

Willow Branch Selection by the Red-naped Sapsucker (*Sphyrapicus nuchalis*)

**The effects of branch characteristics on foraging behavior in
Gothic, CO**

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Abstract:

Foraging Red-naped sapsuckers (*Sphyrapicus nuchalis*) displayed a clear preference for interior willow branches (80% of all total wells) over exterior branches, and for east-facing branches (62% of all total wells) over west-facing ones. Interior branches were most likely favored because of the protection they offered from predators: this theory was supported with observational data in which sapsuckers foraging on exterior branches scanned their surroundings almost twice as often as on interior branches. By contrast, preference for east-facing branches was most likely related to temperature. East-facing branches gained more heat and stayed significantly warmer than their west-facing counterparts for the time intervals of 7 am to 3 pm. Additionally, 72.2% of all total drill sites were found within in the range of 1.072- 1.875 m along the branch and 48.8% found between the range of .92- 1.32 m above the ground, indicating that sapsuckers preferentially create wells within a very specific set of dimensions.

Keywords:

Red-naped sapsucker, double keystone species, willows, sap-feeding, branch selection, orientation, vigilance, optimal foraging theory.

Introduction

How and where animals choose to forage has been a long-standing and extensively researched topic in ecology. As with other behaviors, such as courtship and mating, foraging comes with an associated trade-off: the energy content of the food acquired, balanced against the cost of the energy needed to obtain that food. Optimal foraging theory predicts that an individual should favor the foraging strategy that delivers the greatest net energy intake, thus delivering the highest fitness payoff. (Macarthur, 1966).

Research on avian species has played an important role in furthering our scientific understanding of optimal foraging theory. From studies on the energy trade off associated with well dropping in Northwestern crows (*Corvus caurinus*) (Zach, 1978) to how distance traveled from the nest affects time spent foraging in Cassin's Auklets (*Ptychoramphus aleuticus*) (Adams, 2004), the decision making processes of hundreds of bird species have been examined in the context of the optimal foraging theory.

Although the following study isn't a similarly direct test of the theory, it nonetheless alludes to some of its major concepts while simultaneously providing little known data about the foraging behavior of a Colorado keystone species.

The Red-naped sapsucker (*Sphyrapicus nuchalis*) is a small species of woodpecker found in montane woodlands of the Rocky Mountains. Daily et al. (1993) highlighted the ecological importance of the Red-naped sapsucker in the subalpine ecosystem in Colorado, labeling this bird a "double keystone species". The importance of this species cannot be over-emphasized enough. Abandoned sapsuckers nest cavities in aspen trees provide nest sites for a half dozen other bird species, including the tree swallow and the mountain bluebird, which are incapable of creating their own nest holes (Daily, 1993). Sapsuckers also drill sap wells in all three species of tall willow trees, *Salix*, which provide a food source for hummingbirds, insects, small rodents, and other animals (Daily, 1993).

While all four species of sapsuckers have a varied diet, which includes invertebrates and aspen sap and bast, their diet consists substantially of willow sap. As Tate (1973), Walters (1990), Savignac *et al.* (2006), and Daily *et al.* (1993) concluded, sapsuckers' reliance on willows is an important component of their life history.

The importance of these abundant birds to the Colorado sub alpine ecosystem is evident. Yet, while a substantial amount of research has been done on the habitat and nest site selection of this species, there is little published literature relating to foraging behavior.

In fact, most of the studies conducted on sap-feeding behavior both in mammals and birds have been focused at the level of individual tree or shrub selection. There has been little to no research conducted on how individual branch characteristics influence foraging choice. The goal of this project was to link the foraging and behavioral choices of Red-naped sapsuckers in Gothic, CO, to the characteristics of individual willow branches. These characteristics include whether or not the branch was on a clumped or solitary willow, diameter of the branch, position of the branch (interior or exterior of the shrub), and orientation of the branch (NE, NE, SE, SW). I also attempted to find trends in the creation of the drill site itself, such as whether or not sapsuckers were preferentially drilling at a certain distance along branches and at a certain height above the ground.

An interesting and highly integral component of this study was that several of these variables were most likely influenced by sapsuckers predator avoidance. Adult Red-naped sapsuckers have a varied assortment of natural predators including weasels, foxes, and hawks and their choice of branches might ultimately be influenced by risk of predation.

Accordingly, my hypothesis was two-fold. First, I predicted that there are inherently different branch characteristics such as orientation and position that lend themselves to a "higher quality" branch and thus ensure that not all branches will be drilled on equally. As influence on orientation might be

due less to predation risk and more to temperature differences during the course of a day on the east and west-facing sides of a willow, temperature data was collected to explain orientation preference.

The second part of my hypothesis predicted that a large portion of these 'higher quality' branches will be branches that aid the bird in avoiding predators. I expected to find more wells per branch in willows that are part of a clump as the clump might offer additional protection, and on interior branches where the bird is less exposed. I expected birds foraging on exterior branches to have increased alertness as measured by vigilance looks. I also predicted that drill site should be located an intermediary distance between ground and the crown of the shrub to avoid both terrestrial and aerial predators.

To test these predictions, I conducted the study in two parts. Because sapsuckers do not actively forage on willow sap until their young have hatched, I was given a window of time in which I could collect historical data from past drilling seasons without disturbing the birds or confusing new drills with old. I collected data on ten willows in this manner. This information was later coupled with observations of feeding sapsucker pairs to augment and provide information for any noticeable trends.

Thus, despite the fact that this study only deals tangentially with optimal foraging theory, it nonetheless provides novel data about the foraging behavior of a Colorado keystone species and the willows they rely on. With development spreading further and further into the Rocky Mountains and entire willow ecosystems being leveled to pave the way for ski resorts and private homes, understanding the interactions between *S. nuchalis* and *Salix* has never been more crucial. At the point of this writing, there have been limited to no studies conducted on how the Red-naped Sapsucker selects willow branches to forage from. The information reported in this study will not only allow for a more complete understanding of the birds' interaction with willows, but the behavioral trends will be useful for further and more detailed inquiries on the foraging strategies of the Red-naped Sapsucker.

Methods

The study was conducted in Rocky Mountain Biological Laboratory, a high-elevation field station (9500 ft) located in Gothic, CO just north of the town of Crested Butte. Founded in 1928, RMBL is encircled by Gunnison National Forest land, and is recognized as one of the best places to study the subalpine ecosystems of Colorado. This study area contains a large population of Red-naped sapsuckers and widely distributed clumps of all three sapsucker drilled willow species.

As previously mentioned, this study was conducted in two parts. In order to generate broad, historical trends, I measured old drill sites in both solitary and clumped willow shrubs. It was necessary to sample both clumped and solitary willows, as clumped shrubs may have been used preferentially because they provide more protection. Ten willows were measured in total, four solitary and six clumped.

In order to obtain information about the wells themselves, I divided each tree into four directional quadrants (i.e. NW, SW, NE, and SE) and then numbered each drilled branch, walking in a clockwise path around the shrub. In the interest of time I only recorded detailed measurements from five randomly chosen drilled branches in each quadrant with the exception of two willows whose small size allowed me to obtain detailed measurements for all drilled branches in all quadrants. Once the branches were marked, I wrote down the corresponding numbers on individual slips of paper, shuffled them in a plastic bag, and randomly drew five. These chosen five branches were measured for: diameter (as measured from the thickest part of the drilled area), vertical height of the drill site off the ground, and distance from the lowest well to the base of the tree. For all drilled branches in all quadrants, I recorded the number of individual drill holes, orientation of the branch (NE, SE, NW, SW), and position of the branch relative to the shrub (interior or exterior.) I defined interior branches as those that do not compose the perimeter of the shrub and thus, do not have one or more surfaces exposed to the outside environment.

In order to control for variables such as slope, elevation, and aspect, I sampled only willows on relatively flat ground: i.e. the valley bottoms and not on the surrounding slopes. Willow distance from aspen, while potentially important for determining which willows are fed from first, did not appear to affect preferred branch size or type and so was not considered. Regarding clumped willows and clump size, willows were considered to be 'solitary' only if they did not have a neighboring shrub anywhere within five meters. I attempted to sample only willows from linear patches so that I did not introduce more values such as shrub position within the patch (exterior vs. interior).

Furthermore, for a single representative willow, I recorded ambient air temperature on the east and west facing sides, as well as temperature of east and west facing branch surfaces, (both interior and exterior) with a (FLUKE 53/54) thermocouple each hour from 6 am to 12 pm and then once every two hours until 6pm. For this willow I then determined the average height off the ground of the sap sucker wells and held the probe at the mean distance for my measurements. In order to account for differences in temperature due to wind or other interference, I took five readings of air and branch temperatures for both east and west sides of the tree at every interval. I then averaged each set of readings to obtain a mean temperature.

I also attempted to use a hand-held refractometer to record the sugar content of sap on both east and west facing branches and exterior and interior branches. However, the amount of sap obtained from an individual drilled branch was insufficient enough to obtain a clear reading.

The second part of the study consisted of observing the foraging behavior of sapsuckers. I observed feeding birds in the morning and afternoon, both in clumped and unclumped willows. These observed willows were different individuals than the ones measured for the first part of the study. Prior to beginning observations, I chose a vantage point that would allow me to observe the majority of the willow shrub and the birds' activity within it. I also randomly selected four branches that the bird had already drilled on: 1 and 2 always interior, and 3 and 4 always exterior, as focal branches on which I could take detailed measurements after the observational time was done. The rest of the branches were either unidentified interior (UIs) or unidentified exterior (UEs). In some cases, if the shrub was dense enough to hinder viewing, I applied flagging tape to my numbered branches, but at a sufficient height above the drill site so as not to alarm the bird.

I observed for a minimum of an hour at a time, recording the basic following observations into a digital recorder: time bird arrived, direction bird arrived from, sex of the bird, time bird left, and direction bird left. I also identified each branch it visited as either 1,2,3,4 or a UI or a UE and recorded its activities while on that branch as either drill, look, or feed. A look was recorded only if it was clear that the bird had paused to vigilantly considering its environment. These vigilant scans tended to be longer and involved more head-turning than casual upward glances. Similarly, a branch was considered to be 'visited' only if the bird engaged in one of the three activities and did not simply hop on and then hop off as a means of getting to another part of the willow.

If another sapsucker arrived after a first had landed and begun to forage, sex and time of its arrival and departure were noted, but I continued to follow the activities of the first bird.

If a sapsucker exhibited active defense by chasing away sap robbers, I noted the time of its behavior and the identity of the thief.

If a robber was seen feeding while the sapsucker was absent, I likewise recorded time and species.

During my time at RMBL, I managed to find two actively foraging and easily accessible sapsucker pairs and one single female. Each pair and the female were observed for between 4-9 hours. After the observational period was over, I took the full measurements on the drill site on my four focal branches: well length, well width, diameter of branch, height off the ground, and distance of lowest well to base of the tree. I also recorded the total number of drilled branches, counting well number, position, and orientation for all the UIs and UEs on a given tree.

These observational studies of foraging sapsuckers were then used to provide biological and

behavioral context for any trends that emerged in the collected historical data.

The location of all measured willow shrubs and all shrubs used in observations were mapped using a GEO/XT mapping unit. If the shrub was part of a clump, I also mapped the perimeter of the clump, walking as close to the exterior trees as was possible.

Data was mainly analyzed by using t tests to compare physical branch characteristics (such as diameter) and drill site characteristics (height off the ground and distance along the branch) with total number of drilled branches. Because the effects of position and orientation might be compounded, I ran a 2 way ANOVA to test their effects on total number of individual wells. To analyze my temperature data, I ran t tests for each hourly interval, testing for periods of time when temperatures between the east and west sides of the willow were significantly different. And lastly, I used another set of t tests on the observational data to contrast the sapsuckers' behavior with the position of the branch they were foraging on. All analyses were done in JMP.

Results

Several significant trends were found in the 'historical' willows 1-10. Branch diameter, distance of drill site along the branch, and height from the ground to the drill site, had a distinct range of values in which there were significantly more drilled branches. The effects of branch position and orientation were considered by using the number of individual wells instead of drilled branches and also showed strong patterns, with interior and east-facing branches having more wells than exterior and west-facing branches.

Solitary vs. Clumped Willows: Whether a willow is solitary or part of a clump may affect how many branches a sapsucker drills on and how many individual wells it drills per branch. Because clumped willows might offer more protection from predators, I expected to find both more drilled branches and more wells per branch in willows that were part of a group. I measured six clumped and four solitary willows. Interestingly, the average number of drilled branches was almost identical between clumped and solitary shrubs, (means of 35.5 and 33.75 respectively) but clumped shrubs had an average of 2.13 times as many wells per branch. (Fig. 1)

This difference however, was not enough to prove significant; the t test revealed that, contrary to my predictions, there was no difference in the total number of drilled branches for clumped vs. solitary willows (SE clumped=8.510, SE solitary=10.423, $F = 0.0169$, d.f. = 8, $P = .5501$) and no difference in the mean number of wells per branch (clumped mean= 1547.17, solitary mean= 1143.25, clumped SE= 462.99, solitary SE= 567.05, $F = 0.304$, d.f.=8, $P = .5962$).

I then considered the possibility that foraging sapsuckers might be more inclined to drill on exterior branches when the willow was part of a clump as the clump might offer a measure of protection not found in solitary willows. To compare number of interior and exterior drilled branches for both types of willow, (clumped and solitary) I used a chi squared test which revealed that there was no discernible difference in the average number of drilled branches. ($n=355$, d.f.=1, $t=.3958$).

Branch diameter: Branch diameter was the first of three measured branch characteristics, and was taken from the thickest part of the drill site for all 174 branches on all 10 willows. The data yielded a strong results, with 67.6% of all drilled branches falling between the 5.6 and 9.9 cm diameter interval, and 34.5 % in the 5.6- 7.7 cm diameter interval. (Fig. 2) To run a t test, I divided branch diameter into the nominal categories small (3.4- 12.1 cm, mean number of drilled branches=49.667, SE= 8.894) and large (12.2- 20.9 cm, mean number of drilled branches=6.667, SE=8.894). The t test revealed that branch diameter has a significant impact on number of drilled branches ($F=11.686$, $n=174$, d.f.=4, $P = .0134$) with branches in the 3.4-12.1 cm diameter range drilled on more frequently by sapsuckers. As of the time of writing, I am still collecting data on the diameters of both drilled and undrilled branches. It is my hope that the trend I detected above is not the result of the majority of all willow branches falling

within that 3.4-12.1 cm range, but that there is an equal distribution of diameters in an individual willow tree. This would indicate that birds are preferentially selecting branches of a certain diameter for other reasons than sheer abundance.

Position and Orientation: The final two physical branch characteristics I considered were branch position, whether the branch was interior or exterior, and branch orientation, which of the four quadrants (NE, SE, SW, NW) the branch was found in. Unlike the previous tests, number of individual wells, not number of drilled branches, was used as a measure of sapsucker branch preference as it sidesteps the potential problems of there being more branches in a given quadrant or in the interior of the shrub.

In order to test for trends, I constructed graphs (Fig. 3 and 4) detailing the relationship between average well number per branch and branch position/branch orientation. For all ten measured willows, interior branches had an average of 319.85 wells, (mean= 37.631) while exterior branches only averaged 174.1 wells (mean=3.478). A similar pattern was found when contrasting east and west-facing branches, with an average well number of 817.03 for east branches and only an average well number of 487.7 for west branches.

Because an interaction among orientation and position was possible, a two way ANOVA was run next to test the significance of each variable and the strength of the interaction between them. The 2-way ANOVA revealed that both branch position ($F = 34.427$, d.f.=1, $n=274$, $P < 0.001$) and branch orientation ($F = 7.968$, d.f.=1, $n=274$, $P < 0.001$) had a significant effect on the number of wells occurring on the branches. The interaction term between these factors was not significant ($F = .457$, d.f.=1, $P > 0.05$)

Distance along the branch to the drill site: Distance along the branch to the drill site is not a physical branch characteristic but may provide important information about sapsucker foraging behavior nonetheless. This variable was measured from where the branch emerged from the ground, along its length to the lowest well of the drill site. Another strong pattern was found, with 40.2% of all drilled sites located between 1.072- 1.473 m along the branch and 72.2% in the range of 1.072- 1.875 m. (Fig. 5) In order to run a t test, I divided distance into two categories: close (.67- 1.874 m, with a mean of 49.667 and a SE of 8.894) and far (1.876- 3.081 m, with a mean of 6.667 and an SE of 8.894) The resulting values of ($F=11.686$, $n= 172$, d.f.=4, $P=.0134$), indicating that sapsuckers preferentially drill in the range of .67-1.874 m. along the branch.

Height of the drill site: Again, while not a physical characteristic of the branch itself, height from the ground to the lowest well on a branch, was still indicative of patterns within sapsucker foraging behavior. There were similar results for this variable as well, with the majority of all drilled branches, 48.8% found between the range of .92- 1.32 m. ($n= 174$) (Fig. 6)

Another one way ANOVA was preformed to test the significance of this finding, by dividing height into two categories, short (.5- 1.321 m, mean=30.2, SE=4.886) and tall (1.323- 2.527, mean=4.2, SE=4.886). The ANOVA indicated that sapsuckers preferentially drill within a specific height range, ($F=14.178$, $n=174$, d.f.=8, $p=.0055$), favoring the specific range of .92-1.32 m off the ground. If a branch is not at least as tall as .92 m, it has a significantly lower chance of being drilled on.

Temperature: Both ambient and branch temperatures are factors that could explain why sapsuckers display such a strong preference for the east-facing branches of willow trees. Figure 7 and 8 are graphical representations of the changes in temperatures over the course of a typical summer day. They suggest that both east ambient air and east branch surfaces gain more heat and stay warmer for longer than their west-facing counterparts. Only around sunset (5 pm) does the west side of the willow become warmer than the east side.

I ran a t test for each hour of temperature readings to determine at what daily intervals the difference between east ambient vs. west ambient and east branch surface vs. west branch surface were significant. Intervals of significance are marked on Figure 7 and Figure 8 with stars.

Observational data: I collected observational data to augment my observed historical trends. It was most helpful when used to test the hypothesis that sapsuckers drill more wells on interior branches than exterior ones because internal branches offer more protection. To quantify this idea, I focused on comparing the number of vigilance looks to the number of branch visits, drills, and feeds for interior and exterior branches, with the prediction that birds on exterior branches would interrupt their feeding and drilling more in favor of scanning for potential predators. I also hypothesized that due to increased risk, birds would visit exterior branches less and engage in “risky behaviors” (feeding and drilling) less often while on those branches.

Because of the sheer number of comparisons, I have included a table of t test results testing the significance of branch position on each activity (Table 1). The results were of mixed significance, but when I compared the number of looks per visit for interior and exterior branches, I found that there was a marked increase in the number of vigilance scans performed on exterior branches. Therefore, although the birds do not appear to be drilling, feeding, or visiting exterior branches less frequently, they do display increased vigilance while foraging.

Discussion

The purpose of this study was to investigate if physical characteristics of willow branches affected the foraging choice and behavior of the Red-naped Sapsucker, *Sphyrapicus nuchalis*. Although there was no difference in foraging activity among clumped and solitary willows, I found that sapsuckers favored interior and east-facing branches more than exterior and west-facing ones. Although they were not observed to forage less on exterior branches, sapsuckers were notably more vigilant while doing so. The data gathered supports my general hypothesis that certain branch characteristics influence how many branches are drilled, how many wells are drilled, and where on the willow the bird chooses to forage.

Although the results did not support my component hypothesis that I would find more drilled activity on clumped willows as opposed to solitary ones, my small sample size of only ten willows was most likely insufficient to pinpoint any existing trends. A larger study conducted (Eberhardt, 2000) on yellow-bellied sapsuckers utilized a sample size of thirty six individual trees and reported that sapsuckers attacked trees located in clumps more often than those that were solitary. Therefore I am inclined to believe that the trend does exist, but that more willows would need to be examined to detect it.

As mentioned previously, most of the previous studies conducted on sap-feeding behavior have been focused at the level of individual tree selection. There has been little to no research conducted about how individual branch characteristics influence the foraging choice of sap-feeding animals. However, work done on the foraging behavior of Red-cockaded woodpeckers in South Carolina (Hooper, 1981) suggests that this species also drills within a very specific tree diameter range, with live pine stems greater than 23 cm diameter at dbh representing only a quarter of all pines but receiving over half of the use. The Red-naped sapsuckers' similar tendency to drill mostly on branches between the 5.6-9.9 cm range could be related to a host of interrelated factors. For example, the bird might not be able to physically cling to any branch much smaller than 3.4 cm, or it might have difficulty wounding thicker branches sufficiently to produce continuous sap flow.

The Red-naped sapsucker also exhibited a strong preference for creating drill sites in very specific ranges of distance along the branch and height off the ground. Although predation on sapsuckers is extremely common on their nests and increases with the begging calls of their young, adults of the various species all have natural predators including owl, hawk, weasel, fox and snake

species. The specific distance and height ranges in which the Red-naped sapsucker chooses to drill could be indicative of where it is least exposed to predation. Because the birds are threatened by both terrestrial and aerial predators, it is not surprising that the majority of the drill sites are almost a meter above ground, yet between a meter and a meter and a half below the crown of the willow.

Risk of predation could also explain why sapsuckers preferred interior branches to exterior ones. Certainly the increased amount of vigilance scans per visit per exterior branch supports this hypothesis. The t tests conducted on the observation studies also suggest that feeding is the 'riskiest' behavior performed by sapsuckers visiting a willow: there were significantly more looks/feed exhibited on exterior branches than interior ones, while looks/drill remained essentially the same regardless of where the birds foraged.

Red-naped sapsuckers also displayed preference for east-facing branches over west-facing ones. A study conducted on the endangered Hawaiian honeycreeper Akiapolaau, *Hemignathus munroi*, related tree characteristics and sap-feeding behavior with similar results. Although no trees were sampled from the west-facing slopes of the Mauna Kea volcano, Aki drilled ohia trees were more likely to be found facing east than either north or south. (Pejchar, 2004) Such a strong preference for east-facing branches and trees is most likely related to temperature. Pejchar suggests that facing east allows the ohias to make the most of morning light, uptaking CO₂ while temperatures are still low, ultimately resulting in a more photosynthetic tree. In addition, my temperature data reveals that east-facing branch surfaces gain heat sooner than their west-facing counterparts. The fact that east-facing branches warm faster, implies that their sap also gains heat, and might potentially flow more freely sooner in the day.

There is also the possibility that branches within a certain diameter, position, or orientation might have differing sugar content in their sap. However, due to the difficulty in obtaining enough phloem to test with a standard refractometer, I was unable to test this hypothesis at this time.

The lack of a capable refractometer was this study's largest shortcoming. I could have also benefited from more time in which to measure more willows and locate more pairs of foraging sapsuckers to increase sample size. I should have also attempted to measure 'branch health' either through bark thickness, evidence of old scarring, or indication of damage (snaps or splits) as there is evidence that sapsuckers might target already weakened branches (Eberhardt, 2000).

The novelty of this study is that it focuses on a very specific question that has not been considered in previous analyses of woodpecker foraging behavior. Unlike other woodpeckers, sapsuckers are unique in that they drill on multiple branches of single shrub. Understanding how they select which branches to forage from is critical to further understanding the interaction between this keystone species and the willows they feed from. It also has overarching conservation implications. Locally, there has been intensive debate about the development of Snodgrass and similar development projects have been creeping farther and farther into the Rocky Mountains. Almost all entail the destruction of vast willow clumps. Information about the relationship between the Red-naped sapsucker and the *Salix* species will prove useful in making informed policy decisions and in focusing conservation efforts.

In conclusion, I found that certain physical branch characteristics (diameter, position and orientation) affect Red-naped sapsucker drilling behavior. Birds favored branches between 5.6-9.9 cm in diameter, interior branches, and branches on the east-facing sides of the willow. Potential explanations for these trends are the risk of predation (there was a marked increase in vigilance when birds visited exterior branches) and temperature (with the east side of a willow gaining more heat and staying warmer up until around 5 pm). There were also trends in drill site characteristics themselves, with most drill sites found between 1.072-1.473 m along the branch and .92- 1.32 m above the ground. These patterns might also be attributed to predator avoidance but more conclusive studies are needed to test this hypothesis. The narrow focus of this study lent itself to discovering new information about the relationship between *Sphyrapicus nuchalis* and *Salix* spp, which could potentially be used in willow clump conservation efforts in the Rocky Mountains.

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TABLES AND FIGURES

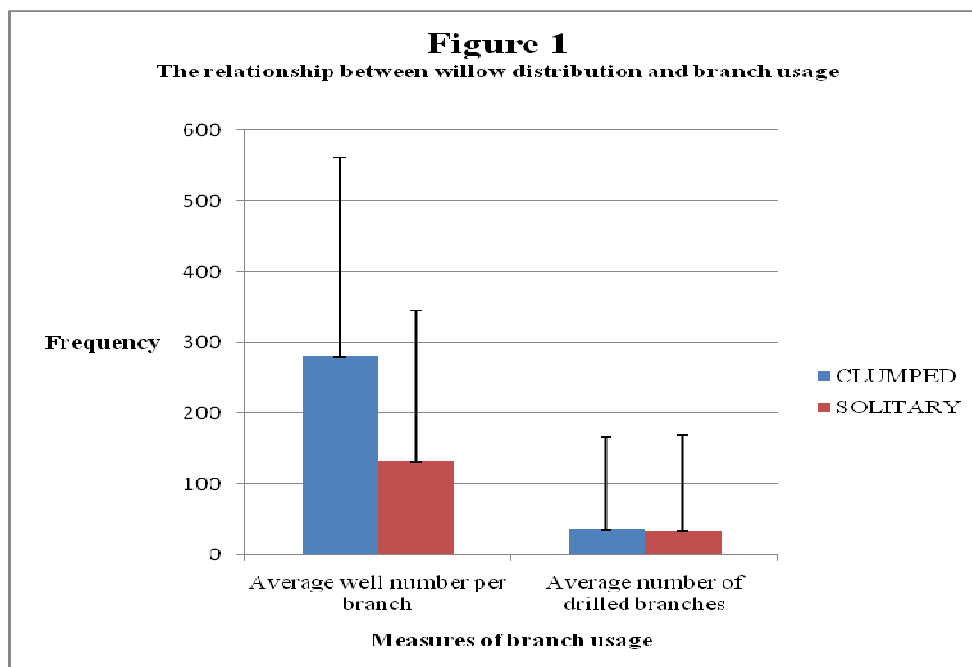


Figure 1: Graph detailing the effect of willow distribution on willow branch usage by sapsuckers for willows 1-10. Willows were either clumped (in a patch) or solitary (lacking a neighboring shrub within 5 meters) and branch usage was measured both by the average number of wells per branch and the average number of drilled branches.

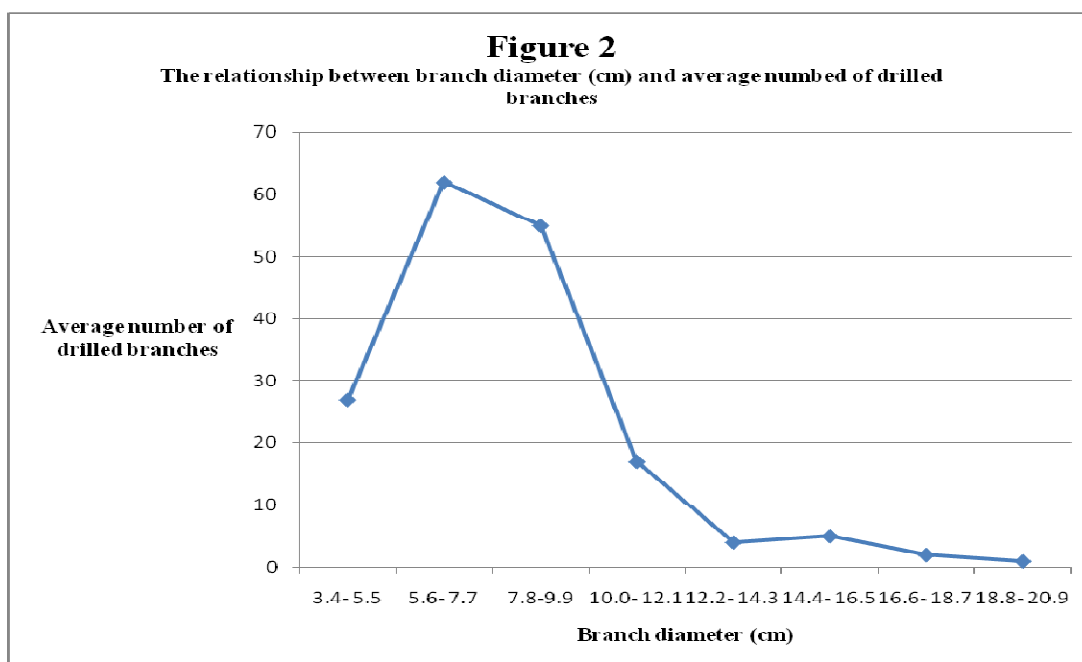


Figure 2: A graph representing the relationship between branch diameter (cm) and the average number of drilled branches for willows 1-10. Branch diameter was measured at the thickest area of the drill site.

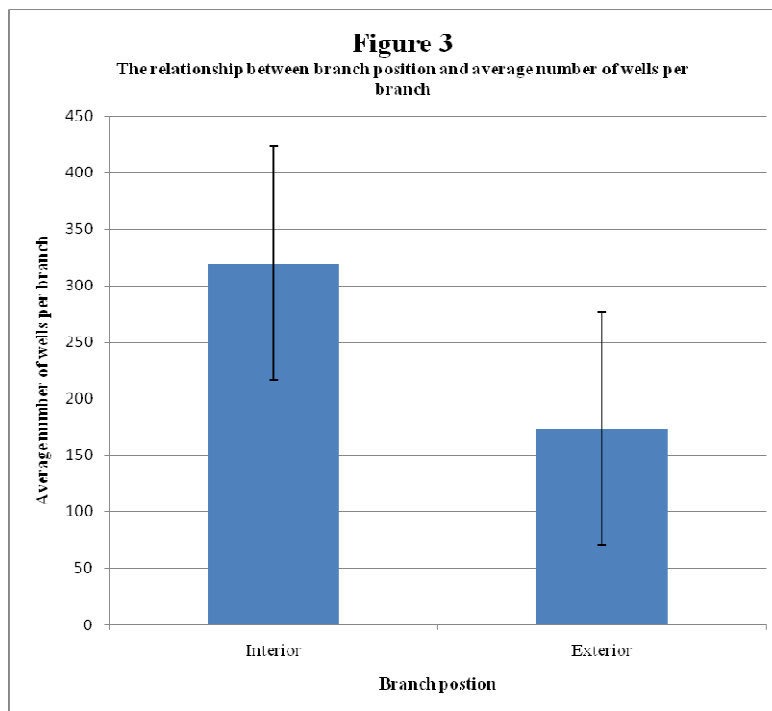


Figure 3: A graph representing the affect of branch position on average number of wells per branch for willows 1-10. Branch position was either interior (the branch did not compose the perimeter of the shrub) or exterior (the branch composed the perimeter of the shrub and so had at least one side facing open air)

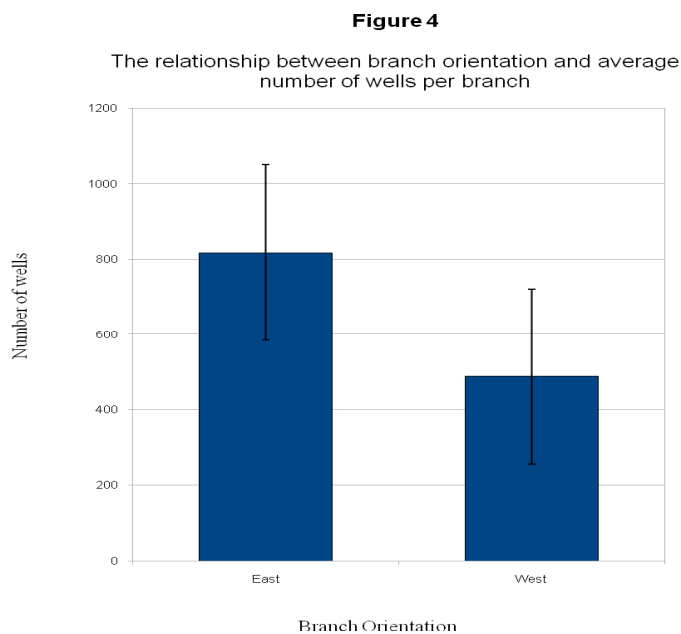


Figure 4: A graph representing the affect of branch orientation on average number of wells per branch for willows 1-10. Branches were categorized as belonging to one of four orientations: SE, NE, SW or NW.

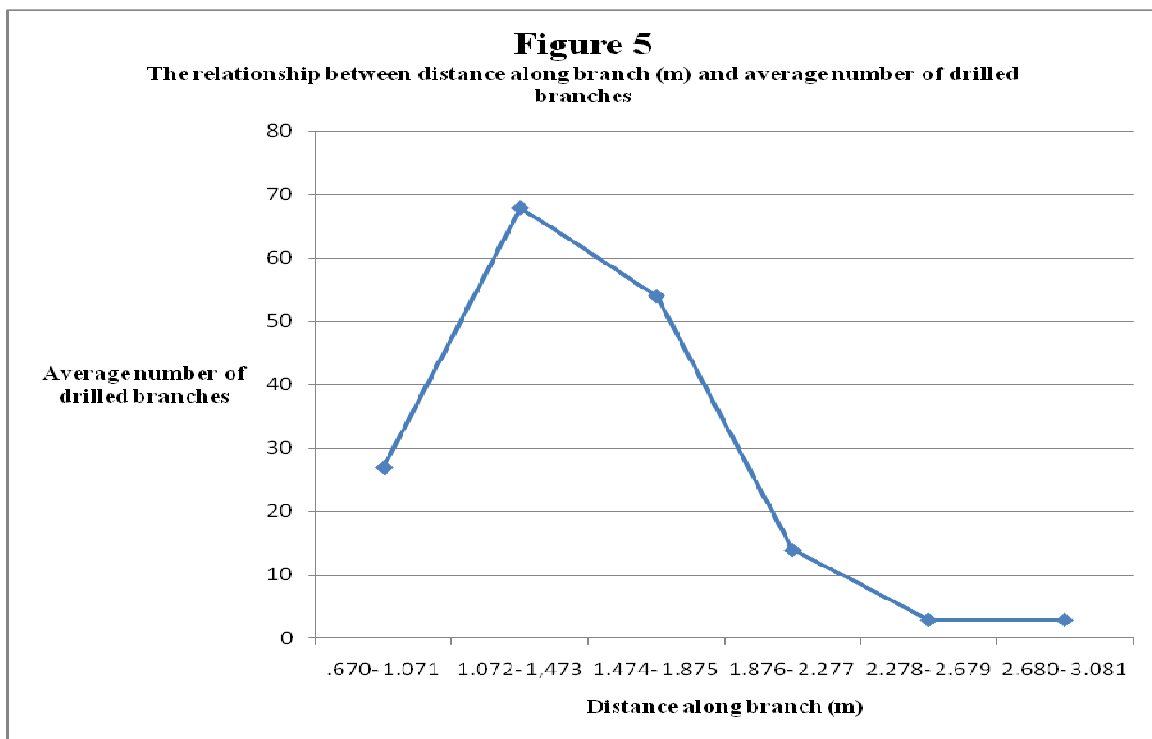


Figure 5: A graph representing the relationship between distance along the branch to the drill site (m) and average number of drilled branches for willows 1-10. Distance was measured from where the branch emerged from the soil along its length to the lowest well.

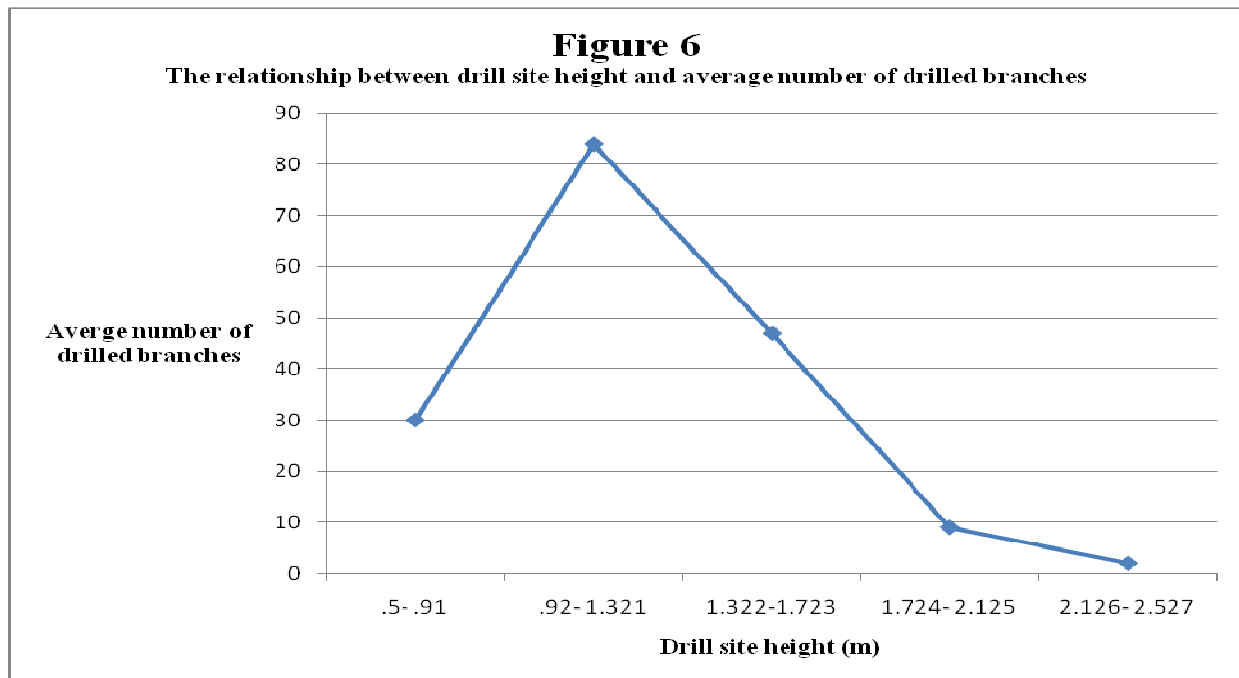


Figure 6: A graph detailing the relationship between height off the ground to the drill site (m) and average number of drilled branches for willows 1-10. Height was measured with a measuring stick from the ground up to the lowest well on a branch.

Figure 7

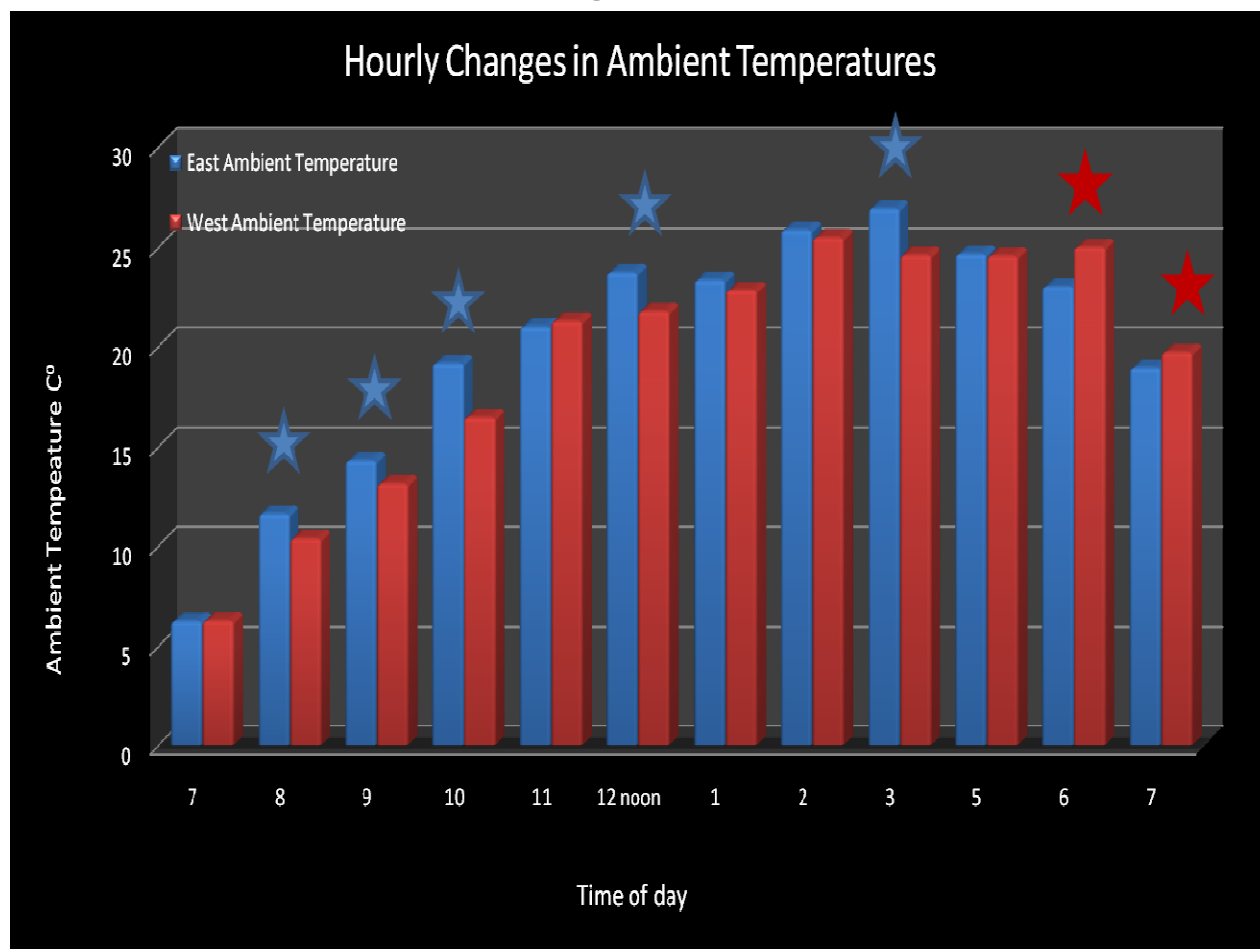


Figure 7: The graphical representation of changes in ambient temperatures (Celsius) for the east and west-facing sides of a representative willow during the course of a typical July 2010 day. Stars indicate in which intervals there is a significant temperature difference (as determined by a t test) between east and west sides.

Figure 8

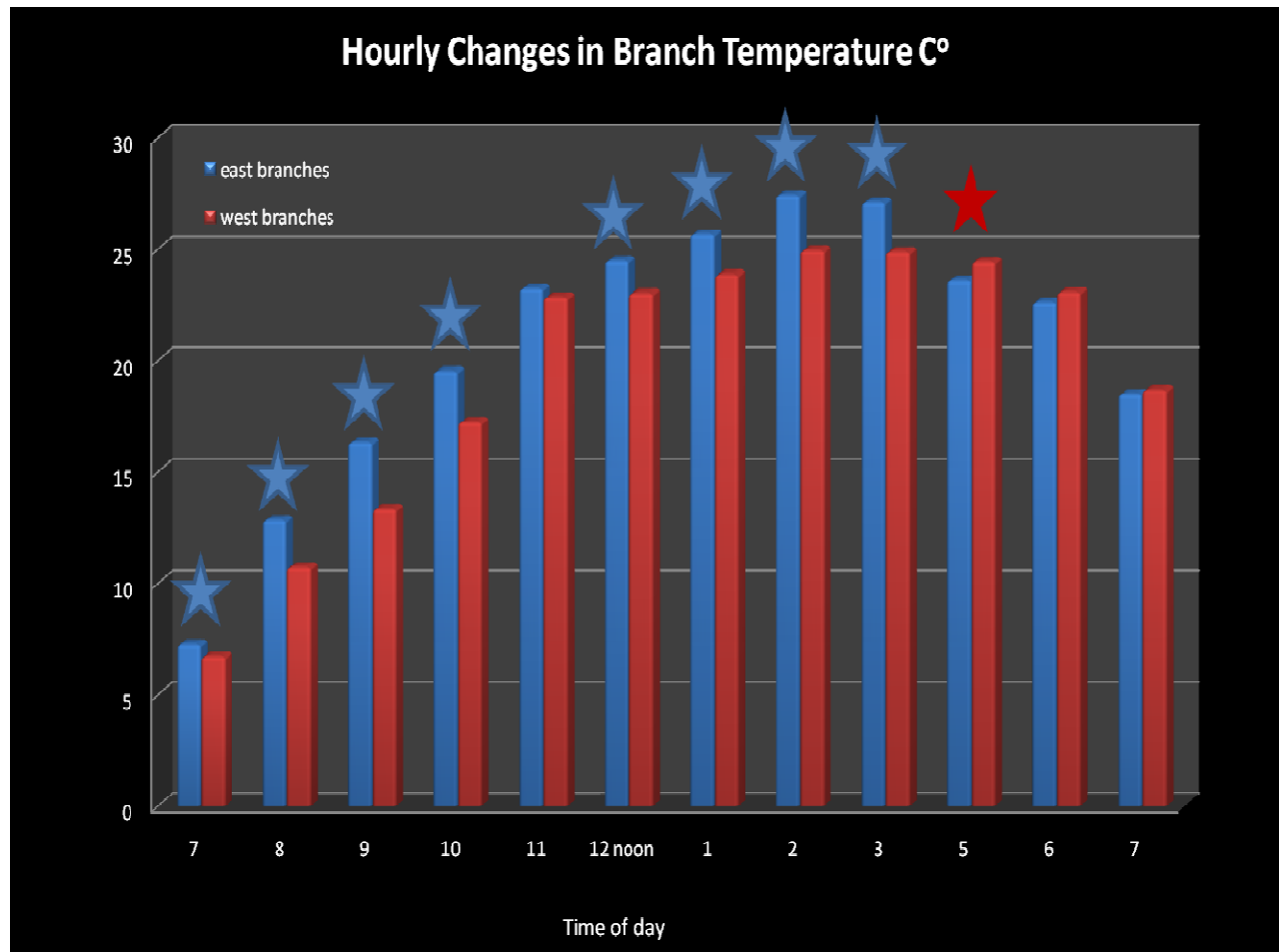


Figure 8: The graphical representation of changes in branch surface temperatures (Celsius) for the east and west-facing sides of a representative willow during the course of a typical July 2010 day. Stars indicate in which intervals there is a significant temperature difference (as determined by a t test) between east and west branches.

Table 1

Activity/Visit Ratio	Exterior branch mean	Interior branch mean	SE Exterior	SE Interior	DF	F Ratio	P value
Looks/Visit	2.10311	1.30459	0.19047	0.19047	1	8.787	0.0091
Looks/Drill	1.93588	1.313	0.3746	0.35318	1	1.463	0.2451
Looks/Feed	2.18475	1.26922	0.28616	0.26979	1	5.419	0.0343
Looks/Combined Feed+ Drill	1.08656	0.53144	0.09792	0.09792	1	16.07	0.001
Drills/Visit	1.15033	1.27086	0.2226	0.2226	1	0.146	0.7096
Feeds/Visit	0.88422	1.21411	0.1571	0.1571	1	2.204	0.157
Visits without drills/visit	0.449	0.44122	0.09661	0.09661	1	0.003	0.9553

Table 1: Summary results for the 2 way ANOVA conducted on all observations. A branch was considered to be visited only if a bird actively looked, fed, or drilled while on it. Looks were defined as vigilance scans, in which a bird actively surveyed its environment for potential predators.