Behavioral Resource Partitioning among *Rana* Species in Northern Wisconsin

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Abstract-

Biodiversity is intricately dependent on the ability of closely related species to survive in proximity to each other without outcompeting one another for the limited resources of an area. A thorough understanding of the means through which closely related species partition limited resources in their ecosystem is therefore essential to conservation ecology. In this study, we examined sympatric species within the genus *Rana*, the true frogs, to test the hypothesis that adults of different species within the genus behaviorally differentiate themselves both temporally and spatially as a means of adhering to a gradient of ecological trade-offs. *Rana* species were observed throughout the day across three habitat types based on the degree of freshwater availability. *Rana sylvatica*—the wood frog—and *Rana clamitans*—the green frog—were found to spatially differentiate themselves along a gradient of freshwater availability, with wood frogs primarily inhabiting wetland habitats and green frogs preferring lakeside habitats. No daily temporal differentiation was found between these two species; however, observations of their foraging habits are suggestive of differential foraging strategies. Wood frogs were more active at all points during the day than green frogs, and foraged primarily in the mornings while green frogs primarily foraged at night. Such means of behavioral differentiation between closely related species of an area are key to a thorough understanding of the mechanisms through which biodiversity is maintained. Through studies such as this, closely related species can be more thoroughly understood, allowing for better protection through well-informed conservation ecology.

Introduction-

Resources within an environment are often limited, forcing species to compete with each other for access to those essential resources such as space and food (Schoener, 1974). Because of this, species settle into a variety of niches in order to best utilize every available aspect of the

environment (Peterson et al, 1999). Studies have shown that the presence of multiple closely related species within a single ecological community is only possible through a partitioning of the available resources, which may be accomplished through a variety of species preferences (Toft, 1980). For example, *distinct* preferences result in the well-known niche differentiation in which species do not overlap in the types of resources utilized. *Shared* preferences, however, result in a differential distribution along gradients due to variation in tolerance and competitive abilities of organisms that have a common preference for a specific segment of an environmental gradient (Wisheu, 1998). These two types of preferences, along with many other behaviorally differentiating characteristics, result in habitat partitioning which allows even closely related species to coexist in the same environment. This raises the question of how closely related species with similar preferences and requirements behaviorally differentiate themselves in order to occupy the same environment.

Behavioral differentiation can occur in multiple ways including separating certain activities in both space and time (Marsh et al., 1999). Food sources are a particularly important resource making differentiation of foraging behavior essential (Van Buskirk, 2003). Foraging behavior can differ in a variety of ways including methods of feeding, diet specialization, and differences in horizontal and vertical feeding positions and behaviors (Allaire and Fisher, 1975). Additionally, preferences in habitat have the potential to spatially distribute species, reducing foraging competition. Studies have been performed to assess a wide variety of foraging behaviors, including preferred foraging habitats, preferred food, time spent foraging, preferred time to forage, manner of foraging, morphological correlations to foraging behavior, and feeding habits (Allaire and Fisher, 1975). For example, in this same study, field sparrows (*Spizella pusilla*) in Eastern Texas utilized higher perches to obtain seeds than other sympatric sparrows,

selecting to spatially forage in an area with little to no competition from other sparrow

types. There are many means through which species behaviorally differentiate themselves, such

as altered foraging behaviors, resulting in a partitioning of resources and decreased interspecific

competition. A further question of investigation is therefore: which aspects of foraging behavior

have the greatest potential to significantly differentiate closely related species, allowing for

survival in proximity?

Six different species of the genus *Rana* are known to live in proximity to each other in

the north woods of North America: *R. palustris*, *R. pipiens*, *R. sylvatica*, *R. septentrionalis*, *R.

clamitans*, and *R. catesbeiana*. *Rana* is a genus of "true frogs" with species that are relatively

large in size compared to many other frog genera. *Rana* species are considered opportunistic

feeders, indiscriminately preying on insects, invertebrates, and even small vertebrates (Parker

and Goldstein, 2004). Because most *Rana* species breed in the early spring, all six species are

expected to be present during the early summer period. This, along with the great diversity of

both vertebrates and invertebrates that can potentially make up the diet of species within this

genus, make the six species of *Rana* present in the north woods ideal candidates for an analysis

of how behavioral characteristics allow closely related species to live in proximity.

This study focuses on the most common species in the north woods, *Rana sylvatica*—the

wood frog— and *Rana clamitans*—the green frog—with particular emphasis on how these

species behaviorally, spatially, and temporally differentiate themselves in order to inhabit the

same area. A similar study was performed in larval anurans to assess whether a previously

established trade-off model was being used to promote ecological specialization along

gradients. According to this model, trade-offs between predator avoidance and rapid growth

prevent species from simultaneously dominating habitats characterized by different types and

numbers of predators, creating species turnover along a gradient and habitat partitioning among related species (Wellborn et al, 2002). It has also been shown that North American *Rana* species replace one another along a gradient according to this model (Van Buskirk, 2003). Therefore, we hypothesize that adults of each *Rana* species will behaviorally differentiate themselves both temporally and spatially as a means of surviving in proximity to one another. To test this, we observed the behaviors of individuals across different habitats throughout the day. We expect species will exhibit distinct foraging behaviors and habitat selection preferences along a gradient of water availability in order to partition the resources of the environment, minimizing competition with closely related species. Through decreasing competition in this way, a greater number of closely related species might live in proximity to each other, allowing for greater biodiversity and species richness of a given ecosystem (Durrett and Levin, 1998).

Methods-

To examine spatial and temporal differentiation in behavior between *Rana clamitans* and *Rana sylvatica*, we visited multiple habitats across the property of the University of Notre Dame Environmental Research Center (UNDERC). This property is a largely undisturbed area of the north woods in northern Wisconsin. Three different habitat types with varying freshwater availability were assessed: dry habitats with no direct water source, wetland and bog areas with intermediate water availability, and deep lake areas. For fifteen days, one 9 X 9 m plot in each habitat type was observed three times a day at the hours of 0900, 1400, and 2000. To avoid order effects, we visited habitats in different orders each day. Individual frogs were observed in the least invasive manner realistically attainable given the terrain of each particular plot. Individuals within the plot were monitored by an observer for 10 minutes upon visualization.

This observational method was utilized to minimize the disturbance of each individual and obtain more accurate data on natural behaviors.

In order to address the hypothesis that *Rana* species show preferential habitat selection along a gradient of water availability, the observer noted the area of the habitat being utilized by the individual, the time of day, and any other types of animals present. A two-way Chi-Square test was performed to determine whether there exists a preference in habitat choice among dry, wetland, and lake habitats for each species. Additionally, a two-way Chi-Square test was run to assess differences in temporal distribution among the different species of *Rana* throughout the day.

To address whether there exists behaviorally modified foraging preferences among *Rana* species, the observer noted both the type of prey for which individuals were foraging and the "activity level" of individuals. Activity levels were scored as follows: 1=no movement; 2=moved upon disturbance, but remained still after initial movement; 3=moved limbs significantly and may have adjusted position one to two times after initial disturbance; 4=moved about a significant amount and held still for no longer than three minutes at a time; 5=actively moving the vast majority of the observational period. Prey were grouped into the following categories: large flying insects, small flying insects, terrestrial insects, worms and grubs, aquatic insects and small vertebrates. In addition to insects pursued, we noted the types of insects within the foraging range of the frog, with foraging range being defined as within approximately 6 inches of the organism. A two-way Chi-Square test was run on the successful foraging attempts to assess whether there is a temporal difference in foraging across different *Rana* species. Two-way Chi-Square tests were also run to test the hypothesis that species will temporally separate their activities throughout the day.

We found a difference in spatial distribution between the two *Rana* species across habitat types (X^2(2, 91)=35.31, p<0.001). Wood frogs were primarily found in wetland habitats, but were also found in smaller numbers in both dry and lake habitats. In contrast, green frogs were found primarily in lake habitats, with fewer individuals in wetland habitats and no individuals in dry habitats (Figure 1). Although both species differ in spatial distribution, there is no difference in temporal distribution between the two species across time of day (X^2(2, 88)=0.058, p=0.971; Figure 2).

We found a trend in the observed successful foraging attempts of each species for each type of insect. Wood frogs were observed to prey only on small, winged insects while green frogs preyed only on grubs and worms (Table 1). The insect types present within the foraging range of each frog type are indicated in Table 2, along with whether each frog pursued the insect or not. Notably, winged insects—both large and small—were pursued by wood frogs 100% of the time that they appeared in the foraging range of the frog, but were pursued 0% of the time that they appeared in the foraging range of green frogs. Similarly, worms and grubs were pursued 100% of the time that they appeared in the range of green frogs. Although no differences were found between the times of day during which successful foraging occurred between the two species, a trend is present (X^2(2, 10)=3.75, p=0.153). Wood frogs successfully foraged primarily in the morning and declined throughout the day, while green frogs successfully foraged primarily at night time.

No differences were found in activity level throughout the day for the two species (morning: X^2(5, 23)=4.966, p=0.420; afternoon: X^2(7, 23)=7.74, p=0.356; evening: X^2(3, 12)=3.200, p=0.3618). However, the data did show notable trends, with wood frogs being, on

average, more active than green frogs at all points throughout the day (Figure 3). Both species showed their highest activity levels at night, but green frogs showed their lowest activity level in the morning while wood frogs showed their lowest activity level in the afternoon (Figure 3).

Discussion-

In accordance with our hypothesis, this study reveals habitat partitioning between *Rana sylvatica* and *Rana clamitans* across habitat types. While wood frogs prefer habitats with intermediate water availability, they are found in both lake and dry habitats as well. Similarly, previous studies show that wood frogs primarily select to reside in closed canopy, forested wetlands post-breeding (Baldwin et al, 2006). Green frogs, however, prefer lake habitats, with fewer individuals residing in intermediate habitats. While *R. sylvatica* and *R. clamitans* composed the core of this study, all *Rana* species within plots were observed, revealing an interesting avenue for further investigation. For example, the mink frog, *Rana septentrionalis,* was observed only in deep lake habitats. This contrasts with both *R. sylvatica* and *R. clamitans*, which were found at different frequencies across multiple habitat types. This is suggestive of a similar potential gradient of distribution based on degree of water availability for all *Rana* species in the area, beyond the two species of primary study. No studies have specifically examined preferences for gradients of water availability for the different species of adult *Rana*; however, our results are in accordance with the distribution model for larval anurans, in which different larval species replace each other along a gradient of water availability (Van Buskirk, 2003).

In contrast to our hypothesis, we found no differences in temporal distribution between green frogs and wood frogs throughout the day. These distributions changed with each other, as both species were the most abundant in the mornings, declining in number throughout the

day. While no differences in daily temporal distribution were found between these two species, the possibility of long-term temporal distributions among the six *Rana* species of the area needs further investigation. The bullfrog—*Rana catesbeiana*—for example, is known to breed primarily in June and July, and emerge in great numbers primarily in the late summer (Willis et al, 1956). This might explain the lack of bullfrog individuals observed during this study, which spanned three weeks in the early summer. Because only two of the six species known to occur in the area were observed in large numbers, this study suggests a longer-term temporal separation in peak activity, as seen in *R. catesbeiana*. In addition, these species have potentially differentiated themselves from *R. sylvatica* and *R. clamitans* by primarily being active at daily time points not assessed during this particular study—in the middle of the night, for example. A study of *Rana dalmatina*, for instance, found 1437 individuals on roads at night and zero during the day (Hartel et al, 2009). This might indicate an almost entirely nocturnal nature to particular species of *Rana*, suggesting the possibility for differentiation from other frogs within the genus.

While few individuals of either species were observed foraging during our study, those individuals that exhibited foraging behaviors revealed a clear trend in prey type preferences. We observed that wood frogs successfully preyed exclusively on winged insects, while green frogs ate only worms and grubs despite having access to other prey types, including winged insects. These observations suggest a distinct preference of green frogs for worms and grubs as compared to the preference of wood frogs for winged insects. However, due to lack of grubs and worms within wood frog foraging range, it is unclear whether this trend is indicative of actual preferences. Further studies are needed to discern whether wood frogs specialize on winged insects or whether they are merely less discriminate feeders than green frogs. For example, stomach content analyses reveal that *Rana septentrionalis* consumes a significantly higher

incidence of aquatic insects compared to terrestrial insects found in the stomachs of the sympatric *Rana pipiens* (Hedeen, 1972). Similarly, a mink frog observed during our study did not pursue a grub within its foraging range although similar prey was consumed by a green frog within the same habitat type. This observation is further suggestive of a preference of *R. septentrionalis* for aquatic insects within deep environments, while *R. clamitans* eats terrestrial grubs.

Food preference is not the only aspect of foraging behavior that can potentially differentiate species. A similar study to this one, explored the means through which closely related species of birds live in proximity, and found two possible food niche differentiation scenarios: 1) the use of different food resources or 2) temporal differences in feeding activities (Riegert et al, 2011). While our results did not support the hypothesis that the temporal aspect of foraging behavior is a primary means of behaviorally differentiating the species of *Rana* on the UNDERC property, a noticeable trend was observed. Our foraging data indicated a preference for wood frogs to forage in the morning and green frogs at night. Further observations could reveal differences in this temporal distribution of foraging behavior despite lack of differences in temporal distribution of the frogs themselves. Studies have shown that the daily foraging windows of individual species are established in response to a complex interaction of environmental and biotic factors (Casas and McCauley, 2012), making daily temporal foraging behavior a viable means of alleviating interspecific competition.

Furthermore, data regarding activity level throughout the day did not show a difference between both species, but suggested that wood frogs potentially spend a greater amount of time foraging than green frogs. Wood frogs show higher activity levels than green frogs at all points throughout the day, while green frog activity levels peak at night which could allow for further

differentiation. Similarly, a study of mesocarnivores in Southwestern Europe showed a substantial flexibility in circadian activity patterns, allowing them to locally adapt their foraging strategies to coexist in an area (Monterroso et al, 2014). Because green frogs show the lowest average propensity for activity in the mornings and the highest at night, wood frogs would likely have the least competition for foraging in the mornings, resulting in the observed wood frog foraging pattern.   Preliminary data regarding mink frog activity levels throughout the day reveals a distinct increase in activity level from the morning to the afternoon. Morning activity level of mink frogs is lower than the observed morning activity of both wood and green frogs. In addition, the mink frog afternoon activity spikes notably, surpassing the activity of wood frogs. This suggests that mink frogs temporally separate themselves from green frogs, which share habitat type, by foraging primarily in the afternoon rather than at night. Because the daily movements of frogs are essential in obtaining food, shelter, and mates (Woolbright, 1985), temporally separating activities allows for greater survival rates across species.

Because every environment provides an intrinsically limited number of resources, the competition between species for these limited resources leads to a partitioning of the available resources among different species (Beaulieu and Sockman, 2012). Those species that occupy similar niches must necessarily compete with each other for the resources essential to survival (Kitchen et al, 1999). This can lead to a decrease in biodiversity, as closely related species outcompete one another for a single niche (Gilpin, 1994). Behavioral differentiation among closely related species is therefore essential to maintaining a high degree of biodiversity in an area (Vandermeer and Yitbareck, 2012).   For this reason, a thorough understanding of the means through which closely related species, such as the *Rana* species examined in this study, exist in proximity to each other is essential to an understanding of biodiversity and how to maintain it.

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Tables-

	Prey	
Species	Small Winged Insects	Grubs/Worms
Wood Frog	6	0
Green Frog	0	4

**Table 1.** Classes of prey successfully foraged for by wood and green frogs across all habitat types.

	Wood Frogs			Green Frogs		
Insects in Range	Pursued	Total	Percentage pursued	Pursued	Total	Percentage pursued
Mosquitos	0	5	0.0%	0	3	0.0%
Large winged insects	1	1	100.0%	0	26	0.0%
Small winged insects (not flying)	4	4	100.0%	0	1	0.0%
Small winged insects (flying)	5	5	100.0%	0	3	0.0%
Surface aquatic insects (large)	0	2	0.0%	0	1	0.0%
Grubs/Worms/Caterpillars	0	0	Not Applicable	5	5	100.0%
Small terrestrial insects	0	0	Not Applicable	0	2	0.0%

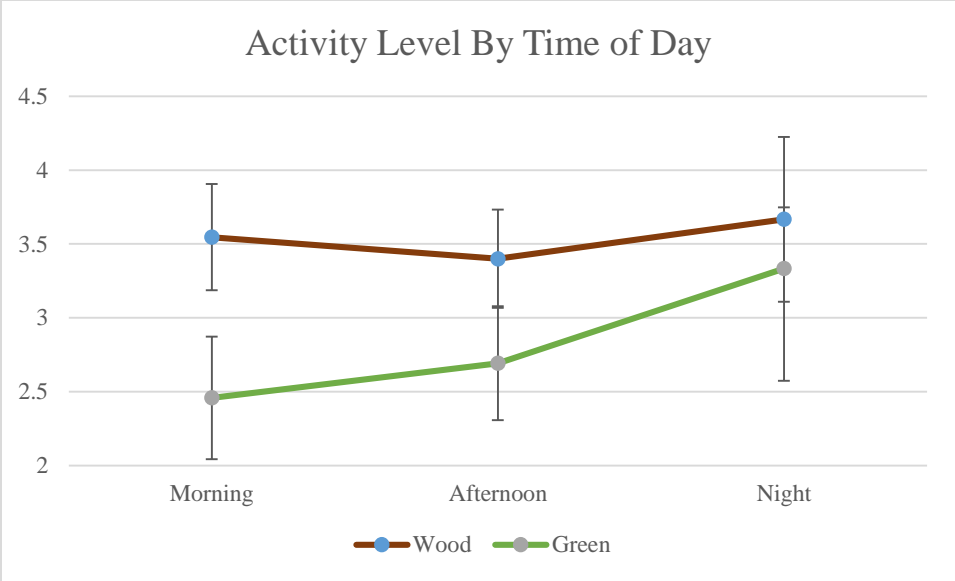**Table 2.** Insects within the foraging range of the observed organisms.
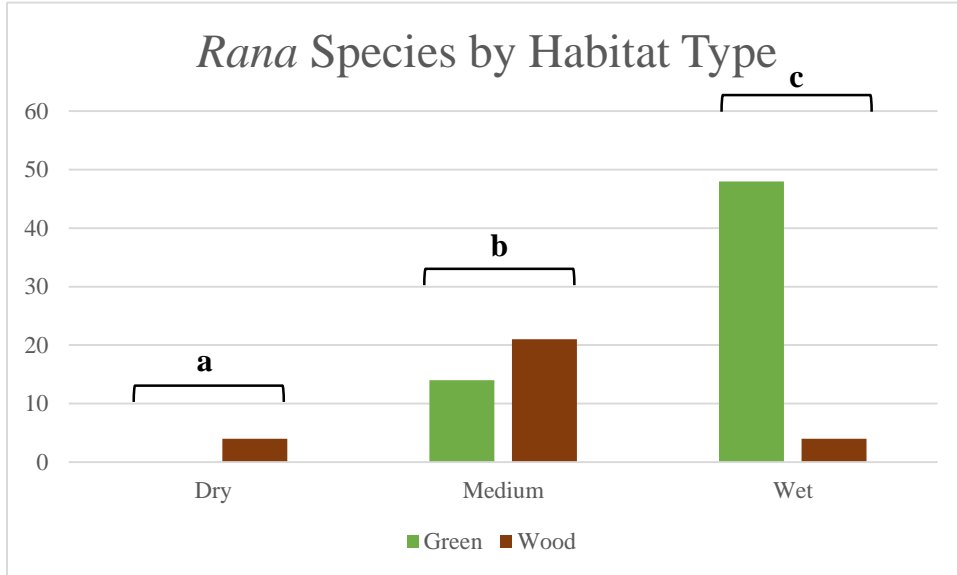
Figure 1. Number of wood and green frogs throughout dry, wetland, and lake habitats at all points during the day. Groups with different letters are different from one another, p<0.001.
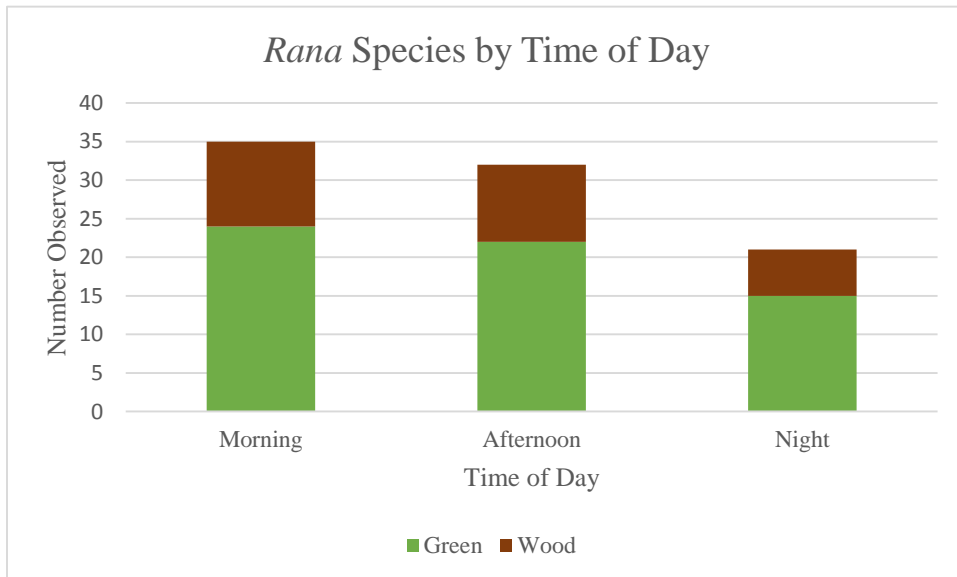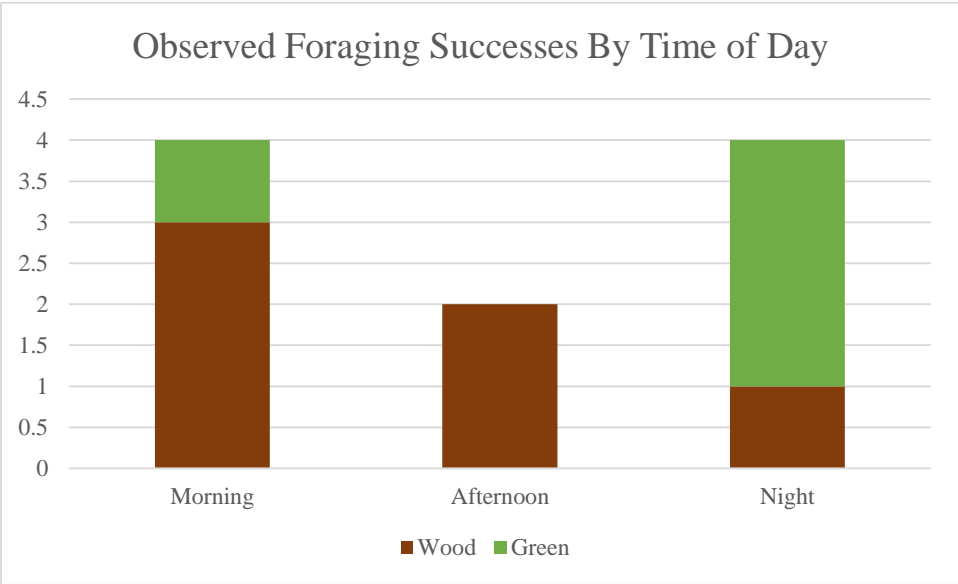

Figure 2. Distribution of wood and green frogs in all habitats throughout different time points in the day.

Figure 3. Average activity level of wood and green frogs throughout the day. Error bars are represented by standard error.

Figure 4. Number of observed foraging attempts by each frog type at each time of day.