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Applying Ecological Theory to Amphibian Populations to Determine if Wood Frogs (*Lithobates sylvaticus*) are Ideal and Free when Selecting Breeding Habitat

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Applying Ecological Theory to Amphibian Populations to determine if Wood Frogs
(*Lithobates sylvaticus*) are Ideal and Free when Selecting Breeding Habitat

A Thesis Presented

By

TAYLOR M. BRAUNAGEL

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(*Lithobates sylvaticus*) are Ideal and Free when Selecting Breeding Habitat

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ABSTRACT

APPLYING ECOLOGICAL THEORY TO AMPHIBIAN POPULATIONS TO
DETERMINE IF WOOD FROGS (*LITHOBATES SYLVATICUS*) ARE IDEAL AND
FREE WHEN SELECTING BREEDING HABITAT

FEBRUARY 2021

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Directed by: Evan H. Campbell Grant

Amphibian populations are declining globally due to a litany of factors including pollution, disease, climate change, and most importantly, habitat destruction. As most amphibian life histories involve their populations being recruitment limited, focusing on the mechanism behind breeding habitat selection will reveal useful cues that managers may use to increase abundance and breeding success. Though there are many theoretical models that describe the distribution of animals in response to a resource, the ideal free distribution (IFD) theory has not yet been applied to amphibian settling decisions. Through this application of the IFD, I have found that a population of wood frogs (*Lithobates sylvaticus*) in Patuxent National Wildlife Refuge select vernal pools that are large, deep, and hold water into the summer months to breed from 2010-2015. This information will provide managers with the ability to predict sites where wood frogs will breed in the future, as well as describe the cues that wood frogs are cueing in on so we can protect, alter, or create ideal breeding habitat.

Key words: amphibian, breeding habitat selection, ideal free distribution, *Lithobates sylvaticus*

TABLE OF CONTENTS

	Page
ACKNOWLEDGEMENTS	iii
ABSTRACT	iii
LIST OF TABLES	v
LIST OF FIGURES	vi
INTRODUCTION	1
CHAPTER	
1. UNDERSTANDING BREEDING HABITAT SELECTION IN AMPHIBIANS USING THE IDEAL FREE DISTRIBUTION	3
Abstract	3
Introduction	4
Part 1: Appraising Models for Breeding Habitat Site Selection	6
Part 2: Using IFD on Amphibian Populations	15
Management Implications	20
2. ARE WOOD FROGS (<i>LITHOBATES SYLVATICUS</i>) IDEAL AND FREE WHEN..... SELECTING BREEDING HABITAT?.....	25
Abstract	25
Introduction	26
Methods	29
Results	33
Discussion	38
BIBLIOGRAPHY.....	47

LIST OF TABLES

Table	Page
1. Results of Spearman Rank Correlation Test.....	36
2. Model Summary for Ending Density.....	37
3. Model Summary for S_{iq}	37

LIST OF FIGURES

Figure	Page
1. Map of Study Area.....	30
2. Observed Rank Order vs. Depth Rank.....	34
3. Observed Rank Order vs. Volume Rank.....	35

INTRODUCTION

General goals of amphibian conservation are to increase, maintain, or slow decline of a target population (Camacho et al. 2010), but each species has a particularly sensitive life stage or process that determines or regulates the number of individuals (Nisbet and Gurney 1982). Early life stage processes are important for recruitment-limited populations, and factors that affect this include habitat availability/predictability, mate availability, and breeding habitat selection (Doligez and Boulinier 2008). Because amphibian recruitment is directly tied to breeding habitat quality, conservation efforts should be focused on creating, enhancing, or protecting productive habitat (Denver et al 1998, Semlitsch 1983, Semlitsch 1987, Wilbur 1972). An individual's fitness is directly related to the quality of the habitat that they select. Therefore, an understanding of breeding habitat selection would lead to more successful conservation of these recruitment-limited amphibian populations (Orians & Wittenberger 1991; Boulinier & Lemel 1996).

Breeding habitat selection studies tend to focus on the result (where individuals settle), instead of the mechanism behind the settling decision (Stewart and Komers 2012, Beckman and Berger 2003). While there are many habitat selection models that can be applied to breeding habitat selection, the ideal free distribution is a promising theory that can be applied over a time series. The ideal free distribution theory has never been used on amphibian populations but delivers promise of a deeper understanding of the mechanisms behind breeding habitat selection.

In my first chapter, I describe habitat selection studies and select a few examples that have been applied to breeding habitat specifically: the habitat preference model,

individual-based model, and the ideal-free distribution. I provide a synthesis and review each model, as well as describe assumptions, data required to run appropriately, advantages, and disadvantages. This appraisal of both example models provides a justification for and describes the benefits of applying the ideal free distribution theory to amphibian populations.

In my second chapter, I apply the ideal free distribution theory to a population of wood frogs in Patuxent Wildlife Refuge (Maryland, USA) over three years. I describe how the IFD can be applied to wood frogs by using census data over a time series. Using daily egg mass counts and vernal pool characteristics over a season, I tested whether wood frogs are ideal and free when selecting breeding habitat.

Together, these chapters describe the importance of breeding habitat selection, and provide some empirical support for the benefit of applying the IFD to amphibian populations. This thesis provides managers with a better understanding of the mechanism behind breeding habitat via a new tool to identify the environmental cues that wood frogs use to select breeding habitat. Managers will now be able to predict the distribution of individuals by assessing environmental cues, as well as understand what ideal habitat is. In the thesis conclusions, I provide potential management recommendations so this information may be used to increase the breeding success and overall abundance of wood frogs.

CHAPTER 1

UNDERSTANDING BREEDING HABITAT SELECTION IN AMPHIBIANS USING THE IDEAL FREE DISTRIBUTION

Abstract

General goals of conservation are to increase, maintain, or slow decline of a target population, but each species has a particularly sensitive life stage or process that determines or regulates the number of individuals (e.g. recruitment). An individual's fitness is directly related to the quality of the habitat that they select. Therefore, an understanding of breeding habitat selection would lead to more successful conservation of these recruitment-limited populations. Breeding habitat selection studies tend to focus on the phenomenon (where individuals settle), instead of the mechanism behind the settling decision. However, the ideal free distribution (IFD) theory can describe these settling mechanism over a time series. The IFD has been applied to numerous taxa, but has not yet been tested on amphibian populations, which are generally recruitment-limited and are experiencing global declines. Here, I argue that incorporating existing ecological theory, specifically the IFD, into conservation management practices for amphibian populations may provide information of breeding habitat selection, and lead to better decisions and resource allocation when protecting, altering, or creating breeding habitat.

Introduction

General goals of conservation are to increase, maintain, or slow decline of a target population (Camacho et al. 2010), but each species has a particularly sensitive life stage or process that determines or regulates the number of individuals (Nisbet and Gurney 1982). These stages are generally dictated by the species' life history, as number of offspring or amount of parental care (Gilbert and Manica 2010). Survival probability varies among age classes, and these differences contribute to relative importance of the ontogenetic variation in these rates to population growth. Species may be categorized as type I (low early-stage mortality), type II (constant mortality), or type III (high early-stage mortality), based on typical survivorship (Demetrius 1978). Most species are limited by birth rates and exhibit a type III survivorship curve, where younger life stages have a high rate of mortality, and older individuals have higher survival rates (Longhurst 2002, Biek et al 2002). Focusing conservation efforts on the most important life stage can improve population growth rates and species persistence (Wisdom et al. 2000).

In addition to survival, maturation rates are important to population growth. The rate of maturation can be described as one element in successful recruitment, which is defined as the addition of individuals to a population via birth and maturation. Recruitment can be highly stochastic in space and time in response to biotic and abiotic factors and includes three main stages: production of offspring, their survival to the adult breeding stage, and their settlement (Gaillard et al. 2008). Recruitment-limited populations experience a sensitive natal or larval period where much of the growth and development occurs, leaving them vulnerable to external threats like predation or environmental stochasticity. Populations that rely heavily on the environment, as opposed to parental

care, for development may be highly susceptible to declines (Hughes and Tanner 2000). As a result, threats that affect early life stages can increase population declines. These populations are characterized by short maximum life spans, early maturation times, high fecundity, and an increased resilience to population decline if recruitment remains high (Hughes and Tanner 2000). Early-life stage processes are important for recruitment-limited populations, and factors that affect this include habitat availability/ predictability, mate availability, and breeding habitat selection.

An individual's fitness is directly related to the quality of the habitat that they select. Therefore, an understanding of breeding habitat selection would lead to more successful conservation of these recruitment-limited populations (Orians & Wittenberger 1991; Boulinier & Lemel 1996). Through observation and experiments, ecologists understand that identification of optimal breeding habitat is paramount for maximizing individual fitness, yet the complex process behind breeding habitat selection is not fully understood (Birkhead 1977, Hatchwell et al. 1996, Poysa 2001). While studies have observed where individuals settle (i.e. where they decide to breed) and compared abundance to habitat characteristics, like pond depth, temperature, cover type, resource availability etc., we lack the understanding of how or why they selected this habitat (MacArthur and Pianka 1966, Verner et al. 1986, Rosenzweig 1991). If the mechanism behind breeding habitat selection was apparent, then managers would not only know which sites individuals choose, but could then also predict the order in which these sites were selected, allowing for an accurate prioritization of conservation efforts. The identification of these ideal breeding habitats and their relative importance to breeding populations can inform managers about refugia to protect and aid in predicting

management outcomes. In addition, managers are frequently called upon to advise and monitor the creation, alteration, or mitigation of breeding habitat (Poiani et al 2000). Creating ideal habitat types or networks could increase individual fitness and recruitment by providing more breeding opportunities (Green et al. 2013); but to make an efficient use of resources, the behavioral process behind habitat selection must be well-understood.

Part 1: Appraising models for breeding habitat site selection

Breeding habitat selection studies tend to focus on the result (where individuals settle), instead of the mechanism behind the settling decision (Stewart and Komers 2012, Beckman and Berger 2003). It is important to note the difference between habitat use, which is a phenomenological result of individuals using specific habitat qualities to meet its life history traits, and habitat selection, which is the mechanistic process behind the hierarchical set of behaviors leading to the disproportionate use of habitats to influence fitness and survival (Hutto 1985, Block and Brennan 1993, Jones 2001). This is an important distinction since the ultimate settling decision by an individual may not align with the optimal habitat (Pulliam 1988, Caughley 1994, Jones 2001). Breeding site selection is similar to the process of dispersal, where individuals make multiple linked decisions in selecting an ultimate destination. Dispersal is comprised of three stages, emigration, movement, and settlement (Travis et al 2012). Understanding how individuals make decisions at each of these points can help understand where selection decisions may be limited.

Habitat selection models can be either phenomenological or mechanistic (Kneib et al 2011) and selecting the correct model for the system depends on the spatio-temporal

scales of the study, and the species and question of interest (Orians and Wittenberger 1991). Phenomenological models describe patterns and correlations between population state variables (e.g., abundance or occurrence) and covariates. Examples include studies on newt occupancy (Denoel & Lehmann, 2006), bird abundance in response to habitat fragmentation (Berg 1997), and butterfly movement across nectar patches (Brommer and Fred 1999). Mechanistic models describe individual behavior and the fitness outcomes leading up to and following a settling decision (Railsback 2001). Examples of mechanistic models include density-dependence in mottled sculpin (Grossman et al, 2006; Grossman 2014), resource abundance in grizzly bears (Nielsen et al. 2010), and dispersal of the long-jawed orb-weaving spider (Gillespie 1987). Published habitat selection models have been developed for many taxa, including salamander occupancy (Price et al 2011), moose habitat preference (Dussault et al 2006), and trout individual-based models (Railsback and Harvey 2001). Habitat selection models tend to focus on the non-breeding stages (e.g., Gillespie 1987, Stewart and Komers 2012, Hughes 1998). In heterogeneous habitats, selection of breeding sites can be understood with similar models for understanding adult habitat preferences, such as moose birthing sites (Stewart and Komers 2012), salmon stream segments (Neville et al. 2006), bird nest sites (Fretwell 1969), amphibian breeding ponds (Gamble et al. 2007).

Choosing the correct model for analyzing breeding habitat selection is crucial for making conservation decisions such as protection of existing refugia, restoration of suboptimal habitat, or creation/mitigation of new habitat. In each of these options, knowing the prioritized list of habitat types and characteristics would be useful for identifying and prioritizing areas to protect, or artificially altering existing habitat to

imitate these successful systems. However, depending on the type of model that is employed, the associated assumptions, and the type of data (e.g. the ultimate distribution vs. tracking individuals), one might be unable to make inferences about the critical ecological processes.. In some cases, an indicator of the outcome of a process does not inform the process directly. For example, Stewart and Komers (2012) used remote sensing to identify ideal birthing habitat for moose and conducted pellet surveys to estimate the population size. While these results give insight into where these moose settled after giving birth, it does not reveal the mechanism behind how they chose this habitat in the first place. When selecting a habitat selection model, it is important to appraise the assumptions of the model and the type of data that is required to run these models, to avoid this misinterpretation of the data.

Breeding-habitat selection models

There are several models used for habitat selection, but many of them are correlative (Piper 2011), including occupancy models, habitat preference models (HPM), and individual-based models (IBM). Occupancy models are used to estimate the proportion of sites occupied by a target species, based upon observed detection/non-detection data (MacKenzie et al. 2003). In a typical occupancy model, the presence/absence of individuals in a population is related to the existing habitat covariates. This model can be extended to a multistate form to understand the reproductive occupancy (i.e. where adults select the breeding/rearing site for their offspring, e.g. Mackenzie et al. 2009). These models are useful for identifying optimal habitat, but because they are correlative (i.e. they relate the decision outcomes to the habitat covariates) they do not reveal the underlying mechanism of breeding habitat selection. In a similar way, the habitat

preference model (HPM) is broadly deductive (Piper 2011), meaning that from the results of this model, one would be able to collect environmental data, and predict the number of individuals that will select that site. Because this model uses individual presence, it must assume individual behavior and fitness outcomes are equal across the population. In contrast, an individual-based model (IBM), which is mechanistic, seeks to describe the movement behavior of a few individuals to predict the behavior of every individual. This can be costly, complex, time-consuming, and produce weaker conclusions because of the typically smaller sample size. Further, in an IBM, assumptions about each individual's behavior and interactions is assumed to be similar across all individuals, including interspecific interactions, accessibility to resources, and genetics. The HPM is considered a top-down model, as the model predicts how many individuals will select a particular habitat type, while the IBM exhibits a bottom-up approach. By focusing on a few individuals, IBMs can predict which habitat other individuals will select, based on their behavior. While these models differ in their scope of focus, they are similar in that the resulting phenomena (*where* they select breeding habitat) are described, as opposed to the applying the underlying mechanism behind breeding habitat selection to each individual within a population (*why* they selected that breeding habitat). While both of these models have been applied to correlative studies, the assumptions and data required to apply these models is also important to appraise.

Habitat Preference Model

The habitat preference model (HPM) describes the expected pattern of space use by a sample of a population (Smouse et al. 2010). Habitat selection modeling includes the frequency of animals that use different habitat types, and their availability. The ratio of

the habitat use and availability of habitat types is used as a measure of habitat preference (Manly et al. 2002). Inference from an HPM assumes that animal density is proportional to habitat quality, as more individuals would settle in the better-quality habitats (Greene and Stamps 2001). Other assumptions include that animals will respond positively to the availability of highly selected habitat (i.e. organisms are more likely to choose the habitat type that is most readily available at a certain point in time; Railsback et al. 1999), and that this higher quality habitat will provide a higher carrying capacity (Van Horne 1983, Garshelis 2000, Railsback et al. 2003).

The assumptions of HPMs are frequently unmet when considering breeding habitats, which reduces the utility of the HPM to recruitment-limited populations (Garshelis 2000). For many species with complex life histories, a combination of habitat types is necessary, regardless of the amount of time spent in one of these habitat types (Garshelis 2000). For example, habitat types that are used for short amounts of time, like breeding habitat or migratory stopovers, may still be critical to overall reproductive success, but the observed density may not indicate the importance. Further, the HPM does not account for competitive interactions, where a smaller number of competitive individuals could inhabit the highest quality habitats, forcing disproportionately more subordinates into lower-quality habitats, lowering the carrying capacity of high quality habitats (VanHorne 1983). The fitness potential of a habitat cannot be assumed based only on the number of individuals observed within it unless a change in density directly correlates with a change in habitat quality (Railsback et al. 2003). In summary, the HPM is a correlative model that describes phenomenon of habitat selection (i.e. the relationships between habitat

qualities and individual abundance), but falters in describing the underlying mechanism behind habitat selection itself.

Individual-based Model

Instead of describing the phenomenon, like the HPM, the individual-based model (IBM) describes the decision rules behind an *individual's* breeding habitat selection in a bottom-up fashion. Animal movement models focus on describing the movement of an individual through space and time (Smouse et al. 2010). In addition to animal movement, visual morphological conditions of individuals at the sites Johnson (2005) can be used to determine habitat quality. However, these physiological indicators are only useful if they are related to individual fitness, as reproductive success can be linked to a particular habitat type. This model makes several assumptions: (i) the physiological responses vary in response to habitat variables (ii) resulting in changes in reproductive success. Body metrics of previously determined high- and low-quality habitats should be collected independently. Though this may seem to be an intuitive solution to determining habitat suitability, it would be difficult to parse out whether the physiological condition was a response to habitat quality, or density of conspecifics within the sites. Johnson also explains that statistically significant variation in these physiological conditions amongst sites is not explicitly indicative of variation in fitness, and that it is not a realistic correlation of habitat quality unless we are completely aware of what resources and ecological constraints govern reproductive success (Johnson 2005). Another assumption of an IBM is that all habitats will contribute to population growth in some way, regardless of quality, and that organisms can assess the mortality risk of each patch (i.e. due to lack of resources or predation). It is difficult to extrapolate the behavior of all

individuals in a population based on a small sample of IBMs because there is a need for many complex assumptions, including the genotype, phenotype, individual space use, potential competitive interactions, and resource availability. Limitations of the utility of the model include the difficulty of identifying and assessing factors that drive habitat selection in the field at the necessary spatial and temporal scales (Railsback 1999). This model provides more potential for gathering information on the mechanism behind breeding habitat selection, because it can link physiology and behavior with habitat factors. However, the financial cost and time investment to collect enough data required to make confident inference about those relationships stands as a disadvantage of individual-based models.

The Ideal Free Distribution

The ideal free distribution (IFD) is attractive as an alternative to the HPM and the IBM because it can be applied to understand breeding habitat selection, requires only two parameters, and has relatively few assumptions which may be more easily met. The IFD considers habitat suitability to be a function of population density. It assumes that animals can assess the quality of all potential sites (individuals are *ideal*), can make the decision to choose the site with the highest quality (individuals are *free*), and that individuals will select the site which maximizes their individual fitness (Fretwell 1969). Other relevant assumptions include that 1) habitat type is evenly distributed (equally accessible) in homogenous patches, 2) no two habitats have the same initial suitability, 3) individuals can move between patches with minimal time or energy consumption, and 4) that fitness is correlated to the abiotic quality of the habitat and the density of conspecific organisms already present (Farnsworth and Beecham 1997; Hakoyama 2003; Stewart and

Komers 2012). The IFD starts by assuming that habitat quality (S) and the reproductive fitness of the individuals that settle there (s) are directly related as:

$$[1] \quad \frac{S_{i1}}{S_{i1}} = \frac{S_{i2}}{S_{i2}}$$

and that the net suitability of a particular habitat (s_i) decreases with an increase in density (n_i):

[2]

$$S_i = \frac{I}{n_i} \sum_{q=1}^{n_i} S_{iq}$$

where S is habitat suitability, n is the number of individuals in the i th habitat, and s_{iq} is the expected success rate of the q th individual (Fretwell and Lucas 1970, Houston 2008).

The basic suitability of a habitat is dependent on the density of that habitat [Equation 3]. The parameters of this model include the individual's fitness (s = expected success rate of the individual), basic suitability (B = the base habitat quality before density effects), the effect of density on the basic suitability ($f_i(d_i)$ = using relevant density cues, such as conspecific presence), and net suitability (S = habitat quality after individuals have selected site i).

[3]

$$S_i = B_i - f_i(d_i), i = 1, 2, \dots, N$$

Where B_i is the basic suitability of the i th habitat, and $f_i(d_i)$ is the lowering effect on suitability of an increase in population density.

The IFD has been applied to multiple taxa because of its ability to describe breeding habitat selection by utilizing only two parameters (individual fitness and habitat suitability, Fretwell and Lucas 1970). For example, Beckmann and Berger (2003) described the habitat quality of black bears by the distribution of food resources, since food availability is a main limiting factor of reproduction. Body condition was measured as black bear mass, because mass is a proxy of reproductive success, and denning chronology were used as the individual fitness variable because competitive individuals hibernated for a shorter amount of time (Beckmann et al. 2003). Further, studies have correlated the number of moose droppings to habitat patch size, gerbil habitat selection with sand stability, and the size of lizards with the competition of resources and territory quality (Stewart and Komers 2012, Rosenzweig and Abramsky 1997, Paterson and Blouin-Demers 2018, Calsbeek and Sinervo 2002). The resulting habitat selection is described in a correlative way, but these studies do not reveal the process behind the selection.

As it was laid out in Fretwell and Lucas (1970), the IFD can describe the process by which animals choose breeding habitat, making this an attractive model. Using this model, managers can determine what the base habitat suitability is of any habitat type, and theoretically quantify how that suitability decreases as density increases. In this theory, managers would assume that individuals will choose the best breeding sites first,

but as the density of that site increases, the quality of the site decreases. This could lead to an individual having to choose between a higher quality habitat that is full, as opposed to a lower quality habitat that is not as full. This can be used to identify optimal breeding habitat in succession over the breeding season, instead of looking at the phenomena of where these animals settled.

The IFD provides some specific theoretical justification for habitat selection that leads to the distribution of animals. Therefore, applying this theoretical model over a time series to produce the mechanism behind breeding habitat selection in recruitment-limited populations would be a novel contribution to conservation management. Managers would have ability to observe habitat selection over time, as opposed to one observation or result. In these observations, the order in which breeding sites are selected would reveal the ranked habitat qualities in a system, providing information about optimal habitat within a metapopulation network of habitat, and allowing for managers to prioritize conservation efforts on the most productive sites. The IFD has been utilized to show the distribution of breeding habitat selection in mammals, reptiles, and birds, however this theory has not yet been applied to amphibian breeding.

Part 2: Using IFD on Amphibian Populations

Amphibian populations are experiencing global declines, in part due to changing climate, but also from habitat loss and alteration, environmental contaminants, and disease (Grant et al. 2016). Nearly one third of amphibian species are threatened with extinction (Stuart et al. 2004, McCallum 2007). Because of their small size and relatively

short life spans, they fall under this type III survivorship curve, where there is a high chance of mortality at a young age, but much less as they reach adulthood (Pinder et al. 1978). We can see this r-strategy exhibited by the number of offspring that amphibians have in one breeding season (e.g. most aquatic breeders deposit up to hundreds or thousands of eggs in one clutch, Mitchell & Pague, 2014). Because these populations are limited by recruitment, understanding where they decide to breed, as well as protecting these breeding sites is imperative to slowing their global decline. Previous studies have examined amphibian breeding habitat selection, but many of these studies are correlative (Appendix A).

The IFD has the potential to add new insights to the mechanism of breeding habitat selection beyond those from previous approaches. For example, Laurila (1998) found that *Bufo bufo* (Common toad) selected the largest pools, specifically those with the largest pool surface area. In the same study, a logistic regression was used to correlate the number of *Lithobates temporaria* (Common frog) with the amount of macrophyte vegetation, as well as pool surface area (Laurila 1998). Cunningham (2007) also used logistic regression to correlate the presence of 11 different amphibian species with habitat characteristics in a beaver-modified landscape. While these correlations provide some information about where these two species end up selecting habitat, it does little to describe the mechanism behind their choice. In a different approach, Strijbosch (1976) decided to focus on the habitat characteristics (e.g. plant composition in fens), and then use the frequency of amphibian occurrence to show habitat selection. This is an example of using the HPM to determine individual selection, however, again, this tactic does not reveal the mechanism behind how individuals decide where to breed. If the IFD were

applied over time, then these studies could have reported a prioritized order of habitat that was selected, at which point the characteristics of these habitats, or the mechanism behind their selection could be revealed (e.g. density, competition, predator-avoidance, prey-abundance).

In another example, Baldwin et al. (2006) employ animal movement techniques and an individual-based model (IBM), using radio transmitters on *Lithobates sylvaticus* (wood frogs) to observe where a sample of wood frogs select post-breeding habitat. This sample of frogs were monitored and recaptured over a season, and a detailed description of where these frogs decided to migrate to after breeding was published in the results. From this study, we observe that some wood frogs select close-canopy, forested wetlands on their way to summer refugia in shady, moist, sphagnum-dominated habitats (Baldwin et al. 2006). Yet, while this study provides insight on where this sample of individuals migrated to after breeding, it is difficult to generalize behavior beyond a sample to all wood frogs. There are a multitude of assumptions that must be placed on this study to imply that all wood frogs behave the same as this sample, including a lack of predation, a lack of resource limiting factors, and conspecific cues (to name a few) that could attribute to different individual behaviors.

While these correlative methods and models have produced valuable information on the amphibian's breeding habitat use, managers still need a better understanding of the mechanism behind the selection processes as opposed to the phenomenological result. Applying the IFD may be useful in these situations. For example, instead of comparing static habitat characteristics to numbers of individuals at one time, using a model that incorporates an axis dedicated to time/density along with habitat quality axis would

reveal daily mechanistic cues and potential density-dependence. The IFD has allowed scientists to gain a better understanding of the distribution of animals in response to habitat quality in other taxa (Kennedy & Grey 1993, Grand & Dill 1997, Beckman & Berger 2003), so it may be useful to apply it to amphibian populations.

Why Vernal Pools?

The studies above describe the breeding habitat selection of pond-breeding individuals, but there are many amphibians that are terrestrial or stream-breeding. To identify breeding habitat selection using the IFD, there needs to be an observable link between habitat quality and individual fitness. While some terrestrial salamanders breed exclusively in vernal pools, there are some species that lay eggs in small moist logs, in moss, or under rocks (i.e. not in aquatic habitat). Terrestrial salamanders are often fossorial, spending most of their time below the surface, making them difficult to consistently detect or observe. Similarly, stream salamanders are difficult to detect because their breeding habitat lies in a continuous area. Not only would it take a lot of effort to detect the individuals but finding where they lay their eggs is an entirely different task that would require more time and energy.

Vernal pool-breeding amphibians, however, breed in discrete vernal pool units that are static, consistently temporal, and often lead to a meta-population structure within a forest ecosystem. A large subset of amphibians includes obligate vernal pool breeders (i.e. those that require temporary fishless pools to breed) because of their sensitive, aquatic larval stages (Baldwin et al. 2006). Vernal pools are ephemeral; consisting of groundwater and melting snow in early spring and drying throughout the summer as plants increase uptake, groundwater recedes, and temperatures rise (Semlitsch and Skelly,

2008). As the changing climate threatens different precipitation and temperature regimes, the altered hydrology may affect the reproductive potential of these obligate vernal-pool breeders (Blaustein et al. 2010). Vernal pool-breeding amphibians (VPBA) are limited by recruitment (Vonesh and DeLaCruz 2002), are declining globally, and are a conservation interest (Stuart et al 2004, Seimlitsch and Rothermel 2003). Not would these VPBA benefit from a greater understanding of their breeding habitat selection, but applying the IFD would be simple, and effective for their overall conservation.

The IFD requires two statistics (measure of habitat quality, and individual fitness indicator) to identify the mechanism of habitat selection in any given system. In vernal pool systems specifically, correlational studies link the abundance of individuals to the depth (DiMauro & Hunter 2002, Skelly 1996, Gamble & Mitsch 2009). It is hypothesized that the larger a pool is (depth, surface area, volume), the more consistently it will be filled, and the longer it will retain water (i.e. hydroperiod). These aquatic larvae need ample time to grow and metamorphose before the pool dries, so selecting a pool that holds water longer allows for stronger offspring. When applying the IFD to VPBA, the depth of a pool would be a sufficient habitat quality indicator. However, an individual fitness indicator must also be identified.

Many vernal pool species breed in large groups that are synchronized with the coming of spring. Consistently warm, wet rains will trigger fossorial migration to breeding habitat (include here that time of day is also important). Once VPBA select their breeding habitat and mating begins, females will often lay only one egg mass (Berven 1988), especially in *R. sylvaticus*. Because each female will lay only one egg mass, the number of egg masses in one pool is an indicator of individual fitness, as well as

selection. In applying the IFD, observing the number of egg masses in a pool over the breeding season, as well as the quality of these pools, would reveal not only which pools accumulated the most egg masses, but also the order in which they did so. Quantifying this mechanism, which may be density-dependent, would lend itself to a greater understanding of breeding habitat selection in vernal pool breeding amphibians, because we could see the successive choices that amphibians make as the season continues.

Management Implications

Managers make difficult decisions when it comes to the conservation of natural resources (Pullin and Knight 2003, Bottrill et al. 2008). Management decisions and recommendations must fulfill the goals set forth by other stakeholders (i.e. trustees, game commissioners, the public) (Smith 2011), but uncertainty complicates these decisions and may lead to the inappropriate allocation of resources. Management strategies may be most useful to declining populations when ecological theory is applied and facilitates an increase of breeding opportunities (Berven 1990, Berven 1988, Gibs & Shriver 2005). A common way to reduce uncertainty that surrounds management decisions is through learning about the systems of interest (Maxwell et al. 2014). Along with consuming published literature, we can learn about a system by monitoring long and short term, predictive modeling, and applying known ecological theory. Monitoring data is useful when there is a need to link environmental learning with management implementation (DOI.gov site). Adaptive resource management (ARM) is a systematic approach for learning about a system through management outcomes and is particularly useful when there is an abundance of uncertainty.

In ARM, managers observe a problem in nature and create a management goal or objective that is mutually agreed upon and reflects the views of all stakeholders (e.g. increase population size, reduce spread of disease, maintain or restore ecosystem functions). Stakeholders then assess possible solutions through literature reviews and short-term monitoring data, and create predictive models using ecological theory (Williams et al. 2009). System state data is estimated using these models, and after a management action is selected and employed, long-term monitoring data facilitates learning about the system after it has been managed (Grant et al. 2013, Walters 1986). Selecting these sub-optimal strategies may lead to a misuse, or inefficient use of these resources, therefore, implementing the best solution for the given objective in the first place is critical (Caughlin and Oakley 2001; Ohlson and Serveiss 2007; Maxwell et al. 2014).

In theory, these steps are simple to apply, but deciding which management strategy is optimal becomes challenging. Merkle et al. 2019 suggest collaboration frameworks between management and researchers, including structured decision-making (SDM) (Merkle et al. 2019). SDM is a process that reduces making a decision to a series of logical steps, taking into account the measurable uncertainties, human bias, and ecological goals (Hammond et al. 1999, Gregory et al. 2012, Runge et al. 2013). This process frames and analyzes making a decision by breaking it down into discrete steps and may be beneficial in ARM between the designing of potential management strategies and their application (Williams et al. 2009). Decision analysis incorporates the beliefs (heavily reliant on ecological information) and values (personal, situational, and rarely influenced by science) of stakeholders and managers when framing management

objectives, but the incorporation of relevant uncertainty is crucial (von Winterfeldt 2013). Looming uncertainty about the system dynamics influences (1) predictions and (2) decisions/choices. Managers would benefit from having a better understanding of how the system responds to change and make the decisions between management alternatives more effective.

The field of resource management is dynamic and unpredictable (resources, funding, policy, stakeholders' values, etc.). Utilizing existing and affordable resources, like theoretical ecology, would not only be cost effective, but would also allow for managers to learn more about their systems and the mechanisms behind these processes of interest. The application of ecological theory to natural and managed systems, along with an analysis of the value of information, could streamline the type, quantity, and quality of data that will be collected, while reducing some structural uncertainty. Paul Ehrlich, well-known for his warnings about human overpopulation, explains that there is an abundance of existing ecological theory, and that we would be foolish to ignore it these existing resources (Ehrlich 1989 *Perspectives in Ecological Theory*).

When relating specifically to amphibian conservation, especially VPBA, managers could stand to know more about the systems they are managing, reducing uncertainty and leading to more successful conservation decisions. To slow the decline of VPBA, managers must identify the highest quality breeding sites, as they are recruitment-limited. Applying the IFD to this system would not only provide managers with information about which breeding sites accumulate the most egg masses, but also a prioritized list of quality habitat, and consequently productivity. Because the IFD predicts that the highest quality site will accumulate the most egg masses, until the base suitability starts to

decline (from conspecific density), and then the next highest quality pool will become the optimal breeding habitat selection.

Improving the persistence of amphibian populations continues to be a main objective of most managers, but there are still relevant uncertainties surrounding these strategies. The three major management alternatives are to protect existing refugia, alter existing pools to mimic ideal habitat conditions, or create entirely new pools or networks (Dodd 2010). In any of the three strategies, identifying where (in space) the conservation action happens is a major uncertainty. If managers had a successive list of the most productive breeding sites for amphibians, then conservation efforts could be much more streamlined and effective.

Ecological theory provides scientists and managers with a shortcut, supplementing mechanisms behind ecological processes, when there is little to no empirical evidence. In the case of vernal pool-breeding amphibians, populations are experiencing global decline, and managers make decisions with great uncertainty (protect, alter, create, or do nothing). Reducing manager uncertainties about the system would yield a more efficient use of resources, and more effective conservation actions towards these declining amphibian populations. Applying ecological theory to how amphibians select breeding habitat not only reveals mechanistic cues about ideal habitat that can be either protected or altered, but also provides opportunities to test minimally applied ecological theory within a time series.

Incorporating theory into conservation management can improve the utilization of scientific evidence when making decisions (Cook et al. 2013). Linking specific system processes with general theoretical models makes scientific discoveries stronger (Grace et

al. 2010). These two pieces along with conservation managers' values would lead to more confident, and effective decisions. Science brings a quantitative, un-biased approach to both predicting future ecosystem states, as well as identifying appropriate management actions. Palmer and Hastings (2003) advocate for more of a mathematical and theoretical approach to biological issues. Bridging the boundary between knowledge and action when it comes to conservation management requires harnessing existing knowledge, creating realistic recommendations, and improving the incorporation of science in management decisions (Cooke et al. 2013). Applying theory to ecological systems and management not only helps to better understand the systems, but also further refine the assumptions of these theories from a mathematical standpoint. Ultimately, utilizing readily available resources can help to drastically reduce the loss of resources by making a suboptimal decision.

CHAPTER 2

ARE WOOD FROGS (*LITHOBATES SYLVATICUS*) IDEAL AND FREE WHEN SELECTING BREEDING HABITAT?

Abstract

Reduction in habitat quality is one of the factors leading to global amphibian declines. For amphibians, which are often recruitment-limited, breeding habitat is disproportionately important to abundance. Breeding habitat selection can be described by the ideal free distribution, where individuals select breeding habitat to maximize their fitness, using habitat and conspecific density cues. In this chapter, I use a census and habitat quality data from multiple wood frog populations within the Patuxent Wildlife Refuge in Maryland, USA to test if wood frogs are ideal and free when selecting breeding habitat. Across three years, wood frogs often selected pools that were larger, deeper, and have a predictable hydroperiod. This suggests that individual wood frogs use existing environmental cues to select breeding habitat that will optimize their fitness. My results add evidence to understand wood frog settling decisions, and may improve management decisions for increasing wood frog abundance, including the reduction of ecological traps that are often associated with anthropogenic/artificial vernal pools.

Introduction

Though there are a handful of factors implicated in global amphibian decline, reduction in habitat quality is considered by many authors to be the most important (Wyman 1990, Blaustein et al. 1994, Pounds 1999). The number and distribution of suitable breeding habitats, in particular, are critical for population growth. For populations that are limited by recruitment, management strategies may be most effective when they increase breeding opportunities (Berven 1990, Berven 1988, Gibbs & Shriver 2005). Many amphibian species have relatively short lifespans, produce many offspring at once, and thus their populations are often recruitment limited (Edge et al 2016, Brockelman 1969). Because amphibian recruitment is directly tied to breeding habitat quality, conservation efforts are often focused on creating, enhancing, or protecting productive habitat (Denver et al 1998, Semlitsch 1983, Semlitsch 1987, Wilbur 1972). Much of what we know about where amphibians decide to breed is correlative, instead of describing the mechanism behind these decisions. (e.g., Kuramoto 1978, Homan et al. 2004, Baldwin et al. 2006, Karraker & Gibbs 2009).

Many vernal pool-breeding amphibians rely on temporary, fishless pools for successful recruitment (Baldwin et al. 2006). Vernal pools are available for breeding wood frogs (*Lithobates sylvaticus*) in early spring, and typically dry before the end of summer, leaving enough time for successful metamorphosis of juveniles. Ideal environmental conditions for amphibian development are temperature and density-dependent and are dynamic and stochastic (Wilbur and Collins 1973, Newman 1998). Pool depth, volume, and hydroperiod are the most important for reproductive success (Skidds et al. 2007, DiMauro and Hunter 2002, Baldwin et al. 2006). In vernal pool

habitats, changing precipitation regimes resulting from climate change may lead to unpredictable annual hydrology, making it difficult for individual frogs to predict what habitat will be successful (Bauder 2005).

Wood frog breeding is temporally predictable, as they emerge and migrate to breeding pools after the earliest warm rains of spring; and the egg masses they produce are clearly visible and distinguishable from one another, which means they can be a useful proxy of population estimates (Grant et al. 2005). Wood frogs select one pool from naturally occurring clusters (VanMeter et al. 2008) for breeding, where females deposit one egg mass (Crouch and Patton 2000). Wood frogs select sites for reproduction based on auditory cues (e.g. vocalizations - Landreth and Ferguson 1966, Tracy and Dole 1969), olfactory cues (Oldham 1967, Dole 1968, Grant et al. 1968), and visual cues (e.g. celestial cues - Landreth and Ferguson 1967, canopy cover – Schiesari 2006, presence of conspecifics – Reeve et al. 2013). These cues suggest that patterns of egg mass accumulation may be informative of individual choices. The speed at which larval development occurs is negatively related to the volume and depth of a pond (Denver et al. 1998, Wilbur and Collins 1973). Pond depth is typically, but not always, correlated with hydroperiod (Snodgrass et al. 2000, Denver et al. 1998, Skidds et al. 2007). A longer hydroperiod allows for greater wood frog larval development and yields a higher survival rate to metamorphosis. This means that individuals should select habitats with more predictable, and longer, hydroperiods which are typically deeper and larger pools.

While these environmental factors described above are correlated with breeding site selection, successful recruitment, and population persistence (Brooks and Hyashi 2002, Homan et al. 2004, deMaynadier and Houlahan 2008, Denton and Richter 2013,

Calhoun et al. 2014), the behavioral mechanism for individual decisions has not been characterized (Skidds et al. 2007). Because breeding site selection is so important for individual fitness in wood frogs, understanding the mechanism behind breeding habitat selection will help managers to increase breeding opportunities and reproductive success. Modeling habitat selection using ecological theory will provide managers with a short-cut that will showcase the environmental cues that amphibians perceive when selecting breeding habitat. Among general habitat selection models, the ideal free distribution (IFD) is a particularly useful theory, which was developed to describe the breeding habitat selection of avifauna (Fretwell and Lucas 1972). The ideal free distribution relates habitat suitability as a function of population density. It assumes that individuals will select the site which maximizes their fitness because animals are ideal (can assess the quality of all potential sites), and free (can make the conscious decision to choose the site with the highest quality) (Fretwell 1969).

I used multiple timeseries of wood frog egg mass counts to answer two questions: 1) are wood frogs ideal and free when selecting breeding habitat, and 2) what environmental cues are wood frogs responding to when they select breeding habitat? For question 1, I will be analyzing the pattern of accumulation, by comparing the rank order of the egg mass accumulation to the rank order of environmental variables, including maximum depth, maximum volume, and hydroperiod predictability. To answer my second question, I will run a mixed effect linear model to compare the same environmental covariates to two fitness variables. I expect egg masses to accumulate in the highest quality sites first (i.e. deepest, largest, most predictable pools). The order in which pools accumulate egg masses should also match with the ending density of egg

masses in each pool (i.e. the largest quality pool should have the highest relative ending density and accumulate the most eggs). Wood frogs exhibit site fidelity, meaning that they are not only expected to return to the same breeding sites each year, but also the returning to their natal sites where they emerged (Vasconcelos and Calhoun 2004). Understanding which pools amphibians select to breed, as well as the cues that they use to make these decisions will provide insight to better management practices in the future.

Methods

Site Description - Patuxent Research Refuge, a ~52 km² forested refuge in suburban Maryland, has multiple clusters of vernal pools which serve as breeding habitat for wood frogs (*Lithobates sylvaticus*). These study sites are within a mixed bottomland hardwood forest, and climate is characterized by hot and humid summers and mild winters, with an average of 1067 mm of rainfall between April and October (U.S. Fish and Wildlife Service 2012).

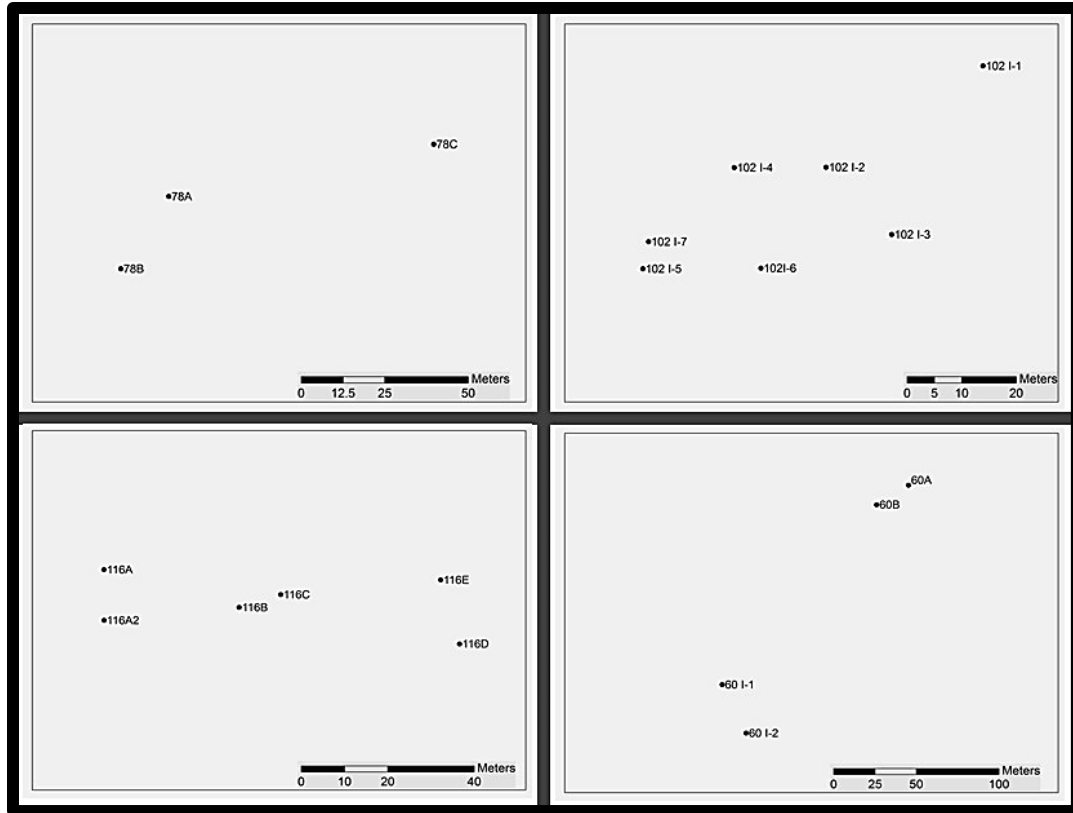


Figure 1. Map of study area, showing the proximity of the pools within each cluster.

Field Methods - Four clusters of pools (Figure 1) were censused daily just prior to and during the breeding season (March-April) for wood frog egg masses. Sites were selected based on the proximity of the pools within a cluster. Four separate clusters, all within 5 km², include between 3-7 pools each. These pools are within 100 m of each other (Figure 1). Two clusters were sampled four times (2010, 2013-2015), and two clusters were sampled only three (2010, 2014, 2015). Along with egg mass counts, site-level covariate data were also recorded, including depth, width, and length. Wood frog egg masses were counted nearly every day at each pool by two independent observers from the first week of March until late April in 2010, and 2013-2015. The highest number of egg masses for each species was recorded each day by either observer was

used in the analysis, due to the operating assumption that egg masses are easily detectable, and not likely to be overcounted (Grant et al. 2005). It is also unlikely for the egg masses of our focal species to be confused with the egg masses of other species because they look fundamentally different. For each pool that had egg masses, we conducted a visual survey of metamorph abundance, using the same double observer method as the egg mass counts (Grant et al. 2005).

Data Description - Four clusters of pools (each with 3-7 pools) were sampled for wood frog egg masses before breeding began through the peak egg mass deposition during the breeding season (early March to June) for three years (2010, 2014, 2015). With data collected in four separate clusters over four years, I will treat each cluster as a replicate (n=14, two clusters were not surveyed in 2013). Once during each survey period, the maximum depth, length and width of each pool was also recorded. I calculated volume using the formula for an ellipse ($\text{volume} = (\pi * \text{length} * \text{width}) / 4$) for each site and year. Hydroperiod is an important feature of wood frog breeding habitat, but there are many ways that hydroperiod can be defined. I decided to use a hydroperiod permanence variable, which is the proportion of how many years out of the previous three the pool held water by 01 June. I also used observations of late summer water availability to construct a categorical hydroperiod variable that describes the site history. This categorization was used to capture the choices of amphibians that emerged from these pools one, two, and three years ago based on the site history (i.e. did it hold water by 01 June). Because wood frogs take at least two years to become sexually mature, and they typically live 4-yrs, this measure of hydroperiod may describe habitat selection that is a function of individual memory (and not related to current conditions). Ponds that held

water through June only in the previous year (termed Lag 1) may not be reliable, though those adults that bred in the pool the previous year may still return even though their offspring did not successfully metamorphose. Lag 2 is defined by pools that held water through 01 June in both of the last two years, and captures sexually mature adults that bred in the pool the year prior, that may have returned, as well as individuals that could have emerged from this pool two years prior. Lag 3 ponds held water through 01 June in all of the last three years and should be the most reliable, as it encompasses a mixture of old and new individuals. I calculated two dependent variables: the total egg mass density (D) by dividing the maximum egg mass count by the pond volume, and the breeding success (S_{iq}) as the number of late-stage tadpoles divided by the max egg mass count (Fretwell 1969). Because the IFD is concerned with the temporal dynamics of habitat choice, I also calculated the date that the first egg mass was deposited in a pool, and compared these ranks to the expected ranks determined by the habitat characteristics (volume and depth).

Breeding Site and Habitat Quality Correlations - I used a Spearman rank correlation test to each pool in all three years combined to test for a relationship between the pattern of accumulation and the pattern of environmental ranks. The observed rank was the order in which each pool was selected (i.e. the first date that an egg mass was deposited) within its cluster. If two pools had the same beginning date, the pool that accumulated more egg masses on that day was assigned a higher rank. To test the whether the patterns of accumulation matched the pattern of environmental variables, I ranked pools by their maximum depth and maximum volume, and hydroperiod permanence. I compared the ranks of all samples (each cluster in each year, n=12), and

then by cluster individually, and by year individually. Pools that were larger, deeper, and held water more consistently were assumed to be higher quality for wood frog breeding (Skidds et al. 2007, DiMauro and Hunter 2002, Baldwin et al. 2006). All pools that did not accumulate any egg masses were assigned the last rank.

Statistical Modeling - I fit the data to two separate models to relate (1) the ending density and (2) breeding success S_{iq} to the independent habitat characteristics: depth, volume, and the three generations described by hydroperiod. The ending density and breeding success were the dependent variables, with a normal error distribution. The year and cluster were included as random effects, allowing us to analyze the non-independent count data by assuming that each year and each cluster have a different “baseline” value for each pool that falls within it. The selected habitat covariates were all fixed effects that we assume independently affect the dependent variables. However, after running both models, there was support for a random effect of cluster and year, so I removed them from the model. Models were fit in the lme4 package (Bates et al. 2015) using R software (R Development Core Team 2020).

Results

Question 1 – Pattern: Order of Accumulation

Pattern of Accumulation via Spearman Rank – Upon visually analyzing the pattern of accumulation and environmental ranks, I found that the deepest pools tended to be colonized first, and the most shallow pools last, however I did observe annual and among-cluster variation (Fig. 2), suggesting that depth alone is not a sufficient predictor for breeding site quality. This pattern was exhibited by cluster 60 and 78, while the

clusters with five or more pools showed more variable adherence to this pattern. For example, in cluster 102 (Fig. 2c), the pool that had the largest depth in all three years was selected second in the first year, not at all in the second year, and then next to last in the third year. In cluster 116 (Fig. 2d), the deepest pool was never selected. This depth ranged from 0.34-0.37 m². Aside from the deepest pool, however, the order of accumulation matched closely to the maximum depth predictions. In this cluster, the deepest pool wasn't always the first selected, but the remaining order matched the depth rankings. A similar, yet less consistent, pattern that varied by cluster was shown when analyzing the maximum volume attained in one year (Fig. 3). Clusters 60 and 78 had larger pools selected first and smaller pools selected last, with exceptions to the year 2014. The rank-order of pond volume, unlike depth, showed no relationship to the pattern of egg mass accumulation in clusters 102 and 116 (Fig 3).

The Spearman rank correlation test allowed for some quantitative evidence between these observed patterns. Using this test, I found hydroperiod permanence, depth, and volume had significant ($p < 0.05$) positive correlations with the order in which ponds were selected for breeding (Table 1). Cluster 60, over all three years, was the only pool to consistently have significantly positive correlations with all three independent variables. Clusters 78 and 102 had positive correlations for all three independent variables, but only hydroperiod was significant for both clusters. Cluster 116 had negative correlations for depth and volume, and no correlation with hydroperiod permanence across all three years. In 2010, 2014, and 2015, all correlations with depth, volume, and hydroperiod permanence were positive, but only hydroperiod was significant. All relationships for

depth and volume were positive across all three years, but only volume in 2014 and 2015 was significant.

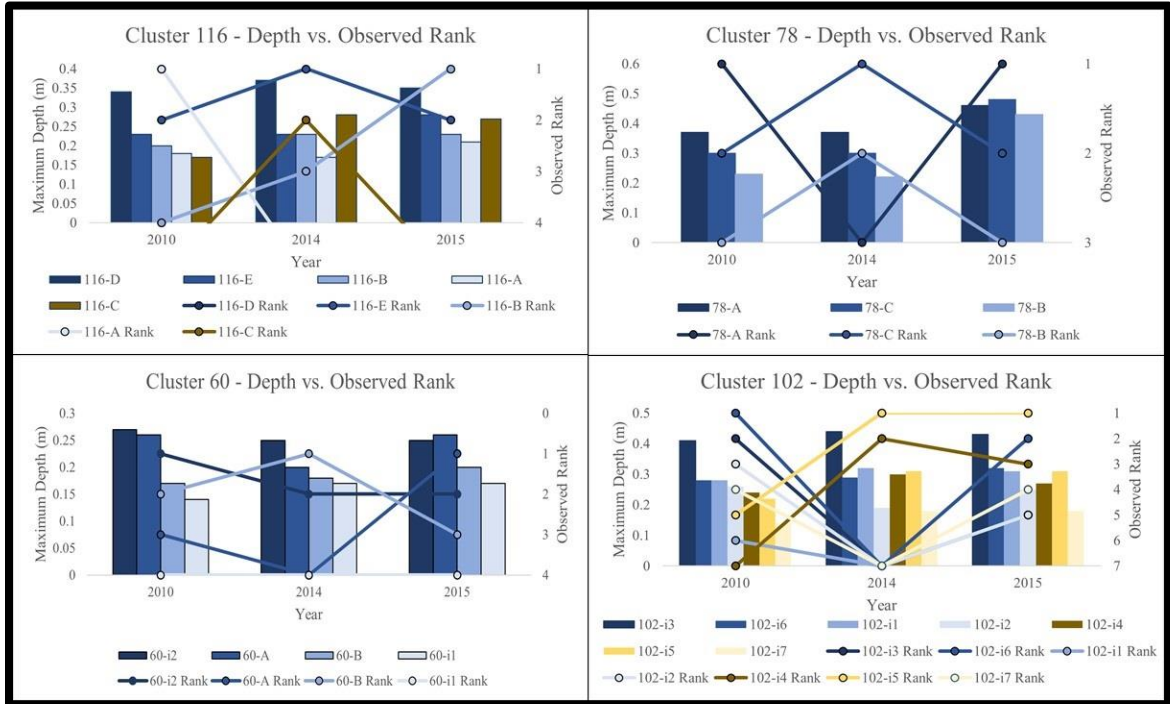


Figure 2. Visual results of the observed rank order that pools were selected compared to their rank according to the maximum depth observed in one year. The maximum depth for each year was plotted first, represented by the bars. These were ranked from largest to smallest. The observed rank order of egg mass

accumulation is shown via the points, and the changes in these ranks from one year to the next is shown by the lines connecting the points.

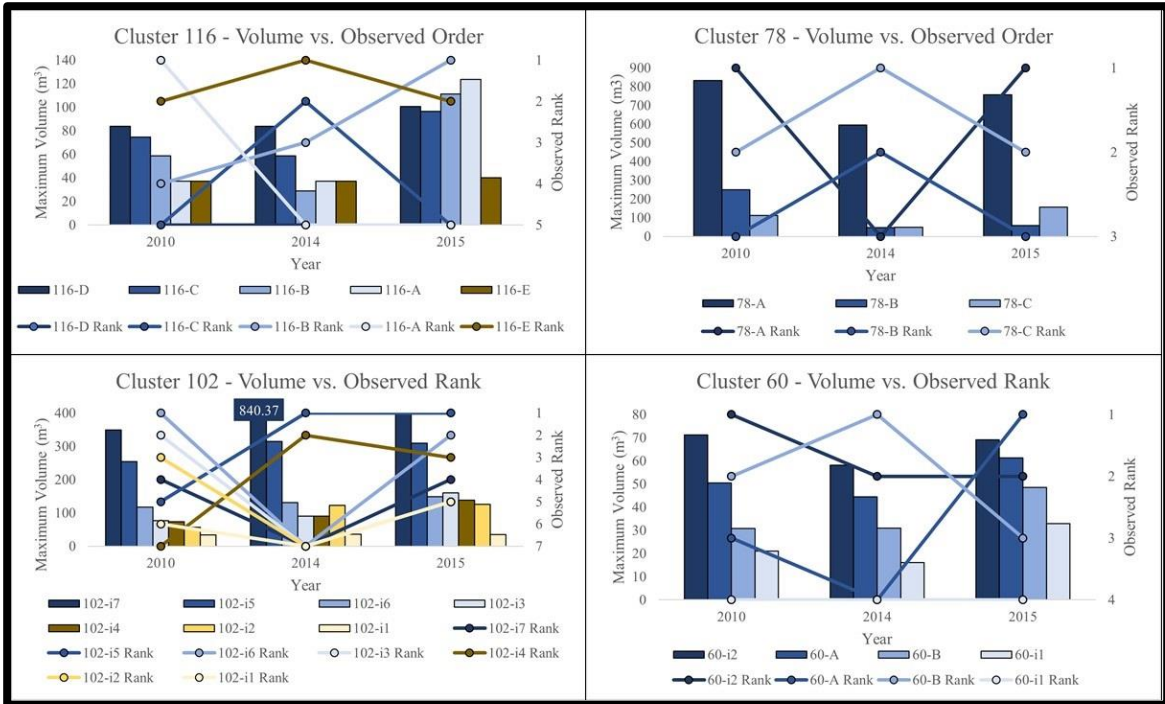


Figure 3. Visual results of the observed rank order that pools were selected compared to their rank according to the maximum volume observed in one year. The maximum volume for each year was plotted first, represented by the bars. These were ranked from largest to smallest. The observed rank order of egg mass accumulation is shown via the points, and the changes in these ranks from one year to the next is shown by the lines connecting the points.

Table 1. Results of Spearman rank correlation test for each cluster over 3 years, and all clusters for each year. Comparing the observed rank order that pools were selected and the ranks of each habitat quality variable. Bold numbers indicate significant relationships.

	Depth (r^2)	Depth p-value	Volume (r^2)	Volume p-value	Hydroperiod Permanence (r^2)	Hydro p-value
<i>All</i>	0.323	0.014	0.363	0.005	0.259	0.005
Cluster						
<i>60</i>	0.683	0.014	0.611	0.034	0.254	0.014
<i>78</i>	0.311	0.415	0.622	0.074	0.359	0.021
<i>102</i>	0.188	0.414	0.320	0.157	0.105	0.008
<i>116</i>	-0.142	0.614	-0.426	0.113	0.000	0.011
Year						
<i>2010</i>	0.346	0.147	0.276	0.253	0.389	0.009
<i>2014</i>	0.259	0.284	0.501	0.029	0.317	0.009
<i>2015</i>	0.259	0.284	0.501	0.029	0.317	0.009

Question 2 – GLM of independent variables

End Density - I found that there was a strong positive relationship between whether a pond held water into June the previous year, and the ending density (Table 2), and the relationship was strong. While hydroperiod in $t-2$ and $t-3$ were also positively related to end density in a given pond (Table 2), their effects were much weaker. Both the maximum depth and maximum volume had negative effects on the ending density (Table 2). Density is indirectly calculated from volume, so this relationship itself is not surprising, but the difference between ending densities across pools/clusters is unexpected. I unexpectedly found that within these clusters, the larger pools have smaller breeding populations per unit volume.

Breeding Success - There was a strong positive relationship between the maximum pond depth and my metric of individual fitness (S_{iq} , which is the number of metamorphs/ the number of egg masses), however, the standard error was large (Table 3). There was a weaker, but still positive effect of the maximum volume in a pool (Table 3). The S_{iq} was most strongly influenced by whether the pond held water in the previous years, with weaker negative relationships with water in $t-2$ and $t-3$, indicating that wood frog fitness is more strongly related to the individual memory from the year prior than experience over a longer time period (Table 3).

Table 2. Model summary of estimated coefficient values and standard errors for a generalized linear model analyzing the fixed effects of maximum volume, maximum depth, and different hydroperiod categories on ending density.

<i>Variable</i>	<i>Estimate</i>	<i>Std. Error</i>
Maximum Depth	-0.241	0.630
Maximum Volume	-0.055	0.047
Lag t-1	0.229	0.140
Lag t-2	0.005	0.118
Lag t-3	0.025	0.137

Table 3. Model summary of estimated coefficient values and standard errors for a generalized linear model analyzing the fixed effects (depth, volume, hydroperiod) and random effects (year and cluster) on the S_{iq} .

<i>Variable</i>	<i>Estimate</i>	<i>Std. Error</i>
Maximum Depth	1.205	1.762
Maximum Volume	0.175	0.130
Lag t-1	0.627	0.394
Lag t-2	-0.234	0.317
Lag t-3	-0.309	0.375

Discussion

Animals that are ideal and free select habitats that optimize their fitness (Fretwell 1969) and identifying characteristics of sites that are selected may aid conservation and management decisions. I found that the pattern of egg mass accumulation suggests that wood frogs make temporally varying selection of optimal habitat. This suggests that individual wood frogs perceive environmental cues used to select breeding habitat that will optimize their fitness. Specifically, I found that where wood frogs chose to breed was related to the depth and volume of the pool. Based on my results, larger and deeper pools were generally selected for the deposition of egg masses before smaller and more

shallow pools. Total pond volume was not as strongly related to selection as the maximum pond depth, but it was a stronger indicator of site selection than the site hydroperiod history, or lags (Table 2, 3). As expected from observations of site-fidelity (Vasconcelos and Calhoun 2004), wood frogs appear to select breeding sites that have predictable hydroperiods (i.e., they held water long enough for successful metamorphosis) in the previous three years (Table 3) – though density and breeding success were not as strongly related as observations of site-fidelity from marked animals would suggest (Green and Bailey 2015). Pools that held water the year prior had the largest egg mass densities and had highest breeding success.

I found evidence to support the non-random selection of breeding sites by wood frogs, consistent with expectations under the IFD. Wood frogs have a complex life cycle that requires sufficiently persistent aquatic habitat to successfully metamorphose. Deeper pools tend to hold water longer (Egan and Paton 2004, Burne and Griffin 2005), which would explain the strong relationship between pond depth and breeding success (Skidds et al. 2007). While the deepest pools were most often selected first, this did not result in higher densities at the end of the breeding season. This low ending density could be a result of predation, because larger pools are more visible and are likely to have more prey (Semlitsch et al. 1996, Morin 1981), or low pond productivity (Berven 1990). Large pools may be an attractive option for wood frogs, with the promise of enough time and resources to metamorphose (Babbitt et al. 2003). However, the hydroperiod is not solely dictated by the size of the pool, but also by other ecological factors (e.g. vegetation, forest type, canopy cover etc.).

Wood frogs did not perfectly demonstrate ideal and free breeding site selection behavior. Wood frogs may not be ‘free’ as an indirect result of their life history. A consistently strong relationship between the last year’s hydroperiod, and a high density and breeding success is supported by this pattern. Wood frogs exhibit site fidelity where individuals may select a lower quality pool than expected because they are using prior information about the success of a site (from which they successfully metamorphosed). Because wood frogs only live for around four years, they are limited in their lifetime reproductive opportunities (i.e. they may only get one or two chances to breed), so selecting their natal pool where they metamorphosed from may be a useful evolutionary strategy. Because wood frogs do not provide parental care, it is impossible to associate their choice of egg deposition site with the consequence of their reproductive fitness. If they are unable to evaluate their breeding success, then they may be subject to ecological traps (DiMauro and Hunter 2002, Schlaepfer et al. 2002). Ecological traps are habitats, usually as a result of anthropogenic interaction, that appear to be suitable based on physical characteristics (a large, deep pool), but because of confounding variables (short hydroperiod), could result in a population sink for those that choose to breed there instead of a source (Best 1986). If site fidelity is a proximate mechanism by which individuals select more stable hydroperiod ponds, then climate change and ecological traps could reduce the benefit of this evolved strategy.

Wood frogs may not be ‘ideal’ in that they may be drawn to suboptimal pools (from a fitness perspective) based on the presence of conspecifics through calling or visual cues. The opposite effect could also occur, where individuals would avoid higher quality habitats because of a surplus of conspecifics, as proposed by the ideal despotic

distribution theory (Fretwell 1972). An extension of this theory includes the effect of intra and interspecific competition on reproductive success and habitat selection, where larger, more superior/experienced individuals could crowd and compete for the best quality habitats, forcing subordinates into lower-quality habitats (Fretwell 1972), however territoriality in adult wood frogs has not been described. While both the ideal despotic and the ideal free distribution theory have been applied to a variety of other taxa including reptiles, mammals, and avifauna (Moeller 1995, Calsbeek and Sinervo 2002, Murray et al. 2007), the ideal free distribution has proven difficult to fully replicate in this study because we were unable to determine a basic habitat suitability.

This study has given insight into the type of information that wood frogs use to select breeding habitat, yet I found that the application of Fretwell's theory to timeseries of census data is not straightforward. Principally, the IFD requires knowledge of a baseline suitability for every habitat, such that as density increases, the suitability of the habitat decreases. This baseline suitability is the maximum suitability when density is zero, and is affected by factors like potential predators, food resources, and conspecific density among others (Fretwell 1972). The concept of habitat suitability has many ecological components (e.g. food, space, predators, mates, etc.), yet when the IFD has been applied to other studies, it often focuses on only one component. For example, in other studies that apply the IFD, the baseline suitability is known to be associated with the amount of food resources that a habitat can produce (Fagen 1988, Beckman and Berger 2003, Calsbeek and Sinervo 2002). While these studies may suggest how the distribution of animals is affecting a limiting food-resource, identifying the factors driving baseline suitability in complex ecological systems is challenging. For wood frogs,

patch size is a strong factor determining the timing of metamorphosis (Skidds et al. 2007), but food availability, competition, and predators also affect the fitness of these individuals, encompassing multiple life history stages (Wilbur and Collins 1973, Denver et al. 1998, Skidds et al. 2007). Our inability to adequately provide baseline suitabilities may also be a reason for wood frog's deviation from an ideal and free distribution.

The lack of fit to the IFD provides us with a greater insight for wood frog breeding habitat selection. In previous research, wood frogs tend to select breeding habitat that is larger, deeper, and has a predictable hydroperiod (Skidds et al. 2007, DiMauro and Hunter 2002, Baldwin et al. 2006), however I found that the pattern of accumulation does not perfectly support those correlations. We assume based on prior studies that bigger, deeper, and more permanent pools are the best (Babbitt et al. 2003), however this assumption is not sufficient to describe the underlying mechanism behind breeding habitat selection in this system. Based on my results, these correlative studies that have been described by the occupancy or abundance of wood frogs are not completely describing the selection process. This lack of fit is indicative that we need to explore more into the dynamic and integrated processes of the system, instead of focusing on the static and observable patterns.

While the IFD uses data of animal accumulation (Messier et al. 1990, Bautista et al. 1995) and distribution (Sutherland et al 1988, Beckman and Berger 2003, Swain and Wade 2003) to describe how populations are regulated in variable environments (Fretwell 1972), other more controlled methods may be useful to understand habitat selection directly. Designing an experiment with the intent to determine which variables that wood frogs respond to most when settling would give more insight to the mechanism behind

breeding habitat selection. Experimentally creating replicated networks of pools with varying hydroperiod, depth, and volume regimes over multiple seasons would allow for more direct estimates of baseline suitability based on habitat quality indices. Other factors that may contribute to basic suitability occur at different scales. Within each pool, the availability or abundance of food resources, size, shape, surface area of the pool, and canopy cover, may be important factors that may interact to create a suitable habitat (Skidds et al. 2007). At a landscape level, hydroperiod regimes, surrounding habitat, and proximity to forests or other forested wetlands are also factors that may contribute to habitat suitability (Kolozsvary and Swihart 1999). In addition, annually tracking individual adults (i.e., via capture-recapture methods, Green and Bailey 2015) that selected the pools to breed would help to understand the relative importance of site fidelity and habitat characteristics in site selection.

Overall, this study suggests that wood frog breeding site selection is predictable and related to habitat features. Understanding breeding site selection may be useful to assess relative quality of pools within a network and improve management to protect vernal pool habitats that are crucial to sustaining amphibian populations. These results add evidence to understand the mechanism behind wood frog breeding site selection decisions, and may enable decisions for increasing wood frog abundance, including the reduction of ecological traps (DiMauro and Hunter 2002).

As amphibian populations are already declining (Miller and Grant 2015), each reproductive season is critical for amphibian population persistence, especially short-generation species like wood frogs (Biek et al. 2002, Vonesh and De La Cruz 2002). Many wood frog populations may benefit from a broader diversity of hydroperiods and

depths when managers are creating, maintaining, altering, or protecting existing habitat.

Providing a greater diversity of habitat may yield more breeding opportunities, increasing potential reproductive success (Brand and Snodgrass 2010), especially as stochasticity in seasonal hydroperiod and urbanization increases (Bertassello et al. 2019).

APPENDIX

System	Species	Methods	Authors
Vernal Pool	<i>Lithobates temporaria</i> <i>Bufo bufo</i>	Linear regression (correlational)	Laurila, 1998
Beaver Pond	<i>Notophthalmus viridescens</i> <i>Ambystoma maculatum</i> <i>Pseudacris crucifer</i> <i>Lithobates clamitans</i> <i>Lithobates sylvaticus</i> <i>Pickrel frog</i> <i>Bullfrogs</i>	Linear regression (correlation)	Cunningham, Calhoun, Glanz, 2007
Vernal Pool	<i>Lithobates sylvaticus</i>	Animal movement via transmitters (IBM)	Baldwin, Calhoun, DeMaynadier, 2006
Fens	Multiple amphibian species	Correlation of habitat type to frequency of occurrence (HPM)	H. Strijbosch, 1979

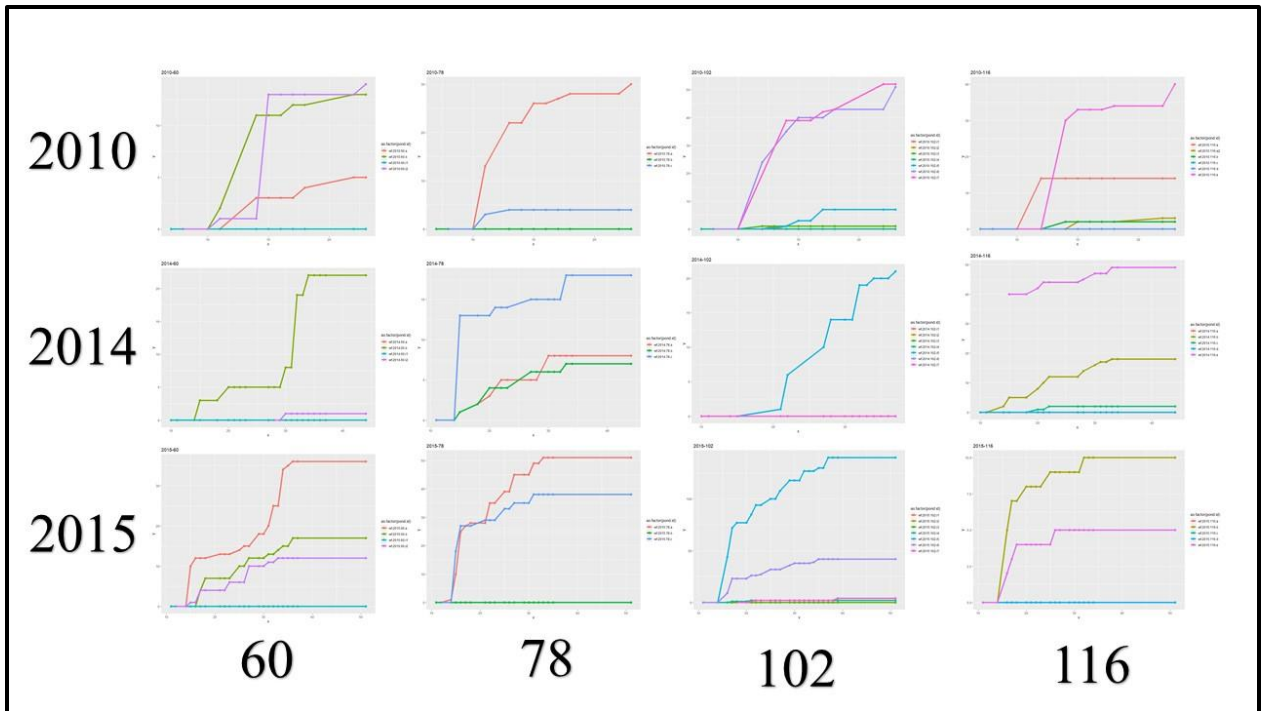


Figure 4. Raw wood frog egg mass counts in four clusters (x-axis) over 3 years (y-axis).

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