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Analysis of Social Dominance in the Green Anole

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ANALYSIS OF SOCIAL DOMINANCE IN THE GREEN ANOLE
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Abstract

Dominance relationships are an important aspect of the social organization of many species. Male dominance often results in successful territory defense and/or access to potential mates, and thus is a central component in establishing social rank. In this study, I used mathematical models to consider social interactions of the green anole lizard (*Anolis carolinensis*) in both territorial and hierarchical contexts. I then identified the behavioral and morphological traits associated with dominance in this species.

I first analyzed a series of ranking algorithms to evaluate their effectiveness as a novel approach to quantifying animal social status. I found that all eight systems considered in this analysis successfully reflected dominance relationships in the green anole; however, no one system consistently predicted ranks using the measured traits. Therefore ranking systems are a viable method of analyzing social hierarchies in anoles, yet multiple systems are required to effectively model these dominance relationships.

I then performed three empirical studies using the eight ranking systems from the previous analysis. In the first study, I performed a tournament of arena trials using pairs of 18 male lizards to identify the traits most closely related to male social status in a dominance hierarchy. These arena trials stimulated aggressive interactions, often resulting in a clearly dominant male. I used the resulting win/loss/tie information in the ranking algorithms to rank the individuals. My results showed that behavioral displays and relative head length were the most predictive of rank in the majority of ranking systems. In my next study, I measured morphological traits, aggressive behavior, territory size, and female overlap (a proxy of territory quality) in 24 green anoles in Palmetto State Park, Gonzales, Texas, to determine how these traits were related to territory size and/or quality in a natural population. Results from this study indicated that body size and head length were important predictors of territory size, and head length was the only significant predictor of territory quality. Finally, I sought to

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validate my results by directly comparing male rank to territory size. In two replicate studies with 10 male lizards each, I first used a series of arena trials to determine individuals' ranks. I then placed the 10 males into an enclosure with 10 females and measured the sizes of male territories over one week. Although I hypothesized that higher ranked males would have larger territories, I found no correlation between rank and territory size.

Overall, these results suggest that head length is an important component of all aspects of dominance (rank, territory size, and territory quality) in the green anole. Head size is closely related to bite force in anoles and is an honest predictor of fighting ability in this species. This study demonstrates that combining animal-based studies with mathematical models is an effective method of analyzing vertebrate social dynamics.

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Chapter One: Overall Introduction

Conflict arises in animal populations when individuals compete for the same limited resources, such as food, mates, and shelters. Physical confrontations between individuals are energetically expensive and dangerous (Clutton-Brock et al. 1979), thus animals in many species have devised social behaviors to allocate valuable resources without fighting. One such system relies on the formation of dominance hierarchies, where higher quality individuals in a population are given priority access to resources by their lower quality conspecifics (Kaufmann 1983). The criteria determining these dominance relationships vary widely, although they are usually related (directly or indirectly) to displays that showcase an animal's health (e.g., beak color signals both dominance and immune function in birds, Murphy et al. 2009, Kelly et al. 2012), size (e.g., pitch of call signals body size in frogs, Ryan 1985), fighting ability (e.g., ritualized displays signal aggression in anoles, Greenberg and Nobel 1944), or physiological preparedness to fight (e.g., baseline testosterone in birds, Pham et al. 2014). Another system of resource allocation is territorial defense, where individuals protect areas from intruders and thus claim exclusive rights to the resources within (Maher and Lott 1995). In this system, superior competitors have access to the territories that contain the highest quantity and/or quality of resources.

Traditionally, hierarchical and territorial methods of social organization have been treated as mutually exclusive. However, this may be an oversimplification. Both

establishing dominance and protecting a territory involve allocating resources depending on quality or social status, and display and fighting behaviors are critical in developing both types of relationships. In this study, I sought to determine the nature of the relationship between these two modes of social organization. Are territorial and hierarchical methods of organization indeed completely distinct systems, established by different behaviors and favoring different traits? Or are they interrelated, where more dominant animals have larger territories or control areas with more valuable resources?

In this thesis, I approached this problem using the green anole lizard (*Anolis carolinensis*) as a model organism (Figure 1.1). This is an ideal species for this investigation, as when anoles are maintained at high population densities they will forgo their natural territoriality and establish dominance hierarchies. My study had three primary goals, through which I aimed to clarify the nature of the relationship between territoriality and hierarchical modes of social organization:

1. To establish a mathematical method of ranking a given population of anoles according to territory size, territory quality, and the ability to win aggressive interactions (aggressive ability).

2. To determine the morphological and/or behavioral traits most closely associated to aggressive ability and territory size/quality.

3. To directly compare individuals' ranks in a dominance hierarchy and their territory size.

To accomplish the first goal, I drew parallels between lizard dominance interactions and sports tournaments, for both arenas contain paired competitions and result in wins, losses, or ties. By placing the aggressive behaviors in this context, I was able to use a wide variety of pre-existing sports ranking algorithms (e.g., Bradley and Terry 1952, Massey 1997, Callaghan et al. 2007) to rank the lizards based on their dominance interactions However, each ranking system emphasizes different statistics about the tournaments, games, or competitors, and each uses different mathematical techniques to

build the ranks. Additionally, all of these algorithms were developed for disciplines other than animal behavior. Thus to identify the systems that would be the most successful at predicting dominance relationships among anoles, I performed an analysis of the underlying mathematical theory of each system to understand the advantages and disadvantages associated with applying them to this system (Chapter 2).

As a second project, I quantified territory size, territory quality, and dominance behavior of natural and lab-maintained populations of *Anolis carolinensis*. I then used ranking algorithms (described above) and compared the model outcomes to results of behavioral interactions of the lizards. I was thus able to identify traits that best predicted social status (Chapter 3). Finally, I calculated the dominance rank of a captive population of green anoles and then allowed them to establish territories inside an artificial enclosure. This allowed me to test whether an animal's territory size is positively related to its hierarchy rank (Chapter 3).

The combination of animal-based studies with a novel mathematical approach provides new insights into both the development of social organization patterns in vertebrates and the mathematical field of ranking. Ranking algorithms are a powerful tool in exploring animal social dynamics, for they provide a nuanced method of quantifying animal behavior patterns in a population-level context. Although ranking algorithms have not been used to model dominance interactions in the past, the success of these systems in this project demonstrates the exciting possibilities they hold for increasing our understanding of the development, maintenance, and ecological context of animal social interactions.

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Figure 1.1: Two adult male green anoles (*Anolis carolinensis*) engaged in an agonistic interaction.

Chapter Two: The Application of Ranking Algorithms to Vertebrate Social Dynamics

1 Introduction

1.1 General Overview

The overall goal of this project is to explore dominance relationships in the green anole (*Anolis carolinensis*). In this species, dominance can be measured in two distinct manners. Green anoles are highly territorial, and territory size and quality (i.e., the number of females residing on a given male territory, Ruby 1984) are measures of social status in wild populations. However, when maintained at high population densities in captivity, these lizards will instead organize themselves using a linear dominance hierarchy based on fighting ability (Stamps 1977). To compare these different metrics of social status, we created systems to rank males in a population according to each measure. Both territory size and quality can be directly measured in the field, and males can be linearly ranked from those with the largest territories and highest female overlap to those with the least. However, quantifying fighting ability is a more complex endeavor. Many different physical and behavioral traits are involved during agonistic interactions, and the processes through which dominance hierarchies are created are still largely unknown. Therefore we explored a novel mathematical framework for ranking animals based on their performance in paired aggressive interactions.

Anole male-male agonistic encounters consist of a series of ritual displays that may even-

tually escalate to lock-jawed fights (Greenberg and Nobel 1944). These displays begin with extensions of the colorful throat fan called the dewlap and pushup displays, followed by the development of dark spots behind the eyes (eye spots) and a dorsal crest. Competitors then begin circling each other in the *face-off* position (Figure 2.1), and will flatten themselves dorsal-ventrally to appear larger and more intimidating. If neither backs down, the aggressors circle closer and closer until they lock jaws, after which they will attempt to throw each other off the perch.

To experimentally measure fighting behavior, we conducted three tournaments of paired aggressive interactions between populations of adult male green anoles. In each agonistic interaction, an individual was declared the winner if it took exclusive control of the provided perch (a clear sign of dominance in this arboreal species, Perry et al. 2004), or if the other individual showed submissive behavior such as running away or attempting to hide. The trial was labeled a tie if competitors did not interact, no resolution was reached in the designated time (10 mins), or if the males attempted to lock jaws. Although a lock-jawed fight would eventually result in a clear winner, we separated individuals before they could fight to prevent injury.

At the end of each tournament, we had a win-loss-tie record for each anole, similar to the record generated in a series of games between sports teams. We decided to treat our collection of lizard interactions as sports tournaments, which then provided a large number of existing sports ranking algorithms (i.e., Page et al. 1999 , Callaghan et al. 2007, Colley n.d.) with which to rank the animals. Generally, a ranking algorithm is an analytical method for determining the relative order of a group of objects given information about how these objects compare to each other. Although the overall goal is always to determine which of these objects is the "best", there is a large amount of variation in the approaches different ranking systems take. Because animal behavior is a relatively novel application of these systems, we were initially unsure which algorithms would produce the most accurate rankings of green anole populations. We thus explored a number of unique ranking algorithms, carefully

analyzing the theory underlying each rank to assess their applicability to our system. We then evaluated the effectiveness of each ranking system using the results of the anole tournament to identify the ranks that most successfully reflected dominance in the green anole.

In the following sections, we describe each of the ranking systems used, including their backgrounds, implementations, and limitations. We will then conclude by returning to the original animal behavior problem by analyzing the applications of these tools to vertebrate social dynamics.

1.2   Mathematical Framework for a Ranking

For the remainder of this thesis, we will discuss all of the ranking systems in the context of a tournament, for in applications these methods are often used in sports (e.g., Colley n.d., Keener 1993, Massey 1977). The objects being ranked will be called *teams*, the interactions between them will be denoted to as *matches* or *games*, and the collection of all the interactions is a *tournament*. Note that many of the ranking methods are also used in applications outside of sports, but maintaining a consistent system of nomenclature increases the clarity of the arguments presented and makes it easier to compare ranking systems.

We will now establish the mathematical framework of a generic ranking algorithm. Consider a collection of n teams $\{t_1, t_2, \ldots, t_n\}$ competing in a tournament T. Within T, each team t_i plays several games where the outcomes can be a win, loss, or a tie based on its ability r_i in relation to its opponent's ability. We interpret r_i as the team's **rating**, or how good it is when compared to the other teams in the tournament. We say t_i is rated higher than t_j if $r_i > r_j$. We call $\mathbf{r} = (r_1, r_2, \ldots, r_n)$ the **rating vector** of the tournament. We can then order the elements of $\mathbf{r}$ to generate the **ranking** of the tournament, where the team t_i with the largest r_i value is ranked 1st, the team with the next highest is ranked 2nd, and so on down to rank n^{th}. Although there is a clear distinction between the rating and ranking of a team, they both provide similar information about the team's standing in the tournament and we will use the terms interchangeably for the remainder of the thesis.

1.3   Ranking Systems

When considering a fixed tournament, there are many ways to define a ranking system to estimate the ranking vector $\mathbf{r}$. We implemented eight ranking systems that each interpret this value in a different way.

The first method is the **Win Percent** method, the simplest ranking algorithm considered. In this system, the rank r_i of a team is a ratio between the number of wins and losses.

Our next two systems can be grouped together as the *Linear Algebra* ranking algorithms, for they estimate $\mathbf{r}$ by solving a system of linear equations. The **Colley** method is a modification of the Win Percent that makes the ranking of each team dependent not just on its wins or losses, but also on the relative ability (i.e., r_i) of the teams it competed against (Colley n.d.). Conversely, the **Massey** method predicts $\mathbf{r}$ based the scores of each game in the tournament using the method of least squares estimation (Massey 1997).

The fourth ranking system considered is the **Bradley-Terry** method, a method of pair comparisons (Bradley and Terry 1952, Agresti 1990). In this system, we interpret $\mathbf{r}$ to determine the probability of a specific outcome of a match.

The next set of algorithms, collectively called the **Markov methods**, uses a different approach. In these methods, we view the initial tournament as a network, where each team is a node and each game is represented as a directed edge between the nodes involved. This then allows us to consider the tournament as a Markov process and the rating vector as the steady-state solution $\mathbf{r}$, if it exists. We explored four different Markov ranks: the **Keener, Biased Voter, PageRank,** and **Oracle** methods. The Keener method finds an ideal weight function for each edge that incorporates the scores of each match (Keener 1993). The Biased Voter method incorporates self-loops as a method of directing the flow of information between two edges towards the winner of the match (Callaghan et al. 2007). The PageRank ranking system is the algorithm that drives the Google search engine, and uses a novel method of ensuring that any network will have a steady-state solution (Page et al. 1999). Finally, the Oracle ranking algorithm is a newly developed system that incorporates an additional node

into the network to prevent the rank inflation of low-winning teams with unexpected wins against highly rated teams (Balreira et al. in press).

2 Win Percent Method

We will begin our discussion of ranking systems with the simplest system in our repertoire, the Win Percent method. In this system, a team's relative ability is interpreted as how often they win. For a given team t_i who won w_i times and lost ℓ_i times, their win percentage ranking r_i is given by

$$r_i = \frac{w_i}{w_i + \ell_i}. \tag{1}$$

In tournaments with ties, we modify the algorithm to become

$$r_i = \frac{w_i + \frac{1}{2}q_i}{w_i + \ell_i + q_i}, \tag{2}$$

where q_i is the number of games team t_i tied. This method is useful in its simplicity, for it requires minimal computations and no additional statistics. However, the Win Percent method has several limitations, for it weighs all wins and losses equally and does not differentiate between the skills of the teams beat or the amount by which they were beat.

3 Colley Method

The Colley method is a ranking system developed by Wesley Colley to address some of the limitations of the Win Percent method (Colley n.d.). Colley's idea was that, rather than treating all wins and losses as the same, teams should instead get more credit for beating better teams. Thus he developed a method that expands the simple win-loss ratio into a system of linear equations. His method is currently used as one of the six methods to generate the BCS Rankings in Division 1 college football.

Consider a tournament T of n teams. As described above, the rank r_i of team t_i calculated by the Win Percent method is given by (1). While this system works well in tournaments with many games played, in situations where teams have not played or have only played few games, the Win Percent method is not effective. For example, consider a situation where teams t_i and t_j only played one game. Then the winner has a rank of 1 and the loser has a rank of 0. This claim that the winner is infinitely better than the loser is a little extreme. To buffer these situations, Colley proposed that the ranking equation be modified to

$$r_i = \frac{w_i + 1}{w_i + \ell_i + 2} \tag{3}$$

so that teams that have not played yet will have a default rank of $\frac{1}{2}$. We can rewrite this as

$$r_i(2 + n_i) = w_i + 1, \tag{4}$$

where n_i is the total number of games played by t_i. Now, let us take a step back and consider the number of games won in a different way. We can write this term as

$$w_i = \frac{w_i - \ell_i}{2} + \frac{n_i}{2} \tag{5}$$

which equals

$$w_i = \frac{w_i - \ell_i}{2} + \sum^{n_i} \frac{1}{2}. \tag{6}$$

Now, we notice that if we did not know anything about any of the teams, we would say that each team had a fifty percent chance of winning any given match, or that they would each have a rank of $\frac{1}{2}$. So if team t_i only played random, unknown teams, we could think about the final summation in (6) as the sum of the ranks of each opponent. But t_i is not going against unknown teams. In fact, we know that the rank of any given opponent t_j is given by r_j. Therefore we can say

$$\sum^{n_i} \frac{1}{2} \approx \sum_{j \in O_i} r_j, \tag{7}$$

where O_i is the set of opponents team t_i played against. We can then combine (4), (6), and (7) to get

$$r_i(2 + n_i) \approx \frac{w_i - \ell_i}{2} + \sum_{j \in O_i} r_j + 1. \tag{8}$$

If we assume equality, this equation can then be rearranged to give

$$r_i(2 + n_i) - \sum_{j \in O_i} r_j = \frac{w_i - \ell_i}{2} + 1. \tag{9}$$

We can repeat this procedure for each team in the tournament, providing n equations and n unknowns $(r_1, r_2, \ldots, r_n)$. We can rewrite this system of equations in matrix form to yield the equation $C\mathbf{r} = \mathbf{b}$, where $\mathbf{r}$ is the ranking vector, C is an $n \times n$ matrix with entries

$$c_{ij} = \begin{cases} 2 + n_i & i = j \\ -g_{ij} & i \neq j \end{cases} \tag{10}$$

(where g_{ij} is the number of games played between teams t_i and t_j), and $\mathbf{b}$ is a vector of length n such that its coordinates are

$$b_i = 1 + \frac{1}{2}(w_i - \ell_i). \tag{11}$$

Then the Colley method finds the exact solution of this matrix system to solve for $\mathbf{r}$.

We note that the Colley method does not have an intuitive modification for integrating ties. Ties will be included in the g_{tot} term as games played, but will not increase the b_i term. This serves as an important limitation in applications that include frequent ties.

4 Massey Method

Like the Colley method, the Massey ranking system also uses a system of linear equations to find the ranking vector of a tournament (Massey 1997). However, while the Colley system emphasizes the skills of the teams beaten, the Massey method instead utilizes the scores of the matches. This system is also used by the BCS. The ranking system we present here is the original method developed by Massey for his undergraduate honors thesis at Bluefield College.

Recall that the Colley system solves the matrix equation $C\mathbf{r} = \mathbf{b}$, where C is a matrix built using the number of games played and $\mathbf{b}$ is a vector containing information about each team's win and loss record. Similarly, the Massey system solves the system $M\mathbf{r} = \mathbf{s}$. Using the same notation as above, here M is an $n \times n$ matrix constructed such that

$$
m_{ij} = \begin{cases}
n_i & i = j, 1 \le i \le n \\
-g_{ij} & i \ne j, 1 \le i \le n \\
1 & i = n
\end{cases}
\tag{12}
$$

and $\mathbf{s}$ is a vector of length n where

$$
s_i = \begin{cases}
\text{(Points scored against } t_i) \text{ - (Points scored by } t_i) & 1 \le i \le n \\
0 & i = n.
\end{cases}
\tag{13}
$$

The Massey system estimates the difference $r_i - r_j$ to be equal to the expected value of the points scored against t_i minus the points scored by t_i. It then defines the ranking vector $\mathbf{r}$ to be the least-squares solution to $M\mathbf{r} = \mathbf{s}$.

5 Bradley-Terry

The Bradley-Terry ranking system takes a completely different approach than any of the other algorithms considered, for it is based on paired comparisons (Bradley and Terry 1952, Agresti 1990). The idea here is that while it is hard to identify the "best" competitor in a large group, it is easy to pinpoint the better object when only considering two things. For example, suppose you were given a selection of 20 cookies and asked to determine the best one. But you love chocolate chip, and snickerdoodle, and peanut butter - how are you ever going to definitely pick your favorite? However, if if asked whether you prefer macaroons to chocolate chips, or snickerdoodles to shortbreads, this becomes a much more manageable problem. Similarly, the Bradley-Terry system compares pairs of teams in a tournament, looking for the relationship between each pair to find the overall ranking.

Specifically, the Bradley-Terry system seeks to calculate the probability one team will beat another. They first establish an overall rating vector $\mathbf{r}$. They then define the probability team t_i beats t_j, denoted π_{ij}, as

$$\pi_{ij} = \frac{r_i}{r_i + r_j} \tag{14}$$

and estimate π_{ij} using iterative maximum-likelihood methods (for a complete description of the method used, see Huang et al. 2006).

Just as not every Markov network has a steady-state solution, not every tournament contains enough paired comparisons to generate a Bradley-Terry rank. One condition absolutely necessary for this ranking to work is that given any partition of the teams into two non-empty subsets, some team in one set must defeat at least one team in the other set. As reported in Ford 1957, this condition is analogous to having a strongly connected network (see description in Section 6 below).

There are a variety of different customizations of the Bradley-Terry method. One interesting alteration introduces the idea of home team advantage, where the team playing on their home field is assumed to have an increased probability of winning. This algorithm is

given as

$$\pi_{ij} = \begin{cases} \dfrac{\theta r_i}{\theta r_i + r_j} & \text{if team } t_i \text{ is at home} \\[2ex] \dfrac{r_i}{r_i + \theta r_j} & \text{if team } t_j \text{ is at home} \end{cases} \tag{15}$$

where $\theta > 0$ represents the strength of the home field advantage/disadvantage (Huang et al. 2006). We note that θ is an unknown parameter that has to be estimated. Another modification of the Bradley-Terry system is the use of scores, where

$$\pi_{ij} \approx \frac{s_{ij}}{s_{ij} + s_{ji}} \tag{16}$$

and s_{ij} is the number of points scored by team t_i against team t_j (Keener 1993). Hence,

$$\frac{r_{ij}}{r_{ij} + r_{ji}} \approx \frac{s_{ij}}{s_{ij} + s_{ji}}. \tag{17}$$

We note that under this system we will increase the likelihood that the tournament is connected and hence that the Bradley-Terry method will provide a meaningful rating vector.

6 Theory of Markov Ranking Systems

6.1 Introduction to Markov Methods

Markov methods build ranks by first representing a tournament as a network. Each node represents a team and edges between nodes represent matches (Figure 2.2). From this directed graph, the tournament can then be viewed as **Markov process**, a stochastic process in which the system alternates between states in a memory-less fashion. The ranking vector is thus the steady-state solution of this process, if it exists. For complete details on the general theory of Markov processes, we refer to Olofsson and Andersson (2012). In the following sections we will describe the theory as it relates to the application in this project.

The steady-state solution of a Markov process is often described in terms of a **random**

walker. Consider a network with n nodes $\{N_1, \ldots, N_n\}$ connected by a series of edges. Imagine placing a *walker* at node N_i with instructions to move through the network by following the directed edges. To leave his initial node, he will have a finite number of edges pointing away from his node from which to choose (Figure 2.3, time step 1). Every edge is associated with a **transitional probability** that influences the likelihood he will choose that path. Each Markov ranking system assigns these transitional probabilities differently; some assign all edges the same weight, while others assign probabilities using specific statistics or functions. When the random walker chooses an edge using to these probabilities, he will follow it to another node, where he is then faced with a similar choice of edges with which to leave that node (Figure 2.3, time step 2). If he were to continue to move around the network in this fashion for as long as he could, keeping track of the nodes on which he spends time, the proportional amount of time he spends on each node *may* converge. The values to which these relative proportions converge is called the steady state solution to the Markov process. In Markov ranking algorithms, the steady state solution is interpreted as the rank of the network, with higher values (i.e., nodes that the walker spent more time on) corresponding to higher ranked teams. To ensure that the Markov process associated with the network will have this steady-state solution, the network must have specific properties that will be described in the following sections.

6.2 Linear Algebra Preliminaries

Although Markov ranking systems are easy to visualize, they are computationally complex and rely on a wide variety of linear algebra properties to function. Before we describe the actual algorithms used to calculate these ranks, we first must review the definitions and matrix properties that form their foundations. For complete details, see Horn and Johnson (1990).

Let A be an $n \times n$ matrix with real entries. If there exists a vector $\mathbf{x} \in \mathbb{R}^n$ such that $A\mathbf{x} = \lambda\mathbf{x}$ and $\mathbf{x} \neq 0$, we define λ as the **eigenvalue** of A associated with the **eigenvector x**.

Another important concept associated with the matrix is the **characteristic polynomial** of A, defined as

$$P_A(t) = \det(A - tI), \tag{18}$$

where I is the identity matrix. We observe that the eigenvalues and characteristic polynomial of a matrix share a close relationship, for if λ is a root of P_A, then λ is an eigenvalue of A. Indeed, we have the following proposition.

Proposition 1. *Let A be an $n \times n$ matrix with the characteristic polynomial $P_A(t)$. We claim that the following statements are equivalent:*

1. *The value $\lambda \in \mathbb{C}$ is an eigenvalue of A.*

2. *The determinant of the matrix $(A - \lambda I)$ equals zero.*

3. *The value $\lambda \in \mathbb{C}$ is a root of $P_A(t)$*

Proof. First, we claim that if λ is an eigenvalue, then $\det(A - \lambda I) = 0$. Consider $A\mathbf{v} = \lambda\mathbf{v}$. Through algebraic manipulation, we get $(A - \lambda I)\mathbf{v} = 0$. By definition, λ is an eigenvalue of A if and only if $A\mathbf{v} = \lambda\mathbf{v}$ has a non-zero solution. Thus $(A - \lambda I)\mathbf{v} = 0$ also has a non-zero solution, so the matrix $A - \lambda I$ is non-invertible. Because this matrix is not invertible, it has a determinant of 0, that is, $\det(A - \lambda I) = 0$.

Next, we claim that if $\lambda \in \sigma(A)$, then λ is a root of $P_A(t)$. Suppose that $\lambda \in \sigma(A)$, and consider $P_A(\lambda)$. By definition,

$$P_A(\lambda) = \det(A - \lambda I).$$

Since $\lambda \in \sigma(A)$, by the previous proof we have $\det(A - \lambda I) = 0$. So

$$P_A(\lambda) = 0,$$

which implies λ is a root of $P_A(t)$. Finally, we note that by definition, $\det(A - \lambda I) = 0$ indicates that λ is a root of $P_A(t)$. Therefore the three statements are equivalent. $\square$

Furthermore, we call the collection of all eigenvalues the **spectrum** of A, denoted $\sigma(A)$.
Given a λ, we can also define the **eigenspace** of λ, denoted $V_\lambda(A)$, to be

$$V_\lambda(A) = \{\mathbf{v}, A\mathbf{v} = \lambda\mathbf{v}\} \tag{19}$$

We note that $V_\lambda(A)$ is a subspace for all $\lambda \in \mathbb{C}$, and that it is non-trivial exactly when
$\lambda \in \sigma(A)$. Finally, we denote the **spectral radius** of A as the magnitude of the largest
eigenvalue,

$$\rho(A) = \max\{|\lambda|, \lambda \in \sigma(A)\} \tag{20}$$

Now that we have these basic definitions to work with, we turn our attention to a special
type of matrix fundamental for Markov ranking systems, the column stochastic matrix. A
matrix is called **column stochastic** if all its elements are non-negative and its columns each
sum to one. These matrices have the property of always having an eigenvalue of 1, which
we will see is important in the following sections. To prove this statement, we must first
consider the following lemma, where A^T denotes the transpose of A.

Lemma 1. *For a matrix A, $\sigma(A) = \sigma(A^T)$, that is, the spectrum of a matrix and its transpose
are the same.*

Proof. Let $\lambda \in \sigma(A^T)$, and consider $\det(A^T - \lambda I)$. We have

$$\begin{aligned}
\det(A^T - \lambda I) &= \det(A^T - \lambda I^T) \\
&= \det((A - \lambda I)^T)
\end{aligned}$$

Now, since we can expand the determinant of a matrix about any row or column, it follows
that for any square matrix B, $\det B = \det B^T$. Thus

$$\det(A^T - \lambda I) = \det(A - \lambda I).$$

By our definition of characteristic polynomials, this implies

$$P_A(t) = P_{A^T}(t)$$

Finally, by the Fundamental Theorem of Algebra, a polynomial is uniquely defined by its set of roots over $\mathbb{C}$. Therefore because A and A^T have the same characteristic polynomials, by Proposition 1 they have the same spectrum. $\square$

We now can find at least one eigenvalue of a column stochastic matrix. Indeed, we have the following.

Proposition 2. *Every column stochastic matrix has an eigenvalue of 1*

Proof. Let $A = (a_{ij})$ be an $n \times n$ column-stochastic matrix. Then for all $i \in \{1, \ldots, n\}$, $\sum_{k=1}^{n} a_{ik} = 1$. Next, let $\mathbf{e} = (1\ 1 \ldots 1)$ and consider

$$A^T \mathbf{e} = \begin{pmatrix} a_{11} & a_{12} & \ldots & a_{1n} \\ a_{21} & a_{22} & \ldots & a_{2n} \\ \vdots & \vdots & & \vdots \\ a_{n1} & a_{n2} & \ldots & a_{nn} \end{pmatrix} \begin{pmatrix} 1 \\ 1 \\ \vdots \\ 1 \end{pmatrix} = \begin{pmatrix} a_{11} + a_{12} + \ldots + a_{1n} \\ a_{21} + a_{22} + \ldots + a_{2n} \\ \vdots \\ a_{n1} + a_{n2} + \ldots + a_{1nn} \end{pmatrix} = \begin{pmatrix} 1 \\ 1 \\ \vdots \\ 1 \end{pmatrix} = \mathbf{e}.$$

Thus $A^T \mathbf{e} = \mathbf{e}$, so 1 is an eigenvalue of A^T. By Lemma 1, we know that A^T has the same eigenvalues as A, so 1 is also an eigenvalue of A. $\square$

In fact, if a matrix is column stochastic, than it also has a spectral radius of 1.

Proposition 3. *If A is a column stochastic matrix, then $\rho(A) = 1$.*

Proof. By Proposition 2, $1 \in \sigma(A)$. Now, assume that there exists another eigenvalue $\lambda \in \sigma(A)$ such that $|\lambda| > 1$. Pick $\mathbf{v}$ such that $A^T \mathbf{v} = \lambda \mathbf{v}$. Then consider the i_{th} coordinate of $A^T \mathbf{v}$

$$(A^T \mathbf{v})_i = \sum_{j=1}^{n} a_{ij} v_j \leq v_{max} \sum_{j=1}^{n} a_{ij}, \text{where } v_{max} \text{ is the largest coordinate of } \mathbf{v}$$

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Now, since A is column-stochastic, $\sum_{j=1}^{n} a_{ij} = 1$, which implies

$$(A^T \mathbf{v})_i \leq v_{max}.$$

However, if we look at the ith coordinate $\lambda\mathbf{v}$, we see

$$|(\lambda v)_i| = |\lambda v_i| > |v_i|.$$

Thus when i is the index corresponding to the max coordinate, than

$$(A^T v)_{max} = |(\lambda v)_{max}| > v_{max}.$$

This is a contradiction, so $\rho(A) = 1$. □

Finally, given an $n \times n$ matrix A, we say $\lambda_1 \in \sigma(A)$ is the **dominant eigenvalue** if $|\lambda_1| > |\lambda|$ for all $\lambda \in \sigma(A)$. The eigenvectors corresponding to λ_1 are called **dominant eigenvectors** of A. In the next section, we will see how these two definitions combine with the previous two propositions to make Markov ranking systems function.

6.3 Calculating Markov Ranks

Recall that we may view a given tournament as a directed graph and then perform a Markov process on this network. This allows us to calculate the steady-state solution of the network, which we interpret as the rank. In practice, Markov ranking systems first convert the networks into column stochastic matrices, and then use the specific properties of these objects described in the previous section to determine the steady-state solution.

We begin by defining the **incidence matrix** associated with the network. This matrix describes the locations and directions of connections between nodes, representing the opponents each team has won/lost against. First, assume the tournament T has n teams

$t_1, t_2, \ldots, t_n$. The incidence matrix A is constructed as follows

$$a_{ij} = \begin{cases} 1 & \text{if } t_i \text{ has beaten } t_j \\ 0.5 & \text{if } t_i \text{ and } t_j \text{ tied} \\ 0 & \text{else.} \end{cases} \tag{21}$$

We remark that technically speaking, the incidence matrix associated with a network should only contain entries of zero or one, however, since we are working in an sport setting where paired comparisons can result in a tie, we shall allow entries of the incidence matrix to be 0.5.

For example, consider the network in Figure 2.4 representing an example tournament between teams $t_1, t_2, t_3,$ and t_4. The associated incidence matrix is given by:

$$A = \begin{array}{c} \\ t_1 \\ t_2 \\ t_3 \\ t_4 \end{array} \begin{array}{cccc} t_1 & t_2 & t_3 & t_4 \\ \begin{pmatrix} 0 & 1/2 & 0 & 1 \\ 1/2 & 0 & 1/2 & 1 \\ 1 & 1/2 & 0 & 0 \\ 0 & 0 & 1 & 0 \end{pmatrix} \end{array}.$$

The incidence matrix thus contains the win-loss-tie information from the tournament as a matrix. However, the more information a system can include, the more accurately it will construct a ranking. Many Markov ranking systems weight edges within the network to incorporate additional information about games, indicating not just who won or lost but how strongly that victory reflects the relative ability of each team. Each ranking system utilizes a different method to assign these values; for example, the Keener method uses the score of each game to generate edge weight. In tournaments where teams play the same opponents more than once, weights are often given by the number of games each team won or lost. To incorporate the additional information contained in these weights, it is necessary to modify the incidence matrix. We construct this new **weighted incidence matrix** , denoted by A^*,

as

$$a_{ij}^* = w_{ij}, \tag{22}$$

where w_{ij} is the weight of the edge from t_j to t_i. We note that for the remainder of our discussion, all of the edges will have non-negative weights. With the completion of the weighted incidence matrix, we have succeeded in converting all of the information in the network into numerical form.

In general, we call a network **strongly connected** if there is a finite path from a given node to any other node in the network. A priori, this is not trivial to check. Fortunately, we have the following analytical tool to determine if a network is strongly connected.

Proposition 4. *Let M be a directed network with n nodes, and let A be the incidence matrix of M. Define the vector $\mathbf{v_0^1} = (1\ 0\ 0 \ldots 0)$, and generalize this form so that $v_0^\alpha = (0\ 0 \ldots 1 \ldots 0)$, where 1 is in the αth position. Now for all $k < n$, recursively define*

$$\mathbf{v_k^\alpha} = sign\left(\mathbf{v_{k-1}^\alpha} + A\mathbf{v_{k-1}^\alpha}\right),$$

where $sign : \mathbb{R} \to \mathbb{R}$ such that

$$sign(x) = \begin{cases} 1 & if\ x > 0 \\ 0 & if\ x \le 0. \end{cases}$$

We claim that there exists $k_0 \le n$ such that $\mathbf{v_{k_0}} = \mathbf{v_{k_0+1}}$. Furthermore, if this $\mathbf{v_{k_0}} = \mathbf{e}$ for all $\alpha \in \{1, \ldots, n\}$, then the network M is strongly connected.

Before we prove this proposition, we will walk through an example to demonstrate how the system works. Recall that the goal of this process is to determine if there is a finite path between each node. To begin, we note that if there exists a path from node N_j to node N_i, then the $(ij)^{th}$ element of the incidence matrix (built without ties) will be equal to 1. Now,

consider the network in Figure 2.1. This network has the incidence matrix

$$A = \begin{pmatrix} 0 & 0 & 1 & 0 \\ 1 & 0 & 0 & 1 \\ 0 & 1 & 0 & 0 \\ 1 & 0 & 1 & 0 \end{pmatrix}.$$

Let $\mathbf{v_0} = (1\ 0\ldots 0)^T$. We can think of this vector as a walker starting at node N_1. First, let us consider the matrix $A\mathbf{v_0}$.

$$A\mathbf{v_0} = \begin{pmatrix} 0 & 0 & 1 & 0 \\ 1 & 0 & 0 & 1 \\ 0 & 1 & 0 & 0 \\ 1 & 0 & 1 & 0 \end{pmatrix} \begin{pmatrix} 1 \\ 0 \\ 0 \\ 0 \end{pmatrix} = \begin{pmatrix} 0(1) + 0(0) + 1(0) + 0(0) \\ 1(1) + 0(0) + 0(0) + 1(0) \\ 0(1) + 1(0) + 0(0) + 0(0) \\ 1(1) + 0(0) + 1(0) + 0(0) \end{pmatrix} = \begin{pmatrix} 0 \\ 1 \\ 0 \\ 1 \end{pmatrix}.$$

We notice that $a_{21} = a_{41} = 1$, so there is a path from node N_1 to both N_2 and N_4. Thus the coordinates in $A\mathbf{v_0}$ that are greater than 0 reflect the nodes that can be reached in one step from the starting node, given by $\mathbf{v_0}$. Now, consider the sum $\mathbf{v_0} + A\mathbf{v_0}$

$$\mathbf{v_0} + A\mathbf{v_0} = \begin{pmatrix} 1 \\ 0 \\ 0 \\ 0 \end{pmatrix} + \begin{pmatrix} 0 & 0 & 1 & 0 \\ 1 & 0 & 0 & 1 \\ 0 & 1 & 0 & 0 \\ 1 & 0 & 1 & 0 \end{pmatrix} \begin{pmatrix} 1 \\ 0 \\ 0 \\ 0 \end{pmatrix} = \begin{pmatrix} 1 \\ 0 \\ 0 \\ 0 \end{pmatrix} + \begin{pmatrix} 0 \\ 1 \\ 0 \\ 1 \end{pmatrix} = \begin{pmatrix} 1 \\ 1 \\ 0 \\ 1 \end{pmatrix}.$$

Now, we notice that in one or fewer steps (zero is a possible number of steps), the walker is able to come into contact with three nodes - the node he started on (N_1), and the nodes he can reach from the starting node in one step (N_2, N_4). Also, each of these nodes can only be reached in exactly one way ($N_1, N_1 \to N_2, N_1 \to N_3$). Therefore the sum $\mathbf{v_0} + A\mathbf{v_0}$ reflects the nodes that can be reached in one or fewer steps, and how many different ways there are

to reach each node. Next, consider $\mathbf{v_1}$

$$\mathbf{v_1} = sign \left(\left(\begin{pmatrix} 1 \\ 0 \\ 0 \\ 0 \end{pmatrix} + \begin{pmatrix} 0 & 0 & 1 & 0 \\ 1 & 0 & 0 & 1 \\ 0 & 1 & 0 & 0 \\ 1 & 0 & 1 & 0 \end{pmatrix} \begin{pmatrix} 1 \\ 0 \\ 0 \\ 0 \end{pmatrix} \right) \right) = sign \left(\left(\begin{pmatrix} 1 \\ 1 \\ 0 \\ 1 \end{pmatrix} \right) \right) = \begin{pmatrix} 1 \\ 1 \\ 0 \\ 1 \end{pmatrix}.$$

Recall that the *sign* function takes each coordinate of the vector v_i and changes it to a 1 if $v_1 > 0$ and to a zero if $v_1 \leq 0$. So $\mathbf{v_1}$ represents the nodes that can be reached from the starting node in zero or one steps. We utilize the *sign* function here to make the process computationally easier, for it reduces the analysis to the manipulation of 1's and 0's and does not remove any important information.

We repeat the above process to find $\mathbf{v_2}$. In this iteration, $\mathbf{v_0}$ is replaced by $\mathbf{v_1}$, so in this round we can think of starting random walkers at nodes $N_1, N_2,$ and N_4 and telling them to each move one time step. Here, we find that $\mathbf{v_2} = (1\ 1\ 1\ 1) = \mathbf{e}$. Thus if the random walker starts at node N_1, he can reach every other node in the network in two or fewer steps.

At this point, our initial intuition is to claim the network is strongly connected, as we have demonstrated that there is a way to reach to every node in the network. However, in a directed graph, the choice of starting node matters. For example, consider a different network L with two nodes, ℓ_1 and ℓ_2, and one edge that points to ℓ_2. Then if we start at ℓ_1 ($\mathbf{v_0} = (1\ 0)^T$), we find that in one step or less we can reach every other node in the network, for

$$\mathbf{v_1} = sign \left(\left(\begin{pmatrix} 1 \\ 0 \end{pmatrix} + \begin{pmatrix} 0 & 0 \\ 1 & 0 \end{pmatrix} \begin{pmatrix} 1 \\ 0 \end{pmatrix} \right) \right) = sign \left(\left(\begin{pmatrix} 1 \\ 0 \end{pmatrix} + \begin{pmatrix} 0 \\ 1 \end{pmatrix} \right) \right) = \begin{pmatrix} 1 \\ 1 \end{pmatrix} = \mathbf{e}.$$

However, if we start at node ℓ_2, there is no way to reach ℓ_1. Thus this network is not strongly connected.

Therefore for directed graphs, we need to prove that if we were to start on any given

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N_i, we could reach every other nodes in the network in a finite number of steps. That is, for each starting node, there must exist some $k \in \mathbb{N}$ such that $\mathbf{v_k} = \mathbf{e}$. To check this, we simply change the $\mathbf{v_0}$. For example, to test the results of starting on node N_2, we begin with $\mathbf{v_0} = (0\ 1\ 0\ 0)^T$, and compute $\mathbf{v_1}, \mathbf{v_2}$, etc.. In our example, we find that starting on N_2, $\mathbf{v_3} = \mathbf{e}$; starting on N_3, $\mathbf{v_2} = \mathbf{e}$; and starting on N_4, $\mathbf{v_3} = \mathbf{e}$. Thus this network is strongly connected.

We now return to the proof.

Proof. To begin, we claim that if $(Av_0^\alpha)_i > 0$, then there exists a path of length one between node N_α and node N_i. First, we observe that

$$(Av_0^\alpha)_i = \sum_{j=1}^{n} a_{ij}(v_0^\alpha)_j.$$

Because all $(av_0^\alpha)_i \geq 0$, the only way for the above sum to be positive is for a_{ij} and $(Av_0^\alpha)_j$ to be greater than zero for some j. The only element of $\mathbf{v}_0^\alpha$ that is positive is in position α, and the only positive elements in the αth column of A will be the elements corresponding to nodes connecting to node N_α. Thus if $(Av_0^\alpha)_i > 0$, there exists a path from node N_α to node N_i. Now, we notice that $\mathbf{v_0^\alpha} + A\mathbf{v_0^\alpha}$ will equal a vector with positive elements in the positions corresponding to the nodes that can be reached in zero steps (the starting node) as well as those that can be reached in one step. Additionally, applying the sign function to this vector will preserve the signs of the elements but reduce them all to zeros or ones. Thus the vector $\mathbf{v_1^\alpha}$ represents the nodes that can be reached from node N_α in one or fewer steps. By repeating a similar analysis, we can see that the vector $\mathbf{v_k^\alpha}$ represents the nodes that can be reached from node N_α in k or fewer steps. If there exists a k such that $\mathbf{v_k^\alpha} = \mathbf{e}$, then every element can be reached from the starting node N_α. If this condition holds for every $\alpha \in \{1, 2, \ldots, n\}$, then every node can be reached from each possible starting vector, and the network M is strongly connected. $\square$

Say M is strongly connected. While this tells us something informative about our net-

work, we do not know anything about the effects of connectivity on the weighted incidence matrix we just compiled. Therefore we introduce another important concept, the irreducible matrix. We say a matrix is **irreducible** if there is no permutation that transforms it into a block matrix of the form

$$\begin{pmatrix} A_{11} & A_{12} \\ 0 & A_{22} \end{pmatrix}.$$

As Keener (1993) demonstrated, this is equivalent to saying that for any two numbers i and j, there is an integer $p \geq 0$ and a sequence of integers $k_1, k_2, \ldots, k_p$ such that the product $a_{ik_1} a_{k_1 k_2} \cdots a_{k_p j} \neq 0$. If a network is strongly connected, it is always irreducible, as demonstrated by the following proposition.

Proposition 5. *Let M be a strongly connected network. Then the resulting weighted incidence matrix A^* is irreducible.*

Proof. Pick two nodes $N_i, N_j \in M$. Because M is strongly connected, there is a finite path between N_i and N_j. List the elements in this path in the order they must be taken to get from N_i to N_j:

$$N_i, N_{k_1}, N_{k_2}, \ldots, N_{k_p}, N_j,$$

where $k_1, k_2, \ldots, k_p$ are natural numbers less than n. Now, consider nodes N_i and N_{k_1}. Because there is a path between these two nodes, we know that $a_{ik_1}^* > 0$. Similarly, $a_{k_1 k_2}^* > 0$, $a_{k_2 k_3}^* > 0$, $\ldots$, $a_{k_p k_j}^* > 0$. Thus

$$a_{ik_1}^* a_{k_1 k_2}^* \cdots a_{k_p kj}^* > 0.$$

So A^* is irreducible. $\qquad\square$

Next, we calculate the **transitional probability matrix** P, defined such that

$$p_{ij} = \frac{a_{ij}^*}{\sum_{k=1}^{n} a_{kj}^*} \tag{23}$$

provided the denominator is nonzero.

Recall from the Random Walker discussion that a transitional probability p_{ij} is the probability that, given multiple choices of edges with which to leave node n_i, the walker will choose to use the one connecting node N_i to N_j.

For Markov methods to generate a successful ranking for a tournament, P must be column-stochastic (i.e., all columns must sum to 1). In matrices where $\sum_{k=1}^{n} a_{kj}^* > 0$ for all $k < n$, this condition is trivially true. However, in matrices with a column of all zeroes, which correspond to nodes with no outgoing edges (called **dangling nodes**), the resulting matrix P will not be column-stochastic. In these cases, there will be no steady-state solution associated to this matrix. Many Markov systems incorporate methods to remove these situations, as we will see in the following sections.

Now, consider the matrix P. This represents the transitional probabilities associated with moving between nodes. Alternatively, we can also think of these values as the proportion of a team's importance that it transfers to each other team. That is, given a node N_i with rating r_i, it will then transfer $p_{ji}r_i$ of its rank to node N_j. So we can think of the rank of a given node as:

$$r_i = p_{i1}r_1 + p_{i2}r_2 + \ldots + p_{in}r_n. \tag{24}$$

As we compute the equations for all of the ranks, we get the following system of n equations and n unknowns:

$$r_1 = p_{11}r_1 + p_{12}r_2 + \ldots + p_{1n}r_n$$

$$r_2 = p_{21}r_1 + p_{22}r_2 + \ldots + p_{2n}r_n$$

$$\vdots$$

$$r_n = p_{n1}r_1 + p_{n2}r_2 + \ldots + p_{nn}r_n.$$

This can be written in matrix form

$$
\begin{pmatrix} r_1 \\ r_2 \\ \vdots \\ r_n \end{pmatrix}
=
\begin{pmatrix}
p_{11} & p_{12} & \cdots & p_{1n} \\
p_{21} & p_{22} & \cdots & p_{2n} \\
\vdots & \vdots & & \vdots \\
p_{n1} & p_{n2} & \cdots & p_{nn}
\end{pmatrix}
\begin{pmatrix} r_1 \\ r_2 \\ \vdots \\ r_n \end{pmatrix}
\tag{25}
$$

and simplifies to $\mathbf{r} = P\mathbf{r}$, where $\mathbf{r}$ is an $n \times 1$ vector representing the rating of each node. Notice that $\mathbf{r}$ is the eigenvector associated with the eigenvalue 1. Although the equation looks simple, solving for $\mathbf{r}$ becomes a highly non-trivial problem if P has many eigenvalues associated with 1.

6.4 Solving r = Pr for the Ranking Vector

Given the complexity of finding eigenvalues and eigenvectors of matrices, we shall devote this section to show that in our application, when the matrix is column stochastic and under some nice conditions, we can indeed solve this problem.

To begin, we note that by Propositions 2 and 3, because P is column stochastic, 1 is an eigenvalue of P and P has a spectral radius of 1. However, if 1 is a repeating eigenvalue, there will be multiple linearly independent eigenvectors associated to 1. A foundational assumption of any ranking algorithm is that there exists an inherent hierarchy within a set of teams; that is, there is only one correct ranking that accurately represents the relationship between these teams. Fortunately, the **Perron-Frobenius Theorem** provides conditions under which 1 is associated with a unique eigenvector.

Theorem 1 (Perron-Frobenius). *If the matrix A has non-negative stochastic entries and the associated network is strongly connected, then there exists an eigenvector r with non-negative*

entries corresponding to a positive eigenvalue λ. Furthermore, if the matrix is irreducible, the eigenvector r has strictly positive entries, is unique and simple, and the corresponding eigenvalue is the largest eigenvalue of A in absolute value.

Remark 1. We note that if A is not stochastic, then by a dilation of the space, i.e., division by the spectral radius, the matrix will become column stochastic. Such alternations will not change the algebraic properties of the matrix, therefore the Perron-Frobenius Theorem will still hold for non-stochastic matrices as well. For a full proof, see Keener (1993).

It is worth spending some time proving the Perron-Frobenius Theorem, for it is the critical result that drives the functionality of Markov ranking systems. We begin by proving a few lemmas.

Lemma 2. *The product of column stochastic matrices is column-stochastic.*

Proof. Let A, B be $n \times n$ column stochastic matrices. Then each entry in AB is given by

$$(ab)_{ij} = \sum_{\ell=1}^{n} a_{i\ell} b_{\ell j}$$

and the sum of column k of AB is

$$
\begin{aligned}
\sum_{i=1}^{n} \sum_{\ell=1}^{n} a_{i\ell} b_{\ell k} &= \sum_{\ell=1}^{n} \sum_{i=1}^{n} a_{i\ell} b_{\ell k} \\
&= \sum_{\ell=1}^{n} b_{\ell k} \sum_{i=1}^{n} a_{i\ell} \\
&= \sum_{\ell=1}^{n} b_{\ell k}(1) \\
&= 1,
\end{aligned}
$$

where the last two equalities are satisfied because A and B are column stochastic. Hence AB is column stochastic. $\square$

Lemma 3. *If M is positive and column stochastic, then any eigenvector in $V_1(M)$ has all positive or all negative components.*

We will proceed by contradiction. First, recall that by the **Triangle Inequality**, $|\sum_i Y_i| < \sum_i |Y_i|$ when the signs of Y_i are mixed. Suppose $\mathbf{x} \in V_i(M)$ contains elements of mixed signs. Since $\mathbf{x}$ is an eigenvector of M, we know that $\mathbf{x} = M\mathbf{x}$, thus $x_i = \sum_{j=1}^{n} M_{ij}x_j$. Since x_j are of mixed signs and $M_{ij} > 0$ for all i, j, we know that $M_{ij}x_j$ are of mixed signs as well. By the Triangle Inequality, we have

$$|x_i| = \left| \sum_{j=1}^{n} M_{ij}x_j \right| < \sum_{j=1}^{n} |M_{ij}x_j| = \sum_{j=1}^{n} M_{ij}|x_j|.$$

Now consider the sum of x_i over all $i \in \{1, 2, \ldots, n\}$.

$$\sum_{i=1}^{n} |x_i| < \sum_{i=1}^{n}\sum_{j=1}^{n} M_{ij}|x_j| = \sum_{j=1}^{n} \left(\sum_{i=1}^{n} M_{ij} \right) |x_{ij}|.$$

Since M is column stochastic, $\sum_{i=1}^{n} M_{ij} = 1$, and we find

$$\sum_{i=1}^{n} |x_i| < \sum_{j=1}^{n} |x_j|,$$

a contradiction. $\qquad\square$

Lemma 4. *Let $\mathbf{v}$ and $\mathbf{w}$ be linearly independent vectors in $\mathbb{R}^m$, where $m \geq 2$. Then for some values s and t that are not both zero, the vector $\mathbf{x} = s\mathbf{v} + t\mathbf{w}$ has both positive and negative components.*

Proof. First, we note that because $\mathbf{v}$ and $\mathbf{w}$ are linearly independent, neither $\mathbf{v}$ nor $\mathbf{w}$ are $\mathbf{0}$. Now let $d = \sum_i v_i$. If $d = 0$, then $\mathbf{v}$ must contain elements of mixed sign, thus for $s = 1$ and $t = 0$, $\mathbf{x} = \mathbf{v}$ and $\mathbf{x}$ has mixed signs. Now, suppose $d \neq 0$, and let $t = 1$ and

$$s = -\frac{\sum_i w_i}{d}.$$

Then

$$\begin{aligned}
\sum_i x_i &= \sum_i sv_i + \sum_i tw_i \\
&= \sum_i \frac{v_i}{d}\left(\sum_j -w_j\right) + \sum_i w_i \\
&= \frac{\sum_i v_i}{\sum_i v_i}\left(\sum_j -w_j\right) + \sum_i w_i, \text{ because } d = \sum_i v_i \\
&= -\sum_i w_i + \sum_i w_i \\
&= 0.
\end{aligned}$$

Since $\mathbf{v}$ and $\mathbf{w}$ are independent, $\mathbf{x} \neq 0$, thus $\mathbf{x}$ contains mixed elements. $\qquad\square$

With these tools established, we will prove the Perron-Frobenius Theorem.

Proof. Let A be an $n \times n$ matrix that is column stochastic and has non-negative entries. Additionally, let the network associated to A be strongly connected. First, we note that if there exists an edge connecting N_j to N_i, $a_{ij} > 0$. Now, we claim that $(a^p)_{ij} > 0$ if and only if node N_i can be reached from node N_j in exactly p steps. To begin, let $(a^p)_{ij} > 0$. Then there exists some set of integers $k_1, k_2, \ldots, k_{p-1}$ such that $a_{ik_1}a_{k_1k_2}\cdots a_{k_{p-1}j} > 0$. Since each element $a_{\ell m} = 0$ or 1, we must have $a_{ik_1} = a_{k_1k_2} = \ldots = a_{k_{p-1}j} = 1$. Thus there is a path from N_j to $N_{k_{p-1}}$, a path from $N_{k_{p-1}}$ to $N_{k_{p-2}}$, $\ldots$, and a path from N_{k_1} to N_i. So a path exists from N_j to N_i and it has exactly p steps. Now, suppose there exists a path from nodes N_j to N_i with p steps. List the sequence of nodes in the path: $N_j, N_{k_{p-1}}, \ldots, N_{k_1}, N_i$. Because there are edges connecting every element next to each other in this sequence, we know $a_{ik_1} = a_{k_1k_2} = \ldots = a_{k_{p-1}j} = 1$, thus the product formed by these terms will be positive. Now, consider $(a^p)_{ij}$, which can be represented as a sum of products of elements of A. The product $a_{ik_1}a_{k_1k_2}\cdots a_{k_{p-1}j}$ is in this sum. Because all a_{ij} are positive, the total sum will be greater than or equal to its components, thus

$$(a^p)_{ij} \geq a_{ik_1}a_{k_1k_2}\cdots a_{k_{p-1}} > 0.$$

Thus $(a^p)_{ij} > 0$ implies that there is a path between nodes N_i and N_j of length p.

Next, we claim that $(i+a+a^2+\ldots+a^p)_{ij}$ is positive if and only if there is a path from node N_j to node N_i that is p or fewer steps long. To begin, let $(i+a+a^2+\ldots+a^p)_{ij} > 0$. Because all elements a_{ij} are positive, this implies that there exists at least one $k \in \{0, 1, \ldots, p\}$ such that $(a^k)_{ij} > 0$. By the previous claim, this implies that there is a path from N_i to N_j that is exactly k steps long. Now, suppose there is a path from N_j to N_i that is k steps long, where k is an integer such that $0 \leq k \leq p$. Then, by the previous proof, $(a^k)_{ij} > 0$. Since all elements of a_{ij} are positive, $(i + a + a^2 + \ldots + a^p)_{ij} \geq (a^k)_{ij} > 0$.

We now claim that because A is strongly connected, $I + A + A^2 + \ldots + A^{n-1}$ is positive. Because A is strongly connected, there exists a finite path between any two nodes. Pick two nodes N_i and N_j and suppose that the path between them is k steps long. By the previous proof, this means that $(i + a + a^2 + \ldots + a^{n-1})_{ij} > 0$. Thus for all $\ell, m < n$, $(i + a + a^2 + \ldots + a^{n-1})_{\ell m} > 0$, so $I + A + A^2 + \ldots + A^{n-1}$ is positive.

Now, let us use this sum to build a new matrix B, where $B = \frac{1}{n}(I + A + A^2 + \ldots + A^{n-1})$. We notice that B is both positive and column stochastic. Indeed, n is positive and by the previous proof $I + A + A^2 + \ldots + A^{n-1}$ is positive as well, so B is positive. Next, we note that the identity matrix I is trivially column stochastic, and A is column stochastic by assumption. By Lemma 2, we know that the product of column stochastic matrices is column stochastic, thus $A^2, A^3, \ldots, A^{n-1}$ are also column-stochastic. Now, consider the sum of column k of B. This equals:

$$
\begin{aligned}
\frac{1}{n}\sum_{j=1}^{n}(i_{jk} + a_{jk} + a_{jk}^2 + \ldots + a_{jk}^n) &= \frac{1}{n}\left(\sum_{j=1}^{n}i_{jk} + \sum_{j=1}^{n}a_{jk} + \sum_{j=1}^{n}(a^2)_{jk} + \ldots + \sum_{j=1}^{n}(a^n)_{jk}\right) \\
&= \frac{1}{n}(1 + 1 + 1 + \ldots + 1), \\
&= \frac{1}{n}(n) \\
&= 1
\end{aligned}
$$

since $I, A, A^2, \ldots, A^{n-1}$ are column stochastic. Thus the sum of column k in B is 1, thus B

is column stochastic. By Proposition 2, because both A and B are column stochastic, 1 is an eigenvalue of both matrices. Additionally, by Proposition 3, 1 is the spectral radius of both A and B. For the remainder of the proof, we will discuss the eigenspace associated to the eigenvalue 1.

Next, we claim that because B is both positive and column stochastic, $\dim(V_1(B)) = 1$. We will proceed by contradiction. Suppose there are two linearly independent eigenvectors $\mathbf{v}$ and $\mathbf{w}$ in the subspace $V_1(B)$. For any $s, t \in \mathbb{R}$ (both not zero), the nonzero vector $\mathbf{x} = s\mathbf{v} + t\mathbf{w} \in V_1(B)$ and, by Lemma 3, $\mathbf{x}$ has components that are either all positive or all negative. But by Lemma 4, there exists some s and t such that $\mathbf{x}$ contains both positive and negative components, a contradiction. Thus $V_1(B)$ cannot contain two linearly independent vectors, so $\dim(V_1(B)) = 1$.

We will now use this information to draw conclusions about the eigenspace of A with respect to 1. We claim that $V_1(A) \subseteq V_1(B)$. To begin, let $\mathbf{x} \in V_1(A)$). Then $A\mathbf{x} = 1\mathbf{x} = \mathbf{x}$. Now, we note that $AA\mathbf{x} = A\mathbf{x}$, which then implies that $A^2\mathbf{x} = \mathbf{x}$. Similarly, $AA^2\mathbf{x} = A\mathbf{x}$ implies that $A^3\mathbf{x} = \mathbf{x}$. It is straightforward to see that $\mathbf{x} = A\mathbf{x} = A^2\mathbf{x} = \ldots = A^{n-1}\mathbf{x}$, thus

$$I\mathbf{x} + A\mathbf{x} + A^2\mathbf{x} + \ldots + A^{n-1}\mathbf{x} = n\mathbf{x}.$$

Therefore

$$\frac{1}{n}(I + A + A^2 + \ldots + A^{n-1})\mathbf{x} = \mathbf{x},$$

which means

$$B\mathbf{x} = \mathbf{x}.$$

Since 1 is an eigenvalue of B, this then implies that $x \in V_1(B)$, thus $V_1(A) \subseteq V_1(B)$.

Finally, we claim that $\dim(V_1(A)) = 1$. Indeed, since $V_1(A) \subseteq V_1(B)$, $\dim(V_1(A)) \leq \dim(V_1(B))$. By a previous result, we know that $\dim(V_1(B)) = 1$, thus $\dim V_1(A)) = 0$ or 1. We note that since 1 is an eigenvalue of A, $V_1(A)$ contains at least one non-zero eigenvalue, thus $\dim(V_1(A)) \neq 0$. Therefore $\dim(V_1(A)) = 1$, that is, A has a single eigenvector

associated with its dominant eigenvalue. $\qquad\square$

We are now ready to solve $\mathbf{r} = P\mathbf{r}$. In applications, computing eigenvectors is often difficult. Fortunately, there is a powerful method to efficiently approximate the dominant eigenvector called the **Power Method**, as stated below.

Theorem 2 (The Power Method). *Let A be an $n \times n$ matrix with real entries and eigenvalues $\lambda_1, \ldots, \lambda_n$ ordered so that*

$$|\lambda_1| > |\lambda_2| \geq \ldots \geq |\lambda_n|.$$

Also, let $x_0 \neq 0$ be the starting vector. Then the iteratively defined vector

$$\mathbf{x}_k = A\mathbf{x}_{k-1} = A^k \mathbf{x_0}$$

converges to the the dominant eigenvector of A.

Remark 2. We note that if x_0 is orthogonal to V_{λ_1}, then $\alpha_1 = 0$ and the Power Method will not generate a correct dominant eigenvalue. However the probability of choosing such a vector is 0, thus we can effectively operate the Power Method with a random vector.

Proof. First, assume A is diagonalizable. Then A has a basis $\mathbf{y}$ that contains all of the eigenvalues of A, therefore the vector $\mathbf{x_0}$ can be expanded along these eigenvectors such that

$$\mathbf{x_0} = \alpha_1 \mathbf{y}_1 + \ldots + \alpha_n \mathbf{y}_n$$

with $\alpha_1 \neq 0$. Thus

$$A^k \mathbf{x} = \mathbf{x}_k = \sum_{j=1}^{n} \lambda_j^k \alpha_j \mathbf{y}_j.$$

We can factor out a constant and slightly expand this expression to get

$$\mathbf{x}_k = \lambda_1^k \left(\alpha_1 \mathbf{y}_1 + \sum_{j=2}^{n} \left(\frac{\lambda_j}{\lambda_1} \right)^k \alpha_j \mathbf{y}_j \right)$$

Now, because $|\lambda_1| > |\lambda_j|$ for all j, $\left(\dfrac{\lambda_j}{\lambda_1}\right)^k \to 0$ as k increases. Thus for large k,

$$\left(\frac{1}{\alpha_1\lambda_1^k}\right)\mathbf{x}_k = \mathbf{y}_1.$$

Thus up to an error term $\left(\dfrac{1}{\alpha_1\lambda_1^k}\right)$, $A^k\mathbf{x}$ approximates the eigenvector associated with the dominant eigenvalue. We note here that this result also holds if A is not diagonalizable, however this proof is outside the scope of this project. (Proof adapted from Kincaid and Chyeney 2002). $\qquad\square$

7 Markov Ranking Systems

Now that we understand how generic Markov ranks are calculated, we will move into a discussion of the four specific Markov ranking systems we used in our analysis: the Keener, Biased Voter, PageRank, and Oracle algorithms.

7.1 Keener

Our first Markov ranking system is a system developed by James Keener as a novel application of the Perron-Frobenius Theorem (Keener 1993). Like Massey, Keener's system ranks each team based on the scores of matches within a tournament. Although this system is not used by any major sports ranking organization, it has been shown to be highly successful in ranking NFL football tournaments (Keener 1993).

The Keener method functions similarly to the generic Markov systems we have seen, however it employs a unique system of weighting each game. Let S_{ij} be the amount of points team t_i scored against team t_j. The most intuitive method of assigning weights using these scores is

$$a_{ij}^* = \frac{S_{ij}}{S_{ij} + Sji}. \tag{26}$$

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Here, each edge is weighted by the proportional amount of points that team scored in comparison the total number of points scored in the match. However, consider a game with a score of 1-0. This would assign the winner a weight of 1 and the loser a weight of 0, effectively weighting the winner infinitely higher than the loser. However, in low-scoring sports such as hockey or soccer, a score of 1-0 could reflect a highly defensive game in which both teams were fairly evenly matched. To remedy this problem, we could instead make the weight equal to

$$a^*_{ij} = \frac{S_{ij} + 1}{S_{ij} + Sji + 2}.$$ (27)

Here, as we saw in the Colley method section, teams start with a rank of $1/2$ and move up/down from there. Unfortunately, under this formula, teams could artificially boost their ranks by driving up scores. Not only would this encourage poor sportsmanship, it would also decrease the accuracy of the ranks.

Keener proposed the weight

$$a^*_{ij} = h\left(\frac{S_{ij} + 1}{S_{ij} + Sji + 2}\right),$$ (28)

where h is the function such that

$$h(x) = \frac{1}{2} + \frac{1}{2}sign\left(x - \frac{1}{2}\right)\sqrt{|2x - 1|}.$$ (29)

The function h was chosen for several reasons. First, $h\left(\frac{1}{2}\right) = \frac{1}{2}$, thus all teams start with a default weight of $1/2$. Additionally, the slope of h decrease as the winner's score increases and the loser's score decreases, as shown in Figure 2.5. Thus the weight is not inflated by high-scoring games.

Notice that this scoring metric provides information about both winning and losing teams, thus in this system each match is represented by two edges: one from the winner to the loser, a^*_{ij}, and one from the loser to the winner, a^*_{ji}. Finally, using the weighted incidence matrix,

the Keener ranking system builds the Transitional Probabilities matrix and uses the power method to solve $\mathbf{r} = P\mathbf{r}$. This system does not automatically ensure a strongly connected network, so the user must check the network using method described in Proposition 4 to ensure that the conditions of the Perron-Frobenius Theorem are met before computing this rank. Observe that using scores, one is more likely to obtain a network without dangling nodes as generally teams do score points even in a loss.

7.2 Biased Voter

In the Markov ranking system we have seen the interaction between two teams is characterized by one edge, where the loser points to the winner. The Biased Voter ranking system takes a different approach, for each match is instead represented by four edges: one from the loser to the winner, one from the winner to the loser, one from the loser to itself, and one from the winner to itself. Each edge is then weighted using a fixed probability. This system was originally developed by Callaghan et. al as a network-based approach to ranking college football games (Callaghan et al. 2007).

To visualize the Biased Voter ranking system, consider a network containing nodes N_i and N_j where N_i beat N_j. Now picture a random walker starting at node N_i. He is faced with a choice: he can either move to node N_j, or he can stay on N_i. Movement away from the starting node still corresponds to a loss of importance, thus arrows pointing towards the winners have higher weights than those pointing towards the losers. The walker will stay on N_i (the winner) with a probability of p, where $p \in [0.5, 1]$, and will move to N_j (the loser) with a probability of $1 - p$. Conversely, he would move from N_j to N_i with a probability of p and would stay on N_j with a probability of $1 - p$ (Figure 2.6).

To calculate the ranking in a tournament using the Biased Voter ranking algorithm, we begin by building the weighted incidence matrix. In this system, if team i beats team j, then $a_{ij}^* = p$ and $a_{ji}^* = 1 - p$. Because every node is also connected to itself, we also calculate

a_{ii}^* for every team i as:

$$a_{ii}^* = \sum_{k=1}^{n} 1 - a_{ki}^*.\tag{30}$$

The transitional probability matrix is calculated in the same manner as in the previously described Markov Methods. Note that as long as every team has played at least one game, then the network will not contain any dangling nodes and the transitional probability matrix will be column stochastic. However, as with the Keener method, the Biased Voter system does not provide a method of ensuring that the network is strongly connected and must be checked before proceeding.

7.3 The PageRank Algorithm

The PageRank algorithm is perhaps the most well-known Markov ranking system, made famous for its efficiency in web-based search engines. It was originally developed by Google founders Larry Page and Sergey Brin as a method of ranking websites for use in the Google search engine (Page et al. 1999), but the algorithm is now used in a wide variety of applications from sports to informatics.

When developing the ranking system, Page and Brin were faced with the challenge of ranking web sites based on the likelihood a page contains information relevant to the searcher. While their competitors simply scanned the page for keywords, they instead sought a method to evaluate not just if the page contained the searched phrase, but if the page exhibited the maximum amount of relevant information. Their innovation came from deciding to rank a page by the other pages it is linked to. Credible pages with large amounts of easily accessible information are often linked to by smaller sites for use as references or additional sources of information. It turns out, ranking a website based on how many sites link to it, and in turn how many sites are connected to these links, etc. is a fast and efficient method of determining the importance of a site.

The PageRank algorithm they developed to interpret this idea is a Markov based ranking

method with a novel modification to ensure that any network will satisfy the conditions of the Perron-Frobenius Theorem. We begin by interpreting our initial data set as a directed graph, and constructing the weighted incidence matrix from this network as described in the previous section. Each edge is assigned a weight of 1, thus the transitional probabilities for the network become:

$$p_{ij} = \frac{1}{\sum\limits_{k=1}^{n} a_{kj}^{*}}. \tag{31}$$

Of course, one must ensure that the denominator of p_{ij} does not equal 0. If a node has any outgoing edges, the corresponding column will contain at least one element greater than zero. Because by definition the weighted incidence matrix only contains positive elements, this means that the corresponding column sum will not equal zero. However, there can exist nodes with no edges pointing away from it, either from undefeated teams or from websites with no exterior links. To deal with these dangling nodes, we replace all the elements in a column of all zeroes with $1/n$. This ensures that all the transitional probabilities can be calculated and that the resulting transitional probability matrix is column stochastic.

However, even after such modifications, we still must ensure that the network is strongly connected. This is especially important when considering networks of websites, where each site contains relatively few links when compared to the total number of websites on the world wide web. To ensure that the matrix is strongly-connected, we first choose $\alpha \in (0, 1)$ and let $\mathbf{e}$ be a $n \times 1$ vector $(1\ 1 \ldots 1)^{T}$. We then define the new Google matrix G_{α}.

$$G_{\alpha} = \alpha P + (1 - \alpha) \left(\frac{1}{n}\right) \mathbf{e}\mathbf{e}^{T} \tag{32}$$

which, in matrix form, expands to

$$
G_\alpha = \alpha \begin{pmatrix} p_{11} & p_{12} & \cdots & p_{1n} \\ p_{21} & p_{22} & \cdots & p_{2n} \\ \vdots & \vdots & & \vdots \\ p_{n1} & p_{n2} & \cdots & p_{nn} \end{pmatrix} + (1-\alpha) \begin{pmatrix} 1/n & 1/n & \cdots & 1/n \\ 1/n & 1/n & \cdots & 1/n \\ \vdots & \vdots & & \vdots \\ 1/n & 1/n & \cdots & 1/n \end{pmatrix}. \tag{33}
$$

Heuristically, one can view α as the probability that the random walker will move around the network according to the transitional probability matrix and $1 - \alpha$ as the probability he will move according to the **teleportation matrix**, or the matrix $T = (1/n)\mathbf{e}\mathbf{e}^T$ (Figure 2.7). Notice that T is column-stochastic, as each element in a given column is $1/n$ and there are n elements per column. If the walker moves according to T, he has an equal probability of moving to any node on the graph.

Now, because G_α is a convex combination of the column stochastic matrices P and T, G_α is also column-stochastic, as shown below.

Proposition 6. *The convex combination of column stochastic matrices is column stochastic.*

Proof. Let A and B be column stochastic $n \times n$ matrices, and let V be a convex combination of these matrices. Then there exists a $t \geq 0$ such that

$$
V = tA + (1-t)B.
$$

Now, for each column $k \in n$, we have

$$
\begin{aligned}
\sum_{j=1}^{n} v_{jk} &= \sum_{j=1}^{n} (ta_{jk} + (1-t)b_{jk}) \\
&= t\sum_{j=1}^{n} a_{jk} + (1-t)\sum_{j=1}^{n} b_{jk}.
\end{aligned}
$$

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Since A and B are column stochastic, for all $i \in n$, $\sum_{j=1}^{n} a_{ji} = 1$ and $\sum_{j=1}^{n} b_{ji} = 1$. Thus

$$\sum_{j=1}^{n} v_{jk} = t(1) + (1-t)(1),$$

which simplifies to

$$\sum_{j=1}^{n} v_{jk} = 1$$

Thus V is column stochastic. $\qquad\qquad\square$

Finally, we note that G_α is also strongly connected, for the convex combination with the teleportation matrix creates connections between every node in the resulting network. Therefore G_α fulfills all the criteria of the Perron-Frobenius Theorem, and we can use the Power Method to solve the matrix equation $\mathbf{r} = G_\alpha \mathbf{r}$ for the dominant eigenvector.

7.4   The Oracle Ranking System

Although the general Markov ranking system is a powerful tool, it experiences an inherent limitation when applied to sports games. Consider the network in Figure 2.8. In the unmodified Markov system, all of the importance flowing through N_1 will also go to N_4, inflating its rank and ranking team t_1 first and team t_4 second. This represents a situation in which t_1 beats every other team and t_4 loses to every other team, yet t_4 somehow managed a spectacular win against t_1. Intuitively, we know that despite their miraculous win, t_1 should still be ranked reasonably low, for they lost four times more than they won. Thus this system creates a ranking that does not appear to accurately represent the abilities of the teams.

The Oracle ranking system is a newly-developed system that was specifically developed to address this issue. The Oracle ranking system has been successful in foresight predictions of regular-season NFL tournaments (Balreira et al. in press), and current work is seeking to apply it to other professional sports as well.

To implement the Oracle ranking algorithm, we begin by building a network from the

tournament and assigning each edge a weight of 1. We now introduce the Oracle as a new node. From every node N_i, there is an edge pointing to the Oracle with a weight of u_i. Also, from the Oracle, there is an edge to every node N_i of weight d_i (Figure 2.9). These u_i and d_i weights are defined by the user, and can be a constant, a game statistic (i.e., score, shots on the goal, etc.), the number of wins of a given team, or anything else the user defines as being important in establishing the rank of a tournament. Note that all of these weights must be greater than 0. The new weighted incidence matrix becomes:

$$
A^* = \begin{pmatrix}
a^*_{11} & a^*_{12} & \dots & a^*_{1n} & u_1 \\
a^*_{21} & a^*_{22} & \dots & a^*_{2n} & u_2 \\
\vdots & \vdots & & \vdots & \vdots \\
a^*_{n1} & a^*_{n2} & \dots & a^*_{nn} & u_n \\
d_1 & d_2 & \dots & d_n & 0
\end{pmatrix}.
\tag{34}
$$

We now calculate the transitional probabilities by dividing each element by the sum of its column, and use these to build the transitional probability matrix. Note that there are no dangling nodes, for every node has at least one edge pointing from it to the Oracle. Consequently, there are no columns of all zeroes and each column sums to one, so P is column-stochastic. This matrix is strongly connected as well, for from any node N_i, there is at least one path to any other node N_j that is two steps long: N_i to the Oracle, and the Oracle to the N_j. Thus the conditions of the Perron-Frobenius Theorem are met, and we can calculate the ranking matrix $\mathbf{r}$ by solving the equation $\mathbf{r} = P\mathbf{r}$ using the Power Method. Observe that the obtained rating vector had dimension $n + 1$, due to the addition of the Oracle node. Hence, we must only consider the first n entries as our ratings. If needed, we can also scale $\mathbf{r}$ so all of the first n entries add up to one.

8   Applying Ranking Systems to Anole Dominance Interactions

After learning the theory behind the eight ranking systems described above, we then set out to test the effectiveness of these algorithms in analyzing dominance behaviors in the green anole (*Anolis carolinensis*). In the summer of 2013, we built a tournament of paired aggressive interactions, called arena trials, between 18 adult male green anoles (denoted Tournament 1, or simply T_1). A year later, we conducted two more tournaments of 10 males each to validate the results of the first experiment, denoted by tournaments T_2 and T_3, respectively. By comparing the ranks generated from these tournaments to lizard characteristics related to dominance, we could then identify the ranks that most accurately reflected social status within anole populations.

Because each of these ranking systems uses different statistics and mathematical approaches to build their ranks, we predicted that some ranks would be consistently more or less reflective of anole social interactions than others. Specifically, we predicted that the Colley method would be the least successful ranking system due to its inability to effectively incorporate ties. Arena trials limit the amount of time competitors have to establish dominance relationships, thus there were often situations in which the winner could not be identified by the end of the trial. However, these ties still reflect important information about the relative abilities of the lizards involved, and must be incorporated into a ranking system for the resulting rank to be accurate. Conversely, we expected the Oracle to be the most effective ranking system, for it has a high degree of customizability and can incorporate a maximal amount of information when building the ranks.

The tournament schedules were each designed to have a diameter of two; that is, for any two lizards i and j, one of the following holds: either lizard i played lizard j, or lizard i played another lizard who also played lizard j. Every male competed once a day for six days in the first tournament and once a day for five days in the second and third tournament. In

each arena trial, we placed the two males to compete in opposite ends of a mesh cage and allowed them to acclimate under opaque containers for ten minutes. A wooden perch was placed between the animals in accordance with standard arena trial procedures in anoles (Tokarz 1985), for anoles are arboreal and male position on the perch is directly related to dominance in this genus. We then lifted the containers and allowed the animals to interact for ten minutes. We recorded the the number of pushup displays and dewlap extensions performed, as well as the latency to eyespot development, the time of the first display, and the number of trials an individual developed a dorsal crest. We declared an individual the winner if it monopolized the perch or if its competitor showed clear submissive behavior, such as running away or hiding. Alternatively, we called the trial a tie if the individuals did not interact, did not reach a resolution in the time allowed, or if they attempted to lock jaws. Finally, we recorded the time to resolution for each individual i as

$$
\text{(Time to Resolution)}_i = \begin{cases} \text{time lizard } i \text{ established dominance, if lizard } i \text{ won the trial} \\ \text{time the individuals attempted to bite each other} \\ 600, \text{ if the trial ended in a tie or lizard } i \text{ lost.} \end{cases}
$$

(For a more thorough description of these arena trials, see Chapter 3, Section 2.1)

At the end of each tournament, we used this win/loss/tie information to calculate the ranks of the competitors using each of the focal ranking algorithms. For the Win Percent, Colley, Bradley-Terry, Keener, and PageRank algorithms, we used the standard parameters described above. For the Biased Voter ranks, we chose $p = 0.75$. However, calculating the Massey and Oracle ranks required more information. Recall that the Oracle algorithm contains two sets of customizable weights, the up and the down weights. Oracle ranks that incorporate score are among the most successful Oracle systems in foresight predictions of NFL games (Balreira et al. in press), thus we chose to make the up weight equal to a metric of score. We then made the down weights a reflection of the number of interactions each team won, so for a given lizard i, $d_i = w_i + 1$, where w_i is the number of arena trials team i

won. (Note that the addition of 1 was to ensure that the down weight is positive for every individual). The Massey system is also largely based on score. Lizard fights do not inherently contain a scoring metric that quantifies how much more dominant one competitor is than another as basketball or soccer do, so we had to create one to calculate these two ranks. We initially tried to interpret score as some behavioral metric (e.g., number of dewlap extensions, number of pushup displays), however we could not find a value that was consistently higher in winners than in losers. Thus we instead chose to interpret score in terms of the time to resolution, or the number of seconds into the encounter that the individual definitively established dominance. Therefore we defined the score of an arena trial as

$$Score = \frac{600 - (\text{Time to Resolution})}{100} + 1, \tag{35}$$

where again the added 1 was to ensure a positive score.

This was a particularly useful scoring system because it distinguished between the different types of ties. Recall that attempting to bite, not interacting, and failing to establish dominance within the ten minute time span were all recorded as ties and in effect treated as equivalent in all of the previous ranking systems. However, an individual that attempts to lock jaws with its opponent is clearly significantly more aggressive than one who allows another male in its space without challenge. Therefore each of these ties reflect different information about the aggressive abilities of the participants. Fortunately, our scoring system weights these ties differently. When we separated individuals attempting to bite each other, we ended the trial and recorded the time, so these individuals always had a score greater than 1. Conversely, individuals who were closely matched or did not interact had a score equal to 1. Additionally, using this metric the winner's score is always larger than the losers, with additional weight going to individuals who won more quickly, i.e., were significantly more dominance than their opponent.

Once we calculated each of the eight ranks, we then used multilinear regression to com-

pare each ranking to six morphological traits (body length, mass, head length, head width, dewlap length, and tail length) and two behavioral traits (cresting behavior and a principle component that combined the rate of pushup displays and dewlap extensions, the time of eyespot development, and the time of the first display, see Chapter 3 Section 2). We chose this specific set of traits because they have each been linked to dominance in the anole literature (e.g., Perry et al. 2004, Tokarz 1985, Vanhooydonck et al. 2005), although the relative importance of each trait in anole dominance interactions is still under investigation (for a full description of these traits, see Chapter 3, Section 2.1). For each rank, we performed a series of multilinear regressions testing all possible combinations of one to eight traits to identify the traits most closely related to that particular hierarchy. We then compared the traits that predicted each of the ranks to identify the traits that serve as the most important criteria of dominance in these populations.

Not only did this analysis identify the traits most predictive of overall social status (see Chapter 3), but it also produced an adjusted R^2 value for each ranking system. I interpreted this value as a measure of the success of the ranks, where methods with higher R^2 values were more reflective of the dominance relationships in this species. In this way, we were able to determine the ranks that performed the best in this animal behavior context.

9   Tournament Results

In the first tournament with 18 lizards, half of the 64 total aggressive interactions resulted in ties. In the second tournament ($n = 10$), 16 out of 25 trials had a clear winner and 9 ended in a tie, while of the 25 trials in the the final tournament ($n = 10$), there were 15 clear wins and 10 ties. Thus the ability of each ranking method to incorporate and interpret ties is going to have an impact on the effectiveness of the systems.

Within each tournament, the rankings were highly correlated (Table 2.3), but there remained variation in each individual's ranks (Tables 2.1 and 2.2). Not surprisingly, there

was also variation in the R^2 values generated in the linear regression analyses of these ranks (min $= 0.40$, max $= 0.97$, see Table 2.4). All of the ranking systems were significant reflections of the dominance traits in Tournaments 1 and 2, however only two (the Keener and PageRank algorithms) were related to the traits in Tournament 3.

When the ranks were ordered from most effective (highest adjusted R^2 value) to least effective (lowest adjusted R^2 value) in each of the three tournaments, there was no clear pattern between the best and the worst ranks (Table 3.5). The Oracle and Biased Voter methods were the only ranking systems not found in the bottom three ranks, and the Massey was the only system not found in the top three ranks. This implies that, while there is no ranking algorithm that works the best in all anole populations, the Oracle and Biased Voter systems are the most consistently reliable ranking methods and the Massey system is the most consistently unreliable system.

10   Discussion

The overall goals of this project were to determine if ranking algorithms are applicable to animal social dynamics, and to identify the ranks best suited for this context. We found that ranking algorithms were indeed successful measures of fighting ability in green anoles (*Anolis carolinensis*), however no one algorithm was the most successful model in every tournament. Markov methods provide a high degree of customization and created successful rankings in all three tournaments, implying that they are particularly well suited for animal social behavior studies. The Massey system was the most consistently unsuccessful ranking, most likely do the choice of scoring system used. All of the other ranking systems worked well in some tournaments but not in others, implying that multiple ranks are needed to accurately interpret dominance relationships in anole populations.

In two of the three tournaments analyzed, including the one with the largest sample size, the ranks modeled dominance interactions within the green anole populations very

successfully. The Biased Voter ranking system explained 97% of the variation in the traits related to dominance in the T_2, and the Oracle system explained 79% of this variation in T_1. Indeed, even in the third tournament, where most of the results were not significantly related to the measured traits, the Keener ranking system explained almost 60% of the observed variation in trait measures. This suggests that ranking systems are indeed a useful method with which to measure animal social hierarchies.

While we found that ranking systems in general successfully reflected the observed social dynamics, individual ranking systems experienced a wide range of success in measuring these dynamics. No method was consistently the most successful or least successful, for most of the ranks performed well in some tournaments and not in others. This, in addition to the variation observed between the ranks, implies that it is wise to consider multiple ranking algorithms when analyzing animal behavior. In fact, by comparing the traits emphasized by the ranks that work the best/worst for a given population, this could highlight important characteristics of the interactions that drove the formation of the relationships.

In our study populations, we found that the Biased Voter and Oracle systems were the algorithms that consistently provided successful quantifications of dominance hierarchies for the green anole. Additionally, the Keener and PageRank methods were the only two methods to significantly reflect the dominance relationships of Tournament 3. It is intuitively favorable to impose network-based ranking systems onto groups of animals, for natural vertebrate populations are often modeled as social networks, in which individuals form nodes and interactions with conspecifics become edges. Indeed, understanding the underlying structure, connectivity, and temporal variation of these networks is a thriving area of research (Wey et al. 2008). Therefore modeling the flow of dominance through a population by treating it like a Markov system is a natural extension of the current work in animal social dynamics. Additionally, it is exciting that these models in particular were successful due to their high degree of customizability. Our specifications of the Oracle rank were highly successful, particularly in the first tournament, implying that including carefully chosen statistics into the ranks can

increase the effectiveness of the ranking. This suggests that testing scoring metrics specific to the species or population being investigated may lead to the development of Markov ranking systems that very accurately represent the social dynamics of the population.

The only system to consistently perform poorly in our three populations was the Massey ranking algorithm. This is a system that was designed very specifically for football ranks, so it could be that this ranking system simply inherently does not work in an animal behavior context. The choice of the h function or the heavy reliance on score, which is not well defined in animal interactions, may not be appropriate in this arena. However, this lack of success could also be due to the scoring metric that we chose in this analysis. Testing different definitions of score could identify the aspects of dominance interactions that the Massey system interprets the best and result in a more successful rank.

All of the other systems performed well in some tournaments and poorly in others, so we cannot draw any strong conclusions to their effectiveness in modeling anole dominance hierarchies. However, we can make educated predictions as to the animal social systems in which each system will perform successfully. To begin, consider the Win Percent rank, which did reasonably well in all of the tournaments. If investigators do not wish to use advanced ranking systems to address their inquiries, it appears that they can still generate successful rankings and answer their questions using this simple and reliable method. Next, we still maintain that the Colley method is not a wise choice in modeling dominance relationships. Although it did well in tournaments T_1 and T_2, this method's general inability to handle ties and low degree of customizability make it an illogical choice when identifying ranking systems to use in a dominance context. However, given enough time, pairs of anoles will almost always establish a dominant-submissive relationship, so there will be a low incidence of ties in field studies or long-term laboratory experiments. The Colley system may be a reasonable choice of ranking system in these situations. Next, when considering the Bradley-Terry model, we note that this system requires a large number of paired comparisons to generate an accurate rank. In fact, in sports applications the Bradley-Terry system is often limited to

Major League Baseball and National Basketball Association tournaments, for sports such as football simply do not play enough games to work in this system. In both field and laboratory experiments, the number of interactions that can be observed is often limited, either by the investigator's ability to find the organism or by the money, time, and equipment available. Therefore the Bradley-Terry model may generally not be an ideal ranking system for animal behavior endeavors. However, the modification of the Bradley-Terry system that uses a metric of score decreases the number of comparisons needed to generate a rank, so this metric may be useful in some behavioral contexts.

Overall, we found that ranking algorithms successfully reflected the dominance relationships observed in populations of green anoles. This indicates that behavior is an exciting new application for ranking algorithms, one which will hopefully provide new insights into how animal social dynamics function.

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Table 2.1: The ranks generated by each of the eight ranking systems for a tournament of aggressive interactions between 18 adult male *Anolis carolinensis* (Tournament 1).

Lizard	Win Percent	Colley	Massey	Bradley-Terry	Keener	Biased Voter	PageRank	Oracle
1	3	4	4	6	8	6	7	5
2	4	2	1	3	2	1	1	2
3	10	5	2	4	6	4	6	6
4	11	11	17	11	15	11	14	12
5	15	16	9	17	17	17	16	16
6	7	10	12	13	14	16	13	10
7	18	18	18	18	18	18	18	18
8	17	17	10	15	16	15	17	17
9	5	9	3	8	1	5	2	4
10	1	1	6	1	5	2	5	1
11	13	15	13	14	12	12	15	14
12	8	7	14	9	9	10	9	9
13	9	8	5	7	4	7	4	8
14	14	12	16	10	7	9	8	11
15	6	3	7	2	3	3	3	3
16	16	14	15	16	10	14	12	15
17	2	6	8	5	11	8	10	7
18	12	13	11	12	13	13	11	13

Table 2.2: The ranks generated by each of the eight ranking systems for two tournaments ($n = 10$ each) of aggressive interactions between adult male green anoles *Anolis carolinensis* (Tournaments 2 and 3, repectively).

Lizard	Win Percent	Colley	Massey	Bradley-Tery	Keener	Biased Voter	PageRank	Oracle
1	7	8	8	7	8	7	7	7
2	6	6	7	8	7	8	6	6
3	7	7	6	6	4	6	3	8
4	4	4	4	4	5	4	5	4
5	1	1	1	1	1	1	2	1
6	2	3	2	3	3	3	4	2
7	10	10	9	10	9	9	10	10
8	2	2	3	2	2	2	1	3
9	9	9	10	9	10	10	9	9
10	4	5	5	5	6	5	8	5
1	4	4	4	4	3	4	2	4
2	7	7	5	5	7	7	7	7
3	2	3	2	3	2	3	3	3
4	2	2	3	2	1	2	1	2
5	4	5	6	6	6	5	5	5
6	6	6	7	7	4	6	4	6
7	9	10	9	10	9	10	8	10
8	9	9	8	9	8	9	10	9
9	1	1	1	1	5	1	6	1
10	7	8	10	8	10	8	9	8

Table 2.3: Pearson correlation values comparing the ranks generated by the 8 different ranking systems. All correlations had $p < 0.01$.

	Win Percent	Colley	Massey	Bradley-Terry	Keener	Biased Voter	PageRank	Oracle
Win Percent	1	0.90	0.64	0.85	0.64	0.76	0.72	0.91
Colley		1.00	0.68	0.96	0.77	0.90	0.84	0.96
Massey			1.00	0.70	0.68	0.73	0.73	0.74
Bradley-Terry				1.00	0.81	0.95	0.86	0.95
Keener					1.00	0.90	0.97	0.86
Biased Voter						1.00	0.92	0.94
PageRank							1.00	0.91
Oracle								1.00

Table 2.4: The adjusted R^2 values generated when each ranking system was compared to optimal combinations of morphological and behavioral characteristics that reflect dominance in the green anole (*Anolis carolinensis*) using linear regression. In this analysis, *** indicates p values < 0.001, ** indicates p values < 0.01, and * indicates p values < 0.05.

	Tournament		
Ranking System	1	2	3
Win Percent	0.724***	0.844**	0.528
Colley	0.753***	0.931**	0.473
Massey	0.490*	0.870**	0.399
Bradley-Terry	0.495*	0.941***	0.452
Keener	0.411*	0.857**	0.590*
Biased Voter	0.563**	0.971***	0.504
PageRank	0.655**	0.832**	0.518*
Oracle	0.796***	0.861***	0.534

Table 2.5: The ranking systems ordered by adjusted R^2 value for each tournament. These R^2 values (Table 2.4) were generated by comparing each ranking system to a series of behavioral and morphological traits using linear regression.

Tournament 1	Tournament 2	Tournament 3
Oracle	Biased Voter	Keener
Colley	Bradley Terry	Page Rank
Win Percent	Colley	Oracle
PageRank	Massey	Win Percent
Biased Voter	Oracle	Biased Voter
Bradley Terry	Keener	Colley
Massey	Win Percent	Bradley Terry
Keener	PageRank	Massey

12   Figure Legends

Figure 2.1: Two male green anoles (*Anolis carolinensis*) in an aggressive interaction. Both individuals are flattened dorsal-ventrally and have developed crests and dark eyespots. They are in the *face off* position, where they align their bodies parallel to each other so that they can circle their opponent. Photograph courtesy of Michele Johnson.

Figure 2.2: An example tournament of six games between four teams, t_1, t_2, t_3, and t_4. **(A)** The outcome of each game **(B)** The network representation of the tournament, where arrows point from the loser to the winner.

Figure 2.3: Picture a random walker positioned on node N_1 (time step 1). From this node, he could use three different edges to move to another node, each associated with a different transitional probability (p_{21}, p_{61}, and p_{31}). Suppose he chooses the edge with transitional probability p_{12} and moves to node N_2. From this node, he now has a choice of two edges with which to move, each with their own transitional probabilities (time step 2). The walker will continue to move around the network in this fashion.

Figure 2.4: A network interpretation of an example tournament of six games between four teams. Edges each represent a match and point from the loser to the winner. Double-headed arrows represent ties. (Note: This network is different than the one in Figure 2.2.)

Figure 2.5: Plot of Keener's weight function $h(x)$(solid line) and the identity function (dashed line). We note that winner's scores will be those above $h(x) = 0.5$ and loser's scores will be scores below $h(x) = 0.5$, with higher-scoring games representing the values closer to both 0 and 1. Figure obtained from Keener (1993).

Figure 2.6: A representation of the network generated by the Biased Voter system from a single match between two teams, where t_1 (corresponding to node N_1) beat t_2 (corresponding to node N_2. Note that all edges pointing to the winner have a weight of p, and all those pointing towards the loser have a weight of $1 - p$, where $p \in (0.5, 1)$.

Figure 2.7: A representation of the network generated by the PageRank system for a tournament between four teams, specifically highlighting the options the random walker positioned at node t_1 has to move. The solid arrows represent each match, where the arrow points from the loser to the winner. The random walker will use these arrows α proportion of the time, where $\alpha \in (0, 1)$. The dashed arrows represent the teleportation matrix, where the walker can move to any node in the network. He will use these arrows $1 - \alpha$ proportion of the time.

Figure 2.8: A network representing a tournament in which an otherwise winless team, n_4, beats and otherwise undefeated team, n_1.

Figure 2.9: A representation of the network generated by the Oracle ranking system. Notice that the network is constructed in the same fashion as general Markov methods, however it also includes an additional node, the Oracle.

Figure 2.1

Figure 2.2

(A)

Game	Winner	Loser
1	t_1	t_2
2	t_1	t_3
3	t_4	t_1
4	t_4	t_3
5	t_2	t_4
6	t_2	t_3

(B)

Figure 2.3

Time Step 1:

N_6

N_4 N_5

N_2 p_{61} N_3

p_{21} N_1 p_{31}

Time Step 2:

N_6

N_4 N_5

p_{42} p_{52}

N_2 N_3

N_1
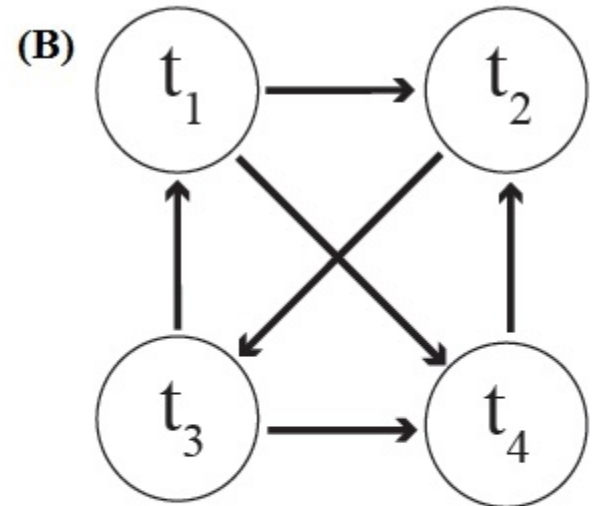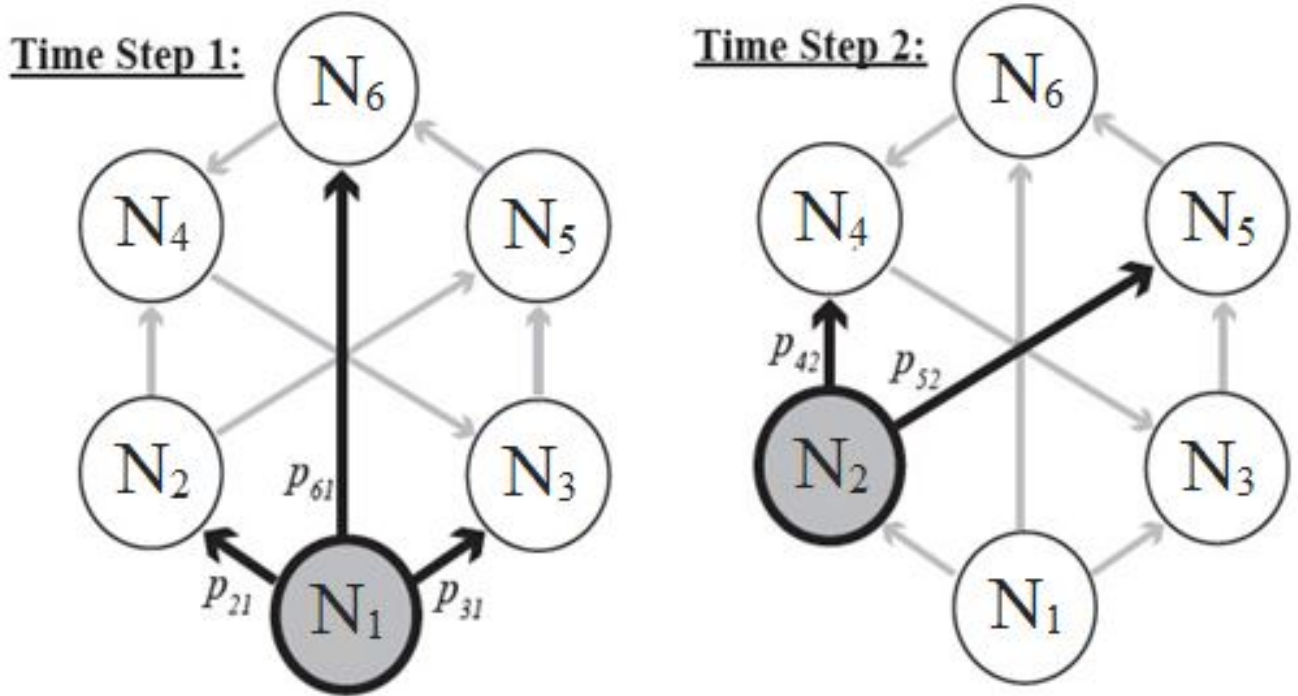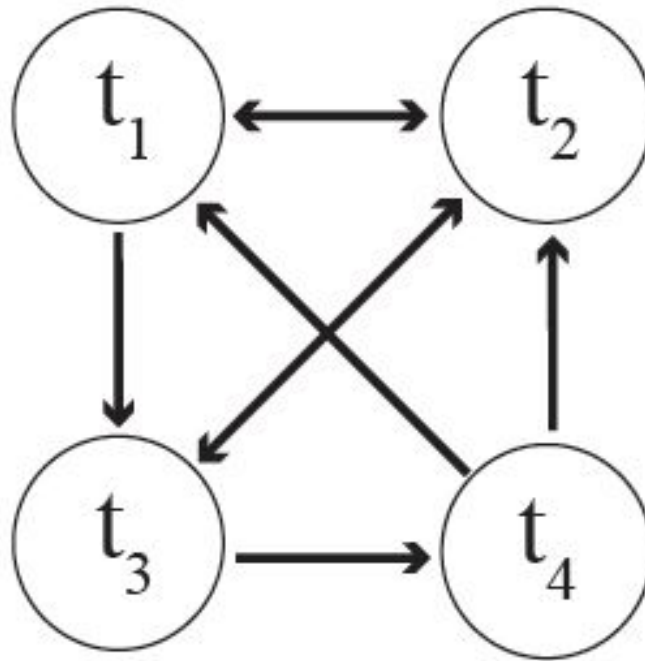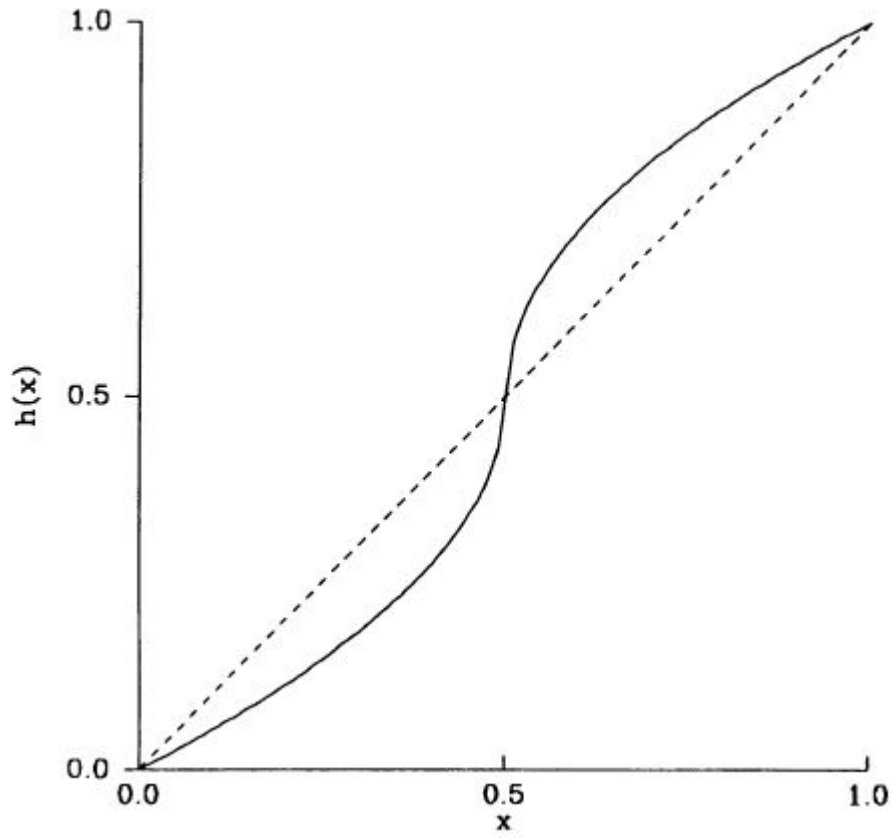
Figure 2.4

Figure 2.5

Figure 2.6
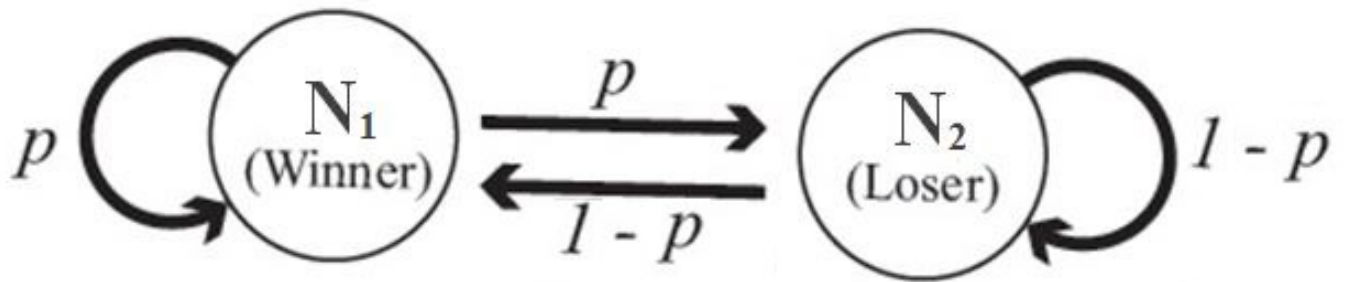
Figure 2.7
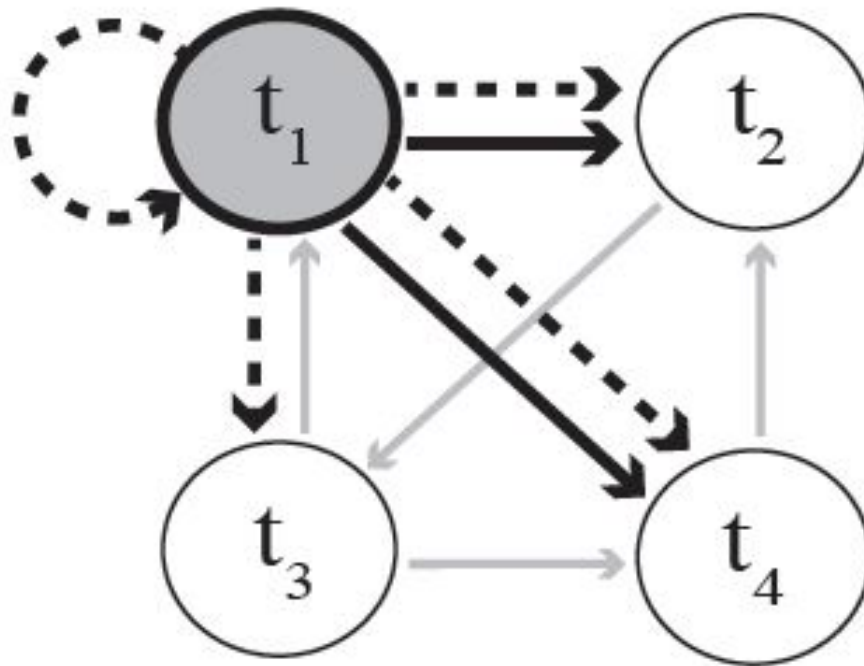
Figure 2.8
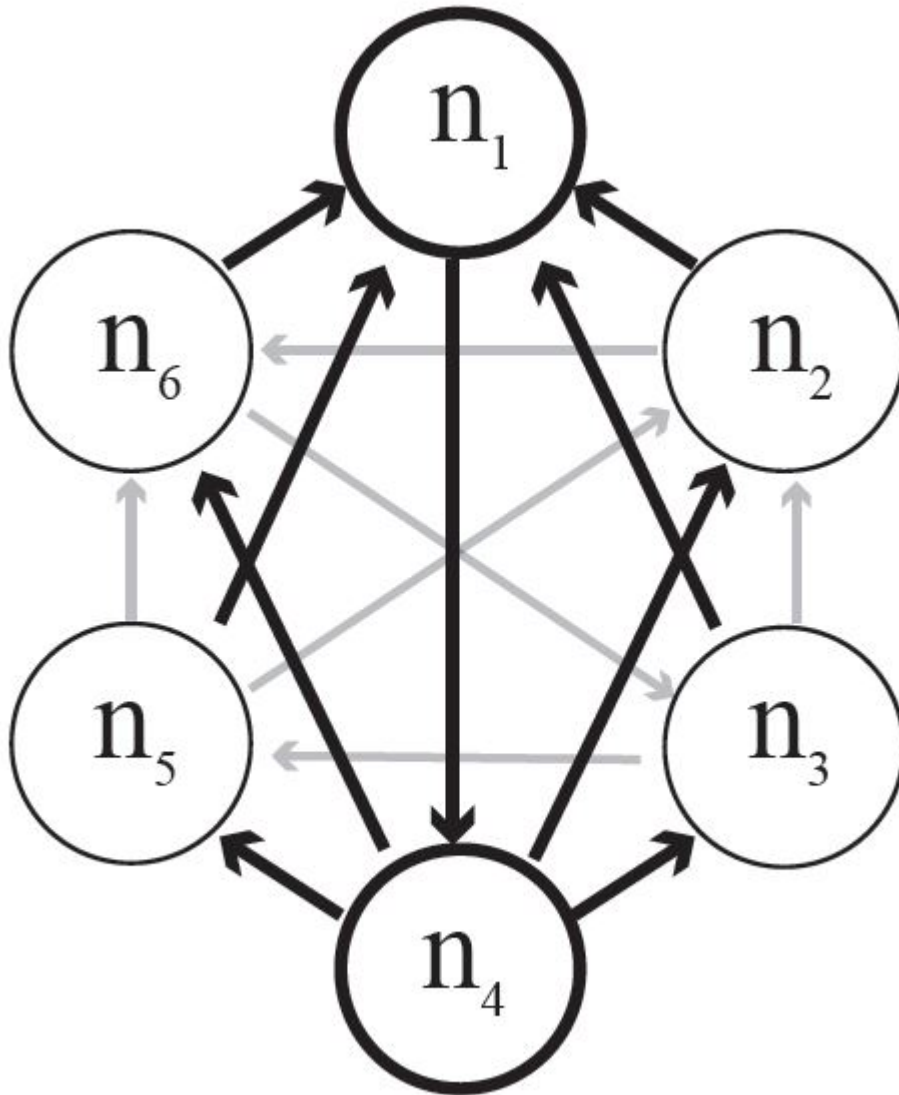
Figure 2.9
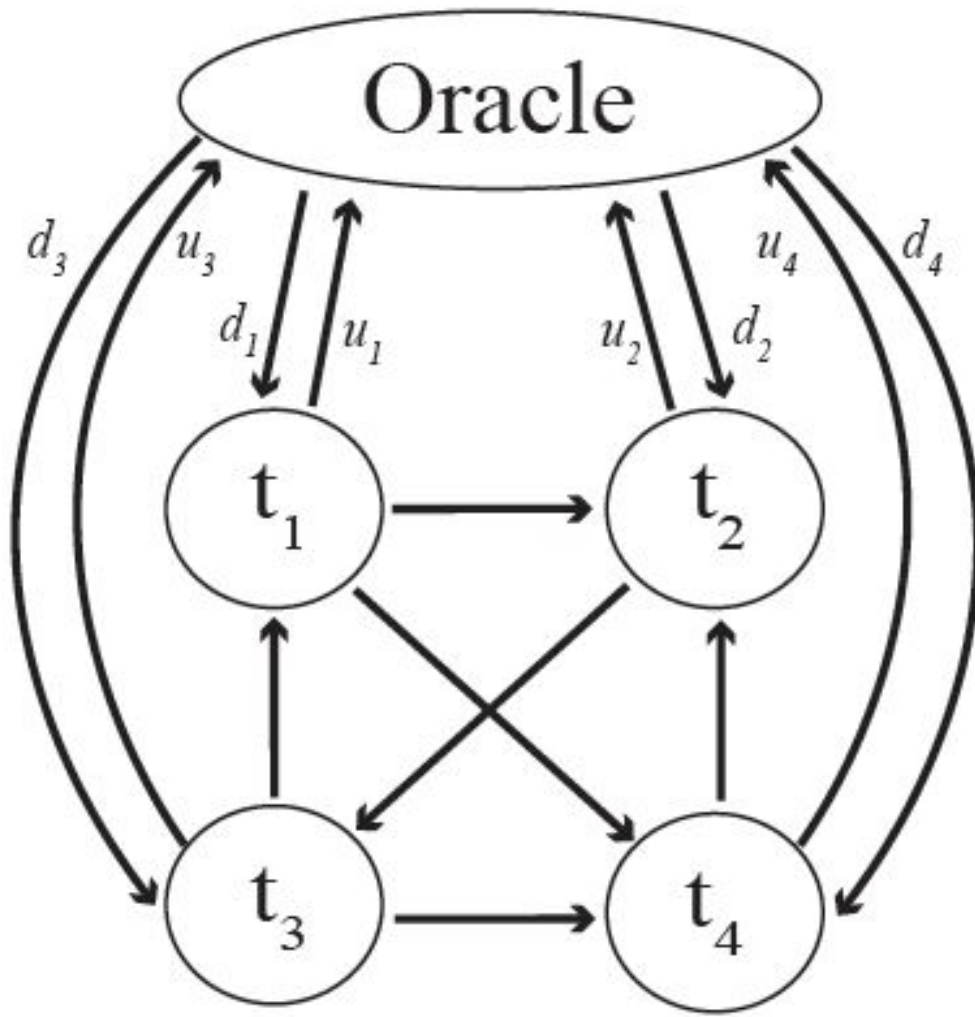
Chapter Three: An Exploration of the Relationship between Dominance and Territoriality in the Green Anole

1 Introduction

1.1 Dominance Structures of Animal Populations

Within many animal populations, conspecifics compete for valuable resources such as food, mates, and shelter. This intraspecific competition is often costly, particularly when it results in physical altercations. Fights between individuals require a large investment of energy from both winners and losers (Neat et al. 1998), and can result in injury or death. For example, nearly 6% of breeding males in a given population of red deer (*Cervus elaphus*) are permanently injured each year in male-male contests (Clutton-Brock et al. 1979). To avoid such expensive confrontations, many animals form dominance relationships within a population as a method of partitioning resources. This is a common form of social organization, observed in a broad range of taxa that includes fish (salmon: Nakano 1994), birds (tits: Lahti et al. 1994), mammals (elephants: Archie et al. 2006), and insects (ants: Monnin and Peeters 1999). In a system of dominance relationships, individuals use their relative rank in a population's hierarchy to determine the outcomes of interactions, where lower-ranked

individuals are expected to defer to higher-ranked ones in subsequent contest situations (Kaufmann 1983). This is beneficial to both parties. Dominant animals are given priority access to resources (Kaufmann 1983) and often experience higher reproductive success (Dewsbury 1982, Frank et al. 1995), and although submissive individuals are denied these obvious fitness benefits, they avoid the energetic costs of fighting and probably losing contests, allowing them to conserve energy for more potentially rewarding situations (Renison et al. 2002).

Dominant-submissive relationships are formed in a variety of ways. Many animals use displays to convey information about their physical fitness and fighting ability to their opponent without having to physically engage them. Different taxa use different types of displays. Coloration and ornamentation are common visual cues in birds (e.g., feather colors, Rohwer 1974, Senar 2006; beak color, Murphy et al. 2009), mammals (e.g., primate fur color, Bradley and Mundy 2008; antlers, Bowyer 1986), and reptiles (e.g., throat color, Thompson and Moor 1991). Bright colors, particularly those related to carotenoid concentrations, are often honest signals of an individual's health and/or quality (Pérex-Rodríguez and Viñuela 2008, Cook et al. 2013), and thus can be used as agonistic signals to also indicate fighting ability (Pryke et. 2001, Senar 2006). Other animals, such as amphibians and some primates, use auditory cues, evaluating their opponents based on their call volume, complexity, pitch, or frequency. For example, in many frogs, the pitch of aggressive calls is related to body size, and larger and stronger males give deeper calls (Ryan 1985). Behavioral displays are also important, for they allow individuals to display their ornamentation, weapons, and size to maximize their effects. However, when individuals are closely matched in ability or are equally invested in the defended resource, displays may not be enough to determine the dominance relationship between two individuals. Instead, closely matched individuals must fight to establish their social status.

Dominant-submissive dynamics are a widely-observed phenomenon, and there are many types of social organizations that include these relationships. Kaufmann (1983)

distinguishes between two broad types of dominance: absolute and relative. Absolute dominance is characterized by linear relationships among individuals that are independent of space and time. That is, if one animal is dominant over another, it will continue to be so regardless of where or when the animals interact in the future. This type of behavior is often observed in animals that live in social groups, particularly social mammals like hyenas (Frank 1986) and bighorn rams (Hass and Jenni 1991). In contrast, relative dominance exists in populations in which the dominance relationships are predictably reversible in certain situations (Kaufmann 1983). The most obvious example of this is territorial animals, where on its own territory an animal is much more likely to win dominance interactions (Evans 1936, Johnsson et al. 1999) than it is on other individuals' territories. Territorial animals presumably only know their dominance relationships to their neighbors, and do not have information on relative fighting ability of individuals they have not yet encountered, as is observed in systems with absolute dominance. Another example of relative dominance is found in social primates, which can have highly complex ranking systems. In these systems, an individual will win more social interactions when in the presence of a high-status family member than it would when their relatives are not present (Kawai 1958). These populations thus incorporate social information such as kin relationships into the ranking system.

1.2 Animal Territoriality

In this thesis, I expand upon the idea of relative social hierarchies by analyzing the dominance behavior of a territorial species. Although territorial behavior has been studied since its initial observation in the 1920's (Howard 1920), there is no one standard definition of territoriality. How this term is used and the behavioral and ecological factors associated with it vary widely, often depending on the taxa being studied. There are three main definitions, as reviewed by Maher and Lott (1995). In the first, a territory is defined as a fixed area (Brown and Orians 1970) that the

owner protects from competitors. In most species, animals only defend against members of their same sex (Maher 2004, Pierro et al. 2008), allowing intraspecific overlap of territories for mating purposes. Often these challenges are limited to behavioral displays (Ficken 1962, Price et al. 1990) and self-advertisement (Wolff et al. 2002), although if the intruder does not back down they may escalate to fights. The second definition describes a territory as an area over which an animal has exclusive use. The threshold value of home range overlap permissible for an area to be considered a territory varies greatly by species. In this definition, all that matters is that the owner has exclusive use of the space, without regards to how it obtained this use (Pitelka 1959). The final definition of territory is characterized by site-specific dominance, in which an individual has priority access to a set of resources in a specific space (Kaufmann 1983). Many scientists also combine these definitions, requiring two or even three of the criteria for an area of home range to be considered a territory. For example, Brown and Orians (1970) required an individual's defense of an area to lead to its exclusive use of that area before it can be called a territory. Still others see territoriality as a continuum, with exclusive, defended territories on one end of the spectrum and overlapping, undefended home ranges on the other (Maher and Lott 1995).

Territoriality has evolved in a wide variety of species, for there are many different situations in which this method of resource allocation is selectively advantageous. For example, territoriality often exists in populations that contain feasibly defensible resources that limit population growth (Brown 1969). This is an economic model, in which we assume that the energetic costs of establishing and defending a territory are outweighed by the fitness benefits of having exclusive access to the resources within this territory. For a resource to be economically defensible, it must satisfy two criteria. First, it must be predictable, for there is a large amount of risk associated with defending a resource that may or may not be there later (Orians 1961). Second, it must also be unevenly distributed to justify the cost of defense (Magnunson 1962). The limiting resources worth defending can generally be categorized as food, habitat

features, mates, and refuges/home sites. The distribution, availability, and importance of each of these resources vary across habitats; thus they can each affect different species in a variety of ways. Territoriality can also evolve as a response to population density. Maher and Lott (2000) proposed a U-shaped curve to explain this relationship. They claim that territoriality is not advantageous in populations with either low or high densities, for at low densities there are simply no conspecifics to defend against and at extremely high densities large intruder pressure makes it energetically unfeasible to keep competitors out. Thus they argue that it is only in populations between these two extremes that territoriality exists. Indeed, when anisopteran dragonflies (*Aeschna cyanea*) live at relatively high densities, males exhibit territoriality, while at lower densities males are nomadic (Poethke and Kaiser 1987). Additional factors such as predation pressure (Candolin and Voigt 2001) and energy availability (Ewald and Carpenter 1978) have also been related to territorial behavior.

1.3 Dominance Behavior and Territoriality of *Anolis* Lizards

One of the major goals of this thesis was to explore the relationship between territoriality and dominance behavior in anole lizards (genus *Anolis*). With over 400 species, this is one of the largest genera of vertebrates (Losos 2009). Generally, these lizards are relatively small (body length < 135mm, Case 1978), arboreal, and insectivorous. Males and females are sexually dimorphic, where males are usually larger and heavier than females (Jenssen et al. 1995). Males (and to a lesser degree, females) have a brightly colored throat fan called a dewlap that they use in both sexual and aggressive displays. Anoles are particularly well-suited for the present study due to their system of social organization. Generally, both males and females are territorial. However, in particularly dense populations (most notably those in

sustained in captivity), some species of this genus will switch to a linear dominance hierarchy system (Stamps 1977). Thus the same lizards may experience populations organized according to both territorial and dominance systems, making it possible to do comparative studies between the two systems.

Within the genus *Anolis*, territory is generally defined as maintaining a defended area (Stamps 1977). With the exception of three species (*A. agassizi, A. tropidolepsis, and A. taylori*), all anole species are territorial under this definition (Losos 2009). There is a large amount of variation in territory sizes (Schoener and Schoener 1982) and degrees to which conspecific territories overlap (Losos 2009, Johnson et al. 2010), although the amount of overlap is similar within a habitat (Johnson et al. 2010). Males typically defend all of the area they occupy, thus territory and home range size are roughly equivalent in anoles (Stamps 1977).

In many anole species, both males and females are territorial (Stamps 1973, Jenssen 1970), although males usually have larger territories than females (Schoener and Schoener 1982). The primary purpose of male territoriality in this genus is mate acquisition (Stamps 1977, Losos 2009) for males with more females on their territory exhibit higher reproductive success (Ruby 1984) and male territory size is often larger than necessary for food acquisition (Andrews 1971, Schoener and Schoener 1982). Generally, males defend their territory against perceived competitors, and are often intolerant of conspecific males intruding on their territory. However, small juvenile males may occupy the territory of established adult males, either because they are mistaken for females (Trivers 1976) or because the territory holder does not view them as a threat. These covert males generally try to remain inconspicuous and rarely display (Fleishman 1988, Orrell and Jenssen 2003). Males do not defend against females and rarely show them aggression (Stamps 1977), while females will challenge all intruding conspecifics of similar size, including other females and both territory-holding and juvenile males (Losos 2009). Female territory defense revolves around protecting food supplies and includes dewlap extensions and/or push-up displays, although they rarely escalate to fights (Jenssen et al. 2000). This defense is

also only effective over short distances when compared to males and does not include assertion displays.

Most anoles show similar patterns of territory defense, despite minor variations between species (Losos 2009). There are two broad categories of anole territory defense: assertion displays and responses to challengers. Assertion displays are spontaneous displays, usually head-bobs, push-ups and dewlap extensions, given by an animal as it moves through its territory to declare the owner's presence and to warn any competitors that may be watching (Carpenter 1967, Jenssen 1977). These displays are highly stereotyped, species-specific, and heritable (Jenssen 1977). During the breeding season, males generally have high rates of such displays, sometimes devoting the majority of their time to them (Losos 2009). But when a competitor is not deterred by advertising displays and instead challenges the territory holder, the lizards will engage in a series of aggressive displays of increasing intensity (Greenberg and Noble 1944). They begin by performing head-bobs, push-ups, and dewlap extensions (which are also used in courtship). Some species also perform additional agonistic displays; for example, male green anoles (*Anolis caroliensis*) will also develop dark spots behind their eyes (called eyespots) and erect a dorsal crest to signal aggression. If neither backs down, the opponents flatten themselves dorsal-ventrally to appear larger and more intimidating (Greenberg and Noble 1944) and begin circling each other in the "face off" position. They will circle closer and closer until they lock jaws, after which they each attempt to throw their opponent off of the perch. Lock jawed fights are relatively rare in the wild, as the majority of aggressive interactions between male anoles are resolved without the use of physical contact (Lailvaux et al. 2004). As in most species, most anoles win the majority of encounters on their own territory (Evans 1936).

A variety of experimental techniques have been used to study dominance relationships and the traits that determine them in anoles. The most common is the use of arena trials (e.g., Lailvaux et al. 2004). These staged confrontations involve placing two anoles into a cage and observing the outcome of the subsequent

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aggressive interaction. By observing the behavior, morphology, and physical abilities of the competitors, experimenters can determine the individual qualities that determine which lizards will win or lose. Another approach is to maintain captive groups of anoles at high population densities and observe the resulting dominance hierarchy that forms (e.g., Stamps 1984). In such situations the lizards use their display and fighting abilities to establish their social rank, then distribute food and mating opportunities throughout the population accordingly. This gives experimenters a continuum of dominant-submissive relationships that can be used to identify the traits most closely related to social status. Still more scientists use field studies, observing the natural dominance interactions associated with territory defense and attempting to distinguish between characteristics of the winners and losers (e.g., Schoener and Schoener 1982).

Although there is still no definitive consensus on which traits predict social dominance in anoles, patterns are emerging from the results of dominance studies. Morphological traits directly related to fighting ability, such as body size (Tokarz 1985, Losos 2009) and head size (which is related to bite force, Perry et al. 2004, Henningsen and Irschick 2012), are often identified as important predictors of dominance interactions. Additionally, performance-based traits such as locomotor ability (Perry et al. 2004) and jumping velocity (Lailvaux et al. 2004) are often heightened in more dominant animals. The importance of signals such as dewlap morphology and tail length are still poorly understood, although dewlap length is related to bite force in some *Anolis* species (Vanhooydonck et al. 2005) and tail length is a status signal in other iguanids (Fox et al. 1990). In green anoles, rapid eyespot development is one of the most reliable visual signals in predicting winners of agonistic encounters. Eyespot darkening is directly related to the aggression-inducing hormone seratraline (Larson and Summers 2001), thus individuals that develop eyespots more rapidly are more likely to win aggressive interactions. However, none of these traits have proven to be predictive in every instance, indicating that there is still more to learn about dominance signaling in anoles.

1.4 Goals of Current Study

In this study, I investigated the relationship between dominance and territorial behavior in the green anole. Dominance and territoriality have traditionally been treated as mutually exclusive methods of social organization, yet as described above, both of these systems are present within green anole populations. Although both types of organization have been extensively studied in this system, the two have never been directly compared. Both are methods of allocating resources based on some kind of rank (i.e., absolute vs relative), yet these ranks are established and the relationships stabilized in very different manners. Do these two means of organizing the population utilize different types of information about competitors while arriving at the same outcomes? Or do the systems favor individuals with different traits, thus creating completely independent ranks? In this thesis, I designed three studies to address these questions.

First, I sought to determine the traits that predict dominance in the green anole. To this end, I conducted a series of arena trials using 18 adult male green anoles and used a collection of ranking algorithms to rank each individual based on its resulting win-loss-tie record. I then performed a series of multilinear regressions to compare these ranks to various morphological and behavioral traits to determine the traits that best predicted dominance. In the second study, I conducted a parallel investigation in a natural setting to determine the traits that best predicted territory size and the extent of male overlap with female territories. I marked 24 adult male green anoles within a 1000 m^2 study plot in Palmetto State Park, Gonzales, Texas and performed behavioral observations on these individuals over the next three weeks. I then used a set of multilinear regressions to determine which morphological and behavioral variables were associated with the two measures of territorial success (size and female overlap). Finally, I designed an experiment to directly compare territory size and dominance. In each of two replicate trials, I ran ten adult male

green anoles through an arena trial tournament and ranked them as in the first experiment. I then placed these males into an artificial enclosure, measured the sizes of the territories the males established over the next week, and compared these measures to the males' ranks. Overall, I predicted that the same traits would predict territory size, overlap with female territories, and dominance in green anoles. I also expected these measures to be related at least in part to body size, which is generally associated to both dominance and territorial success in anoles (Losos 2009). Additionally, I predicted that these measures would be complementary, thus highly-ranked lizards in the dominance trials would in turn establish larger territories in the enclosure.

2 Materials and Methods

2.1 Study 1: Arena Trial Tournament

2.1.1 Collecting and Housing Lizards

Twenty adult male green anoles (*Anolis carolinensis*) were caught by hand or noose in and around San Antonio in summer 2012. Seventeen of the lizards were caught in early June and had their body size and mass measured at three day intervals for forty days as a part of a different experiment. The remaining three lizards were captured at the end of July, however there was no significant difference between any morphological or behavioral traits between the two groups (results not shown). All lizards were housed at Trinity University following standard procedures (Sanger et al. 2008). In brief, each lizard was individually housed in a standard rodent cage of dimensions 20 x 21 x 27 cm, with each cage containing a wooden perch and a small lemon grass plant (*Cymbopogon spp.*) to maintain the humidity within the cage. I covered the floor of each cage with cage carpet (r'zilla), and heated cages using a full

spectrum UV and heat lamp (Flunker's Sun Spot) on a 12:12 light cycle to maintain the temperature and humidity between 25.4-38°C and 37-80%, respectively. I misted lizards daily and fed them two crickets every other day. Cages were separated by wooden dividers to prevent the lizards from visually interacting with each other before the trials.

2.1.2 Arena Trials

I designed a tournament of paired arena trials to allow each lizard to compete in one trial each day for six consecutive days. The resulting tournament network had a diameter of two, thus at the end of the six days every lizard i had either played lizard j or had played another lizard who played lizard j. I randomly assigned the 20 male lizards identification numbers between 1 and 20 and marked each individual with permanent marker, indicating numbers on their sides to allow identification during the arena trials.

Before each trial, I placed the two lizards under opaque plastic containers (5 x 10 x 7 cm) positioned on opposite sides of a mesh cage (63 x 39 x 37 cm). I positioned a single wooden perch between the two containers following standard procedures for anole dominance trials (Garland et al. 1990, Perry et al. 2004), for anoles are arboreal and being higher on a perch than an opponent signals dominance. After a 10 min acclimation period, we lifted the containers and the 10 min trial began. Two experimenters observed the lizards (with each experimenter recording information for a single lizard) from behind a blind 5 m away from the cage. Experimenters recorded the number of pushups and dewlap extensions performed, the time at which an eyespot developed, whether a crest appeared, the latency until the first dewlap or pushup display, and the time at which the lizard climbed onto the perch. After each trial, the experimenters determined the winner (i.e., the more dominant animal, described below) and recorded the time the individual definitively established dominance (time to resolution). In most cases, this was the time the dominant lizard

took the perch. I determined the lizard to be the winner if it monopolized the perch, was higher on the perch than the other lizard at the end of the trial, or if the other lizard clearly showed submissive behavior, such as running away or attempting to hide. If the lizards were at the same height on the perch at the end of the trial, did not interact, or attempted to lock jaws, I called the trial a tie. When the lizards tried to lock jaws, the trial was immediately stopped and the lizards separated. In the event of a tie, the length of the trial was recorded as the time to resolution, while for trials with locked jaws, the time to biting was used as the time to resolution. After the trials each day, I returned the anoles to their cages and gave them food and water. Over the course of the tournament, two anoles died of natural causes, thus results from the trials in which they participated were not included in the ranking analysis.

2.1.3 Morphological Measurements

After the arena trial tournament was completed, I performed morphological measurements for each lizard. Snout-vent length (SVL) was measured from the vent to the tip of the snout to the nearest mm using a plastic ruler. Head length, head width, and dewlap length were all measured to the nearest 0.01 mm using digital calipers. Head length was measured as the distance from behind the ear opening to the tip of the snout. Head width was defined as the length of the widest part of the skull, measured at the anterior base of the cranium. Dewlap length was measured from the insertion point of the second ceratobranchial cartilage (the cartilage that lines the exterior of the extended dewlap) in the lower jaw to the distal end of the cartilage at the abdomen. The mass of each lizard was also measured with a 10 g Pesola scale to the nearest 0.1 g. Finally, tail length was measured from the vent to the tip of the tail to the nearest mm using a plastic ruler.

2.1.4 Calculating the Rankings

I calculated ranks based on the win-loss-tie information from the arena trial tournament using the programs MATLAB R2012a (2012) and R (R Development Core Team 2011, Turner and Firth 2012). I used eight different ranking systems: Win Percent, PageRank, Oracle, Keener, Biased Voter, Colley, Massey, and Bradley-Terry. While most of the ranks were calculated using standard parameters, the Oracle and Biased Voter systems required user-defined parameters. The Oracle system was calculated using an up weight of time to resolution and a down weight of the number of wins plus one (to make the value always positive), and the Biased Voter was calculated using p = 0.75. (For a detailed explanation of the theory and calculation of these ranks, see Chapter 2 of this thesis.)

2.1.5 Data Analysis

I used multilinear regression to determine the morphological and behavioral characteristics that best predicted individuals' rank in multiple ranking systems. Because of the relatively large number of variables considered (11), and the relatively small number of lizards in the study (18), I used a series of Principal Component Analysis (PCA) in the program SPSS 21.0 (2012) to reduce the number of variables. The PCA included four correlated measures of behavioral data (rate of dewlap extensions, rate of pushup displays, time to eyespot development, and time of first display). Because it was not correlated to the other four behavioral measures, the percentage of time an individual crested (crest) was included in our subsequent analyses on its own. The PCA produced one PC with an eigenvalue greater than one. This PC, called Behavior PC, loaded highly for all four of these behavioral variables (Table 3.1), and described 73% of the variation in the behavioral data. Additionally, because morphological variables were associated with overall body size, I conducted a regression with head length, head width, and mass against SVL. Standardized residuals from each regression were used in subsequent analyses. Dewlap length and

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tail length did not correlate to SVL, and were thus included in the analysis without transformation.

In this analysis, I tested for a linear relationship between the morphological and/or behavioral measurements and rank. Thus I performed a series of linear regressions in R comparing the different ranks to eight variables: SVL, relative head length, relative head width, relative mass, dewlap length, tail length, behavioral PC, and crest. For each ranking system, I performed linear regressions using all combinations of 1-7 variables to determine the combination of variables that maximized R^2, the proportion of variance in ranking explained by behavior and morphology. For this analysis, I used adjusted R^2 values, which correct for the artificial inflation in R^2 caused by increasing the number of variables in a regression. I then compared the best models of each separate ranking system to determine which variables appeared most frequently. The variables that appear in the best models for multiple ranking systems are most likely to be important in determining lizard dominance in the arena trials.

2.2 Study 2: Territory Size and Quality in the Wild

2.2.1 Behavioral Observations

To determine the territory sizes and behavioral profiles of a natural population of male green anoles, I established a plot of roughly 50 m x 50 m in Palmetto State Park, Gonzales, Texas in a seasonal swamp dominated mainly by dwarf palmettos (*Sabal minor*). Between May 29 and June 12, 2013, I caught 73 adult green anoles (33 males, 40 females) in the plot. Upon capture, each lizard had a bead tag with a unique color sewn into the muscles at the base of its tail using surgical wire (Fisher and Muth 1989). I then measured the SVL, mass, head length, head width, tail length, and dewlap length of all captured males as described above, and released the lizard at its site of capture. Females were bead-tagged and released at the site of

capture, without measuring morphological traits. After tagging an individual, I waited a minimum of 24 h before conducting behavioral observations on that lizard. Over the course of the three weeks, I performed 5-30 min focal behavioral observations (average = 24.2 min) on the tagged males between the hours of 900 and 1700. During focal observations, I particularly focused on dewlap extensions and pushup displays, as well as any interactions with other lizards. I waited a minimum of 2 h after watching a lizard before performing another observation on that individual, up to a maximum of 3 h of observation per lizard. At the end of the data collection, all lizards with a combined total of at least 2 h of observation and those that were observed at least four times were included in the data analysis.

2.2.2 Territory Measurements

To estimate the territory location of each lizard (including both males and females), I established reference points throughout the study plot. Each time a tagged lizard was sighted, its location was determined by measuring (to the nearest cm) the distance from the lizard's perch location to the closest reference point using measuring tape. I then measured the angle from north between the two points to the nearest degree using a compass. When I performed a behavioral observation of a lizard, I measured up to three perches utilized by the lizard during the observation. Males included in the analysis had a minimum of nine locations recorded (min = 9, max = 51, average = 24.9). Because one goal of this study was to estimate the number of females interacting with each male rather than to accurately measure female territory sizes, we used all females with at least one observation in analyses of female overlap.

I then calculated each male's territory size by first converting the location data into Cartesian (x,y) coordinates using basic trigonometry principles. I used these coordinates in the adehabitatHR package in R (Calenge 2006) to compute the minimum convex polygon (MCP), or total area, for each lizard. To further analyze male territory dynamics, I then designed code in R to calculate exclusive male

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territory size using the vertices of the minimum convex polygon obtained in the previous analysis (exclusive area; code provided in Appendix A).

I also calculated the number of females living within each male's home range as a measure of territory quality. To achieve this, I first created polygons that represented the locations of each female territory. I performed MCP analysis on all females with more than five territory observations (the minimum needed for MCP estimation) to identify the vertices of polygons encompassing 95% of the territory observations. If a female had three or four observations, I used the polygon created by these points as its territory estimate. For those females with only one or two observations, I added ffi0.05 to the observed point to generate enough points to create a polygon. I then created a code in R to count the number of female polygons that overlapped each male territory estimate (Appendix B).

2.2.3 Data Analysis

To identify the variables most predictive of territory size and female overlap in male green anoles, I performed a series of linear regressions with territory size or female overlap as the dependent variable and combinations of morphological and behavioral measures as independent variables. I first determined the relative sizes of mass, head length, and head height using regressions against SVL, as described above. Using the same linear regression procedure described above, I then determined the relationship between two measures of territory size (total area and exclusive area) and seven variables: relative head width, relative head length, relative mass, SVL, tail length, dewlap length, and overall display rate (the total combined rate of dewlap extensions and pushups). Finally, I used a Pearson correlation test to determine the relationship between the size of a male's territory and the number of females that occurred within it. All analyses were performed using R.

2.3 Study 3: Enclosure Study with Arena Trial Tournament

2.3.1 Collecting and Housing Lizards

To determine the relationship between an individual's social rank and its territory size, I conducted two enclosure studies with 10 males in each study. Thirty adult green anoles (20 males, 10 females) were caught on the campus of Trinity University in June 2013. For approximately three weeks, these lizards were housed at Trinity University as described above. Arena trials began after the lizards had been in captivity for approximately one week.

2.3.2 Arena Trials

For each enclosure study, 10 male anoles were run through a tournament of arena trials, as described above. Again, these tournaments were designed so that each lizard i either played lizard j or it played another individual who played lizard j. The same 8 ranks were calculated in MATLAB and R based on the tournament's resulting win-loss-tie information. Additionally, we repeated the data analysis from the first arena trial tournament for each arena trial tournament in this study to validate the results of the first study. However, due to the small sample size of 10 individuals in each round, we limited the maximum number of predictive variables to three in the linear regression analyses.

2.3.3 Enclosure

After the completion of the arena trials, lizards were placed in an artificial enclosure and allowed to establish territories to permit a comparison between an individual's social rank and its territory size. The territory enclosure was a 15 x15 x 5 ft

structure built using 1' PVC pipe (Figure 3.1a), where all PVC joints of the frame were glued to add additional stability. The structure was enclosed using translucent screen door mesh (Costdot Mesh Fiberglass, Milpitas, California USA) along the perimeter and opaque screed door mesh (Phifer Black Pet Screen, Tuscaloosa, Alabama USA) on the roof. Seems were either sewn together with fishing line or stapled, and were reinforced on both the interior and exterior using duct tape. To prevent lizards from escaping under the mesh along the perimeter, bricks were stacked along the bottom of the mesh and covered with topsoil and mulch. Twenty-two potted plants of varying size and species were placed in clusters around the interior of the enclosure to provide habitat (Figure 3.1b). A brick structure approximately 3 x 3 x 0.5 ft was built in the middle of the enclosure to provide lizards with additional shelter and shade (Figure 1b). Ten adult female anoles were introduced to the enclosure to make the social dynamics of the enclosure more natural for the males. No territory data were recorded for the females, and they were not given permanent identification tags. The same females were used for both of the two enclosure trials

For each of the two enclosure studies, the 10 males used in the arena trial tournament were placed in the enclosure. Immediately before introducing the lizards to the enclosure, each male was given a unique bead tag as described above. I then released all 10 males and 10 females in the center of the enclosure simultaneously. Beginning the next day, I collected male territory measurements three times a day (900, 1300, and 1800) by recording each lizard's position on a map of the enclosure, drawn to scale. Data were collected for one week. Lizard territories were generally in flux over the first two days, thus I only used the last five days of data to calculate territory size. In the enclosure, lizards were misted daily and fed roughly two crickets every other day.

We used the five days of territory measurements to calculate each lizard's total and exclusive area as described above. To determine the relationship between the two measures of territory size in the enclosure and the ranks calculated in the arena

trial tournament, we performed a series of Spearman correlation tests comparing each of the 8 ranks to total area and exclusive area. Due to the small sample size, Spearman correlation tests were more appropriate here because they do not assume a linear relationship between variables as Pearson correlations do. I also performed linear regressions comparing total and exclusive territory size to the same seven variables used in Study 2 for each set of enclosure territories to validate the results of the second study. As above, I limited the maximum number of predictive variables to three.

3 Results

3.1 Study 1: Arena Trial Tournament

All eight ranking systems were predicted by at least one of the two measures of behavior (behavior PC or crest; Table 3.2). In fact, the most successful trait combinations of all eight ranks included the behavior PC variable and six ranks included cresting behavior. Additionally, seven of the systems were predicted by some measure of head size, either relative head length or relative head width (Table 3.2). No other trait was predictive of more than half of the ranks, and body size (either relative mass or SVL) was not significant in any ranking system. Thus aggressive behavior and head size are the traits that are most closely related to aggressive ability in this tournament of anoles.

3.2 Study 2: Territory Size and Quality in the Wild

There was a high degree of territory overlap in male *Anolis carolinensis* territories (n = 24), with 79.2% of males overlapping at least three other male territories, 33.3% overlapping at least five neighboring territories, and 8.33% overlapping at least seven

other territories (Figure 3.2). All males overlapped at least one female (min = 1, max = 10, average = 5.2). Total male territory size was correlated with the number of female territories overlapped (r = 0.69, p = 0.00017), however exclusive territory size was not (r = 0.32, p = 0.13). Thus, generally, males with larger overall territories overlapped more female home ranges.

Total male territory size was positively associated with SVL, dewlap length, and relative head length (R^2 = 0.26, p = 0.031, Table 3.3). Exclusive territory size was also predicted by a measure of body size (relative mass) and head size (relative head width), however this result was not significant (R^2 = 0.099, p = 0.13). The number of females overlapped was significantly predicted by relative head length (R^2 = 0.29, p = 0.0038). Therefore in contrast to the results from the arena trial tournament in Study 1, in this population, body size, head size, and dewlap length (but not aggressive behavior) were the traits most closely related to territory size, and head size was most related to territory quality (i.e., female overlap).

3.3 Study 3: Enclosure Study with Arena Trial Tournament

The territories of males in both rounds of the enclosure study were mapped using minimum convex polygons (MCP; Rose 1982; Round 1: Figure 3.3A, Round 2: Figure 3.3B). When territory estimates were compared to the results of the arena trial tournaments, there was no clear relationship between an individual's rank and its territory size (Table 3.4). There were no significant relationships between any of the ranking systems and either total or exclusive territory size in Round 1(all p ¿ 0.05), and in Round 2 the only significant relationship was between the Oracle rank and exclusive territory size (r = -0.71, p = 0.023). Round 2 also contained two marginally significant correlations between rank and exclusive territory size (Win Percent: r = -0.56, p = 0.090; Massey: r = -0.56, p = 0.093). Thus in Round 2, lizards with larger

Oracle, Win Percent, and Massey ranks (i.e., less dominant lizards) had smaller exclusive territories. Although more dominant lizards did not necessarily have larger territories (as was originally predicted), they did exclusively control larger areas.

In the linear regressions using the Round 1 arena trial tournament results, the behavior PC, crest, and relative mass terms were predictive of the highest number of ranks, and the regressions were significant for all eight ranks (all p ¡ 0.01, Table 3.5). Conversely, in the second round, SVL and relative mass were the most predictive traits, although six of the regressions were not significant. The two ranks with significant results (PageRank: $p = 0.041$, Keener: $p = 0.040$) were best predicted by SVL, dewlap length, and head length.

The final linear regression analysis examined the relationship between animal's territory sizes established in the enclosure and various morphological and behavioral traits (Table 3.5). In the first round, total territory size was significantly predicted by relative mass, SVL, and total display rate ($p = 0.0008$). Exclusive territory size was most closely associated with tail length, dewlap length, and total display rate in this round, however this regression was not significant ($p = 0.13$). In Round 2, the best regression for total territory size included the relative mass and dewlap length terms ($p = 0.0032$; Table 3.5), while those for exclusive territory size included SVL ($p = 0.0008$; Table 3.5).

Finally, I compared the body sizes of the males in both rounds of the enclosure study (Study 3) to those in the population in Study 1 (arena trial, Table 3.6). The range of SVL observed in Round 1 (Study 3) of the enclosure studies and relative masses observed in Study 1 were lower than those in either of the two other populations. Additionally, the standard deviations of both SVL and relative mass in the Study 1 males were lower than those in Round 1 and Round 2 (Study 3).

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4 Discussion

The overall goal of this study was to determine the relationship between rank in a dominance hierarchy and territoriality. I originally hypothesized that rank and territorial success to be complementary, thus lizards of higher rank would have larger total territory sizes, larger exclusive areas of territory, and territories that overlapped more females. I also anticipated that the morphological traits that were related to success in territoriality would predict all three measures of social status (rank, territory size, and female overlap), and that all three measures would be related to body size. I found that head length, a visual signal associated with bite force (Vahooydonck et al. 2005), was the only trait to be predictive of territory size, female overlap, and social rank. Other traits, such as body size and dewlap length, were predictive of both territory size and rank, however rank and territory size were not correlated, indicating that these relationships are maintained through different mechanisms.

4.1 Predictors of social rank

This study suggests that the traits most closely related to social rank are body size, aggressive behavior, head size, and dewlap size. The notion that larger males often win aggressive interactions is well documented in anoles (Stamps 1984, Tokarz 1985, Losos 2009), however these results indicate that the system is more nuanced. Although snout-vent length (SVL) and body mass were highly predictive of rank in both enclosure studies, neither was included in the best regressions in the first arena trial study. I suggest that body size only appeared in the two enclosure populations due to differences in variance in SVL and mass observed in each population. In the first round of the enclosure study, when the standard deviation in SVL was 33% higher than it was in the first arena trial population, SVL was predictive of rank. Similarly, in the second round of the enclosure study, the variance in relative mass was four times higher than it was in first arena trial population, and relative mass

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was predictive of rank. This suggests that anoles first consider their opponents based on body size. If the opponents are roughly the same size, as was observed in the first arena trial population, the males then use aggressive behavior as a primary criteria for determining dominance. Indeed, aggressive behavior is a logical next choice, for male green anoles that form eyespots more quickly (Larson and Summers 2001) and perform more displays are more likely to attack. If, however, there is a significant disparity between competitor's body sizes, the larger individual will win. This has been recorded in individual arena trial results, for many studies have found that significantly larger males often win arena trials (e.g., Tokarz 1985). However, the effect of body size discrepancies on dominance behavior has never been recorded at the population level.

This transition from body size to aggressive behavior as the primary determinant of dominance could result in interesting patterns in anole populations over the course of the breeding season. At the beginning of the breeding season, the population consists of adults and young males (i.e., last year's juveniles), thus there will be many different body sizes observed in the population. However, younger lizards grow more quickly than their older counterparts (Shine and Charnov 1992), so this variation will decrease across the season. Therefore we would expect social rank at the beginning of the season to be determined by body size, while at the end of the season it is more likely predicted by aggressive behavior. This potential shift in the criteria of dominance within the population is similar to the age-specific forced polymorphism proposed by Lailvaux et al. (2004). They observed two different morphs among adult male green anoles (lightweight and heavyweight) that select for different traits within two distinct ranges of body size. They did not discuss how these light- and heavyweight morphs interact, or their effect on the dominance structure of the population as a whole. Further studies of temporal variation in dominance behavior of anoles could reveal more about the development and maintenance of these morphs and their function within the population.

Another trait to consistently reflect social rank in the arena trial experiments was head size. Lizards with wider, longer, and/or taller heads are able to generate more force when they bite in agonistic interactions (Herrel et al. 2001, Huyghe et al 2005). As such, both bite force (Perry et al. 2004, Henningsen and Irschick 2012) and head size (Perry et al. 2004) are often identified as important predictors of dominance in anoles. Anole fights consist of "locking jaws," where the two individuals bite each other's jaws and attempt to throw their opponents off their perch. Biting harder will cause more damage to the opponent, increasing the individual's chance of winning the altercation (Husak et al. 2006). In this study, two different measures of head size were identified as important, relative head length and relative head width. Head width is often cited as being the important biomechanical driver of bite force in anoles (Vahooydonck et al. 2005), for a wider head increases the force the lizard can generate as it clamps down (Herrel et al. 2001). However, in fights anoles align their bodies horizontally, thus they are only able to see the length of their opponent's head rather than its width. Head length and width are highly correlated in the present study (r = 0.625, p = 0.0056), thus head length may be the visual signal associated with bite force while head width is the actual mechanism that drives its role in fighting ability.

The final trait related to rank in the arena trial tournaments was dewlap size. Dewlaps are an important visual signal in anoles and are part of a wide variety of signals to competitors, potential mates, and predators. Yet the function of dewlap displays in agonistic interactions is still largely unknown. Studies have found that dewlap size positively correlates to bite force in some *Anolis* species (Hennignsen and Irschick 2012); however these results are not consistent among all species (Vanhooydonck et al. 2005). Additionally, experimentally reducing dewlap size or extension rate does not change the outcomes of paired agonistic interactions (Tokarz et al. 2003, Hennignsen and Irschick 2012). In the present study, dewlap length was only significant in one round (Round 2) of the enclosure study. This implies that it

either is only relevant to dominance interactions in specific situations, or it appeared by chance. The Round 2 animals did not have a greater range or standard deviation in dewlap sizes than the other two populations, indicating that the relationship between dewlap size and rank in this population was not driven by increased variation of the trait as was observed with body size.

4.2 Predictors of Territory Size

In this study, I measured three different metrics of territorial success: total territory size, exclusive territory size, and the number of female territories overlapped. I expected these measures to provide different information about territory acquisition and quality in anoles. Total territory size corresponds to the size of the area defended by the individual, and thus is the traditional definition of territory in anoles (Stamps 1977). However, I reasoned that this may not be the best metric of social status in anoles, as there may be variations in territory quality or individuals' defensive abilities that convey fitness benefits as well. Thus I also calculated exclusive territory size, or the area that an individual successfully protected from conspecifics. I hypothesized that this measure would be more closely related to rank than total territory size, for it would highlight animals with more successful territorial defense. Additionally, I measured the number of female territories overlapped by each male territory as a measure of male territory quality, for access to females directly relates to reproductive success in anoles (Ruby 1984).

In line with my predictions, total territory size was predicted by a similar set of traits as social rank, for body size, head length, and dewlap length were related to territory size in both Study 2 and Study 3. However, female overlap was only predicted by head length. Therefore although total territory size and female overlap are closely related (above results, Johnson et al. 2010), the discrepancy between predictive variables indicates that they are not equivalent measures of territorial

success. Exclusive territory size was only successfully predicted by the measured traits in Round 2 of the enclosure study, where it was related to body size.

Body size was the variable most consistently related to both total and exclusive territory size. Although the direct correlation between body size and territory size has been observed in interspecific comparisons between *Anolis* species (Losos 2009) and in other taxa including birds (Butchart et al. 1999) and fish (Keeley 2000), it has mixed support when viewed within an anole species (Schoener and Schoener 1982). Larger individuals will have greater energetic demands than smaller individuals, so this relationship may simply be due to the increased food supply offered by a more expansive territory. However, as male territory size in anoles is almost always larger than required for caloric needs (Andrews 1971, Schoener and Schoener 1982), this explanation alone is unlikely. Another potential justification relates anoles' size to their age. Iguanids experience indeterminate growth, so a lizard's size is closely related to its age (Shine and Charnov 1992). Larger individuals in anole populations will be older than smaller individuals, indicating that they have had more time to accumulate territory or have more experience establishing and defending territories than their younger conspecifics. This has been observed in the coot *Fulica atra*, where individuals that are older than their neighbors hold larger territories (Cavé et al. 1989).

Although the relationships between body size and both energetic demands and age are plausible explanations for the direct connection between body size and territory size, the most intuitive explanation is that larger lizards are more dominant and thus are able to establish and defend larger territories. Indeed, in the arena trial experiments, size was an important component of social dominance. However, the results of Study 3 indicate that social rank and total territory size are not necessarily related. This could mean one of three things. It could be that interactions between conspecifics are not the major factors limiting territory expansions in the green anole. There is evidence to indicate food availability affects optimal territory size and shape in other taxa, for animals will often decrease their territory size in response to

increased food abundance (Adams 2001). However, other studies suggest that this may in fact be an indirect consequence of the increased conspecific overlap caused by the resource boom (Myers et al. 1979). Another possible explanation for this disparity between total territory size and social rank is that more dominant animals may not necessarily seek larger territories. As I have previously discussed, the number of females overlapped is the most useful predictor of territory quality in anoles. Female territory size and location are primarily dependent on food availability and nesting sites (Jenssen et al. 2001), so females are likely to clump around resource-rich locations. Therefore it is conceivable that males that hold such territories will have high densities of females in a relatively small area, while males that do not hold resource rich areas expand their territories to overlap more females. Finally, the lack of correlation between rank and territory size could be an artifact of the study itself. The lizards may have experienced stress from their captivity that prevented them from behaving normally, or they may have experienced constraints in space, density, habitat type, solar radiation, etc. that caused them to not establish territories in an optimal manner. Although I took care to set up this experiment in the most natural manner possible, behavioral results of captive animals must always be interpreted cautiously.

While the Study 3 results suggested that social rank was not correlated to total territory size, they did potentially identify a weak relationship between exclusive territory size and rank. All three ranks with significant or marginally significant correlation values indicated that more dominant animals have higher exclusive territories, following the pattern I originally predicted. This relationship, in addition to the result that both exclusive territory size and rank were predicted by body size, suggest that larger, more dominant animals are better able to defend an exclusive territory from intruders. Frequency of aggressive behavior observed in laboratory arena trials are closely related to the amount of assertion displays performed in the wild (Perry et al. 2004), thus the aggressive males identified in the ranking analysis likely perform more warning displays during territory defense and are more likely to

defeat challengers in agonistic interactions. While this makes intuitive sense, it was only observed in one of the three study populations. Thus more study is needed to confirm the nature of this relationship. Additionally, exclusive territory size was not related to the number of females overlapped (i.e., territory quality) in the field study, so this successful defense did not guarantee increased territory quality in this study.

Both dewlap size and head length were the other traits related to territory size in this study. In the frequent assertion displays performed by green anoles in territory defense, dewlap displays are an important mechanism for attracting conspecifics' attention. The bright red dewlap contrasts highly against the greens and browns of their forested habitat and thus makes it easier to see the displaying anole from farther away. Since larger dewlaps will be easier to see from a distance, perhaps they decrease the intruder pressure experienced by the individual and result in an increased territory size. Indeed, both lark bunting (*Calamospiza melanocorys*) and collared flycatcher (*Ficedula albicollis*) individuals with larger colored patches on their wings have fewer territorial intruders than birds with smaller ornaments (Chaine and Lyon 2008, Hegyi et al. 2008). This indicates that ornamentation does in fact play a role in maintaining territory size in other species. Similarly, head length is also a trait that can be seen from a distance and from a wide variety of angles. As previously discussed, I believe that head length is the visual signal associated with bite force, so individuals with larger heads are theoretically less likely to be challenged by conspecifics. This would allow them to expand their territories, resulting in larger total territory sizes.

Finally, female overlap, the third metric of territorial success, was only predicted by head length. Head length was an important predictor of dominance in populations with both high and low variance in body size, thus this study suggests that it is one of the best predictors of dominance. The observed relationship between head size and female overlap (the most important measure of territory quality in anoles) indicates that more dominant animals do indeed have higher quality territory, as would be expected. An alternative explanation could be that females preferentially choose to

live in territories held by males with larger heads due to their presumed elevated fighting ability. However, female mate choice is strongly disputed in lizards, with most studies indicating that food availability is more important to female territory locations than the males that reside there (reviewed in Tokarz (1995)).

4.3 Summary

Overall, the results of this study suggest that dominance trials of green anoles in the lab do indeed reflect aspects of the natural interactions of this territorial species, and that there is a relationship between rank in a linear hierarchy and territoriality. I found that social rank, territory size, and territory quality were all predicted by the same trait (head size), and that rank and exclusive territory size were weakly correlated. Thus more dominant individuals do indeed reside on higher quality territories and more successfully defend their home ranges from intruders. The complimentary results observed between these lab and field studies suggest that both venues provide valuable information about natural dominance interactions in anoles. However, the complex nature of most of the relationships observed imply that multivariate analyses are needed when investigating dominance in the wild, for many behaviors are context-specific or only make sense when viewed in a larger ecological context. Additionally, the sometimes contradictory results obtained from different populations within this study further emphasize the necessity for replication in animal behavior experiments to completely understand the nuances within these complex social arenas.

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Table 3.1: Component matrix for the principle component analysis performed on four correlated behavioral variables measured in a tournament of green anoles (*Anolis carolinensis*).

Variable	Loading Coefficient
Dewlaps per min	0.911
Pushups per min	0.907
Time to first display	-0.848
Time to eyespot development	-0.754
Eigenvalue	2.94
% Variation Explained	73.5

Table 3.2: Morphological and behavioral traits that best predict rank in a tournament of paired aggressive interactions between male green anoles (*Anolis carolinensis*).

Ranking Systems	Variable								Adjusted R^2
	SVL	Relative Mass	Tail Length	Dewlap Length	Relative Head Length	Relative Head Width	Behavior PC	Crest	
Win %					●		●	●	0.724***
Colley					●		●	●	0.753***
Massey			●	●		●	●		0.490*
Bradley -Terry			●	●		●	●		0.495*
PageRank			●	●	●		●	●	0.655**
Oracle					●		●	●	0.796***
Biased Voter				●	●		●	●	0.563**
Keener		●					●	●	0.411*
***Indicates $p < 0.001$, ** indicates $p < 0.01$, and * indicates $p < 0.05$.									

Table 3.3: Morphological and behavioral traits that best predicted three territory metrics of 24 adult male green anoles (*Anolis carolinensis*).

Territory Metric	Variable							Adjusted R^2
	SVL	Relative Mass	Dewlap Length	Tail Length	Relative Head Length	Relative Head Width	Total Display Rate	
Total	●		●		●			0.255*
Exclusive		●				●		0.099
Female Overlap					●			0.291*
***Indicates p < 0.001, ** indicates p < 0.01, and * indicates p < 0.05.								

Table 3.4: Spearman correlation values comparing the rank and territory sizes of two replicate populations of green anoles (*Anolis carolinensis*). Each group was run through a series of paired aggressive interactions and ranked using eight ranking algorithms. These anoles were then placed in a 15 x 15 x 5ft enclosure, and the territories they established over the next week were measured. Total area represents the overall size of the individual's home range, while exclusive area represents the amount of territory an individual occupied that did not overlap any conspecifics' territories.

Ranking Systems	Spearman Correlation Values			
	Round 1		Round 2	
	Total	Exclusive	Total	Exclusive
Win %	-0.567	-0.204	0.356	-0.563†
Colley	-0.236	-0.214	0.345	-0.541
Massey	-0.297	-0.202	0.248	-0.559†
Bradley-Terry	-0.188	-0.092	0.430	-0.413
PageRank	-0.394	-0.166	0.261	-0.255
Oracle	-0.200	-0.117	0.297	-0.705*
Biased Voter	-0.200	-0.166	0.345	-0.541
Keener	-0.406	-0.252	0.224	0.401
* Indicates $p < 0.05$, and † indicates $p < 0.1$.				

Table 3.5: The morphological and behavioral traits that best predicted both rank and territory size of two replicate populations (Round 1: ●, Round 2: □) of 10 adult male green anoles (*Anolis carolinensis*). The eight ranks were calculated using the win-loss-tie results of a tournament of paired interactions, and the territory sizes measured after placing the anoles into a 15 x 15 x 5 ft for one week. In the Ranking System analysis (Study 1), the Behavior term refers to the behavior PC, while in the Territory Metric analysis (Study 2) it is the overall display rate (the total rate of dewlap and pushup displays).

| | Variable | | | | | | | | Adjusted R^2 | |
	SVL	Relative Mass	Tail Length	Dewlap Length	Relative Head Length	Relative Head Width	Behavior	Crest	Round 1 (●)	Round 2 (□)
Ranking System										
Win %	□	●,□	□				●	●	0.844**	0.528
Colley	□	●,□	□				●	●	0.931**	0.473
Massey	□	●,□		□			●	●	0.870**	0.399
Bradley-Terry		●					●,□	●	0.941***	0.452
PageRank	●,□		●	□			●		0.832**	0.518*
Oracle	□	□	□				●	●	0.861***	0.534
Biased Voter	□	●,□	□				●	●	0.971***	0.504
Keener	□	●		●,□	□		●		0.857**	0.590*
Territory Metric										
Total	●	●,□		□			●	---	0.892***	0.750**
Exclusive	□		●	●			●	---	0.381	0.743***

***Indicates p < 0.001, ** indicates p < 0.01, and * indicates p < 0.05.

Table 3.6: A comparison between the body sizes of the populations of adult male green anoles (*Anolis carolinensis*) used in Study 1 and Study 3. Recall that relative mass measures are the residuals of a regression between mass and SVL, and thus do not have units. By construction, the average relative mass for each population is equal to zero.

		Study 1	Study 3	
			Round 1	Round 2
SVL	Average (mm)	62.6	65.6	65.1
	Range (mm)	13.7	10.0	14.5
	Standard Deviation	3.50	3.47	4.18
Relative Mass	Range	2.04	4.41	6.30
	Standard Deviation	0.54	1.26	2.07

6 Figure Legends

Figure 3.1: I constructed an artificial habitat enclosure using PVC pipe and mesh (**A**). Twenty *Anolis carolinensis* at a time (10 males, 10 females) were placed in the enclosure and allowed to establish territories. A brick structure and plants were included in the enclosure to provide habitat structure (**B**).

Figure 3.2: The territories of 24 male *Anolis carolinensis* living in Palmetto State Park, Gonzales, Texas were mapped using minimum convex polygons between May 29 and June 12, 2013. Each polygon represents the territory of a different lizard.

Figure 3.3: Two populations of 10 male green anoles (*Anolis carolinensis*) were placed in a 15 x 15 x 5 ft enclosure and their territories were mapped using minimum convex polygon estimates. Each polygon represents the territory of a different lizard. Panel A represents the male territories from the first round of the enclosure study, while Panel B represents those from the second round.

Figure 3.1

A

B

Figure 3.2

Figure 3.3

7

A

B
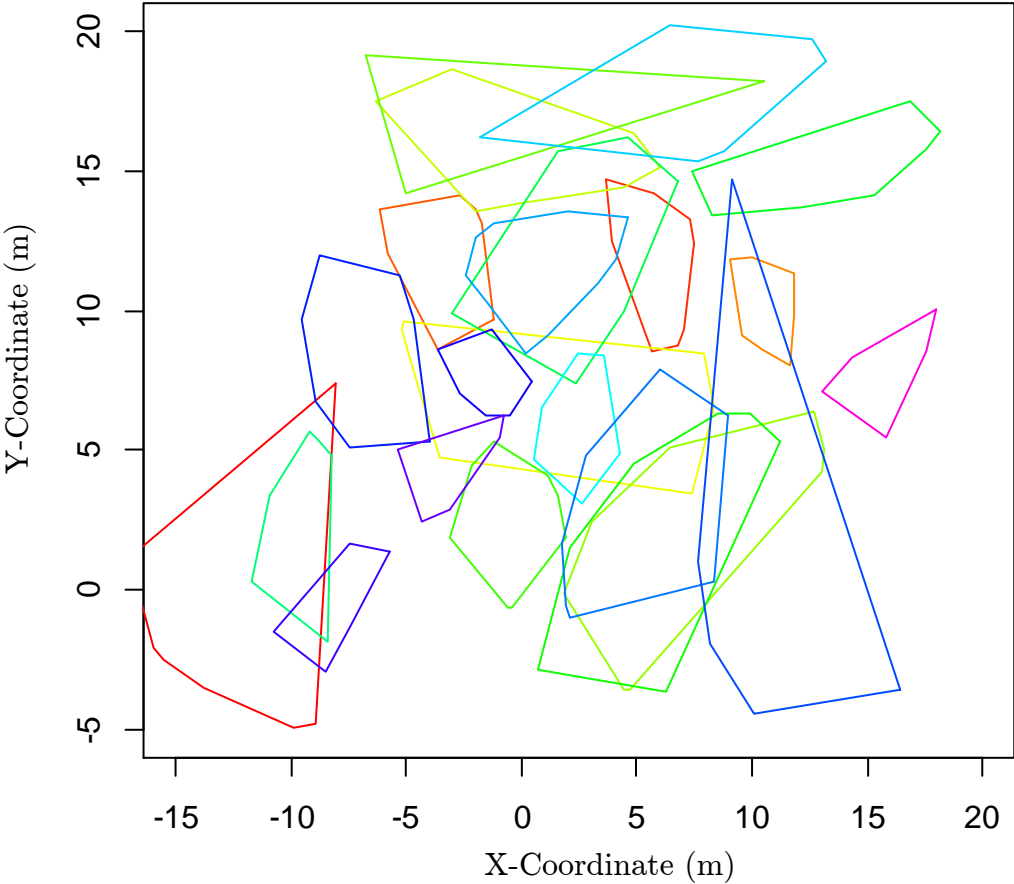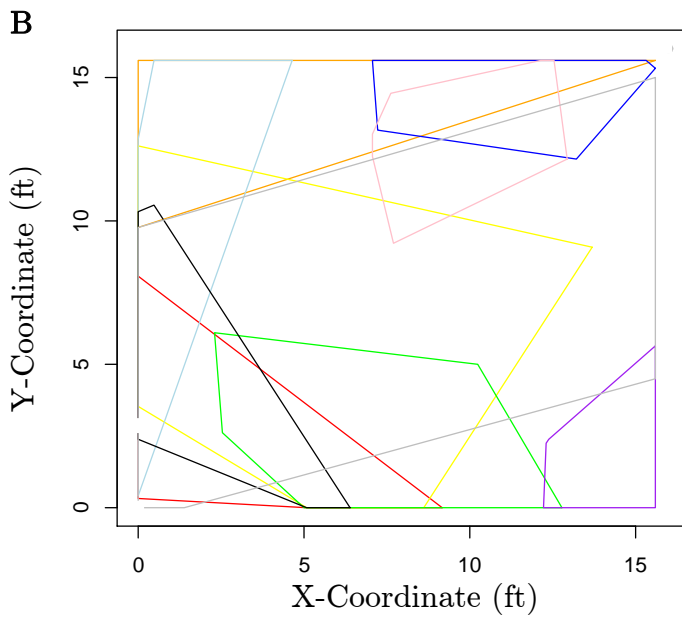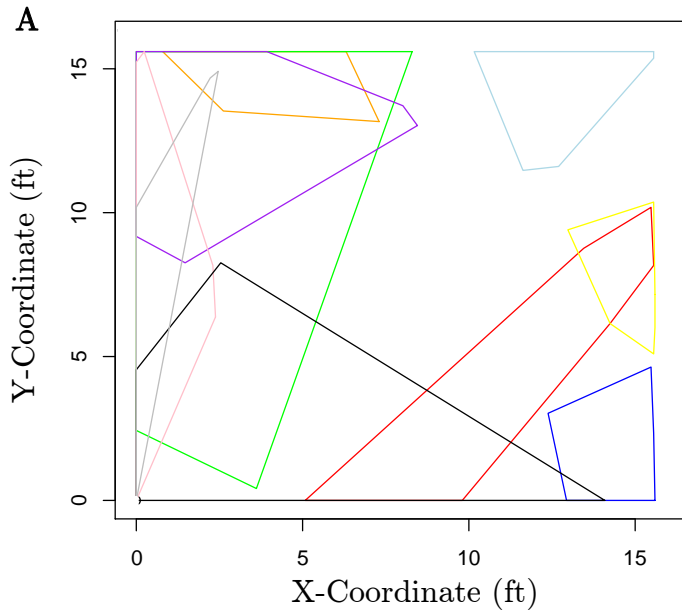
6 Appendix A: Exclusive Area Code

The following code was written in R (version 2.14.1) to calculate the area each male occupied exclusively, and to generate territory graphics (Figures 3.2 and 3.3). Initial input files were labeled "M1xx.txt", and contained the XY coordinates of all sightings of individual with the two-digit ID number xx. The file was formatted:

Closest Reference Point | ID Number | X coordinate | Y coordinate

Note that the data in the first two columns are not used in this code.

This code uses the adehabitatHR (Calenge 2006), plyr (Wickham 2011), splancs (Rowlingson and Diggle 2013), and gpclib (Peng et al. 2012) packages. Each of the functions I created and their inputs are described below. Note that I distinguish between the Main Functions, which generate the output I then used in my analysis, and the Accessory Functions, which perform functions that allow the Main Functions to work. The "GraphingPolygons" function generated Figures 3.2 and 3.3, and the output of the "I_E_Formula" function was used as the exclusive territory measures in the above analysis. This "I_E_Formula" function is based on the inclusion-exclusion formula from probabilistic theory, which is used to compute the union of multiple overlapping sets.

There are three pieces of user-defined information that must be changed before the code will work for a new data set: the highest ID number used in the analysis (m), the path to the directory in use (Folder), and the desired name of the output file generated by the "I_E_Formula" function (FinalFile).

*Remark: The "Mine" function is modified from the "mcp" function in the adehabitatHR package. Because I truncated the code for the "mcp" function to only include the attributes I needed in this study, the "Mine" function generates an output file of the correct MCP vertices, however it no longer functions correctly as the "mcp" function. Thus an error appears when the function is used in isolation. I

emphasize that this error does not affect the portion of the output used in this study, and does not detract from the validity of these results.

```
##===================================================================##
##===================================================================##
##=========            Calculating Exclusive Area          =========##
##===================================================================##
##===================================================================##
##== Goal: To use the polygon coordinates given by a MCP output to calculate the
##==       area of a lizard's territory that the lizard exclusively inhabits, as well
##==       as to graphically depict the lizard's territory.
##==
##== Main Functions
##== Polygon_Coords(): Outputs a text file "PolygonMxx.txt" for each individual that
##==            contains the vertices of the minimum convex polygon
##==            representing that lizard's territory
##== GraphingPolygons(): Graphs MCP polygon of all individuals in one plot; note that
##==            code contains multiple options to color the polygons; also
##==            note that the plot size has to be defined manually through
##==            the x0 and y0 variables
##== I_E_Formula(): Returns a matrix containing the exclusive territory measures of
##==            each individual
##==
##== Accessory Functions
##== Mine(table,name): Function I created by modifying the MCP function from the
##==      adehabitatHR package; inputs are the "M1xx.txt" file and desired output file
##==      name. The output file contains the coordinates of the vertices of the
##==      MCP representing the individual's territory
##== ListOfPolygons(): Generates a list of all "PolygonMxx.txt" files in directory
##== Polygon(n): Gives the polygon for individual (n) in a format the gpclib package can
##==      use to calculate areas
##== InPolygonSet(n): Determines if the polygon file of individual (n) is in the directory
##== NIntersects(n): Calculates the number of territories the territory of individual (n)
##==          overlaps
##== TwoU2(n): Calculates the area of all intersections of lizard (n) and 1 other lizard
##== ThreeU2(n): Calculates the area of all intersections of lizard (n) and 2 others
##== FourU2(n): Calculates the area of all intersections of lizard (n) and 3 others
##== FiveU2(n): Calculates the area of all intersections of lizard (n) and 4 others
##==   (No lizards had 5 intersections or more)
##===================================================================##
##== Created by: Jordan Bush                        Date: 09/05/2013  ==##
##===================================================================##
##===================================================================##

library(adehabitatHR)
library(plyr)
library(splancs)
library(gpclib)
```

```
### Things for user to change:
        m=33 #Highest ID number, re-index to make them all in order
        Folder = "C:\\Users\\Jordan\\Documents\\Research 2013\\Field Work\\Territory R Stuff Final"
        FinalFile = "C:\\Users\\Jordan\\Documents\\Research 2013\\Field Work\\Territory R Stuff
FINAL\\Excl_Territories.txt"
###

Location = paste(c(Folder, "\\"), collapse="")

Mine <- function (xy, percent = 95, unin = c("m", "km"), unout = c("ha",
 "km2", "m2"), name)
{
 if (!inherits(xy, "SpatialPoints"))
   stop("xy should be of class SpatialPoints")
 if (ncol(coordinates(xy)) > 2)
   stop("xy should be defined in two dimensions")
 pfs <- proj4string(xy)
 if (length(percent) > 1)
   stop("only one value is required for percent")
 if (percent > 100) {
   warning("The MCP is estimated using all relocations (percent>100)")
   percent <- 100
 }
 unin <- match.arg(unin)
 unout <- match.arg(unout)
 if (inherits(xy, "SpatialPointsDataFrame")) {
  if (ncol(xy) != 1) {
    warning("xy should contain only one column (the id of the animals), id ignored")
    id <- factor(rep("a", nrow(as.data.frame(xy))))
  }
  else {
    id <- as.data.frame(xy)[, 1]
  }
 }
 else {
  id <- factor(rep("a", nrow(as.data.frame(xy))))
 }
 if (percent > 100) {
   warning("The MCP is estimated using all relocations (percent>100)")
   percent <- 100
 }
 if (min(table(id)) < 5)
   stop("At least 5 relocations are required to fit an home range")
 id <- factor(id)
 xy <- as.data.frame(coordinates(xy))
 r <- split(xy, id)
 est.cdg <- function(xy) apply(xy, 2, mean)
 cdg <- lapply(r, est.cdg)
 levid <- levels(id)
 res <- SpatialPolygons(lapply(1:length(r), function(i) {
  k <- levid[i]
  df.t <- r[[levid[i]]]
  cdg.t <- cdg[[levid[i]]]
  dist.cdg <- function(xyt) {
   d <- sqrt((((xyt[1] - cdg.t[1])^2) + ((xyt[2] - cdg.t[2])^2))
   return(d)
  }
  di <- apply(df.t, 1, dist.cdg)
```

```r
    key <- c(1:length(di))
    acons <- key[di <= quantile(di, percent/100)]
    xy.t <- df.t[acons, ]
    coords.t <- chull(xy.t[, 1], xy.t[, 2])
    xy.bord <- xy.t[coords.t, ]
    xy.bord <- rbind(xy.bord[nrow(xy.bord), ], xy.bord)
          #print(xy.bord)
          write.table(xy.bord, name, sep="\t")
    #cat("DONE\n")
          #so <- Polygons(list(Polygon(as.matrix(xy.bord))), k)
    #return(xy.bord)
  })) }


ListOfLizards<-function()
{
        LizardList = c()
        FileList = list.files(Folder)
        for(i in 0:m){
                if(i < 10) Name = paste(c("M10", i, ".txt"), collapse="")
                if (i >= 10) Name = paste(c("M1", i, ".txt"), collapse="")
                for(j in 1:length(FileList)){
                        File = as.character(FileList[j])
                        if(File == Name) LizardList = c(LizardList, Name)}}
        return(LizardList)
}

Polygon_Coords<-function()
{
        dataTables = c()
        for(i in 0:m){
                if(i < 10) Name = paste(c("M10", i, ".txt"), collapse="")
                if (i >= 10) Name = paste(c("M1", i, ".txt"), collapse="")
                dataTables = c(dataTables, Name)}
        for(i in 0:m){
                if(length(grep(as.character(dataTables[i+1]), ListOfLizards())) > 0){
                        Lizard = read.table(as.character(dataTables[i+1]))
                        Lizard = data.frame(Lizard[,3],Lizard[,4])
                        Lizard = SpatialPoints(Lizard)
                        clu = clusthr(Lizard)
                        safef = failwith(NULL, Mine, quiet=TRUE)
                        name = c("Polygon", as.character(dataTables[i+1]))
                        name = paste(name, collapse="")
                        #cat(as.character(dataTables[i+1]), name, "\n")
                        DocName = paste(c(Location,name), collapse="")
                        LizardMCP = safef(Lizard, name=DocName)}}
}

ListOfPolygons<-function()
{
        LizardList = c()
        FileList = list.files(Folder)
        for(i in 0:m){
                if(i < 10) Name = paste(c("PolygonM10", i, ".txt"), collapse="")
                if (i >= 10) Name = paste(c("PolygonM1", i, ".txt"), collapse="")
                for(j in 1:length(FileList)){
                        File = as.character(FileList[j])
                        if(File == Name) LizardList = c(LizardList, Name)}}
        return(LizardList)
}
```

```
GraphingPolygons<-function()
{
        x0=c(20, -15)
        y0=c(20, -5)
        plot(x0,y0)

        dataTables = c()
        for(i in 0:m){
                if(i < 10) Name = paste(c("PolygonM10", i, ".txt"), collapse="")
                if (i >= 10) Name = paste(c("PolygonM1", i, ".txt"), collapse="")
                dataTables = c(dataTables, Name)}

        Colors = as.list(c(rainbow(length(dataTables))))
        #Colors = as.list(c(heat.colors(m)))
        #Colors = as.list(c(terrain.colors(m)))
        #Colors = as.list(c(topo.colors(m)))

        LizardName = c()
        for(i in 0:m){
                if(i < 10) Name = paste(c("M10", i), collapse="")
                if (i >= 10) Name = paste(c("M1", i), collapse="")
                LizardName = c(LizardName, Name)}

        for(i in 1:m){
                if(length(grep(as.character(dataTables[i]), ListOfPolygons())) > 0){
                        print(as.character(dataTables[i]))
                        LizName = as.character(dataTables[i])
                        Data=read.table(as.character(LizName), header=TRUE)
                        x=Data[,1]
                        y=Data[,2]
                        #polygon(x, y, border="black")
                        polygon(x, y, border=as.character(Colors[i]))}}
}


Polygon<-function(n)
{
        if(n < 10) Name = paste(c("PolygonM10", n, ".txt"), collapse="")
        if (n >= 10) Name = paste(c("PolygonM1", n, ".txt"), collapse="")
        if(length(grep(as.character(Name), ListOfPolygons())) > 0){
                Data = read.table(as.character(Name), header=TRUE)
                x = Data[,1]
                y = Data[,2]
                m = cbind(x, y)
                p = as(m, "gpc.poly")}
        else p=0
        return(p)
}

InPolygonSet <- function(n)
{
        if(n < 10) Name = paste(c("PolygonM10", n, ".txt"), collapse="")
        if (n >= 10) Name = paste(c("PolygonM1", n, ".txt"), collapse="")
        if(length(grep(as.character(Name), ListOfPolygons())) > 0) return(TRUE)
        else return(FALSE)
}

NIntersects <-function(n)
{
        IntersectingPolygons = c()
```

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```r
                if(InPolygonSet(n) == TRUE){
                        Poly1 = Polygon(n)
                        for(a in 0:m){
                                if(InPolygonSet(a) == TRUE){
                                        Poly2 = Polygon(a)
                                        if(area.poly(intersect(Poly1, Poly2)) > 0) IntersectingPolygons =
c(IntersectingPolygons, a)}}
                        return(IntersectingPolygons)}
                else return(0)
}


TwoU2 <-function(n)
{
        if(InPolygonSet(n) == TRUE){
                intList = NIntersects(n)
                Sum = 0
                for(b in intList) {if(b != n) Sum = Sum + area.poly(intersect(Polygon(n), Polygon(b))))}
                return(Sum)}
        else return("n Not In Data Set")
}

ThreeU2 <-function(n)
{
        if(InPolygonSet(n) == TRUE){
                intList = NIntersects(n)
                Sum = 0
                #print(intList)
                for(b in intList){
                        for(a in intList){
                                if((a < b) && (a != n) && (b != n)){
                                        Inter = intersect(Polygon(a), Polygon(b))
                                        Sum = Sum + area.poly(intersect(Polygon(n), Inter))}}}
                return(Sum)}
        else return("n Not In Data Set")
}

FourU2 <-function(n)
{
        if(InPolygonSet(n) == TRUE){
                intList = NIntersects(n)
                Sum = 0
                #print(intList)
                for(b in intList){
                        for(a in intList){
                                for(c in intList){
                                        if((a < b) && (b < c) && (a != n) && (b != n) && (c != n))
                                        {
                                                #cat(a, b, c, "\n")
                                                Inter1 = intersect(Polygon(a), Polygon(b))
                                                Inter2 = intersect(Polygon(c), Polygon(n))
                                                Sum = Sum + area.poly(intersect(Inter1, Inter2))
                                        }}}}
                return(Sum)}
        else return("n Not In Data Set")
}

FiveU2 <-function(n)
{
        if(InPolygonSet(n) == TRUE){
```

```
                        intList = NIntersects(n)
                        Sum = 0
                        #print(intList)
                        for(b in intList){
                                for(a in intList){
                                        for(c in intList){
                                                for(d in intList){
                                                        if((a < b) && (b < c) &&(c < d) && (a != n) && (b != n)
&& (c != n) && (d != n)){

                                                                #cat(a, b, c, d, "\n")
                                                                Inter1 = intersect(Polygon(a), Polygon(b))
                                                                Inter2 = intersect(Polygon(c), Polygon(n))
                                                                Inter3 = intersect(Inter1, Polygon(d))
                                                                Sum = Sum + area.poly(intersect(Inter2, Inter3))
                                                        }}}}}
                        return(Sum)}
                else return("n Not In Data Set")
}

I_E_Formula<-function()
{
        m_new = length(ListOfPolygons())
        TotalAreaCol = c()
        ExclAreaCol = c()
        for(n in 0:m){
                if(InPolygonSet(n) == TRUE){
                        Area = area.poly(Polygon(n)) - TwoU2(n) + ThreeU2(n) - FourU2(n) + FiveU2(n)
                        ExclAreaCol = c(ExclAreaCol, round(Area, 3))
                        TotalAreaCol = c(TotalAreaCol, round(area.poly(Polygon(n)), 3))
                        #E_n = paste("E", n, collapse="")
                        #ExclAreaCol = c(ExclAreaCol, E_n)
                        #A_n = paste("A", n, collapse="")
                        #TotalAreaCol = c(TotalAreaCol, A_n)}}
        print(TotalAreaCol)
        print(ExclAreaCol)
        Matrix = matrix(c(TotalAreaCol, ExclAreaCol), ncol=2)
        colnames(Matrix) = c("Total Area", "Exclusive Area")
        rownames(Matrix) = c(ListOfLizards())
        write.table(Matrix,FinalFile, sep="\t")
        return(Matrix)
}
```

8 Appendix B: Female Overlap Code

The following code was written in R (version 2.14.1) to calculate the number of female territories overlapped by each male territory to provide a measure territory quality. Each male and female in the analysis had individual files containing the coordinates of the vertices of the minimum convex polygon representing their territory. Files for male anoles were named "PolygonM1xx.txt", where xx represents the two digit identification number of the animal. Female files were named "PolygonF1xx.txt." These files were formatted in the following manner:

"Vertex Number" | X coordinate | Y coordinate

Note that to generate a polygon, this code requires a minimum of three vertices per individual. As described in the body of this chapter, for lizards with less than three vertices, I added ±0.05 to the existing coordinates to create additional vertices.

The code uses the plyr (Wickham 2011), splancs (Rowlingson and Diggle 2013), and gpclib (Peng et al. 2012) packages. The purpose and required inputs of each function I created is detailed below. The output of the "MaleAndFemaleInt" function was used as the female overlap term in the above analysis.

There are four pieces of user-defined data that must be inputted for the code to work with new data: the number of male territories in the analysis (mM), the number of female territories in the analysis (mF), the directory the data files are in (Folder), and the name of the final output file created by the "MaleAndFemaleInt" function (FemInt˙FileName).

```
##===============================================================##
##===============================================================##
##====            Male and Female Territory Intersections    ====##
##===============================================================##
##===============================================================##
##== Purpose: Calculates the number of females whos territories overlap each male territory
##==
##== Functions:
##==  ListOfLizardsM(): Creates a list of all male lizard names
##==  ListOfLizardsF(): Creates a list of all female lizard names
```

```
##==  InPolygonSetM(n): Determines if the given number n corresponds to a male polygon
##==  InPolygonSetF(n): Determines if the given number n corresponds to a female polygon
##==  PolygonM(n): Turns the Polygon text file of male n into a form the plyr package
##==          can read
##==  PolygonM(n): Turns the Polygon text file of female n into a form the plyr package
##==          can read
##==  NIntersects(n): Returns the number of females that male n's territory intersects
##==  MaleAndFemaleInt(): Returns a table of the number of females each male intersects
##==
##== Packages Required: plyr, splancs, gpclib
##==
##==================================================================##
##== Code By: Jordan Bush                          Date: 3/10/2014 ==##
##==================================================================##
##==================================================================##


library(plyr)
library(splancs)
library(gpclib)


### User Defined Information:
    mM = 33 #Highest ID number of Males
    mF = 40 #Highest ID number of Females
    Folder = "C:\\Users\\Jordan\\Documents\\Research 2013\\Field Work\\Territory R Stuff FINAL"
    FemInt_FileName = "C:\\Users\\Jordan\\Documents\\Research 2013\\Field Work\\Territory R Stuff
FINAL\\NumFemaleInt.txt"


ListOfPolygonsM<-function(){
    LizardList = c()
    FileList = list.files(Folder)
    for(i in 0:mM){
            if(i < 10) Name = paste(c("PolygonM10", i, ".txt"), collapse="")
            if (i >= 10) Name = paste(c("PolygonM1", i, ".txt"), collapse="")
            for(j in 1:length(FileList)){
                    File = as.character(FileList[j])
                    if(File == Name) LizardList = c(LizardList, Name)}}
    return(LizardList)}

ListOfPolygonsF<-function(){
    LizardList = c()
    FileList = list.files(Folder)
    for(i in 0:mF){
            if(i < 10) Name = paste(c("PolygonF10", i, ".txt"), collapse="")
            if (i >= 10) Name = paste(c("PolygonF1", i, ".txt"), collapse="")
            for(j in 1:length(FileList)){
                    File = as.character(FileList[j])
                    if(File == Name) LizardList = c(LizardList, Name)}}
    return(LizardList)}

InPolygonSetM <- function(n){
    if(n < 10) Name = paste(c("PolygonM10", n, ".txt"), collapse="")
    if (n >= 10) Name = paste(c("PolygonM1", n, ".txt"), collapse="")
    if(length(grep(as.character(Name), ListOfPolygonsM())) > 0) return(TRUE)
    else return(FALSE)}

InPolygonSetF <- function(n){
    if(n < 10) Name = paste(c("PolygonF10", n, ".txt"), collapse="")
```

```r
        if (n >= 10) Name = paste(c("PolygonF1", n, ".txt"), collapse="")
        if(length(grep(as.character(Name), ListOfPolygonsF())) > 0) return(TRUE)
        else return(FALSE)}


PolygonM<-function(n){
        if(n < 10) Name = paste(c("PolygonM10", n, ".txt"), collapse="")
        if (n >= 10) Name = paste(c("PolygonM1", n, ".txt"), collapse="")
        if(length(grep(as.character(Name), ListOfPolygonsM())) > 0){
                Data = read.table(as.character(Name), header=TRUE)
                x = Data[,1]
                y = Data[,2]
                m = cbind(x, y)
                p = as(m, "gpc.poly")}
        else p=0
        return(p)}


PolygonF<-function(n){
        if(n < 10) Name = paste(c("PolygonF10", n, ".txt"), collapse="")
        if (n >= 10) Name = paste(c("PolygonF1", n, ".txt"), collapse="")
        if(length(grep(as.character(Name), ListOfPolygonsF())) > 0){
                Data = read.table(as.character(Name), header=TRUE)
                x = Data[,1]
                y = Data[,2]
                m = cbind(x, y)
                p = as(m, "gpc.poly")}
        else p=0
        return(p)}


NIntersects<-function(n){
        IntersectingPolygons = 0
        if(InPolygonSetM(n) == TRUE){
                Poly1 = PolygonM(n)
                for(a in 0:mF){
                        if(InPolygonSetF(a) == TRUE){
                                Poly2 = PolygonF(a)
                                if(area.poly(intersect(Poly1, Poly2)) > 0) IntersectingPolygons =
IntersectingPolygons + 1}}
                return(IntersectingPolygons)}
        else return(0)}

MaleAndFemaleInt<-function(){
        Matrix = matrix(ncol=1, nrow=length(ListOfPolygonsM()))
        rownames(Matrix) = c(ListOfPolygonsM())
        index = 1
        for(i in 0:mM){
                if(InPolygonSetM(i) == TRUE){
                        Matrix[index,] = NIntersects(i)
                        index = index + 1}}
        write.table(Matrix, FemInt_FileName, sep="\t")
        return(Matrix)}
```