Scraping Network Analysis: A Method to Explore Complex White-tailed Deer Mating Systems

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Abstract - *Odocoileus virginianus* (White-tailed Deer) are social animals that thrive in rural and urban settings. Scraping behavior is an olfactory reproductive communication used by White-tailed Deer to establish breeding networks. Male scraping is a complex scent-marking behavior which advertises sociosexual status and location to potential females as well as to competing males. Female scraping behavior is thought to be an estrus signal alerting males during times of optimal fertility. This study describes a new method to examine White-tailed Deer mating systems using social network analyses of scraping behavior using an urban population of White-tailed Deer as a model. First, we validated the scraping behavior at our study site in Tougaloo, MS, during the 2019–2020 breeding season. Using remote monitoring, we continuously documented scraping behaviors over 8 different scrape-site locations and found similar behavioral, temporal, and spatial patterns in our urban breeding network as reported in rural and captive deer studies. Next, we describe methods detailing how social network analyses can reveal sociality, dominance, importance, and social structure within male scraping networks. Using centrality measures, we were able to rank dominant male influencers, anticipate social conflict among rivals, and made predictions regarding the spread of communicable diseases through a male scraping network. We also detail network analyses combining both male and female scraping behavior to reveal a glimpse into the complexity of breeding networks. Using network measures, we were able to rank males based on competitiveness and female preference. Lastly, we generated a theoretical breeding network to explore female sociability, competitiveness, preference, and mate choice. Taken together, this work describes a new method using scraping network analysis to investigate the complexity of White-tailed Deer breeding networks. This work also demonstrates the future applications of this method for predicting the spread of communicable diseases and for predicting mate selection within White-tailed Deer mating systems.

Introduction

Odocoileus virginianus (Zimmermann) (White-tailed Deer, hereafter "Deer") are sexually dimorphic, have reproductive seasonality, and exhibit seasonal breeding behaviors. One such behavior is scraping, which produces physical and chemical signposts (Moore and Marchinton 1974). Male deer conduct elaborate scent-marking behaviors that advertise their sociosexual status and location (DeVos 1967, Hirth 1977, Moore and Marchinton 1974). Scraping involves pawing the soil, chewing vegetation of overhanging branches, and depositing scent from 6 different glands including forehead glands, preorbital glands, and even salivary glands

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(DeVos 1967; Hirth 1977; Gassett et al. 1996, 2000; Miller et al. 1998; Moore and Marchinton 1974; Osborn et al. 2000). Male Deer make long-distance movements during the breeding season (Karns et al. 2011, Ozoga and Verme 1975). On forays, males create and visit scrape sites to assert dominance to competing males and to display prowess to potential female mates (Marchinton et al. 1990, Miller and Marchinton 1999, Moore and Marchinton 1974). Most scraping behavior is performed by males >2.5 years old and occurs before or during the peak of the breeding season (Kile and Marchinton 1977; Miller and Marchinton 1999; Ozoga and Verme1975, 1985). Scraping behavior is influenced by experience, age, social rank, and testosterone levels (Miller et al. 1987). Mature males are responsible for most scraping behavior and use scrapes to communicate dominance to suppress breeding by younger males (Hirth 1977, Marchinton et al. 1990, McCullough 1979). Females also scrape, but less often than males (Moore and Marchinton 1974, Sawyer et al. 1982). Scrapes are thought to be a form of reproductive communication between sexes to establish breeding networks; however, the role of this behavior in mate selection and reproductive outcomes remains unclear (Sawyer and Miller 1989). We speculate that female scrape communications are directed at potential mates based upon individual female preference. Documentation of female Deer mating preference has been reported in the literature using spatial data and behavioral cue data (Kolodzinski et al. 2010, Labisky and Fritzen 1998, Morina et al. 2018, Sullivan et al. 2017). How these preferences and behaviors impact Deer social networks remains unclear. Social networks have been studied in a wide variety of animals such as: *Macaca* spp. (macaques), *Papio* spp. (baboons), dolphins, sharks, *Orcinus orca* (L.) (Killer Whale), wasps, kangaroos, elephants, hyenas, and sparrows, just to name a few (Barrett et al. 2012, Beisner et al. 2015, Carter et al. 2009, Fedurek and Lehmann 2017, Flack et al. 2006, Franz et al. 2015, Goldenberg et al. 2016, Ilany et al. 2015, Lusseau 2003, Naug 2009, Mourier et al. 2017, Shizuka et al. 2014, Williams and Lusseau 2006). Previous social network analyses of rural White-tailed Deer have demonstrated the importance of landscape features and its impact on social behavior (Koen et al. 2017). Social network analysis can also be used to better understand social complexity in breeding systems (McDonald et al. 2020). In this study, we validate scraping behavior in urban Deer and describe a new method to examine the complexity of Deer-mating systems using social network analyses of scraping behaviors. Our study demonstrates how scraping behavior shapes Deer-breeding networks. Using network measures, we were able to rank principal network influencers, predict social conflict, demonstrate female preference, and make predictions about the spread of communicable diseases through scraping networks. Overall, this study demonstrates the application of social network analysis of scraping networks and the significance of scraping behavior in Deer-mating systems.

Field-site Description

Our survey location was a 202-ha (496-acre) plot of woodland surrounding the Tougaloo College Campus in Tougaloo, MS, and included hardwood forests, mixed hardwood–pine forests, suburban plantings, and open pastures where hunting is highly restricted (Fig. 1; Tougaloo College 2019). Tougaloo College is positioned within the intersection of Madison, Hinds, and Rankin counties in Mississippi. Tougaloo College campus is bordered by 3 major interstates (I-220, I-55 and US-51) and 1 busy state road (County Line Road) and is located near 3 urban centers (Jackson, Ridgeland, and Madison), making Tougaloo an urban haven for wildlife.

Methods

Remote monitoring

The Tougaloo College campus is a refuge for many types of urban wildlife including White-tailed Deer. We speculated that the college campus housed an ample deer herd that would be sufficient for social network analyses. However, the number of White-tailed Deer and the impact of a busy college campus on reproductive behaviors were not known. Also, a survey of urban White-tailed Deer scraping behavior has never been reported in the literature. For these reasons, we surveyed the woodlands surrounding Tougaloo College for deer activity and found 22 scrape sites (Fig. 1). Sixteen of the 22 scrapes formed a line on an old abandoned road (Fig. 1). Scrape sites were found on creek crossings, on woodland edges in open areas, and near deer trails (Fig. 1). These are typical locations, as Deer scrapes are often found near trails, creek crossings, in open areas, woodland edges, and old roads (Kile and Marchinton 1977, Miller and Marchinton 1999). To survey the scraping behavior of Tougaloo's deer population, we used 8 Tasco Trail Cameras

Figure 1. Tougaloo campus field-site. Shown is the QGIS map of the survey site at Tougaloo College, Tougaloo, MS. Scrape sites were marked using a white circle with a centered black dot. Cameras markers are shown as grey diamond markers.

(Model #: 119270CW, Tasco Worldwide, Miami FL) positioned at active scrape-site locations, on high-traffic trail sites, and at feeding stations according to the manufacturer's instructions and using methods as previously described (Alexy et al. 2001, Curtis et al. 2010, Jacobson et al. 1997). Digital images with date and time stamps were stored on SanDisk Ultra 16GB flash memory. We set up the cameras in the 3/5 mode, which allows the camera to take 3 digital images every 5 seconds during motion-sensor activation. We stored the digital images long term on external hard drives for image analysis. We placed the cameras in the field from 5 November 2019 to 31 January 2020 and left them undisturbed except for memory card and battery changes, which we performed at 30-day intervals. For cameras set in areas of high scrape density, we maintained at least 250 feet separation between camera placements.

Identification of scrape sites

We identified scrape sites using methods as previously described in Alexy et al. (2001). Briefly, we identified scrape sites by large circular depressions of disturbed ground under low-lying tree limbs. Tougaloo woodlands were searched for scrapes in a grid pattern by teams of 3 to 5 individuals starting in late October 2019 and ceasing in early November to minimize added human disturbances from the study. We recorded scrape-site locations using GPS. We created a map of scrape-site and camera-site locations by entering the GPS data into QGIS software and then layering it on Google (Fig. 1).

Deer identification and population analysis

We identified Deer in the digital images using methods as previously described in Jacobson et al. (1997). We identified unique profiles for individual male antlered Deer from digital images using parameters such as: antler patterns, pelage, and body size. We defined females as antlerless deer in this study, which included any spotless fawns. Fawns with spots were not seen on camera during the defined study period. We used methods described by Jacobson et al. (1997) to estimate Tougaloo's urban Deer population. Although this population method has been shown to be less accurate in rural settings, it has been shown to be highly effective at estimating deer populations in suburban areas such as our survey location (Curtis et al. 2009). We were unaware of any proven method to uniquely identify females or antlerless deer without a tagging or collar system. Therefore, we focused on unique antlered males in this study. We defined mature males as > 2.5 years of age and immature adult males as <2.5 years of age as previously described (Alexy et al. 2001, Ozoga and Verme 1985). Each unique male was assigned a number as the data was parsed.

Scraping behavior analysis

Literature has reported many types of Deer behaviors recorded at scrape sites such as: pawing the ground, marking overhead branches, urination, and smelling of the scrape itself (Alexy et al. 2001; Kile and Marchinton 1977; Marchinton et al. 1990; Miller et al. 1987, 1998; Moore and Marchinton 1974; Sawyer and Miller 1989; Sawyer et al. 1982). Mature males have been noted to paw the ground, mark overhead branches with antlers, forehead glands and preorbital glands, and urinate on the scrapes. Females display similar behavior, but less often as compared to males (Sawyer et al. 1982). In this study, we used methods as previously described (Alexy et al. 2001; Kile and Marchinton 1977; Marchinton et al. 1990; Miller et al. 1987, 1998; Moore and Marchinton 1974; Sawyer and Miller 1989; Sawyer et al. 1982) to define male and female scraping behavior as any marking behavior that might leave behind a scent such as: pawing the ground, marking overhead branches, and urination. Smelling or sniffing the scrape was not considered in this study because, although an important behavior, it does not leave behind a scent on the scrape (Alexy et al. 2001). We analyzed scraping behaviors based on date, time, sex, scrape-site location, and male maturity over the survey period. We averaged scraping behavior per day over all 8 scraping sites to calculate the mean scraping behavior per day for mature males, immature adult males, and females. We used the Student *t*-test to determine statistical significance with a *P* value less than 0.05 considered significant. We counted male scraping behavior for each unique male, where males received one point for each scrape visit during which scraping behavior was observed. Figure 2a shows how mature males are easily identifiable. We scored each unique male's scraping activity based upon the percentage of that male's number of scraping behaviors compared to the total scrape activity of all males combined over all scrape locations. We recorded female scrape responses for each unique male as female scraping behavior seen within a 24-hour period after that unique male's scraping behavior was recorded. We then gave each unique male a value based upon the percentage of total female scrape responses during the survey period. We also noted the time of day when scraping behaviors occurred and also how the days of the month impacted scraping behavior leading into the breeding season.

Social network analyses

Since scrapes are important competitive communication between male White-tailed Deer, we used scraping data to generate a male scraping network. We performed social network construction and hypothesis testing using methods previously described in Bastian et al. (2009), Croft et al. (2011), and Farine and

Figure 2 (following page). The male scraping network. (a) Images of mature Males 1–8 displaying easily identifiable unique antler and body characteristics. (b) Graph showing the percentage of total scrape activity over the survey period for each individual from Male 1 to Male 14. (c) Network graph showing scraping interactions between 3 males at one scrape site location. Males are number nodes, where M represents Male. The edges are scraping messages marked as directional arrows from one male to his target male. The size of the arrow indicates the message size and is based on the number of times the male scraped at this scrape location. (d) Depiction of the male scraping network, which is a combination of all scrape interactions over all 8 scrape site locations during the survey period. The size of each node represents the total weighted degree or total scrape messages sent and received. The weighted edges are based on total scraping messages. Not all males demonstrated scraping behavior and therefore are represented as nodes only without edges.

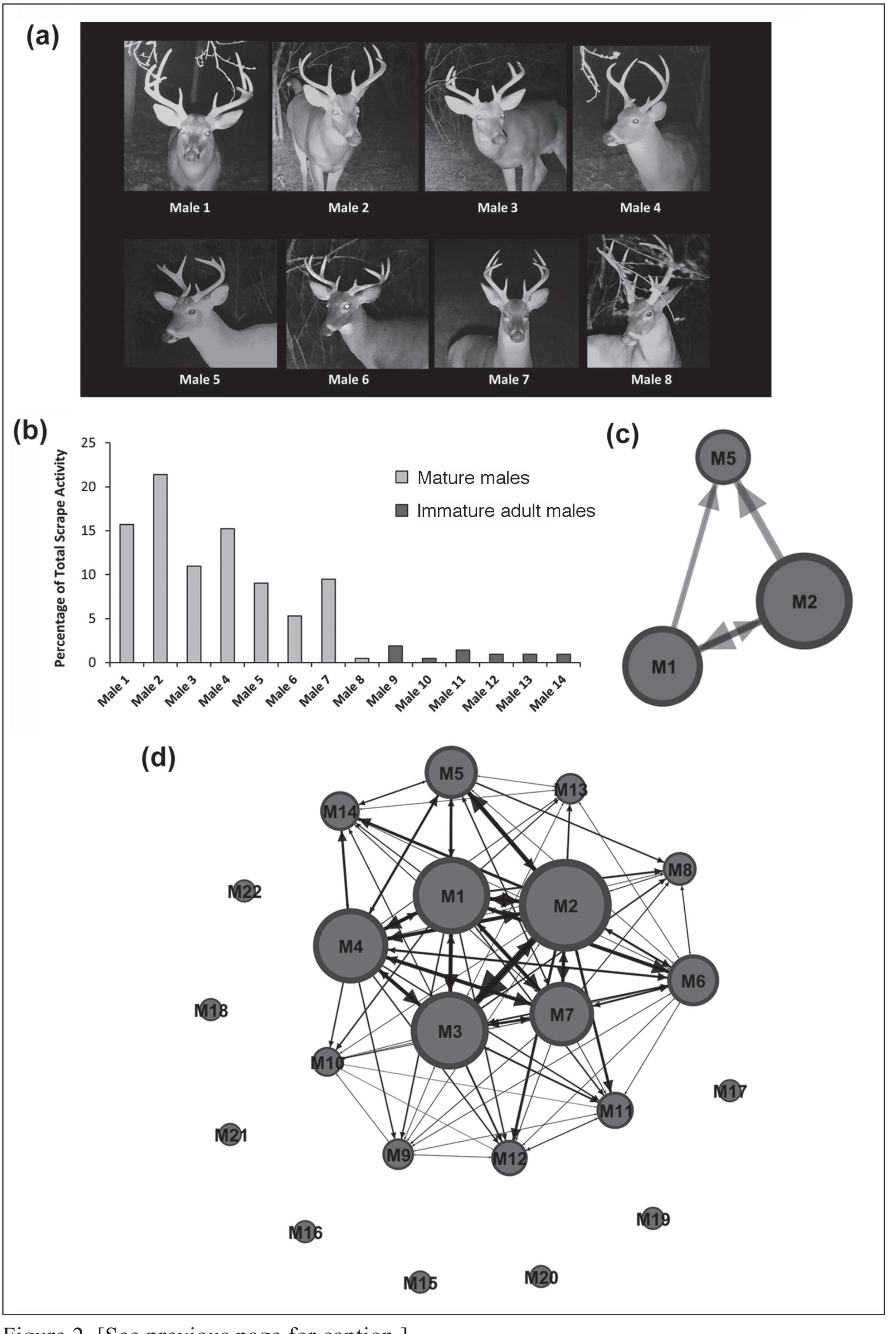


Figure 2. [See previous page for caption.]

Whitehead (2015). For the male scraping network, we recorded the number of scraping behaviors and the scrape site location for each unique male, which we designated as a unique node number. We inferred that males using the same scrape site were communicating with one another in a competition for dominance. Thus, we interpreted scraping data as a message edge or directional weighted degree targeted to each of the other males (nodes) that scraped at the same scrape; 1 node targets all other nodes scraping at the same scrape. The weight of the degree is the number of scraping behaviors counted for each node at that scrape site and is targeted at all other nodes scraping at the same scrape site. We placed the node number, target node, and weighted degree data in open source Gephi software to generate the male scraping network (Bastian et al. 2009). For the breeding network, individual females were not identifiable, and instead we grouped them into 1 node and gave them edges directed at each unique male node based upon data from 24-hour female scrape-response analysis. Therefore, the female network node targeted male nodes that scraped at the same scrape site within a 24-hour period before a female scrape response. The female node targeted each male node with a weighted degree equal to the percentage of female responses. Male nodes targeted the female node as a weighted degree based upon the percentage of scraping behaviors observed for each male node. We placed the node number, target node, and weighted degree data in open source Gephi software to generate the breeding network (Bastian et al. 2009).

To better understand the social role of each male, out degree centrality, in degree centrality, and closeness centrality for each male was measured and ranked. Such network measures can provide a better understanding of the relational states between nodes and node influence over a network (Opsahl et al. 2010). For example, out degree centrality is a measure of gregariousness and influence, specifying highly connected individuals sending important communications; however, in the case of a scraping network, it can measure dominating, or domineering individuals (Miller et al. 1987, Wey et al. 2008). On the other hand, in degree centrality is a measure of popularity and demand, specifying highly connected individuals receiving important communications; however, in the case of a competitive scraping network, it can measure individuals posing the biggest threat and a major target for suppression (Miller et al. 1987, Wey et al. 2008). Closeness centrality measures how well connected an individual is to all others within the network, specifying highly centralized and connected individuals sending and receiving important

(a)
In Degree Centrality Calculation:

$$\text{In DC} = K_i^{(1-\alpha)} \times S_i^{\alpha}$$

where,
K_i = Number of In Degree Connections
S_i = In Degree Weight
$\alpha = 0.5$

(b)
Out Degree Centrality Calculation:

$$\text{Out DC} = K_o^{(1-\alpha)} \times S_o^{\alpha}$$

where,
Ko = Number of Out Degree Connections
So = Out Degree Weight
$\alpha = 0.5$

(c)
Closeness Centrality Calculation:

$$\text{CC} = [\,\Sigma S_T^{\alpha}\,]^{-1}$$

where,
S_T = Total Degree Weight Between Nodes
$\alpha = 0.5$

Figure 3. Network centrality formulas. Shown are the formulas used to calculate (a) in degree centrality, (b) out degree centrality, and (c) closeness centrality adapted from Opsahl et al. (2010).

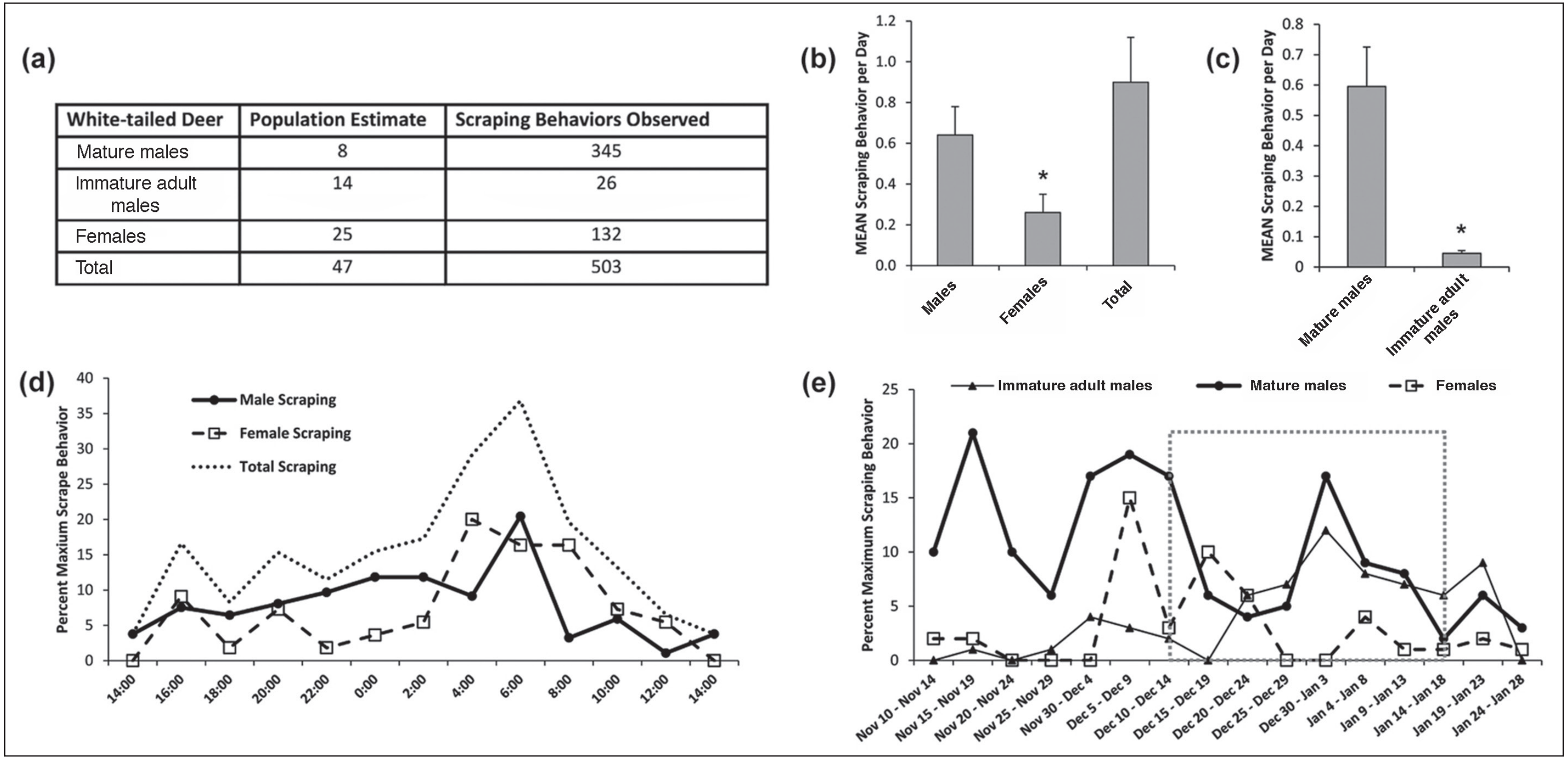
communications (Wey et al. 2008). In a scraping network, we suggest that closeness centrality measures importance. To determine in degree centrality, out degree centrality, and closeness centrality, we adapted the following formulas for calculating node centrality in weighted networks from Opsahl et al. (2010) (Fig. 3). For all calculations, we used an α value of $\alpha = 0.5$ to give both node strength and number of connections proportional influence over the data being parsed. For in degree centrality and out degree centrality, we ranked the nodes with higher scores higher than nodes with lower scores (Opsahl et al. 2010). For closeness or closeness centrality, we ranked the nodes with lowest scores higher than nodes with higher scores. For predicting disease transmission or mating preference, we used the heat-mapping function in Gephi software to generate prediction graphs by selecting a color scheme and node of interest within the graphed network. We carried out closeness calculations between 2 nodes using the closeness centrality formula described in Figure 3c.

Results and Discussion

Population estimate and scraping activity

Over the survey period, we collected 36,707 digital images from the wildlife cameras. Population analysis estimated Tougaloo's urban Deer population to be ~47 Deer (Fig. 4a). We identified 25 females (antlerless Deer) and 22 unique antlered male Deer. These males were then categorized as mature males or immature adult males. Over the survey period, our wildlife cameras recorded both male and female scrape-site visitations and scraping interactions. We captured 503 observations of scraping behavior in male and female deer (Fig. 4a). Both males and females repeatedly visited the same scrape sites. Also, multiple males were recorded using the same scrape sites, and every scrape site observed was used by more than 1 male. Most scraping behavior was observed by mature males (Fig. 4a). Males displayed statistically more scraping behavior per day as compared to females (Fig. 4b); and mature males significantly scraped more per day as compared to immature adult males (Fig. 4c). These data are similar to data reported in the literature on rural and captive deer herds, where mature males scrape more often than females and immature adult males (Alexy et al. 2001, Miller et al. 1987, Ozoga and Verme 1985).

Scraping behavior started at ~14:00, increased to a peak at ~7:00, then quickly decreased from 8:00 to 12:00, and then started back ~14:00 the next day (Fig. 4d). Our scraping behavior times aligned with previous reports in rural populations (Alexy et al. 2001). Scraping activity over the breeding season was documented in 5-day intervals starting from 5 November 2019 to 31 January 2020 (Fig. 4e). Figure 4e shows that mature male and female scraping activity occurs in waves. Using the data from Mississippi Department of Wildlife Fisheries and Parks' (MDWFP) deer monitoring program, we estimated that the 4-week breeding period for Tougaloo's deer population as occurring from 14 December to 14 January (MDWFP 2019). We saw a drastic decrease in mature male scraping behavior that occurred at the start of the projected breeding window (Fig. 4e). Again, our data was supported by the literature, where scraping behavior is reported to decrease during the peak breeding



(a)

White-tailed Deer	Population Estimate	Scraping Behaviors Observed
Mature males	8	345
Immature adult males	14	26
Females	25	132
Total	47	503

Figure 4. Population estimate and scraping data. (a) The table shows the White-tailed Deer population estimate and the number of observed scraping behaviors. (b) The graphs displays the mean scraping behavior per day± SE for males and females were * $P < 0.05$ is considered significant. (c) The graph shows the mean scraping behavior per day± SE for mature males and immature adult males were * $P < 0.05$ is considered significant. (d) The graph shows the percent maximum scraping behavior of males and females over time (hours) beginning from 14:00 to 14:00 the next day. Total scraping behavior is a combination of both male and female data displayed as the black dotted line. (e) The graph shows the percent maximum acraping behavior of immature adult males, mature males, and females from 10 November to 28 January analyzed over 5 day intervals. The grey dotted line forms a box around the 4 week breeding period estimated from data taken from MDWFP (2019).

time (Alexy et al. 2001, Kile and Marchinton 1977, Miller and Marchinton 1999, Ozoga 1989). Taken together, our scraping data was in line with the current literature, which supports the validity of social network analysis of scraping behavior at our study site.

Analysis of competitive male scraping networks

Figure 2b shows the scrape activity for each individual male over the survey period, where mature males have higher scrape activity as compared to immature adult males. Figure 2c shows the scraping communications at just 1 scape site. Three males or nodes are scraping at this location, where the arrow or degree edge is indicating the direction and the size of the communication. In this example, Male 2 has the highest scrape activity at this location and is sending dominating signals to the other males at this scrape (Fig. 2c). Male 1 is also sending sizable messages at this location; however, Male 5's scraping messages are over shadowed by the magnitude of the messages sent by Male 1 and Male 2. Next, we expanded the data from all scrape sites to generate the complete male scraping network (Fig. 2d). Figure 2d shows the scraping interactions between all 22 individual males, where the size of each node represents the total weighted degree or total scrape messages sent and received. Not all males displayed scraping behavior and did not participate in scrape activity; these males are shown on the outer edge of the social network graph (Fig. 2d). Males with the stronger scrape communications were closer to the center of the network and displayed their influence over the network by their node size (Fig. 2d). The proximity of one node to another represents the strength of the relationship and competition for dominance between nodes, as scrapes are an advertisement of presence and dominance in a highly competitive breeding system (Hirth 1977, Marchinton et al. 1990, Sawyer and Miller 1989, Sawyer et al. 1982).

Figure 5 shows the out degree centrality, in degree centrality, and closeness centrality for each male and their ranks. Male 2 and then Male 1 ranked the highest for out degree centrality (Fig. 5a), which correlates with their high level of scrape activity (Fig. 2b). These data suggest that Male 2 and Male 1 are dominant influencers over the scraping network. Interestingly, Male 3 ranked the highest for in degree centraility, suggesting Male 3 poses the biggest threat to others or is being targeted for suppression (Fig. 5a). Male 2 ranked 2nd for in degree centrality, which is no surprise, since Male 2 is the most dominating influencer. Based on very tight closeness centrality ranking scores, Males 1, 2, 3, and 4 are the most important males or top competitors battling for breeding rights in the male scraping network (Figs. 2d, 5a). Since, Male 2 ranked high in all centrality measures, we measured Males 2's closeness to other males to determine which males are Male 2's major competitors and found that Male 3 was the closest competitor (Fig. 5b). Taking Male 3's closeness measures, we found that Male 2 was the closest competitor. Based on Male 2 (Fig. 5b) and Male 3 (Fig. 5c) closeness rankings, Male 2 and Male 3 are major rivals. The few alterations recorded were all between Males 2 and 3 (Fig. 5d), suggesting that network measures may be important predictors of rivalry and physical conflicts within socially structured scraping networks.

Predicting disease transmission in scraping networks

Out degree centrality, in degree centrality, and closeness centrality measures have been suggested to be important predictors in disease transmission and are used to identify potential super-spreaders within social networks (Hu et al. 2018, Kitsak et al. 2010, Zhang et al. 2019). Individuals with high ranked out degree centrality and closeness centrality scores would seem more likely to spread communicable diseases due to their influencing network positions. Likewise, individuals with high ranked in degree centrality and closeness centrality scores would likely be more vulnerable to disease due to their closeness and incoming connections with others. Based upon centrality rankings, Males 1, 2, 3, and 4 would be considered potential super-spreaders who could easily transmit disease to individuals within the scraping network (Fig. 5a). Using our male scraping network as a model, we show

(a)

	Connections	Out DC	Out DC Rank	In DC	In DC Rank	CC	CC Rank
Male 1	13	91.60	2	62.90	5	0.032	2
Male 2	13	99.70	1	76.90	2	0.029	1
Male 3	13	74.60	4	83.20	1	0.032	2
Male 4	13	85.70	3	67.20	4	0.033	3
Male 5	8	49.30	7	45.30	7	0.044	5
Male 6	13	54.70	6	59.60	6	0.045	6
Male 7	13	67.10	5	70.20	3	0.037	4
Male 8	7	14.70	14	32.40	11	0.073	10
Male 9	9	22.10	10	29.20	12	0.082	11
Male 10	9	21.70	11	23.50	14	0.092	13
Male 11	9	23.20	9	40.90	9	0.064	8
Male 12	9	18.70	12	41.70	8	0.066	9
Male 13	8	17.90	13	29.10	13	0.083	12
Male 14	8	26.10	8	40.20	10	0.059	7

(b)

	Closeness	Rank
Male 1	0.012	3
Male 3	0.006	1
Male 4	0.014	4
Male 5	0.010	2
Male 6	0.200	10
Male 7	0.014	4
Male 8	0.090	8
Male 9	0.140	9
Male 10	0.140	9
Male 11	0.018	6
Male 12	0.018	6
Male 13	0.033	7
Male 14	0.017	5

(c)

	Closeness	Rank
Male 1	0.023	2
Male 2	0.011	1
Male 4	0.023	2
Male 5	0.030	4
Male 6	0.032	5
Male 7	0.023	2
Male 8	0.033	6
Male 9	0.143	8
Male 10	0.143	8
Male 11	0.027	3
Male 12	0.027	3
Male 13	0.143	8
Male 14	0.050	7

(d)

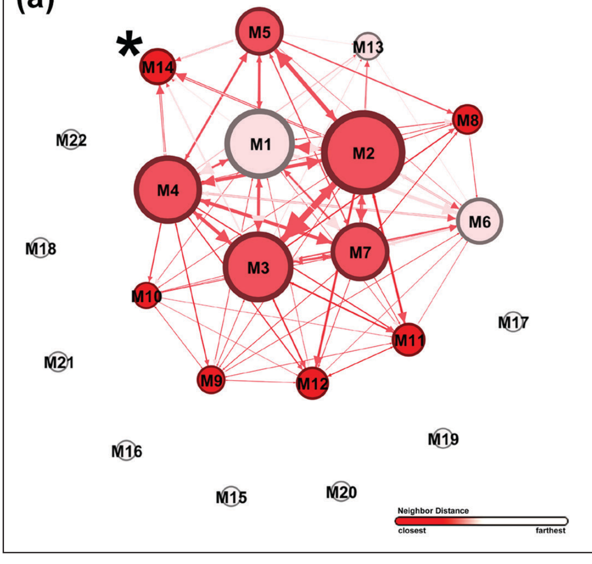
Figure 5. Analysis of the male scraping network. (a) The table shows the out degree centrality (Out DC), in degree centrality (In DC), and closeness centrality (CC) for each male in the scraping network and their corresponding rank. (b) Shown are the closeness scores and rank between Male 2 and other males in the network. (c) Shown are the closeness scores and rank between Male 3 and other males in the network. (d) Shown is a physical altercation between Male 2 and Male 3 at a scrape site.

hypothetical disease transmission through the network from a sick male. Using Male 14 as an example, Figure 6a predicts the spread of disease into the scraping network using heat mapping of neighbor closeness. Assessing Male 14's closeness rankings, we determined that Males 8, 9, 10, 11 and 12 are highly susceptible for disease transmission from Male 14 (Fig. 6b). In this manner, network measures might be useful predictors to model disease transmission in scraping networks.

Analysis of breeding networks

Since scraping behavior is also an olfactory communication between the sexes used to establish breeding networks (DeVos 1967, Hirth 1977, Marchinton et al. 1990, Moore and Marchinton 1974, Sawyer and Miller 1989, Sawyer et al. 1982), we examined how females responded to individual males during a 24-hr period after a male left a scraping signal. Figure 7a shows the female responses to each individual mate male's scraping communications over the survey period. Interestingly, some mature males received more female responses as compared to other males (Fig. 7a). Male 1 received over 2 times as many female scraping responses as compared to other males. Male 1 also received multiple responses from groups of females simultaneously, which was a response not seen for other males. Figure 7b shows Male 1 scraping, followed by multiple females responses (Fig. 7c, d) within 2 hrs post scraping. Taken together, these data suggest that female scraping response

(a)

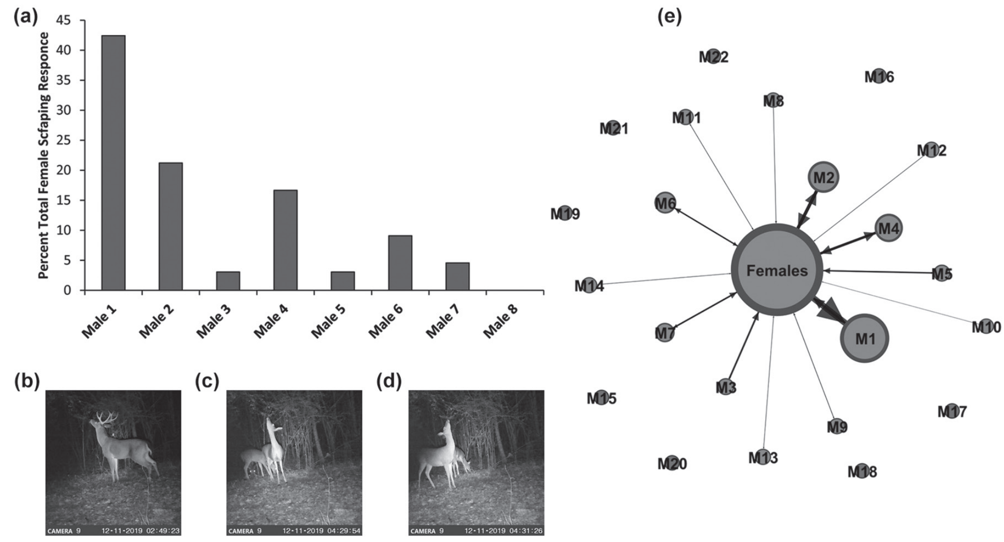


(b)

	Closeness	Rank
Male 1	0.20	3
Male 2	0.07	2
Male 3	0.07	2
Male 4	0.07	2
Male 5	0.07	2
Male 6	0.20	3
Male 7	0.07	2
Male 8	0.05	1
Male 9	0.05	1
Male 10	0.05	1
Male 11	0.05	1
Male 12	0.05	1
Male 13	0.20	3

Figure 6. Predicting disease transmission within scraping networks. (a) Displayed is the predicted disease transmission pathway from infected Male 14 (*M14) to other males within the scraping network. Shown in red is the heat map function, where males closer to M14 are red hot and more susceptible to disease as compared to males who are farther away and display lighter node shading. (b) Closeness scores and rank between Male 14 and other males in the network, where males with higher ranking are closer to Male 14 and more susceptible to disease transmission.

is a communication directed at specific males based on female preference. To explore this idea further, we placed the female scraping-response data to both mature and immature adult males alongside all male scraping data into Gephi software to generate the breeding network (Fig. 7e). Using out degree centrality and in degree centrality, we ranked males within the breeding network. Male 2 ranked highest

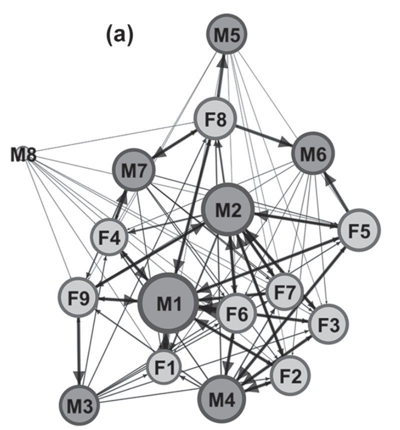


(f)

	Connections	Out DC	Out DC Rank	In DC	In DC Rank
Male 1	1	3.96	2	6.48	1
Male 2	1	4.63	1	4.47	2
Male 3	1	3.32	4	1.41	6
Male 4	1	3.90	3	4.00	3
Male 5	1	3.00	6	1.41	6
Male 6	1	2.28	7	2.83	4
Male 7	1	3.08	5	2.24	5
Male 8	1	1.38	8	0.00	8
Male 9	1	1.38	8	1.00	7
Male 10	1	0.69	11	0.00	8
Male 11	1	1.18	9	1.00	7
Male 12	1	0.97	10	1.00	7
Male 13	1	0.97	10	1.00	7
Male 14	1	0.97	10	1.00	7

Figure 7. Analysis of the breeding network. (a) Graph showing the percentage of total female scraping responses for each mature male. (b) Image showing Male 1 scraping, followed by multiple females scraping responses (c) and (d) within a 2hr time period. (e) Graph showing the breeding network generated from both male (M) and female scraping data over the survey period. The weighted edges are based on scraping percentage. Individual females were not identifiable and were grouped into one node noted as Females. (f) The out degree centrality (Out DC) and in degree centrality (In DC) for each male in the scraping network and their corresponding rank.

in out degree centrality due to the weight of his dominant scraping behavior (Fig. 7f). Male 1 ranked highest in in degree centrality due to his popularity among females within the breeding network (Fig. 7f). The major drawback of this simulated breeding network is the lack of female identification. If individual females were identifiable, we could generate a more intricate breeding network. Expanding on this idea, we used scraping data from 8 mature males to generate a theoretical breeding network where 9 unique females were identifiable (Fig. 8a). Using out degree centrality and in degree centrality, we ranked males and females within the breeding network (Fig. 8b, c). Females 5 and 8 ranked highest for out degree centrality, demonstrating possible female dominance, competition, high sociality, or flirtatiousness. Female 8 and 9 ranked highest for in degree centrality, demonstrating their popularity among male nodes (Fig. 8b). Female 8 ranked highest in closeness centrality due to high network connectivity and importance. Male 1 ranked highest in in degree centrality and closeness centrality based upon high network connectivity and popularity among females (Fig. 8c). Male 2 ranked highest in out degree centrality due to dominant and competitive scraping behavior. Since this theoretical breeding network displays female mate preferences, we explored the possibility of predicting female mate selection using heat mapping and closeness measures using Female 9 as an example. Heat mapping of Female 9's connections displayed strong preferences for Males 1, 2, and 3 (Fig. 9a). Closeness ranking revealed Female 9's mate preferences for Males 1, 2, and 3 in that order (Fig. 9b). Overall, this method supports the generation of breeding networks from scraping data to explore the complexity of Deer mating systems to investigate sociality, dominance, competitiveness, importance, preference, and to predict mate selection.



(b)

	Connections	Out DC	Out DC Rank	In DC	In DC Rank	CC	CC Rank
Female 1	7	8.94	5	22.91	3	0.0065	8
Female 2	7	18.97	3	23.59	2	0.0050	5
Female 3	7	18.97	3	22.61	4	0.0052	6
Female 4	7	12.65	4	21.33	5	0.0069	9
Female 5	7	25.30	1	23.59	2	0.0042	2
Female 6	7	21.91	2	20.83	6	0.0045	3
Female 7	7	12.65	4	23.59	2	0.0063	7
Female 8	7	25.30	1	24.54	1	0.0041	1
Female 9	7	18.97	3	24.54	1	0.0049	4

(c)

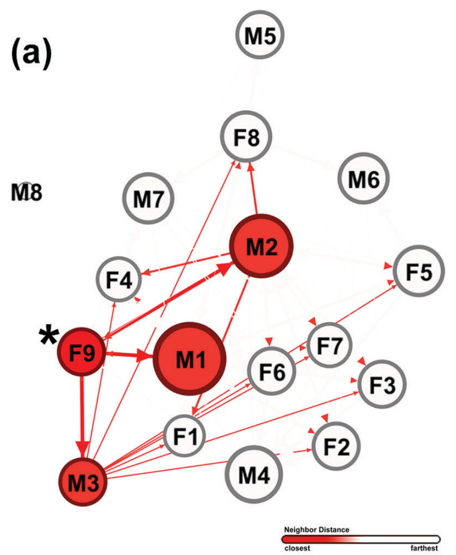
	Connections	Out DC	Out DC Rank	In DC	In DC Rank	CC	CC Rank
Male 1	9	36.00	2	62.93	1	0.0017	1
Male 2	9	41.24	1	37.95	2	0.0023	2
Male 3	9	29.85	4	6.32	5	0.0072	5
Male 4	9	34.86	3	25.30	3	0.0034	3
Male 5	9	12.73	7	6.32	5	0.0172	7
Male 6	9	20.12	6	12.65	4	0.0080	6
Male 7	9	29.77	5	12.65	4	0.0056	4
Male 8	9	9.00	8	0.00	6	0.1111	8

Figure 8. Analysis of a theoretical breeding network. (a) Depiction of the theoretical breeding network generated from both male (M) and female (F) scraping data where individual females were identifiable. (b) The out degree centrality (Out DC), in degree centrality (In DC), and closeness centrality (CC) for each female in the scraping network and their corresponding rank. (c) The out degree centrality (Out DC), in degree centrality (In DC), and closeness centrality (CC) for each male in the scraping network and their corresponding rank.

The goal of this study was to develop a method to explore the complexity of Deer social networks using scraping data. To achieve this goal, we first validated Tougaloo College's campus as a potential study site for urban Deer research. Population analysis estimated a deer herd totaling ~47 individuals using the campus during the survey period (Fig. 4a). Though population estimating methods described by Jacobson et al. (1997) have been shown to be less accurate in rural settings, these methods have been shown to be highly effective in suburban areas such as our survey location (Curtis et al. 2009). Survey of the college campus terrain revealed evidence of deer activity and 22 scrape sites (Fig. 1). Using remote monitoring over scrape sites, we collected over 36,000 digital images and recorded over 500 scraping observations. We documented urban scraping behaviors (Fig. 4) comparable with those reported in captive and rural deer (Alexy et al. 2001; Beier and McCullough 1990; Hirth 1977; Kile and Marchinton 1977; Marchinton et al. 1990; Miller et al. 1987, 1998, 2003; Moore and Marchinton 1974; Ozoga 1989; Sawyer et al. 1982; Sawyer and Miller 1989). Overall, our scraping behavior data correlated with the current literature and validated our study site as appropriate for social network analysis.

Scrapes are important sociosexual communications used by Deer to build breeding networks. Prior research has shown that patterns within social networks prior to breeding have demonstrated strategies in mate competition and mate choice in

(a)



(b)

	Closeness	Rank
Male 1	0.016	1
Male 2	0.018	2
Male 3	0.024	3
Male 4	0.067	4
Male 5	0.500	7
Male 6	0.200	6
Male 7	0.105	5
Male 8	0.900	8

Figure 9. Predicting mate selection within a hypothetical breeding network. (a) Displayed is the predicted mate selection pathway from Female 9 (*F9) to preferred males within the breeding network. Shown in red is the heat map function, where males closer to F9 are red hot and more likely to be selected as a mate as compared to males who are farther away and display lighter node shading. (b) Closeness scores and rank between Female 9 and males in the network, where males with higher ranking are closer to Female 9 and most likely to be selected as a mate.

other species, making social network analysis a useful tool to study mating systems (McDonald et al. 2013, 2020; Oh and Badyaev 2010; Wey et al. 2013). In our study, Males 1, 2, 3, and 4 were ranked as the top contenders due to their importance for network structure and their high connectivity. Male 2 was ranked the most domineering (dominating others) and Male 3 was deemed the biggest threat (targeted for suppression). Using closeness calculations, we were able to identify male rivalry between Males 2 and 3, which may be useful for predicting physical altercations (Fig. 5b, c, d). Taken together, these findings provide deeper insight into the complex competition and social struggle within male scraping networks to establish breeding roles.

Strategies to prevent and control the transmission of communicable diseases, such as chronic wasting disease in Deer populations, are an area of major concern for biologists and land managers (MDWFP 2020, Rivera et al. 2019). Network measures can be usd to predict disease transmission and identify potential super-spreaders within social networks (Hu et al. 2018, Kitsak et al. 2010, Zhang et al. 2019). Individuals with high ranked out degree centrality and closeness centrality scores are likely to more easily spread communicable diseases due to their influencing network positions. High-ranked in degree centrality and closeness centrality scores would make individuals more vulnerable to disease due to their closeness and incoming connections. In our study, Males 1, 2, 3, and 4 can be ranked as super-spreaders due to their centrality rankings (Fig. 5a). Using the male scraping network as a model, we can model the spread of communicable disease and predict the most vulnerable individuals (Fig. 6). We foresee scraping network analysis as a valuable tool used by biologists and land managers in future efforts to monitor and control transmission of communicable diseases within Deer populations.

Scrapes are also important social sites for female–male reproductive communications (Alexy et al. 2001, Hirth 1977, Moore and Marchinton 1974, Sawyer and Miller 1989, Sawyer et al. 1982). Two factors most likely influenced female scraping response: female estrus level and female mating preferences. Literature suggests that male scraping behavior stimulates estrus in females and therefore stimulates female scraping behavior (Alexy et al. 2001, Hirth 1977, Marchinton et al. 1990, Miller et al. 1987, Moore and Marchinton 1974, Sawyer and Miller 1989). A wide variety of semiochemicals have been described in urine, tarsal glands, forehead glands, interdigital glands, and microbial flora, giving individual Deer a unique chemical signature (Gassett et al. 1996, 2000; Miller et al. 1998; Osborn et al. 2000). Scent recognition in Deer is not a new theory; previous reports suggest that Deer identify each other from previous encounters and can even identify each other in low light using scent (Forand and Marchinton 1989, Muller-Schwarze 1971). Dominant males and subordinate males secrete different concentration of these volatile compounds, which allows females to preview male quality at scrape sites using scent (Gassett et al. 1996, 2000; Miller et al. 1998; Osborn et al. 2000). Spatial movement data suggests that just prior to entering estrus, females attempt to increase mate quality by excursive behaviors which advertise their presence to a larger number of competing males (Kolodzinski et al. 2010, Sullivan et al. 2017).

We speculate that during excursive behavior, females survey scrapes for mate quality, and develop mate preferences.

Documentation of female Deer mating preferences have been reported in the literature using spatial data and behavioral data (Kolodzinski et al. 2010, Labisky and Fritzen 1998, Morina et al. 2018, Sullivan et al. 2017). Studies have shown that females prefer large-antlered males as compared to smaller-antlered males, because large antlers signal better genetics quality and greater offspring success (Morina et al. 2018, Vanpé et al. 2007). Would females not also have a mate preference based upon scent? Here, we report further evidence of female mate preference at scrape sites, where individual male Deer received differing levels of female scraping responses (Fig. 7a). Using both female and male scraping data, we were able to model the local breeding network (Fig. 7e). Currently, there is no method to uniquely identify females without a tagging or tracking system, creating a major limitation to this study. Constrained by the lack of female identification, we grouped all the females into 1 node and analyzed the network. Based upon network measures, we ranked males based upon competiveness and female preference (Fig. 7f). To demonstrate future applications for this method, we generated a theoretical breeding network where both females and males were identifiable (Fig. 8a). Using network measures, we ranked females based upon sociability and popularity (Fig. 8b). Using closeness measure, we demonstrated how this method can be used to predict mate selection (Fig. 9). In conclusion, this work describes a new method of scraping network analysis of Deer mating systems with future applications for predicting social structure, modeling the spread of disease, and predicting mate selection. This method can be easily adapted to study many other aspects of Deer sociobiology such as bachelor grouping behavior, family grouping, and GPS proximity data to assist biologist and land managers in areas of research beyond scraping.

Acknowledgments

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Literature Cited

Alexy, K.J., J.W. Gassett, D.A. Osborn, and K.V. Miller. 2001. Remote monitoring of scraping behaviors of a wild population of White-tailed Deer. Wildlife Society Bulletin 29:873–878.

Barrett, L., S. Henzi, and D. Lusseau. 2012. Taking sociality seriously: The structure of multi-dimensional social networks as a source of information for individuals. Philosophical Transactions of the Royal Society B: Biological Sciences 367:2108–2118.

Bastian, M., S. Heymann, and M. Jacomy. 2009. Gephi: An open source software for exploring and manipulating networks. International AAAI Conference on Weblogs and Social Media. 2 pp. Available online at https://gephi.org/publications/gephi-bastian-feb09.pdf.

Beier, P., and D.R. McCullough. 1990. Factors influencing White-tailed Deer activity patterns and habitat use. Wildlife Monographs 109. 49 pp.

Beisner, B.A., J. Jin, H. Fushing , and B. Mccowan. 2015. Detection of social group instability among captive Rhesus Macaques using joint network modeling. Current Zoology 61:70–84.

Carter, A.J., S.L. Macdonald, V.A.Thomson, and A.W. Goldizen. 2009. Structured association patterns and their energetic benefits in female Eastern Grey Kangaroos, *Macropus giganteus*. Animal Behaviour 77:839–846.

Croft, D., J.R. Madden, D.W. Franks, and R. James. 2011. Hypothesis testing in animal social networks. Trends in Ecology and Evolution 26:502–507.

Curtis, P.D., B. Boldgiv, P.M. Mattison, and J.R. Boulanger. 2009. Estimating deer abundance in suburban areas with infrared-triggered cameras. Human–Wildlife Interactions 3:116–128.

De Vos, A. 1967. Rubbing of conifers by White-tailed Deer in successive years. Journal of Mammalogy 48:146–147.

Farine, D., and H. Whitehead. 2015. Constructing, conducting, and interpreting animal social network analysis. Journal of Animal Ecology 84:1144–1163.

Fedurek P., and J. Lehmann. 2017. The effect of excluding juveniles on apparent adult Olive Baboons (*Papio anubis*) social networks. PLoS One 12:e0173146.

Flack J.C, M. Girvan, F.B. de Waal, and D.C. Krakauer. 2006. Policing stabilizes construction of social niches in primates. Nature 439:426–429.

Forand, K., and L.R. Marchinton. 1989. Patterns of social grooming in adult White-tailed Deer. American Midland Naturalist 122:357–364.

Franz M., J. Altmann, and S.C. Alberts. 2015. Knockouts of high-ranking males have limited impact on baboon social networks. Current Zoology 61:107–113.

Gassett, J., K.A. Dasher, K.V. Miller, D.A. Osborn, and S.M. Russell. 2000. White-tailed Deer tarsal glands: Sex and age-related variation in microbial flora. Mammalia 64:371–377.

Gassett, W., D.P. Wiesler, A.G. Baker, D.A. Osborn, K.V. Miller, R.L. Marchinton, and M. Novotny. 1996. Volatile compounds from the forehead region of male White-tailed Deer (*Odocoileus virginianus*). Journal of Chemical Ecology 23:569–578.

Goldenberg, S.Z., I. Dougalus-Hamilton, and G. Wittemyer. 2016. Vertical transmission of social roles drives resilience to poaching in elephant networks. Curr Biol. 26:75–79.

Hirth, D.H. 1977. Social behavior of White-tailed Deer in relation to habitat. Wildlife Monographs 53. 53 pp.

Hu, Y., S. Ji, Y. Jin, L. Feng, H.E. Stanley, and S. Havlin. 2018. Local structure can identify and quantify influential global spreaders in large-scale social networks. PNAS 115:7468–7472.

Ilany A., A.S. Broom, and K.E. Holekamp. 2015. Topological effects of network structure on long-term social network dynamics in a wild mammal. Ecology Letters 18:687–695.

Jacobson, H., J.C. Kroll, R.W. Browning, B.H. Koerth, and M.H. Conway. 1997. Infrared-triggered cameras for censusing White-tailed Deer. Wildlife Society Bulletin 25:547–556.

Karns, G., R.A. Lancia, C.S. DePerno, and M.C. Conner. 2011. Investigation of adult male White-tailed Deer excursions outside their home range. Southeastern Naturalist 10:39–52.

Kile, T.L., and R.L. Marchinton. 1977. White-tailed Deer rubs and scrapes: Spatial, temporal, and physical characteristics and social role. American Midland Naturalist 97:257–266.

Kitsak, M., L.K.Gallos, , S. Havlin, and H.A. Makse. 2010. Identification of influential spreaders in complex networks. Nature Physics 6:888–893.

Koen, E., M.I. Tosa, C.K. Nielsen, and E.M. Schauber. 2017. Does landscape connectivity shape local and global social network structure in White-tailed Deer? PLoS ONE 12:e0173570.

Kolodzinski, J., L.V. Tannenbaum, L.I. Muller, D.A. Osborn, K.A. Adams, M.C. Conner, W.M. Ford, and K.V. Miller. 2010. Excursive behaviors by female White-tailed Deer during estrus at two Mid-Atlantic sites. American Midland Naturalist 163:366–373.

Labisky, R.F., and D.E. Fritzen. 1998. Spatial mobility of breeding female White-tailed Deer in low-density populations. Journal of Wildlife Management 62:1329–1334.

Lusseau, D. 2003. The emergent properties of a dolphin social network. Proceedings of the Royal Society B: Biological Sciences 270:S186–S188.

Marchinton, R.L., K.L. Johansen, and K.V. Miller. 1990. Behavioral components of White-tailed Deer scent marking: Social and seasonal effects. Pp. 295–301, *In* D.W. MacDonald, D. Müller-Schwarze, and S.E. Natynczuk (Eds.). Chemical Signals in Vertebrates. 5th Edition. Oxford University, London, UK. 688 pp.

McCullough, D.R. 1979. The George Reserve Deer Herd: Population Ecology of a K-selected Species. University of Michigan Press, Ann Arbor, MI. 271 pp.

McDonald, G., R. James, J. Krause, and T. Pizzari. 2013. Sexual networks: Measuring sexual selection in structured, polyandrous populations. Philosophical Transactions of the Royal Society B: Biological Sciences 368:20120356.

McDonald, G.C., N. Engel, S.S. Ratão, T. Tamás Székely, and A. Kosztolányi. 2020. The impact of social structure on breeding strategies in an island bird. Science Reports 10:13872.

Miller, K.V., and R.L. Marchinton. 1999. Temporal distribution of rubbing and scraping by a high-density White-tailed Deer, *Odocoileus virginianus*, population in Georgia. Canadian Field-Naturalist 113:519–521.

Miller, K.V., R.L. Marchinton, K.J. Forand, and K.L. Johansen. 1987. Dominance, testosterone levels, and scraping activity in a captive herd of White-tailed Deer. Journal of Mammalogy 68:812–817.

Miller, K.V., B. Jemiolo, J.W. Gassett, I. Jelinek, D. Wiesler, and M. Novotny. 1998. Putative chemical signals from the White-tailed Deer (*Odocoileus virginianus*): Social and seasonal effects on urinary volatile excretion in males. Journal of Chemical Ecology 24:673–683.

Miller, K., L.I. Muller, and S. Demarais. 2003. White-tailed Deer. Pp. 906–930, *In* G.A. Feldhamer, B.C. Thompson, and J.A. Chapman (Eds.). Wild Mammals of North America, John Hopkins University Press, Baltimore, MD. 1232 pp.

Mississippi Department of Wildlife Fisheries and Parks (MDWFP). 2019. Mississippi White-tailed Deer simulated mean conception date map. Available online at http://www.mdwfp.com/wildlife-hunting/deer-program/deer-breeding-date-map/. Accessed 01 December 2019.

MDWFP. 2020. Chronic wasting disease. Available online at http://www.mdwfp.com/wildlife-hunting/chronic-wasting-disease/. Accessed 15 December 2020.

Moore, W.G., and R.L. Marchinton. 1974. Marking behavior and its social significance in White-tailed Deer. Pp. 447–456, *In* V. Geist and F.R. Walther (Eds.). The Behavior of Ungulates and its Relation to Management. International Union for the Conservation of Nature, Gland, Switzerland. 940 pp.

Morina, D., S. Demarais, B.K. Strickland, and J.E. Larson. 2018. While males fight, females choose: Male phenotypic quality informs female mate choice in mammals. Animal Behaviour 138:69–74.

Mourier, J., C. Brown, and S. Planes. 2017. Learning and robustness to catch-and-release fishing in a shark social network. Biologyl Letters 13:20160824.

Muller-Schwarze, D. 1971. Pheromones in Black-tailed Deer (*Odocoileus hemiounus columbianus*). Animal Behaviour 19:141–152.

Naug, D. 2009. Structure and resilience of the social network in an insect colony as a function of colony size. Behavioral Ecology and Sociobiology 63:1023–1028.

Oh, K.P., and A.V. Badyaev. 2010. Structure of social networks in a passerine bird: Consequences for sexual selection and the evolution of mating strategies. American Naturalist 176:E80–E89.

Opsahl, T., F. Agneessens, and J. Skvoretz, J. 2010. Node centrality in weighted networks: Generalizing degree and shortest paths. Social Networks 32:245–251

Osborn, D.A., K.V. Miller, D.M. Hoffman, W.H. Dickerson, J.W. Gassett, and C.F. Quist. 2000. Morphology of the White-tailed Deer tarsal gland. Acta Theriologica 45:117–122.

Ozoga, J.J. 1989. Temporal pattern of scraping behavior in White-tailed Deer. Journal of Mammalogy 70:633–636.

Ozoga, J.J., and L.J. Verme. 1975. Activity patterns of White-tailed Deer during estrus. Journal of Wildlife Management 39:679–683.

Ozoga, J.J., and L.J. Verme. 1985. Comparative breeding behavior and performance of yearling vs. prime-age White-tailed bucks. Journal of Wildlife Management 49:365–372.

Rivera, N.A., A.L. Brandt, J.E. Novakofski, and N.E. Mateus-Pinilla. 2019. Chronic wasting disease in cervids: Prevalence, impact, and management strategies. Veterinary Medicine: Research and Reports 10:123–139

Sawyer, T.G., and K.V. Miller. 1989. Response of female White-tailed Deer to scrapes and antler rubs. Journal of Mammalogy 70:432–433.

Sawyer, T.G., R.L. Marchinton, and C.W. Berisford. 1982. Scraping behavior of female White-tailed Deer. Journal of Mammalogy 63:696–697.

Shizuka, D., A. Chaine, J. Anderson, O. Johnson, I.M. Laursen, and B.E. Lyon. 2014. Across-year social stability shapes network structure in wintering migrant sparrows. Ecology Letters 17:998–1007.

Sullivan, J., S.S. Ditchkoff, B.A. Collier, C.R. Ruth, and J.B. Raglin. 2017. Breeding behavior of female White-tailed Deer relative to conception: Evidence for female mate choice. Ecology and Evolution 7:2395–2402.

Tougaloo College. 2019. Our history. Available online at https://www.tougaloo.edu/about-tougaloo-college/our-history. Accessed 01 October 2020.

Vanpé, C., J.M. Gaillard, P. Kjellander, A. Mysterud, P. Magnien, D. Delorme, G.V. Laere, F. Klein, A.J. Olof Liberg, and M. Hewison. 2007. Antler size provides an honest signal of male phenotypic quality in Roe Deer. American Naturalist 16:481–493.

Wey, T., D.T. Blumstein, W. Shen, and F. Jordán. 2008. Social network analysis of animal behaviour: A promising tool for the study of sociality. Animal Behaviour 75:333–344.

Wey, T., J.R. Burger, L.A. Ebensperger, and L.D. Hayes. 2013. Reproductive correlates of social network variation in plurally breeding Degus (*Octodon degus*). Animal Behaviour 85:1407–1414.

Williams, R., and D. Lusseau. 2006. A Killer Whale social network is vulnerable to targeted removals. Biology Letters 2:497–500.

Zhang, D., Y. Wang, and Z. Zhang. 2019.Identifying and quantifying potential superspreaders in social networks. Science Reports 9:14811.