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Scraping Behavior in Male White-tailed Deer as a Potential Means of Transmitting Chronic Wasting Disease

Travis C. Kinsell
University of Nebraska at Lincoln, tckinsell@hotmail.com

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SCRAPING BEHAVIOR IN MALE WHITE-TAILED DEER
AS A POTENTIAL MEANS OF
TRANSMITTING CHRONIC WASTING DISEASE

by

Travis C. Kinsell

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SCRAPING BEHAVIOR IN MALE WHITE-TAILED DEER AS A POTENTIAL MEANS OF TRANSMITTING CHRONIC WASTING DISEASE

Travis C. Kinsell, M.S.

University of Nebraska, 2010

Advisor: Scott E. Hygnstrom

Chronic wasting disease (CWD) has become a concern for wildlife managers and hunters across the United States. High prevalence of chronic wasting disease (CWD) in older male white-tailed deer (*Odocoileus virginianus*) suggests that sex-specific social behavior may contribute to the spread of the disease among males. Scraping is a marking behavior performed by male white-tailed deer during the rut in which a pawed depression and associated over-hanging branch are marked with saliva, glandular secretions, urine, and feces. We placed 71 and 35 motion-activated cameras on scrapes in DeSoto National Wildlife Refuge in western Nebraska and eastern Iowa from Oct. – Nov. 2005 and Sept. – Nov. 2006, respectively. We recorded 5009 encounters and 1830 direct interactions. We developed an ethogram of behaviors of interest at scrapes. We found that males interacted with scrapes more frequently than females ($P < 0.001$). Male interactions were more complex, with 69% consisting of ≥2 observed behaviors versus 25% and 13% for females and fawns. We identified individual male deer ≥2.5 years old and determined the minimum number of different scrapes individuals visited and the number of individuals that visit a single scrape. Individuals that appeared on camera ≥5 times visited a mean of 3.9 scrapes (range = 1-15) and traveled a mean minimum distance of 978 m between consecutive scrapes. A mean of 5.1 individuals visited a single scrape, and up to 43% of individuals returned to a scrape previously visited at least once. We modeled Risk Values based on frequency of occurrence, duration, and Threat Values of each behavior, for contacting and transmitting CWD prions at scrapes. Adult males had the highest total Risk Values for contacting CWD prions (114.1) and shedding prions (59.4). The "grasp-lick branch" behavior had the highest Risk Value for adult males for both contacting and transmitting prions. Our study reveals a sex specific social behavior in male white-tailed deer that has the potential to spread chronic wasting disease between adult males in the population.

DEDICATION

I would like to dedicate this to my Parents:
Clint and Gloria Kinsell
They have supported and encouraged me in everything I do,
and have done everything they could to help me succeed.
I can’t thank them enough for that.

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INTRODUCTION

Chronic wasting disease (CWD) has become a concern for wildlife managers and hunters across the United States. Despite years of research on the disease, much is still unknown. Miller and Conner (2005) indicated that the influence of social behaviors on the spread of the disease may be an important area of research. Scraping behavior in male white-tailed deer is a marking behavior which is thought to have social and communicational significance (Moore and Marchinton, 1974; Hirth, 1977; Sawyer *et al.,* 1989). The following is a literature review of chronic wasting disease, scraping behavior in white-tailed deer (*Odocoileus virginianus*), and ethograms used to study behavior.

CHRONIC WASTING DISEASE

Chronic wasting disease is a fatal transmissible spongiform encephalopathy (TSE) of cervids that is similar to scrapie in sheep and goats, Creutzfeldt-Jakob disease in humans, transmissible mink encephalopathy in mink (*Mustela vison*), and bovine spongiform encephalopathy (BSE) in cattle (Williams and Young, 1980; Williams *et al.,* 2001). Chronic wasting disease has been found in mule deer (*Odocoileus hemionus*), white-tailed deer, Rocky Mountain elk (*Cervus elaphus nelsoni*, Williams and Young 1980; Spraker *et al.,* 1997), and moose (*Alces alces*, Baeten, 2007). The disease has not been proven to be naturally transmissible to humans, sheep, cattle, or other non-cervid species (Raymond *et al.,* 2000; Hill *et al.,* 2000; Belay *et al.,* 2004). Chronic wasting disease is the only TSE that is known to affect free-ranging wildlife (Williams and Young, 1993; Spraker *et al.,* 1997). Chronic Wasting Disease was first documented in a captive wildlife facility in Colorado in 1967 (Williams and Young, 1980).

The term “prion” is used to distinguish the causative agent for TSEs and is described as a proteinaceous infectious agent that is a protease-resistant form of natural cellular proteins (Prusiner, 1982; 1991). As with most TSEs, natural cellular proteins (PrP^c) are transformed into infectious proteins (PrP^{res}) which results in CWD infection (Soto, 2004; Weissmann, 2004). The disease agent is found in the central nervous system, lymphoid tissues, blood, and saliva of infected cervids (Williams *et al.,* 2001; Mathiason, 2006). Clinical signs and symptoms of CWD include emaciation, repetitive or unnatural behavior, lowered head and ears, increased salivation, weight loss, increased urination, low urine specific gravity, and terminal anorexia (Williams and Young, 1980; Spraker *et al.,* 1997; O’Rourke *et al.,* 1999). Pathological signs include lesions on the dorsal portion of the medulla oblongata, neuronal degeneration, and spongiform encephalopathy (Williams and Young, 1980; 1993; Spraker *et al.,* 1997; O’Rourke *et al.,* 1999).

The core endemic area for CWD consists of northeastern Colorado, southeastern Wyoming, and western Nebraska (Williams *et al.,* 2002). The disease has also been found in free ranging or captive animals in New Mexico, Wisconsin, Illinois, Utah, South Dakota, Kansas, Oklahoma, Montana, Minnesota, New York, West Virginia, Saskatchewan, Alberta, and Korea (Belay *et al.,* 2004; Williams, 2005; Sigurdson and Aguzzi, 2007).

The emergence of CWD in Nebraska is a major concern for hunters and wildlife officials because it has the potential to decimate cervid populations (Gross and Miller, 2001). Deer hunting and other cervid-related activities play a significant role in Nebraska's economy. The first case of CWD in Nebraska was found in a captive elk farm in Cherry County in 1998 (Nebraska Department of Agriculture, 2008). Nebraska's first documented case of CWD in the wild was in 2000 and since then, infected mule deer and white-tailed deer have been found across the Panhandle region of western Nebraska. The disease has now been detected as far east as Grand Island (Nebraska Game and Parks Commission, 2008).

Estimates of prevalence rates for wild populations are 5% in mule deer, 2% in white-tailed deer, and <1% in Rocky Mountain elk (Belay *et al.,* 2004). Prevalence rates have been found to be >13% for 4.5 to 5.5 year-old male white-tailed deer in Wisconsin (Osnas *et al.,* 2009). Prevalence has been found to be up to 2 times higher in males than in females for both mule deer (Miller *et al.,* 2000; Farnsworth *et al.* 2005; Miller and Conner 2005) and white-tailed deer (Grear *et al.,* 2006). The prevalence of CWD tends to increase with age in deer (Miller *et al.,* 2000; Farnsworth *et al.,* 2005; Grear *et al.,* 2006; Miller and Conner, 2005).

Transmission routes of CWD are relatively unknown. Mathiason *et al.,* (2006) confirmed that the disease can be passed through blood and saliva. It is also hypothesized that CWD prions are spread through feces, urine, direct contact with infected deer, and living in an area contaminated with CWD prions (Spraker *et al.,* 1997; Miller *et al.,* 1998; Gross and Miller, 2001; Miller *et al.,* 2004, Nichols *et al.,* 2009). Kincaid and Bartz (2007) showed that the nasal cavity is an efficient route of infection in hamsters. Prions have been found in feces (Safar *et al.,* 2008; Tamgüney, 2009) and in low concentrations in urine (Haley *et al.,* 2009). Prions have been shown to bond with soil particles, such as some types of clay and quartz sand, sometimes enhancing their infectivity through oral exposure (Cooke *et al.,* 2007; Johnson *et al.,* 2007; Ma *et al.,* 2007). Prions have been shown to persist in the environment for >2 years, and maintain their ability to infect (Miller *et al.,* 2004; Johnson *et al.,* 2006; Mathiason *et al.,* 2006; Seidel *et al.,* 2007). Manganese oxides however, may degrade prions in environments that are rich in manganese minerals (Russo *et al.,* 2009). White *et al.* (2010) found that increased manganese in elk brain matter with decreased magnesium appeared to increase the risk of CWD infection.

SCRAPES

Scrapes are chemical signposts made by white-tailed deer to communicate with other deer in the area. Scrapes are thought to assist in the induction and synchronization of estrus in females (Moore and Marchinton, 1974; Hirth, 1977; Sawyer *et al.,* 1989). Scrapes are often located in open, highly visible areas, such as game trails, old roads, forest edges, clearcuts, and forest openings (Kile and Marchinton, 1977; Miller and Marchinton, 1999). The first scientific description of a male white-tailed deer creating a scrape was provided by Pruitt (1953). In a short note, he described how a large male came to the edge of a forest and pawed at the ground, creating a circular depression. Scrape depressions are typically 0.7 m long and 0.3 m wide (Hirth, 1977). Urination, rub-urination, and to a lesser extent, defecation in the depression are associated with the creation and maintenance of scrapes (Hirth, 1977; Kile and Marchinton, 1977; Miller *et* *al.,* 1987). Pawing is thought to be a means of scent marking the scrape with the interdigital glands (Moore and Marchinton, 1974). Females have been documented making and maintaining scrapes, although this occurrence appears to be rare, and is not restricted to the breeding season (Sawyer *et al.,* 1982; 1989).

Scrapes typically are associated with an over-hanging branch 1-2 m above the ground (Hirth, 1977; Kile and Marchinton, 1977; Marchinton and Hirth, 1984). Kile and Marchinton (1977) showed that the scrape-branch association is highly significant ($P < 0.001$). Over-hanging branches are marked with secretions from the forehead glands (Atkeson and Marchinton, 1982), pre-orbital glands, and/or saliva (Miller *et al.,* 1987). The male that Pruitt (1953) described alternately pawed at the ground and manipulated over-hanging branches. The deer grasped the over-hanging branches in his mouth, pulled them down, and raked his antlers through them. Males also nuzzle, lick, and pull over-hanging branches with their mouths (Moore and Marchinton, 1974; Kile and Marchinton, 1977; Hirth, 1977). Manipulation of the over-hanging branch is believed to be a means of scent marking (Moore and Marchinton, 1974; Kile and Marchinton, 1977; Miller *et al.,* 1987).

Older male white-tailed deer make the majority of the scrapes (Ozoga and Verme, 1985; Miller *et al.,* 1987; Marchinton *et al.,* 1990; Alexy *et al.,* 2001). The degree of involvement by younger males is still unclear. Yearling or 2.5-year-old males interacted with scrapes little or not at all in captive facilities (Miller *et al.,* 1987; Marchinton *et al.,* 1990). In another study on captive deer, Ozoga and Verme (1985) reported that yearlings made only 15% of the scrapes and began scraping later than mature males. Alexy *et al.* (2001), however, reported that the scraping activity of yearlings was not delayed in relation to older males, in a study done on wild deer with remote cameras. Alexy also reported that 42% of the scrapes observed were created by yearling males, although they noted that yearlings marked less frequently than older males.

Males begin making scrapes approximately 1-2 months prior to breeding. The activity intensifies and peaks around late October or early November, then drops off through the end of November and into December (Kile and Marchinton, 1977; Ozoga and Verme, 1985; Ozoga, 1989; Miller and Marchinton, 1999; Alexy *et al.,* 2001). Most scraping behavior occurs at night (Alexy *et al.,* 2001).

CONCLUSION: SCRAPING AND CWD

The behavior of scraping is likely a contributor to the transmission of CWD in white-tailed deer. Miller and Conner (2005) suggested that sex-specific social behavior is important to understanding why prevalence of CWD varies between the sexes. I believe that infectious prions could be transmitted through scrapes in several ways. They could be transferred to another deer near the scrape by direct contact of mucosal membranes, such as the nose. They could be transmitted via over-hanging branches because of contaminated saliva and glandular substances on the branches. They could also be transmitted through the pawed depression on the ground as deer paw and sniff at soil contaminated with urine, feces, and glandular substances.

Manipulation of the over-hanging branch may be a focal point for environmental contamination. Saliva has been identified as a vehicle of transmission (Mathiason *et al.,* 2006). Prions could be shed onto a branch when a deer takes the branch into its mouth.

Any other deer that subsequently interact with the scrape and lick or grasp the branch may come into contact with CWD prions.

ETHOGRAMS

To begin understanding behavior, behaviors of interest should be defined and catalogued in an ethogram. To most, the definition of an ethogram is a list of precise, detailed descriptions of the behavior patterns of a species (Brown, 1975; Eibl-Eibesfeldt, 1975; Immelmann, 1980; Dawkins, 2007). An ethogram does not always catalog the entire behavioral repertoire of a species. Ethograms of more specific subsets or functional systems of behaviors are often used (Immelmann, 1980; Lehner, 1996). An ethogram often is accompanied by illustrations or photographs depicting the climax of the behavior. The science that goes into creating an ethogram has been referred to as the morphology of behavior, because behavioral patterns can be just as unique as the morphological characteristics used to identify a species (Immelmann, 1980).

Ethograms have taken many different forms over the years, with some ethologists including excruciating detail, while others have minimized descriptions. Schleidt *et al.* (1983) proposed a standardized ethogram using the bluebreasted quail (*Coturnix chinenesis*) as an example. The position and angle of the trunk and extremities of the bird were taken into account as a code for each body position of each behavior. Other ethograms, including a more recent ethogram of predatory behavior (MacNulty *et al.,* 2007), have taken a simpler approach. MacNulty's ethogram provided a verbal description of each state and then quantified the probability of an animal entering a given state, conditional on the current state (i.e. attacking, after approaching a group of prey).

I was unable to find many examples of ungulate ethograms in the primary scientific literature, but some examples were found in the secondary literature. A very good example of an ungulate ethogram was provided by Clutton-Brock (1982) on the displays and interactions of red deer (*Cervus elaphus*) stags during the breeding season. He listed each display and interaction, followed by detailed descriptions of the actions that made up the behaviors. Geist (1981) provided a detailed description of behaviors exhibited by mule deer, including the functional groups of feeding, predator avoidance, and courtship. Geist (2002) provided similar descriptions of the behavior of elk in North America.

Pruitt (1956) was the first to describe a male white-tailed deer making a scrape when he described the creation of a “pawed circle.” Hirth (1977) provided an informal ethogram of scent marking behaviors. He described thrashing, rubbing, scraping, and rub-urination, with an emphasis on the social behavior and situations which lead up to the scent marking behaviors. He described a ‘typical’ scraping sequence that involved pulling the branches with the mouth, raking the antlers across the branches, rubbing the branches against the forehead, pawing the ground, urinating, and rub-urinating. Nothing was mentioned in this description about the use of the pre-orbital gland or deer smelling or licking either the branch or the scrape. A similar, but shorter description was provided by Marchinton and Hirth (1984). Woods (1988) listed 8 behaviors at scrapes in his study. These behaviors were listed under 2 categories: limb events and ground events. Limb events consisted of smelling the limb, licking the limb, rubbing the pre-orbital gland on the limb, and rubbing the forehead on the limb. Ground events consisted of smelling the scrape, pawing the scrape, urinating in the scrape, and auto-erotic behavior. No descriptions of these behaviors were provided. While we have found some descriptions of the scraping process in the literature, we have not been able to find a formal ethogram describing all of the behaviors associated with scraping in the primary scientific literature.

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CHAPTER 2 : AN ETHOGRAM FOR SCRAPING BEHAVIOR BY WHITE-TAILED DEER

KINSELL, TRAVIS C.[1], HYGNSTROM, SCOTT E., CLEMENTS, GREGORY M., FROST, CHARLES J.,

School of Natural Resources, University of Nebraska-Lincoln, Lincoln 68583-0974

VERCAUTEREN, KURT C.

USDA, APHIS, WS, National Wildlife Research Center, Fort Collins, CO 80521-2154

Abstract.-- Whereas white-tailed deer (*Odocoileus virginianus*) are a widely studied species, previous studies have not provided an ethogram that fully describes their behavior at scrapes. We placed 71 motion-triggered cameras on 85 scrapes on DeSoto National Wildlife Refuge for a total of 1492.5 functional camera days in the fall of 2005. We recorded 3106 encounters (the deer came within 2 m) with scrapes by deer of all sex and age classes; 1218 of those resulted in direct interactions (the deer performed a scrape-related behavior) with scrapes. Out of 1477 adult and yearling male encounters with scrapes, interactions were observed 57% (n = 893) of the time. Daily interactions by males peaked during the nighttime hours of 00:00 – 02:59 and 18:00-20:59. Average interaction time for males was 72 s (95% CI = [1 ; 258]). The smell branch and smell scrape behaviors were the most common, appearing in 63% and 57% of male interactions, respectively. Adult females encountered scrapes 896 times and interacted 25% (n = 223) of the time. Daily interactions by adult females peaked during the nighttime hours of 03:00 – 5:59 and 18:00-20:59. Average interaction time was 63 s

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[1] Corresponding author: email: tckinsell@huskers.unl.edu

(95% CI = [1 ; 216]). Fifty-four percent of female interactions consisted of smelling the scrape. Males (57%) interacted with scrapes more frequently than females (25%; $P < .0001$). Male interactions were more complex, with 69% consisting of ≥ 2 scrape-related behaviors versus 25% and 13% for females and fawns, respectively. We observed “flag-up” departure from scrapes in 21% of the interactions and pre-orbital gland marking of overhanging branches in 22% of the interactions. Increased understanding of scrape-related behavior by white-tailed deer may enable us to better understand dominance, mate selection, and disease transmission in deer.

Keywords: behavior, ethogram, Nebraska, *Odocoileus virginianus,* overhanging branch, rub-urination, scrape, scraping, white-tailed deer

INTRODUCTION

Scrapes (Figure 2-1) are chemical signposts made by male white-tailed deer (*Odocoileus virginianus*) to communicate with other deer in the area during the breeding season (Moore and Marchinton, 1974; Hirth, 1977). Scrapes are also thought to be a way for males to express dominance and establish a hierarchy (Moore and Marchinton, 1974; Hirth, 1977; Miller *et al.*, 1987). Pruitt (1956) was the first to describe a male white-tailed deer that created a circular depression, or “pawed circle” by scraping the ground with its hooves and antlers and alternately interacting with an over-hanging branch. Rub-urination, and to a lesser extent normal urination and defecation in the depression are associated with the creation and maintenance of scrapes (Hirth, 1977; Kile and

Marchinton, 1977; Miller *et al.*, 1987). It is likely that scent from interdigital sebaceous and sudoriferous gland secretions (Quay and Müller-Schwarze, 1970) are deposited in the scrape during the process of pawing a depression. The scent may indicate the age and dominance of a male (Gassett *et al.*, 1996).

Scrapes typically are associated with an over-hanging branch 1-2 m above the ground (Hirth, 1977; Kile and Marchinton, 1977; Marchinton and Hirth, 1984). Over-hanging branches are marked with pre-orbital glands, forehead glands and/or saliva (Miller *et al.*, 1987). Atkeson and Marchinton (1982) show that forehead secretions are used to mark rubs and may be used in other signpost marking behaviors. Hirth (1977) observed that males allowed branches to rub across, or spring up across the forehead.

Males begin making scrapes approximately 1-2 months prior to breeding. The activity intensifies and peaks in late-Oct. to early-Nov., and drops off through the end of Nov. and Dec. (Kile and Marchinton, 1977; Ozoga and Verme, 1985; Ozoga, 1989; Miller and Marchinton, 1999; Alexy *et al.*, 2001). Most scrape-related behavior of deer in wooded habitats of the southern United States occurs at night (Alexy *et al.*, 2001). Females have been observed making and maintaining scrapes, although this occurrence appears to be rare and is not restricted to the breeding season (Sawyer *et al.,* 1982). Females also walked through scrapes, sniffed them, and often urinated within 20 m of scrapes (Sawyer *et al.*, 1982; 1989).

To study behavior of animals, it is helpful to first develop a comprehensive list of behavioral patterns of a species (ethogram) with precise, detailed descriptions of those behaviors (Brown, 1975; Eibl-Eibesfeldt, 1975; Immelmann, 1980; Dawkins, 2007). Hirth (1977) described scent-marking behaviors in white-tailed deer with an emphasis on the social behaviors and situations that led up to scent marking events. He described a ‘typical’ scraping sequence that involved pulling over-hanging branches with the mouth, raking antlers across the branches, rubbing over-hanging branches against the forehead, pawing the ground, urinating, and rub-urinating. Although anecdotal accounts exist, we were unable to find prior detailed research that documents white-tailed deer using the pre-orbital gland for marking, or licking and smelling the scrape depression or branch. Marchinton and Hirth (1984) provide a brief description similar to the Hirth (1977) account. Frequency of occurrence of distinct scrape-related behaviors has not previously been reported. In this study we provide a detailed ethogram for scrape-related behavior by white-tailed deer.

METHODS

STUDY AREA

DeSoto National Wildlife Refuge (DNWR) is located in the flood plain of the Missouri River, about 32 km north of Omaha, Nebraska between Blair, Nebraska and Missouri Valley, Iowa, USA. The DNWR consists of a 3,384-ha patchwork of riparian hardwood forest, grassland, wetland, and cropland administered by the US Fish and Wildlife Service. The interspersion of habitat supports a diverse range of flora and fauna (US Fish and Wildlife Service, 2008).

Estimates of pre-harvest densities of white-tailed deer at DNWR were 41-51 deer/km^2 from 2004–2007 (Hefley *et al.,* 2010). Estimates of female:male ratios were 2.15:1 and 1.86:1 and fawn:doe ratios were 1.28:1 and 1.43:1 in 2005 and 2006, respectively (Clements *et al.,* 2010). As part of other research efforts in the study area, 20-25 females and 20-30 males were radio-collared and ear-tagged on DNWR during the time of this study. An estimated 42 additional males and 17 females were marked with ear tags alone. We estimate that up to 24% of the males and 6% of the females were marked on DNWR during the study (Gilsdorf and Clements, pers. comm.).

MATERIALS AND METHODS

We located scrapes during the fall breeding season from mid-Oct. through Nov. of 2005 by walking forest-field edges, trails, and 2-track roads through the forest. Each was marked with a Global Positioning System (GPS; Garmin, Olathe, KS, USA). We selected scrapes if they appeared to be recently active (*i.e.* freshly disturbed soil in the depression or freshly broken over-hanging branches), and were within 8 m of a tree that would support a camera for more detailed monitoring. All monitored scrapes were associated with over-hanging branches. We monitored 85 scrapes with remote infrared motion-activated video cameras (StumpCam^{tm} Inc., Tyler, Texas, USA) and motion-activated digital camera systems (Reconyx Silent Image, LaCrosse, Wisconsin, USA). Sixty-two of the 85 scrapes were located on forest-field edges and 23 were located in the forest interior (Figure 2-2). We hung cameras from trees 4-8 m away from the scrape and 1-3 m above ground, and focused them to provide a field of view that included a scrape, an over-hanging branch, and a minimum 2-m radius of the surrounding area. We programmed StumpCams to record for 3 min when triggered with a 10 s (hardware minimum) recycle period between triggers. We programmed Reconyx cameras to take 1 frame per second for 30 s, with a 1 s recycle time between triggers. We moved cameras if scrapes were inactive >1 week. We checked StumpCams every 3-4 days and Reconyx cameras 1 time per week. Batteries and recording media were replaced as needed to keep the cameras functional. Each time cameras were checked we recorded the individually-coded scrape name (GPS waypoint name + camera ID), time, battery condition, and any other pertinent comments regarding condition of the scrape or camera. We labeled each video tape with the scrape name, and date and time of insertion and removal from the camera. Reconyx media were labeled with the camera ID and images were downloaded onto a laptop after each camera was checked. Video tapes were viewed and any encounters were digitized and saved to a hard drive and placed in a folder labeled with the individually-coded scrape name and tape number for easy reference. StumpCams monitored scrapes for a combined 976 functional camera days. Reconyx cameras monitored scrapes for a combined 519 functional camera days.

We defined an “encounter” with a scrape as an event in which a deer came within 2 adult body lengths (~2 m) of a scrape, with a high likelihood that the deer could identify the scrape and interact with it if so inclined (*i.e.* a deer walks nearby the scrape, versus running past the scrape). We noted an “interaction” with a scrape when a deer approached a scrape and performed ≥1 scrape-related behavior as defined below. All interactions were also encounters, however, not all encounters resulted in interactions. We classified males as adult, yearling or fawn based on antler size, body size, body condition, height and length of rostrum. We classified females as fawn or adult, based on body size, body condition, height and length of rostrum. We examined the video images and still pictures frame by frame to identify behaviors associated with scrapes and over-hanging branches.

Behavioral categories identified in the ethogram included: smell scrape, scrape ground, smell branch, grasp-lick branch, mark branch with pre-orbital gland, other branch interactions (*i.e.* rake antlers and non-saliva or glandular contact with the branch), rub-urinate, urinate, defecate, Flehmen (lip-curl), and flag-up departure. Each behavior was recorded in Microsoft Access (Microsoft Corporation, Redmond, Washington, USA) as present or absent during the time of an interaction. Dates and times were recorded for the beginning and end of each encounter. Data were queried out of Microsoft Access into a Microsoft Excel (Microsoft Corporation, Redmond, WA, USA) database, where it was formatted to be imported into Program R (R Development Core Team, 2009) for statistical analysis. We used Program R, package Chron (James and Hornik, 2009) to analyze interaction time and duration data. We split the day into 8, 3-hour time periods beginning at 00:00-02:59 and created distributions of time-of-day of scrape visitations. We performed a test for equality of proportions on the proportion of encounters that resulted in interactions for males versus females. We quantified each behavior as a percentage of the total number of interactions by sex. We recorded the time spent at a scrape from the moment an animal came within 2 m of a scrape, to the time it exited for encounters and interactions, and used Excel to find the average, median and 95% confidence intervals for males and females.

RESULTS

We observed 3106 encounters with scrapes in Oct. – Nov. 2005 across all sex and age classes. Of those encounters, 39% (n=1218) resulted in interactions with scrapes. Of those interactions, 69% (n = 839) were performed by adult (n = 566) and yearling (n = 273) males. Thirty-eight percent of all adult and yearling male encounters (n = 2415) were observed during the peak times of 18:00 – 20:59 (n = 473), and 03:00 – 05:59 (n = 451). Encounters remained high during the night (Figure 2-3) and dropped off dramatically (4%) from 09:00 – 14:59 (n = 105).

Adult and yearling males encountered scrapes 1477 times and interacted with scrapes 57% (n = 839) of the time. Males interacted with scrapes more frequently (test for equality of proportions, $p < 0.001$) than adult females when they encountered a scrape. Interactions by males typically consisted of a combination of 2 (21%, n = 177), 3 (20%, n = 168), 4 (12%, n = 102), or more (16%, n = 132) of the behaviors described above (Table 2-1). Single-behavior interactions made up 31% (n = 260) of the male interactions. The most common male single-behavior interactions (Table 2-2) were smell scrape (53%, n = 139), and smell branch (34%, n = 88). Male interactions were more complex than female or fawn interactions. Sixty-nine percent of male interactions consisted of ≥2 behaviors, while only 25% and 13% consisted of ≥2 behaviors for females and fawns, respectively (Table 2-1). Females and fawns were not observed performing more than 3 behaviors during an interaction. One male was observed performing 9 of the 11 described behaviors during a single interaction (Table 2-1).

Average time for an encounter by a male was 56 s (95% CI = [1 ; 235]) with a median of 26 s. Average time for an interaction by a male was 72 s (95% CI = [1 ; 258]) with a median of 43 s. Males interacted with scrapes the most from the hours of 00:00 – 02:59 and 18:00 – 20:59, and the least from 09:00 – 14:59 (Figure 2-3).

Adult females encountered scrapes 896 times and interacted 25% (n = 223) of the time. Adult female encounters consisted of walking by (52%, n = 463), grazing in the area (11%, n = 99), walking by and grazing (4%, n = 34), walking by and acknowledging (looked at the depression or branch or paused at the scrape without interacting) the presence of a scrape (7%, n = 59), and other non-interactions (2%, n = 18). Interactions by adult females (n = 223) with a scrape consisted of smell scrape (54%, n = 120), smell branch (17%, n = 37) (Table 2-2), smelling both (21%, n = 46), and other scrape-related behaviors (10%, n = 22). Average time for an encounter was 41 s (95% CI = [1 ; 149]) with a median of 16 s. Average time for an interaction was 63 s (95% CI = [1 ; 216]) with a median of 37 s. Females interacted with scrapes the most from the hours of 03:00 – 05:59 and 18:00 – 20:59, and least from 09:00 – 14:59 (Figure 2-3).

SCRAPE DEPRESSION-RELATED BEHAVIORS

The following behaviors were associated with the creation, maintenance, or inspection of scrape depressions by males in order of frequency of occurrence. Percentages are for adult and yearling males only. Females only participated in the smell scrape behavior and percentages are reported above.

Smell scrape (61%, n = 510).-- The deer paused at the scrape and lowered its nose to within 10 cm of the scrape depression, without immediately grazing or manipulating the scrape in any way, rarely making direct contact with the soil (Figure 2-4a). Smell scrape made up 23% of all observed behaviors (n = 2227) by male white-tailed deer (Table 2-3). Smell scrape most often was accompanied by smell branch (59%) or grasp-lick branch (37%; Table 2-4).

Scrape ground (27%, n = 225).-- The deer pawed the ground directly below the over-hanging branch. The pawing action cleared the ground of any loose vegetation or leaves creating a bare area of ground under the over-hanging branch (Figure 2-4b). The action occurred even in areas where the ground was covered in short, thick grass that could not be cleared in a single scraping event. Scrape ground made up 10% of all observed behaviors (n = 2227) by male white-tailed deer (Table 2-3). Scrape ground was often directly followed by smell scrape. Scrape ground most often was accompanied by smell branch (77%) or smell scrape (66%; Table 2-4).

Rub-urinate over scrape (14%, n = 118).-- The deer moved its posterior legs slightly forward and together ventro-medially in a way that brought the tarsal glands into proximity below the penis. The deer then urinated onto the tarsal glands while rubbing the glands together (Figure 2-4c). Rub-urinate over scrape made up 5% of all observed behaviors (n = 2227) by male white-tailed deer (Table 2-3). Rub-urinate over scrape most often was accompanied by smell branch (65%) or smell scrape (62%; Table 2-4).

OVER-HANGING BRANCH-RELATED BEHAVIORS

The following behaviors are associated with the marking, manipulation, or inspection of over-hanging branches by males in order of frequency of occurrence. Percentages are for interactions of adult and yearling males only. Female behaviors consisted of smell branch and lick-grasp branch and are reported above.

Smell branch (67%, n = 561).-- The deer lifted or held its nose within 10 cm of or in contact with an over-hanging branch (Figure 2-4d) and made no immediate effort to mark the branch. Nose-to-branch contact was common. Smell branch made up 25% of all observed behaviors (n = 2227) by male white-tailed deer (Table 2-3). Smell branch most often was accompanied by grasp-lick branch (48%) or smell scrape (53%; Table 2-4).

Grasp-lick branch (39%, n = 330).-- The deer made contact with the over-hanging branch in 1 of 2 ways, either lifting its head to an over-hanging branch and take the branch into its mouth, occasionally pulling down on the branch, resulting in the breaking or biting off of the tip of the branch (Figure 2-4e), or lifting its head to an over-hanging branch and extend its tongue to make contact with the branch. Males occasionally would stand on their hind legs to reach higher branches. Grasp-lick branch made up 15% of all observed behaviors (n = 2227) in male white-tailed deer (Table 2-3). Grasp-lick branch was most often accompanied by smell branch (82%) or smell scrape (58%; Table 2-4).

Mark branch with pre-orbital gland (22%, n = 187).-- The deer lifted its head to the over-hanging branch, closed its eye(s), and moved its head in a way that caused the branches to make contact with or pass over the pre-orbital glands near the eyes (Figure 2-4g). Deer would often lift the head to position the branch under the chin, then pull down to allow the branch to spring back up, along the cheek, and over the eye. Branches often made incidental contact with forehead or antlers. Males occasionally would stand on their hind legs to reach higher branches. Mark branch with pre-orbital gland made up 8% of all observed behaviors (n = 2227) by male white-tailed deer (Table 2-3). Mark branch with pre-orbital gland most often was accompanied by smell branch (80%) or grasp-lick branch (62%; Table 2-4).

Other branch contact (2%, n = 17).-- 'Other branch contact' included all interactions with over-hanging branches that did not involve saliva or pre-orbital gland contact with the branch. Incidental contact with antlers or forehead in the process of manipulating the branch for mouth or eye contact was not included. The primary behavior seen in this category was raking of antlers through over-hanging branches. The deer would lift its antlers to the over-hanging branch and move its head in a circular, side-to-side, and/or front-to-back motion, which caused the antlers and forehead to rake through the over-hanging branches (Figure 2-4f). The behavior occasionally resulted in the breaking of branches and entanglement of antlers in the branches. Other branch contact made up 8% of all observed behaviors (n = 2227) by male white-tailed deer (Table 2-3). Other branch contact most often was accompanied by smell branch (71%), grasp-lick branch (53%) or mark branch with pre-orbital gland (53%; Table 2-4).

OTHER SCRAPE-RELATED BEHAVIORS

The following behaviors occurred at scrapes, but were not always associated with the over-hanging branch or the scrape depression in order of frequency of occurrence. Percentages are for interactions of males only. We did not observe females conducting these other scrape-related behaviors.

Flag-up departure (21%, n = 175).-- The male left the vicinity of the scrape with its tail erect and fully or partially showing the “white flag” and rump patch (Figure 2-4i). The tail was held steady and did not wag side to side. Males displaying this behavior did not bolt from the scrape or show other signs of alarm. The tail was considered to be raised if it was within 45 degrees of being vertical and the white underside was clearly visible. Flag-up departure made up 8% of all observed behaviors (n = 2227) by male white-tailed deer (Table 2-3). Flag-up departure most often was accompanied by smell branch (70%) and smell scrape (61%; Table 2-4).

Flehmen (<1,. n = 3).-- “Flehmen,” or lipcurl is a term first used by Schneider (1930) for a grimace-like response to urine inspection observed in a variety of mammals during the breeding season, including most ungulates and felids (Schneider, 1930; Estes, 1972; Altieri and Müller-Schwarze, 1980).

The male smelled a location where we had observed a female urinating previously and lifted its head to approximately a 45-degree angle and raised its upper lip (*i.e.* lip curl). The lip curl was accompanied by swinging of the head from side to side in 1 observation. Each time, smell scrape occurred in the same interaction as Flehmen (Table 2-4).

AUXILIARY BEHAVIORS

The following behaviors occurred in the vicinity of a scrape, but were not necessarily related to scraping behavior by adult and yearling males. Behaviors are discussed in order of frequency of appearance. The following categories were considered encounters unless otherwise noted in the description. Percentages are based on all male encounters with scrapes (n = 1477).

Walk-by scrape (30%, n = 440).-- The deer moved past the scrape within a 2 m radius with 2-3 hooves in contact with the ground at the same time (as opposed to running in which <2 hooves may be in contact with the ground at the same time). The deer did not interact with or by any noticeable means acknowledge the presence of the scrape.

Walk-by and acknowledge scrape (11%, n = 157).-- The deer moved past the scrape within a 2 m radius with ≥3 hooves in contact with the ground at all times. The deer made some indication that it was aware of the presence of the scrape, but did not stop to interact with the scrape, such as it glanced down at the ground in the direction of the scrape as it passed, lifted its head as it passed under the licking branch, and/or looked at or smelled the over-hanging branch without breaking stride. Walk-by and acknowledge scrape was considered an interaction if the deer appeared to smell either the scrape or the over-hanging branch; otherwise it was considered an encounter.

Graze (11%, n = 162).-- The deer consumed forage within 2 m of the scrape. A grazing event could also be associated with a walk-by scrape, or walk-by and acknowledge scrape as the deer grazed through the area near the scrape. When grazing occurred near the scrape, it was considered an encounter if no other scrape-related activities took place.

Defecation (3%, n = 51).-- The deer deposited fecal material in or near the scrape. Defecation occurred in 6% of male interactions. Whereas defecation is not exclusive to scraping behavior, all defecation events recorded in this study occurred with 2 m of a scrape. Therefore, we considered defecating to be part of an interaction.

Urination (3%, n = 49).-- The deer urinated in or near the scrape without any effort to urinate over the tarsal glands. Normal urination occurred in 6% of male interactions. Whereas urinating is not exclusive to scraping behavior, all urination events recorded in this study occurred within 2 m of a scrape. Therefore, we considered urination to be part of an interaction.

DISCUSSION

Males performed 69% of all observed interactions, and 68% of the total male interactions were performed by adult males (≥2.5 year olds) versus 32% by yearlings. We found that most encounters and interactions took place from dusk to dawn, which is consistent with what Alexy *et al.* (2001) found in Georgia. Male encounters resulted in interactions 57% of the time, versus 25% for females ($P > 0.001$) which concurs with findings from Alexy *et al*. (2001)of 52% (males) and 21% (females). Male interactions ranged from smelling the scrape or branch, to participating in 9 of the 11 described behaviors during a single interaction. Females and fawns were not seen performing >3 behaviors during an interaction (Table 2-1). Nearly half (48%) of interactions by males consisted of ≥3 behaviors whereas 74% of interactions by females consisted of only 1 behavior. Female interactions consisted mostly of smelling the overhanging branch or scrape depression. Smell branch (67%) and smell scrape (61%) were the most common behaviors performed by males during an interaction, followed by grasp-lick branch (39%).

Females that interacted with scrapes ($n = 223$) typically smelled the scrape (54%), or smelled the over-hanging branch (17%), further re-enforcing the idea that scrapes are chemical signposts used to communicate between the sexes. Creation or maintenance of scrapes by females, as described by Sawyer *et al*. (1982), was not observed in this study. We recorded few instances of females urinating near scrapes during an interaction (1%, $n = 3$), whereas Sawyer *et al.* (1989) and Moore and Marchinton (1974) indicated that females commonly urinated in the vicinity (<20 m) of scrapes. Events of female urination in our study may have been taking place outside the 2 m radius around the scrape. Infrequent female urination likely influenced the number of observations of Flehmen in males (n = 3), as this behavior is triggered by the inspection of a female's urine while in the presences of the female (Geist, 1981; Marchinton and Hirth, 1984). It is interesting to note that 2 of the 3 Flehmen events we observed occurred over urine that was not fresh. Both events took place at the same scrape and urine location, 6 and 29 h after the observed female urination event occurred.

A hypothetical scraping sequence by an adult male that would include most of the above described behaviors might unfold as follows: a male would approach a scrape, smell the over-hanging branch, then grasp it in its mouth and pull (or lick the branch repeatedly). The deer would then manipulate the branch so that it would pass over the pre-orbital gland and finally smell the branch again. Subsequently, the deer would paw the depression, smell the pawed area, and rub-urinate over the depression before slowly moving away from the location with tail erect. Our ethogram of scrape-related behavior is consistent with previous descriptions (Hirth, 1977; Marchinton and Hirth, 1984) with the exception that we found only 1 mention pre-orbital gland marking in the primary literature (Miller *et al.*, 1987), and flag-up departure, to our knowledge, has not been described in the past. Pruitt (1959), however, noted that the male he observed raised its tail in the process of creating the scrape. Interactions with the over-hanging branch were almost always followed by smelling the branch again, confirming the idea that scrapes are marked with chemical substances (Miller *et al.*, 1987) and serve as chemical "signposts" (Moore and Marchinton, 1974; Hirth, 1977).

The “tail erect” posture has been described in black-tailed deer (*Odocoileus hemionus columbianus*) by Stankowich (2008), who associated the posture with excited states such as aggression and alarm. In white-tailed deer, the raised tail, exposing the rump patch, is thought to be associated with conspecific communication and group cohesion during flight from a predator and is used when fleeing across an open field or through thick vegetation (Smith, 1991). Flagging may indicate the deer’s good health and ability to escape from a predator (Caro *et al.*, 1995). Raising the tail increases the visibility of the deer to predators and conspecifics. Pruitt (1953) described a male raising its tail in the process of making a scrape, however, we have not found reports of males raising their tail as they leave a scrape in the scientific literature.

The significance of flag-up departure from a scrape is unclear. Deer often raise their tails in a similar manner when defecating. Of all observed male defecation events, flag-up departures also were observed 60% of the time. Out of all the flag-up departures, however, defecation was observed only 18% of the time (Table 2-3). The lower resolution of the cameras at night may have made it difficult to observe fecal pellets dropping to the ground. Even so, if deer were defecating 100% of the time when the flag-up departure was observed, we would expect to have greater detection rate than 18%. Smell scrape (61%), scrape ground (59%), smell branch (70%), and grasp-lick branch (57%) all had high rates of co-occurrence when flag-up departure was observed in the same interaction (Table 2-4). Flag-up departure was observed 46%, 47%, 36% of the time when scrape ground, other branch interaction, and rub-urinate behaviors occurred, respectively (Table 2-4). Only 1 doe was observed raising her tail while with-in 2 m of the scrape. While flag-up departure may indicate nothing more than a forthcoming defecation event, the high co-occurrence with branch and scrape related behaviors may suggest some behavioral significance.

Flag-up departure may by a physical cue designed to attract the attention of females, a sign of dominance, or a motor reflex of an aroused state induced by interacting with a scrape. It would be interesting to know if other males or females were nearby when flag-up departures occurred, however our cameras did not provide a view of the surrounding area. Flag-up departure may be a sign of dominance if it is displayed in the presence of other males. A raised tail is highly associated with dominant male wolves (Fatjó *et al*. 2007). Flag-up departure may be a courtship signal if directed towards females. Scrapes are thought to assist in the induction and synchronization of estrus in females (Moore and Marchinton, 1974; Hirth, 1977; Sawyer *et al.*, 1989). A motor reflex of an aroused state might be inferred if it commonly occurs when no other deer are nearby.

Rub-urination, urination, and defecation are often reported to some degree in association with scraping activity (Hirth, 1977; Kile and Marchinton, 1977; Miller *et al.*, 1987). We found that urination and defecation rarely occurred (3% each) within 2 m of a scrape, and rub-urination was only conducted by males in 14% of the interactions. The scrape ground behavior occurred in nearly 30% of interactions. This may suggest that scent left in the scrape from interdigital glands is more important in the marking of a scrape than scent from urine and tarsal glands. Gassett *et al.* (1996) reported that some compounds found in interdigital gland secretions were significantly higher in males ≥3.5 years old than in younger males, and may be indicative of a dominant male. We found no evidence that males will lick the scrape depression.

Forehead secretions and compounds often have been discussed in relation to scent marking by ungulates, particularly in black-tailed deer (Quay and Müller-Schwarze , 1970; Müller-Schwarze, 1971; Volkman *et al*., 1978; Atkeson and Marchinton, 1982; Gassett *et al*., 1997). Hirth (1977) reported that males allowed branches to move across the forehead while marking scrapes. However, our observations indicate that forehead glands and secretions might not be used by white-tailed deer in the marking of scrapes. The over-hanging branch often makes contact with the forehead as the deer attempts to manipulate the branch into a position in which it will pass over the pre-orbital gland. We believe that this contact with the forehead is incidental in the process of pre-orbital marking, and not intentionally done to mark the branch with forehead substances. Forehead gland secretions are more likely to be associated with rubs as described by Atkeson and Marchinton (1982).

It has been suggested that scraping behavior plays a role in the establishment and maintenance of a dominance hierarchy among males (Miller *et al.* 1987). We found that older males (≥2.5 years old) participated in more interactions than yearling males. We also observed flag-up departure from a scrape which may be a dominance display drawing attention to the male who performed the marking.

Animal behaviors may play an important role in disease transmission. Chronic wasting disease (CWD) has become a major concern for wildlife managers in recent years. Miller and Conner (2005) suggested that understanding sex-specific social behavior may be important to understanding why chronic wasting disease prevalence varies between the sexes. Transmission rates of CWD may be dependent on frequency of contact between individuals or the density of populations (Gross and Miller, 2001;

Schauber and Woolf, 2003). Understanding the nature and frequency of these behaviors in white-tailed deer may be critical in understanding the probability of disease transmission among adult males, due to the concentration of urine, feces, saliva, and glandular substances at scrapes, some of which are known to contain CWD prions (Mathiason *et al*., 2006; Safar *et al.*, 2008; Tamgüney *et al*., 2009; Haley *et al*., 2009).

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TABLES AND FIGURES

Table 2-1: Number of scrape-related behaviors occurring within interactions by male, female, and fawn white-tailed deer at DeSoto National Wildlife Refuge in eastern Nebraska and western Iowa, 2005.

Behaviors per Interaction	**Males**	**Females**	**Fawns**
1	260	167	133
2	177	52	18
3	168	6	2
4	102	0	0
5	86	0	0
6	33	0	0
7	11	0	0
8	1	0	0
9	1	0	0
Total	839	223	153

Table 2-2: Behaviors performed in interactions with scrapes in which only 1 behavior was exhibited by male, female, and fawn white-tailed deer at DeSoto National Wildlife Refuge in eastern Nebraska and western Iowa, 2005.

Behavior	**Males**	**Females**	**Fawns**
Smell scrape	139	120	107
Scrape ground	4	0	0
Smell branch	88	37	17
Other branch contact	1	0	1
Grasp-lick branch	4	2	3
Branch eye contact	1	0	1
Rub-urinate	7	0	0
Urinate	3	2	1
Defecate	7	5	2
Flehmen	0	0	0
Flag-up	6	0	0
Total	260	167	133

Table 2-3: Number of scrape-related behaviors exhibited by male, female, and fawn white-tailed deer at DeSoto National Wildlife Refuge in eastern Nebraska and western Iowa, 2005.

Behaviors	**Males**	**Females**	**Fawns**
Smell scrape	510	172	121
Scrape ground	225	0	0
Smell branch	561	92	34
Other branch contact	17	0	2
Grasp-lick branch	330	9	9
Branch eye contact	187	4	1
Rub-urinate	118	0	0
Urinate	49	3	2
Defecate	52	6	3
Flehmen	3	0	0
Flag-up	175	1	1
Total	2,227	287	173

Table 2-4: Percentages of the co-occurrence of behaviors during a scrape interaction for male white-tailed deer at DeSoto National Wildlife Refuge in eastern Nebraska and western Iowa, 2005. Percentages at the intersections of rows and columns represent the number of times the behaviors were seen together, divided by the total number of times the behavior in the column was observed, multiplied by 100. Total number of observations are in ().

	Smell scrape (510)	**Scrape ground (225)**	**Smell branch (561)**	**Other branch contact (17)**	**Branch saliva contact (330)**	**Branch eye contact (187)**	**Rub-urinate (118)**	**Urinate (49)**	**Defecate (52)**	**Flehmen (3)**	**Flag-up (175)**
Smell scrape (510)	NA	66	53	47	58	56	62	59	58	100	61
Scrape ground (225)	29	NA	31	47	44	46	43	29	44	33	59
Smell branch (561)	59	77	NA	71	82	80	65	76	56	33	70
Other branch contact (17)	2	4	2	NA	3	5	2	2	2	0	5
Branch saliva contact (330)	37	65	48	53	NA	62	49	53	40	67	57
Branch eye Contact (187)	21	38	27	53	35	NA	31	29	23	33	30
Rub-urinate (118)	14	23	14	12	18	19	NA	2	17	0	25
Urinate (49)	6	6	7	6	8	7	1	NA	13	0	7
Defecate (52)	6	10	5	6	6	6	8	14	NA	0	18
Flehmen (3)	1	0	0	0	1	1	0	0	0	NA	0
Flag-up (175)	21	46	22	47	30	28	36	27	60	0	NA

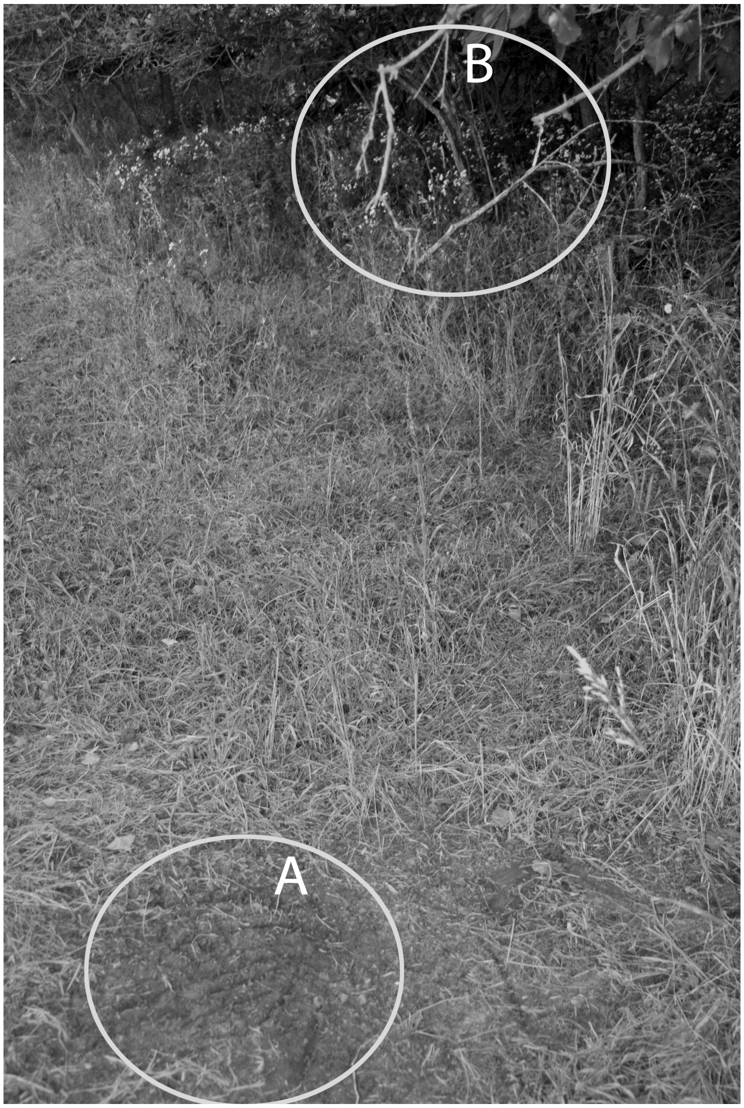

Figure 2-1: A typical scrape (A) with a depression (B) and an over-hanging branch, made by a male white-tailed deer at DeSoto National Wildlife Refuge in eastern Nebraska and western Iowa, 2005.

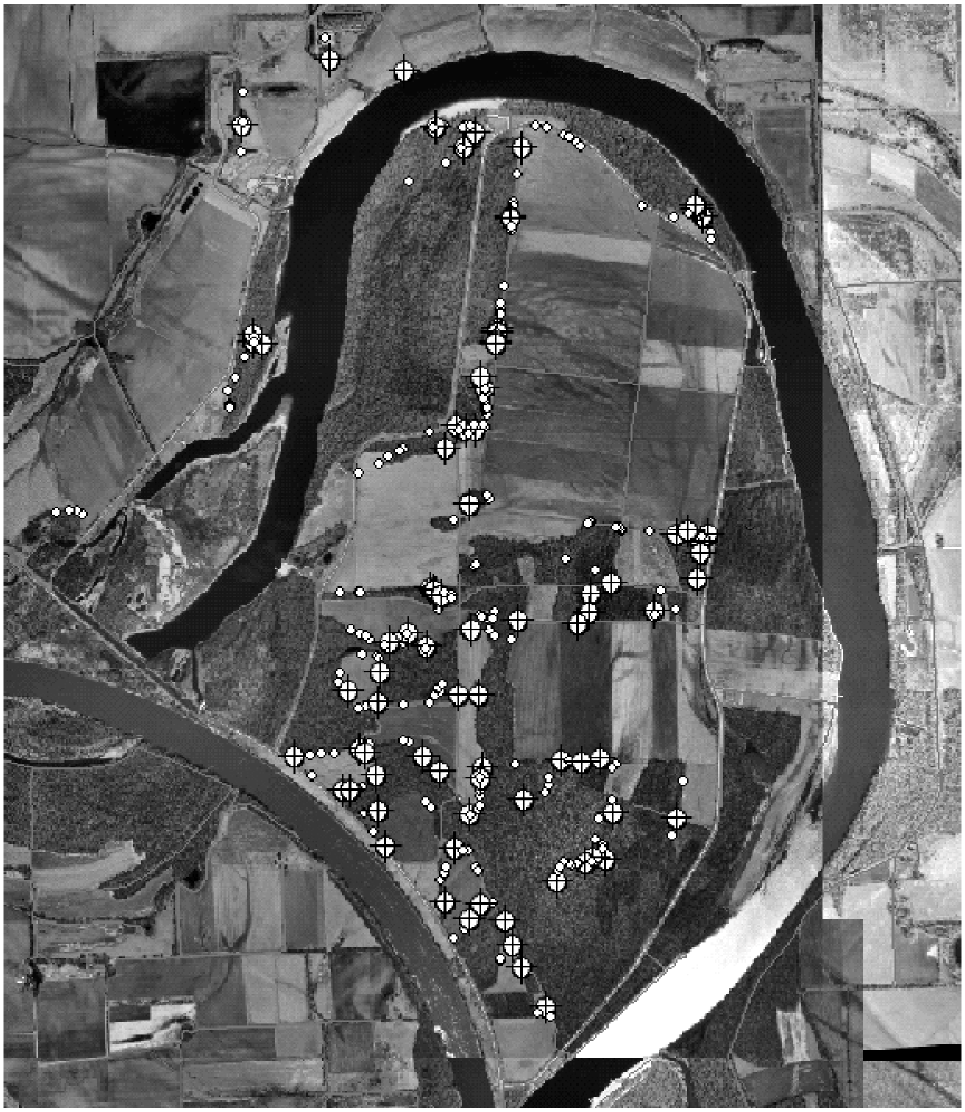

Figure 2-2: Located scrapes (°) made by male white-tailed deer at DeSoto National Wildlife Refuge in eastern Nebraska and western Iowa, 2005. Twenty-seven percent of the observed scrapes were monitored with animal-activated cameras (⌖).

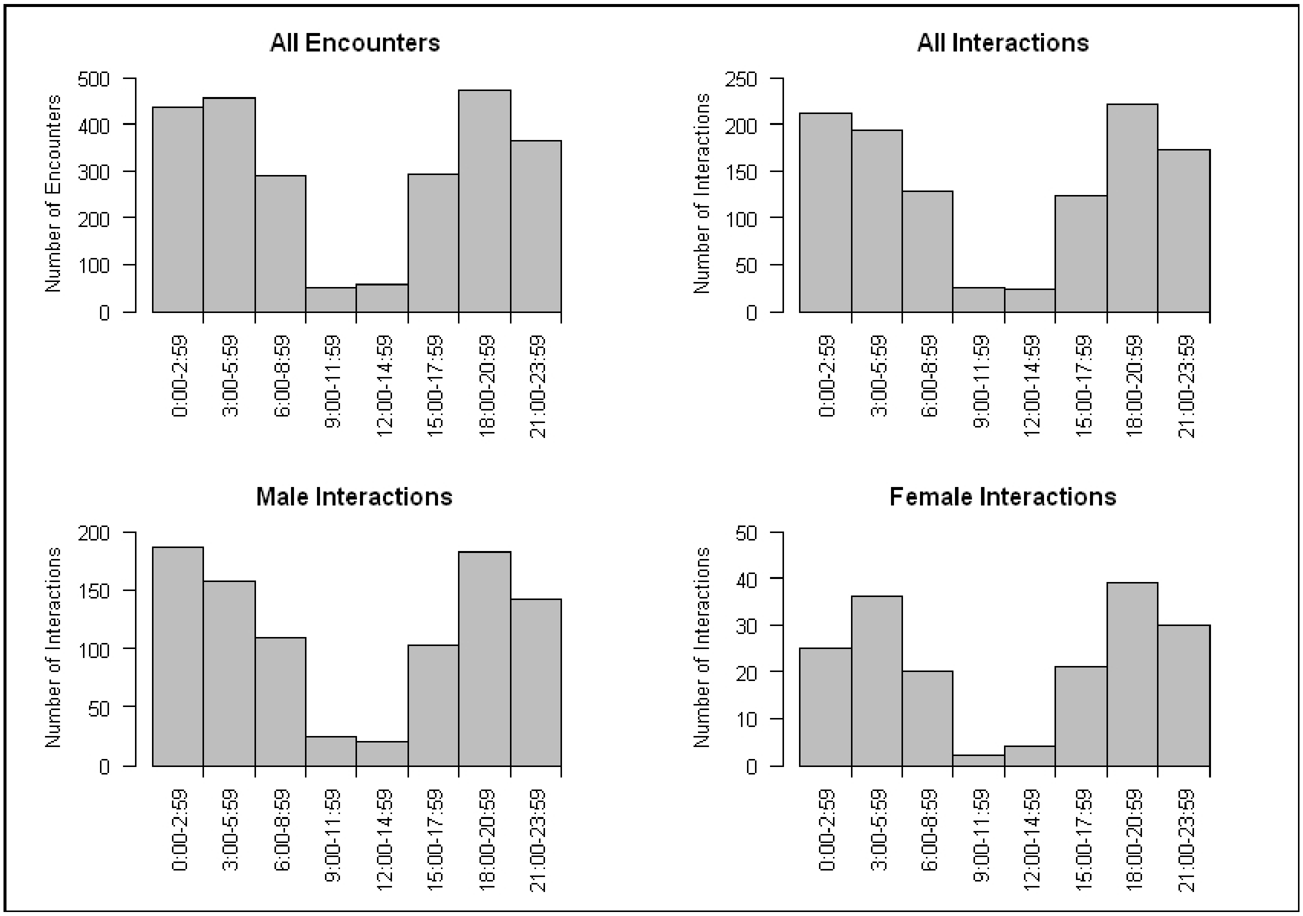

Figure 2-3: Time of day that encounters and interactions at scrapes took place by male and female white-tailed deer at DeSoto National Wildlife Refuge in eastern Nebraska and western Iowa, 2005.

Figure 2-4: Typical scrape-related behaviors of male white-tailed deer, including (a) smell scrape, (b) scrape ground, and (c) rub-urinate. Branch related behaviors include (d) smell branch, (e) grasp-lick branch, (f) mark branch with pre-orbital gland, (g) other branch contact (rake the antlers through the branches), and (h) flag-up departure.

CHAPTER 3 : SPATIAL AND TEMPORAL USE OF SCRAPES BY MALE WHITE-TAILED DEER

KINSELL, TRAVIS C.[a], HYGNSTROM, SCOTT E., CLEMENTS, GREGORY M., FROST, CHARLES J.,

School of Natural Resources, University of Nebraska-Lincoln, Lincoln 68583-0974

VERCAUTEREN, KURT C.

USDA, APHIS, WS, National Wildlife Research Center, Fort Collins, Colorado 80521-2154

Abstract.-- We placed 71 and 35 motion-activated cameras on scrapes made by white-tailed deer (Odocoileus virginianus) on DeSoto National Wildlife Refuge, in eastern Nebraska and western Iowa, from Oct. – Nov. 2005 and Sept. – Nov. 2006, respectively. Cameras were operational for 1495 and 1303 camera days in 2005 and 2006, respectively, resulting in 5009 encounters (deer came near scrapes) and 1830 interactions (deer performed a scrape-related behavior) with scrapes across all sex-age classes. Most scrape-related activity occurred at night between the hours of 18:00 and 06:00. Deer were 6-13 times more active in the daytime at scrapes within forest interiors than scrapes along forest edges. We identified 184 unique male white-tailed deer in 2005 and 119 in 2006: 12-17% of identified males appeared ≥5 times at monitored scrapes. Individuals visited a mean of 3.9 unique scrapes (range 1-8). Mean minimum distance moved among scrapes for individuals that appeared ≥5 times was 978 m. Sub-dominant males were more likely to have larger mean minimum movements (>978 m) among scrapes than

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[a] Corresponding author: email: tckinsell@huskers.unl.edu

other dominance categories. Post-dominant males visited a different scrape more often than returning to a previously visited scrape. We observed a mean of 5.1 (range 1-15) individual adult males interacting with individual scrapes, with 43% of them returning to a previously visited scrape at least 1 time. Visiting many scrapes may increase a male's chances of encountering receptive females that inspect scrapes while in estrous. Scrape-related behavior may be important in the transmission of diseases such as chronic wasting disease, therefore it is important to know how many individuals make use of a single scrape, and how individuals use scrapes across the landscape.

Keywords: behavior, *Odocoileus virginianus*, spatial, scrape, temporal, white-tailed deer.

INTRODUCTION

Scrapes are chemical signposts made by male white-tailed deer (*Odocoileus virginianus*, hereafter referred to as deer) to communicate with other deer in an area (Moore and Marchinton, 1974; Hirth 1977). Scrapes are also thought to be a way for males to express dominance and establish a hierarchy (Hirth, 1977; Miller *et al.,* 1987; Moore and Marchinton, 1974). Scrape depressions are areas on the ground that are pawed and "scraped" free of ground litter by male white-tailed deer. Scrapes typically are about 0.7 m long and 0.3 m wide (Hirth, 1977). Males rub-urinate and to a lesser extent, urinate and defecate in the depression (Hirth, 1977; Kile and Marchinton, 1977; Miller *et al.* 1987). Scrapes typically are associated with an over-hanging branch 1-2 m above the ground (Hirth, 1977; Kile and Marchinton, 1977; Marchinton and Hirth, 1984) which is marked with saliva and secretions from pre-orbital glands (Miller *et al.,* 1987;

Kinsell *et al.*, in prep [a]). It is likely that scent from interdigital sebaceous and sudoriferous gland secretions (Quay and Müller-Schwarze, 1970) are deposited in the scrape during the process of pawing a depression. The scent may indicate the age and dominance of a male (Gassett *et al*., 1996).

Older (≥2.5 years old) male deer made the majority of the scrapes in Michigan and Georgia (Ozoga and Verme, 1985; Miller *et al.,* 1987; Marchinton *et al.,* 1990; Alexy *et al.,* 2001). Yearling or 2.5-year-old males interacted with scrapes little or not at all in a captive facility in Georgia (Miller *et al.,* 1987; Marchinton *et al.,* 1990). Yearlings made only 15% of the scrapes in a captive facility in Michigan and began scraping later in the breeding season than older males (Ozoga and Verme, 1985). Free-ranging yearling males created 42% of the scrapes in Georgia, but marked (branch marking, pawing, or urination) less frequently than older males (Alexy *et al.,* 2001). Yearlings accounted for 33% of scrape interactions by males in Nebraska (Kinsell *et al.*, in prep [a]).

Males began making scrapes about 1-2 months prior to breeding in Georgia and Michigan. The activity intensified and peaked around late-Oct. or early-Nov., then dropped off through the end of Nov. and into Dec. (Kile and Marchinton, 1977; Ozoga and Verme, 1985; Ozoga, 1989; Miller and Marchinton, 1999; Alexy *et al.,* 2001). Most scrape-related behavior occurred at night in Georgia (Alexy *et al.,* 2001).

A review of the literature revealed 1 study (Alexy *et al.,* 2001) that reported multiple identifiable males using the same scrape. The Alexy study monitored 9 scrapes over a 2-year study period, and rarely recorded individuals visiting >1 monitored scrape. The objectives of this study were to determine how individual scrapes are used by multiple males and how individual males use multiple scrapes across the landscape. We believe it is important to study the use of scrapes by individual male deer due to the possibility of disease transmission through scrape-related behavior.

METHODS

STUDY AREA

DeSoto National Wildlife Refuge (DNWR) is located in the flood plain of the Missouri River, about 32 km north of Omaha, Nebraska between Blair, Nebraska and Missouri Valley, Iowa, USA. The DNWR consists of a 3,384-ha patchwork of riparian hardwood forest, grassland, wetland, and cropland administered by the US Fish and Wildlife Service. The interspersion of habitat supports a diverse range of flora and fauna (US Fish and Wildlife Service, 2009).

The soil on DNWR is quite variable because of past flooding and shifts of the Missouri river channel. The soil types are of Albaton-Haynie Associations. Albaton series soils are predominantly silty clay or clay in the Ap horizon, with 40-60% clay and 1-5% sand. Haynie series soils are predominantly silt loam, very fine sandy loam and silty clay loam in the Ap horizon, with 15-30% clay and 18-55% sand (Soil Survey Staff, 2008). The topography is relatively flat with slopes of 0-2% (US Department of Agriculture, 1976).

The forests of DNWR are dominated by mature eastern cottonwood (*Populus deltoides*), but also include black walnut (*Juglans nigra*), box elder (*Acer negundo*), American elm (*Ulmus americana*), eastern red cedar (*Juniperus virginiana*), black willow (*Salix nigra*), sandbar willow (*Salix interior*), and Chinese elm (*Ulmus parvifolia*). The understory includes hackberry (*Celtis occidentalis*), mulberry (*Morus rubra*), and green ash (*Fraxinus pennsylvanica*). Poison ivy (*Rhus radicans*) and common scouring-rush (*Equisetum hyemale*) dominate the ground layer (US Fish and Wildlife Service 2009). The grasslands of DNWR consist mostly of warm-season native species and to a lesser extent, cool-season species. Dominant native species include big bluestem (*Andropogon gerardii*), little bluestem (*Schizachyrium scoparium*), switchgrass (*Panicum virgatum*), Indian grass (*Sorghastrum nutans*), Canada wild rye (*Elymus canadensis*), and at least 160 species of native forbs and flowers. Cropland on DNWR includes corn (*Zea mays*), soybeans (*Glycine max*), and sweet clover (*Melilotus* spp.; US Fish and Wildlife Service 2009).

Estimates of pre-harvest densities of white-tailed deer at DNWR were 41-51 deer/km^2 from 2004–2007 (Hefley *et al.,* 2010). Estimates of female:male ratios were 2.15:1 and 1.86:1 and fawn:doe ratios were 1.28:1 and 1.43:1 in 2005 and 2006, respectively (Clements *et al.,* 2010). As part of other research efforts in the study area, 20-25 females and 20-30 males were radio-collared and ear-tagged on DNWR during the time of this study. An estimated 42 additional males and 17 females were marked with ear tags alone. We estimate that up to 24% of the males and 6% of the females were marked on DNWR during the study (Gilsdorf and Clements, pers. com.).

MATERIALS AND METHODS

We remotely monitored scrapes made by white-tailed deer during the fall breeding season from mid-Oct. - Nov., 2005 and mid-Sept. - Nov., 2006. We located scrapes by walking forest-field edges, trails, and 2-track roads through the forest and geo-referenced them with a Global Positioning System (GPS; Garmin, Olathe, KS, USA). We deployed cameras on selected scrapes if they appeared to be recently active (*i. e.* freshly disturbed soil in the depression or freshly broken over-hanging branches) and were within 8 m of a tree that could support a camera. We only monitored scrapes associated with over-hanging branches. Trees with a circumference ≥30 cm were needed to support StumpCams (StumpCam^{tm} Inc., Tyler, Texas, USA), while trees with a circumference of ≥18 cm were sufficient for Reconyx cameras (Reconyx Silent Image, LaCrosse, Wisconsin, USA). We did not attempt to locate every scrape on the refuge, but rather searched for scrapes until all cameras were deployed on active scrapes (Figure 3-1). In 2005, we monitored 85 scrapes with 37 infrared motion-activated StumpCam video cameras and 34 motion-activated Reconyx digital camera systems. In 2006, we monitored 44 scrapes with 31 StumpCams and 4 Reconyx cameras. Few Reconyx cameras were available in 2006 due to use on another study. We hung cameras in trees 4-8 m from each scrape and 1-3 m above ground and focused each to provide a field of view that included a scrape, an over-hanging branch, and ≥2-m radius of the surrounding area. We programmed StumpCams to record for 3 min when triggered, with a 10-sec lag between triggers (hardware minimum) and Reconyx digital cameras to take 1 frame per sec for 30 sec, with a 1-sec lag between triggers. We removed cameras if scrapes were inactive for >1 week. We checked StumpCams once every 3-4 days, and Reconyx cameras once per week. We replaced batteries and recording media as needed. Each time cameras were checked, we recorded the camera identification code (ID), GPS location, date, time, and condition of the battery. We labeled each videotape with the camera ID, GPS location, and date and time of both insertion and removal from the camera. We reviewed StumpCam video tapes and digitized encounters and interactions to a hard drive. We defined an "encounter" with a scrape as an event in which a deer came within 2 adult body lengths (~2 m) of a scrape and could identify and interact with the scrape (i. *e.* a deer walks near the scrape versus running past the scrape). An "interaction" with a scrape occurred when a deer approached a scrape and performed ≥1 scrape-related behaviors (all interactions were also encounters, but not all encounters resulted in interactions). We placed digitized encounters and interactions in a folder labeled with the camera ID, GPS location, and tape number for easy reference. We labeled Reconyx media with the camera ID and downloaded images from compact flash cards to a laptop following each camera inspection.

We attempted to identify all males ≥2.5 years old (hereafter adults). Individuals were identified by radio-collars, numbered ear-tags, body size and condition, and antler characteristics such as: number of tines on each side, symmetry, width and height of antlers compared to the ears, longest tine relative to the other tines (*i.e.* the third tine on the left), relative length and aspect (*i.e.* slanting in, out, back or forward) of the brow tines, broken tines, and presence and location of non-typical points. We used a series of 3-6 still images captured from the digital video, with a view of each side, front, and back of the antlers to identify unmarked males. Images were sorted into categories such as; 4x4s, 5x4s, 5x5s, 6x6s, non-typical and marked animals to facilitate identification. We labeled these images with a deer identification number (ID) and saved them in a reference collection for future comparison to other males. We are confident in our identification procedures and the identifications we made of individual deer. Any males that we could not identify with certainty were classified by sex and age (fawn, yearling, adult). We examined the video images and still pictures frame by frame and recorded each encounter and interaction with a scrape. We recorded time-of-day the animal entered and left the scrape, animal ID when possible, sex, age class, behaviors performed while at the scrape, and notes about identifiable features of the animal.

We split the day into 8, 3-hour time periods beginning at 00:00-02:59 and created distributions of time-of-day of scrape visitations. We created an empirical cumulative distribution function of the proportion of the identified population that made ≥1 visits to monitored scrapes using program R (R Development Core Team 2008). We created a histogram showing the number of different scrapes visited by individuals that were observed ≥5 times. To explain the differences in movement and appearance we grouped the 70 males that were observed ≥5 times into 4 physical categories; subordinate (typically small bodied, ≤4 points on each side, little antler mass, ears wider than antlers; likely 2.5-year-olds or large yearlings), sub-dominant (typically 4-5 points on each side, more antler mass and larger bodies than subordinates but smaller than dominants, antlers as wide or wider than ears; relatively average individuals), dominant (large bodies and necks, antlers with ≥5 points on each side and with more mass than sub-dominants and subordinates, often have non-typical points; prime aged animals), and post-dominant (individuals with large, scarred bodies, but small antlers, likely past their prime). We ran a X^2 analysis on the following: animals that encountered ≥4 different scrapes versus <4 different scrapes, animals that appeared ≥7 times versus <7 times, animals that had an average movement ≥978 m versus <978 m, and animals that had a scrape fidelity rating of ≤0.40 versus > 0.40, where scrape fidelity = 1-(# scrapes visited/# observations) with 0 meaning every observation was at a different scrape. Scrape fidelity was used to show the propensity of an individual to return to the same scrape or to encounter a number of different scrapes. Each of the numbers we used as the split points above, were the mean of the corresponding category for the 70 animals that appeared at monitored scrapes ≥5 times. We calculated minimum distances between consecutive scrape visits by sorting our data by animal ID and time of encounter. We then used the Pythagorean Theorem on UTM coordinates of consecutive scrape locations for each individual. We examined data from each scrape to determine the number of individual male visits per scrape. We conducted a linear regression to assess the effect of the number of functional camera days on the number of individuals observed at each scrape.

RESULTS

Cameras were operational for 1495 and 1303 camera days in 2005 and 2006, respectively. We recorded 3106 and 1903 encounters with scrapes across all sex-age classes in 2005 and 2006, respectively. Of those encounters, 39% (n = 1218) and 32% (n=612) resulted in interactions with scrapes. Interactions were made up of adult males (46% and 49%), yearling males (22% and 25%), females (18% and 17%), fawns (12% and 9%) and unknown adults (1% and <1%), in 2005 and 2006 respectively. When encountering a scrape, adult males performed an interaction 60% of the time in both 2005 and 2006, followed by yearling males (50% and 41%), females (25% and 18%), and fawns (22% and 12%), respectively (Tables and FIGURES
Table 3-1).

Most interactions (75%) with scrapes occurred at night and between the hours of 18:00 – 06:00 for all sex-age classes, with a pronounced decrease in activity (3%) during daylight hours of 09:00 – 15:00 (Figure 3-2). Interactions during the dawn and dusk hours (21%) of 06:00 – 09:00 and 15:00 – 18:00 were 50% fewer than any single 3-hour time period during the night for adult males and females. Eighty-one percent of adult male interactions occurred at night. Time-of-day of scrape interactions by adult males was significantly different between forest-edge and forest interior scrape scrapes (X^2 = 1223, df = 7, P < 0.001), with interactions at forest interior locations 5.9-13.2 times more likely to occur during mid-day hours, 2.3-4.0 times more likely at dawn and dusk, and 1.4-2.4 times less likely during night-time hours as compared to scrapes located along forest-field edges.

We focus the remainder of the analysis on adult males (≥2.5 years old) because we were able to identify adult males and they were responsible for nearly 50% of all interactions. We observed 628 encounters by 184 unique adult males in 2005, and 355 encounters by 119 unique adult males in 2006. Individual adult males that interacted with a scrape were successfully identified more often (80%) than individuals that merely encountered a scrape (67%). The empirical cumulative distribution function (Figure 3-3) shows that 12-17% of the identified individual males were observed ≥5 times. These individuals were observed either repeatedly visiting the same scrape or visiting multiple scrapes across the landscape. They visited an average of 3.9 unique scrapes (range 1-8, Figure 3-4), and were observed 5-22 times. We found that proportions of individuals in each dominance category were not different among identified adult males that encountered ≥4 different scrapes versus <4 (X^2 = 1.39, df = 3, P = 0.708), and that proportions were not different among males that were observed ≥7 times versus <7 times (X^2 = 5.48, df = 3, P = 0.140). However, we found significantly more sub-dominant males that moved a minimum distance of ≥978 m on average, among scrapes (X^2 = 14.33, df = 3, $P = 0.002$) versus <978 m, and more post-dominant males that had a fidelity rating of ≤0.40 versus > 0.40 ($X^2 = 11.15$, df = 3, $P = 0.011$; Table 3-2).

Mean minimum distance between consecutive encounters with different scrapes for individual adult males (excluding 0s for returns to the same scrape) was 978 m. Mean minimum distance between consecutive encounters (including 0s for returns to the same scrape) was 642 m. The largest minimum distance moved between scrapes on consecutive recorded visits was 3.85 km in 2005, and 3.24 km in 2006. Longest observed minimum distances in a single night was 2.69 km over 3 hr in 2005, and 2.56 km over 8 hr 22 min in 2006. Largest mean minimum distance for an individual was 2.28 km among 3 scrapes (6 observations). One individual repeatedly moved between 2 scrapes 2.69 km apart over the course of 3 days (7 observations).

We observed a mean of 5.1 (range 1-15, median = 4) identified adult males interacting with a single scrape. On average, 43% of adult males that interacted with a scrape returned to the same scrape at least once. We detected no relationship between number of identified adult males interacting with a scrape and the number of functional camera days for the corresponding scrape because the slope coefficient approaches 0 and R^2 <0.001 (Figure 3-5). Of the 16 scrapes in the forest interior where at least 1 identifiable buck was observed interacting, 8 were among the 46 most active scrapes (≥5 unique interactions), and 8 were among the 47 least active scrapes.

DISCUSSION

Adult male white-tailed deer were the most active sex-age class at scrapes. Adult males accounted for nearly half of all interactions, with yearling males accounting for one-forth, and females, fawns and unknown (sex) adults making up the remaining one-forth. When encountering scrapes, adult males stopped to interact 60% of the time. While adult females encountered just as many scrapes as adult males, they stopped to interact only 18-25% of the time (Tables and FIGURES

Table 3-1). These results are consistent with Alexy *et al.* (2001) who reported a 52% interaction rate for males and 21% for females, out of 562 scrape visitations in Georgia.

Interactions at scrapes were largely nocturnal (81% for adult males), occurring between the hours of 18:00-06:00. Activity declined as dawn approached, and increased as dusk approached. Very little activity occurred during daylight hours. These findings were consistent with deer in Georgia (Alexy *et al.,* 2001), where 85% of male visits occurred after dark. Scraping activity was up to 13 times more likely to occur at forest interior scrape sites during daylight hours and up to 2.4 times less likely to occur after dark compared to scrapes located along forest-field edges. We believe this is due to interior scrapes being proximate to daytime bedding areas and forest-field edge scrapes being proximate to nightly foraging areas (*i. e.* crops). Daytime scrape use in the forest interior may also be related to predator avoidance instincts causing deer to remain near cover in the daylight.

By deploying numerous remote cameras on scrapes across DNWR, we had a unique opportunity to observe how adult males move among scrapes. Positive identification of adult males was necessary to determine which males were returning to the same scrapes and which were moving to other scrapes across the refuge. We were able to positively identify 80% of the adult males that interacted with monitored scrapes by comparing antler and body characteristics such as the number of points on each side, number and location of non-typical points, relative length of points compared to other points, symmetry between the sides and body condition and size. We were confident in our ability to identify individual males. Jacobson *et al.* (1997) also found that antler and body characteristics were sufficient to positively identify individual adult white-tailed deer captured by remote infrared-triggered video cameras.

Twelve to 17% of the identified adult males were the most active (Figure 3-3), appearing at monitored scrapes ≥5 times, either moving around to many different scrapes or returning to the same scrape several times. Our cumulative distribution function (Figure 3-3) was similar to what Frost *et al.* (2009) observed regarding movements of white-tailed deer and mule deer in western Nebraska, in which 10% of the population was the most mobile. The number of different scrapes each individual (of the 70 most active) visited followed a normal distribution with a mean of 3.9 different scrapes (Figure 3-4). Some animals returned to the same scrape repeatedly and some visited up to 8 different scrapes. We categorized those active individuals (*i. e.* the top 12-17% observed ≥5 times) into 4 categories based on antler and body characteristics: subordinate (14 animals), sub-dominant (14), dominant (35), and post-dominant (5). A large number of dominant individuals at our scrapes is consistent with previous research which found that most scraping activity is done by prime-age or dominant males (Ozoga and Verme, 1985; Miller *et al.,* 1987; Marchinton *et al.,* 1990; Alexy *et al.,* 2001). DeSoto National Wildlife Refuge is particularly prone to a large number of dominant males due to the relatively high male:female ratios, and older age classes due to limited hunting pressure on male deer at the refuge (1 2-day season per year). We found no difference in the proportion of dominance classes among the individuals that appeared at ≥4 different scrapes versus <4, or those that were observed ≥7 times versus those observed <7 times. We did however, find a difference among proportions of dominance classes that moved mean minimum distance of >978 m among scrapes versus <978 m (*P* = 0.002, Table 3-2). Sub-dominant adult males were more likely to be among those individuals who moved >978 m. Dominant males occasionally displaced smaller males at scrapes if they were nearby, but we saw no evidence of dominant males protecting a particular scrape. Displacement of subordinate males from scrapes by older males was also reported by Alexy *et al.* (2001). We believe this displacement may explain why sub-dominant males moved longer distances among scrapes. Post-dominant males were more likely to be among those individuals with a fidelity rating of ≤0.40 (*P* = 0.011, Table 3-2). Four of the 5 post-dominant bucks had a scrape fidelity rating in the range of 0.33-0.40, indicating that they were more likely to encounter a new scrape than return to 1 they had already visited. However, these individuals did not typically have large mean minimum movement distances, which may suggest that they had smaller use-areas than sub-dominants. To our knowledge, the minimum number of unique scrapes an individual adult male white-tailed deer will visit, and the likelihood of the individual returning to a previously visited scrape (fidelity) versus appearing at a new scrape has not been reported previously.

By identifying individual adult males, we were able analyze patterns in the number of individuals that interacted with a single scrape. A mean of 5.1 identifiable males interacted with a single scrape and up to 43% of individuals returned at least 1 time to a scrape they had already visited, which is consistent with the 44-57% reported by Ozoga and Verme (1985) and the 50% reported by Alexy *et al.* (2001). Our range of 1-

15 identifiable deer observed interacting with individual scrapes is consistent with the 3-13 observed by Alexy *et al.* (2001). We were concerned that the number of functional camera days at different scrapes might bias the number of observed individuals interacting with the scrape; however, we found no relationship ($R^2 < 0.001$, Figure 3-5). We also found that the location of the scrape (forest-edge or interior) had no effect on the number of different individuals visiting a particular scrape.

While it appears that scrape density is dependent on deer density (Miller and Marchinton (1999), individual scrape usage may not be density dependent. Miller and Marchinton (1999) reported a density of 211 scrapes/ km^2 in an area of Georgia where density was 37 deer/ km^2. Kile and Marchinton (1977) reported 70 scrapes on 81 ha (86 scrapes/ km^2) in an area with about 10 deer/ km^2. However, Alexy *et al.* (2001) reported similar single scrape usage numbers to ours for a population with less than half (15-17 deer/km^2) the density of our population (41-51 deer/km^2). So it appears that while the density of scrapes may increase with increased deer density, the number of individual males using each active scrape may remain relatively constant.

Mineral licks and wallows (related to elk), may function as focal points for transmission of chronic wasting disease in elk (*Cervus elaphus*), moose (*Alces alces*), and deer (*Odocoilius* spp.; VerCauteren *et al.,* 2007). Similarly, scrape-related behaviors may result in the creation of many small environmental focal points for disease transmission among white-tailed deer that visit scrapes. By monitoring a large number of scrapes and attempting to identify individual adult males at DNWR, we were able to observe the way adult males interacted with scrapes across the landscape. These findings may help biologists better understand the way diseases such as CWD may be transmitted among males in a population. Adult male white-tailed deer participate in many scrape-related behaviors that increase the potential to bring them into contact with or cause them to shed infectious matter such as CWD prions at scrapes (Kinsell *et al.,* [b] in prep).

We found that an average of 5 (range = 1-15) different adult male white-tailed deer visited single scrapes at DNWR. The most mobile males (top 12-17%) visited an average of 3.9 different scrapes and those scrapes were a mean minimum distance of 978 m (maximum 3.85 km) apart. Males that we classified as sub-dominant were more likely to move longer distances to encounter scrapes and post-dominant males were more likely to have a lower fidelity rating than other dominance classes; however, post-dominant males traveled shorter distances among scrapes than sub-dominants.

Miller *et al.* (1987) introduced the idea that estrous females may seek out dominant males by visiting scrape sites. It follows that it would be beneficial for males to maintain many scrapes to increase the chance that an estrous female will investigate scrapes saturated with their scent. Females have been known to leave olfactory signals at scrapes (Moore and Marchinton, 1974; Sawer *et al.,* 1989), which allow a male to easily follow an estrous female.

Disease transmission may be facilitated at scrapes due to multiple males using the same scrape and then going on to interact with other scrapes across the landscape. Prevalence of CWD increases with age in white-tailed deer (Grear *et al.,* 2006; Osnas *et al.,* 2009), therefore, dominant and post-dominant males are the most likely to be infected with the disease. These males may interact with several different scrapes in a small area, and contaminate those scrapes with CWD. Younger males may subsequently interact with those scrapes and become infected, spreading the disease to more scrapes across a larger area as they roam about the landscape.

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TABLES AND FIGURES

Table 3-1: Number of recorded encounters and interactions with scrapes by sex-age class of white-tailed deer at DeSoto National Wildlife Refuge in eastern Nebraska and western Iowa, 2005-2006.

	2005			**2006**		
	Encounters	**Interactions**	**Percent**	**Encounters**	**Interactions**	**Percent**
All	3106	1218	39%	1903	612	32%
Adult Male	936	566	60%	504	300	60%
Yearling Male	541	273	50%	375	154	41%
Adult Female	896	225	25%	549	101	18%
Fawn	691	153	22%	459	56	12%
Unknown adult	42	1	2%	16	1	6%

Table 3-2: Values of X^2 tests for subordinate, sub-dominant, dominant, and post-dominant identified adult male white-tailed deer at DeSoto National Wildlife Refuge in eastern Nebraska and western Iowa, 2005-2006. Significance at the 0.05 level is 7.82 for 3 degrees of freedom.

Dominance[e]	**# Scrapes**[a]	**# Obs.** [b]	**Avg move**[c]	**Fidelity**[d]
Subordinate	0.08	0.13	0.05	0.34
Sub-dominant	0.97	3.84	8.21*	0.34
Dominant	0.33	1.51	4.19	0.00
Post-dominant	0.01	0.00	1.87	10.47*
Total X^2	1.39	5.48	14.33	11.15
P	0.708	0.140	0.002	0.011

[a] Encountered ≥4 different scrapes vs. <4

[b] Observed ≥7 times vs. < 7 times

[c] Moved ≥978 m on average between scrapes vs. <978 m

[d] Fidelity rating ≤0.40 vs. >0.40, where fidelity = 1 – (# scrapes/# observations)

[e] dominance categories were determined by relative antler and body sizes. The smallest individuals were ranked as subordinates, average sized individuals as sub-dominants, and the largest as dominants. Post-dominants were large bodied, scarred males with disproportionately small antlers.

* Indicates the most significant dominance category.

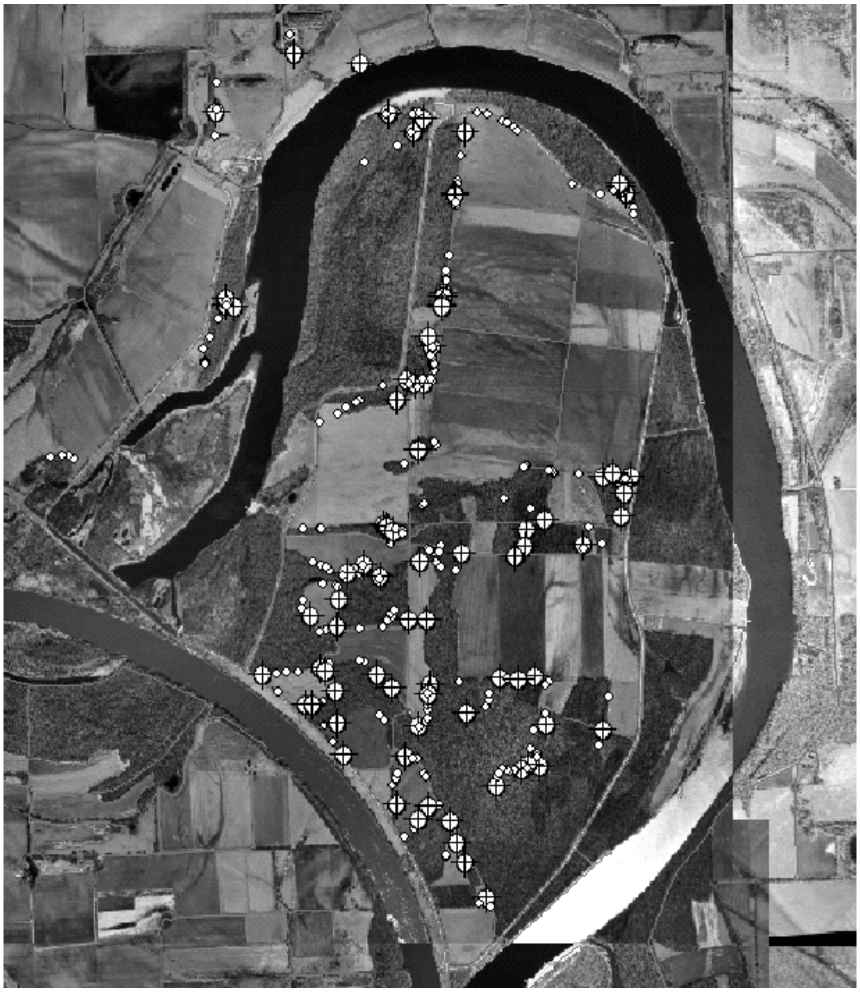

Figure 3-1: Located scrapes (°) made by male white-tailed deer at DeSoto National Wildlife Refuge in eastern Nebraska and western Iowa, 2005. Twenty-seven percent of the observed scrapes were monitored with animal-activated cameras (⌖). Cameras were distributed similarly in 2006 and are not shown here.

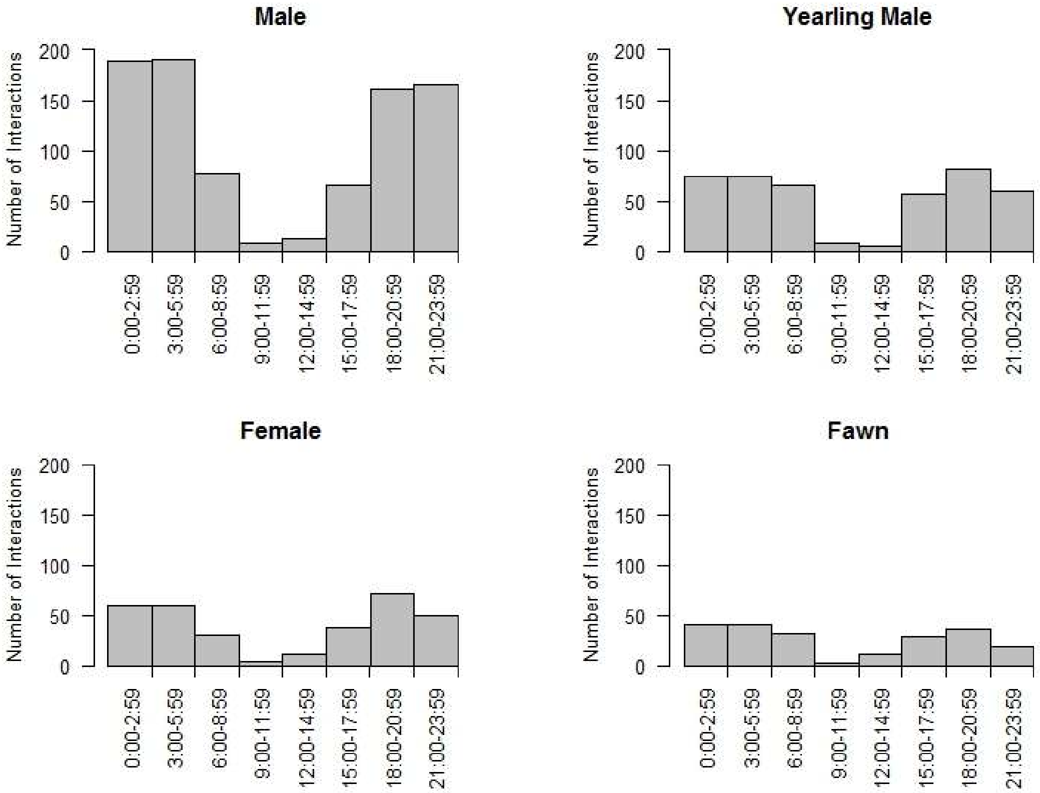

Figure 3-2: Time-of-day that interactions at scrapes took place by male, yearling male female, and fawn white-tailed deer at DeSoto National Wildlife Refuge in eastern Nebraska and western Iowa, 2005-2006.

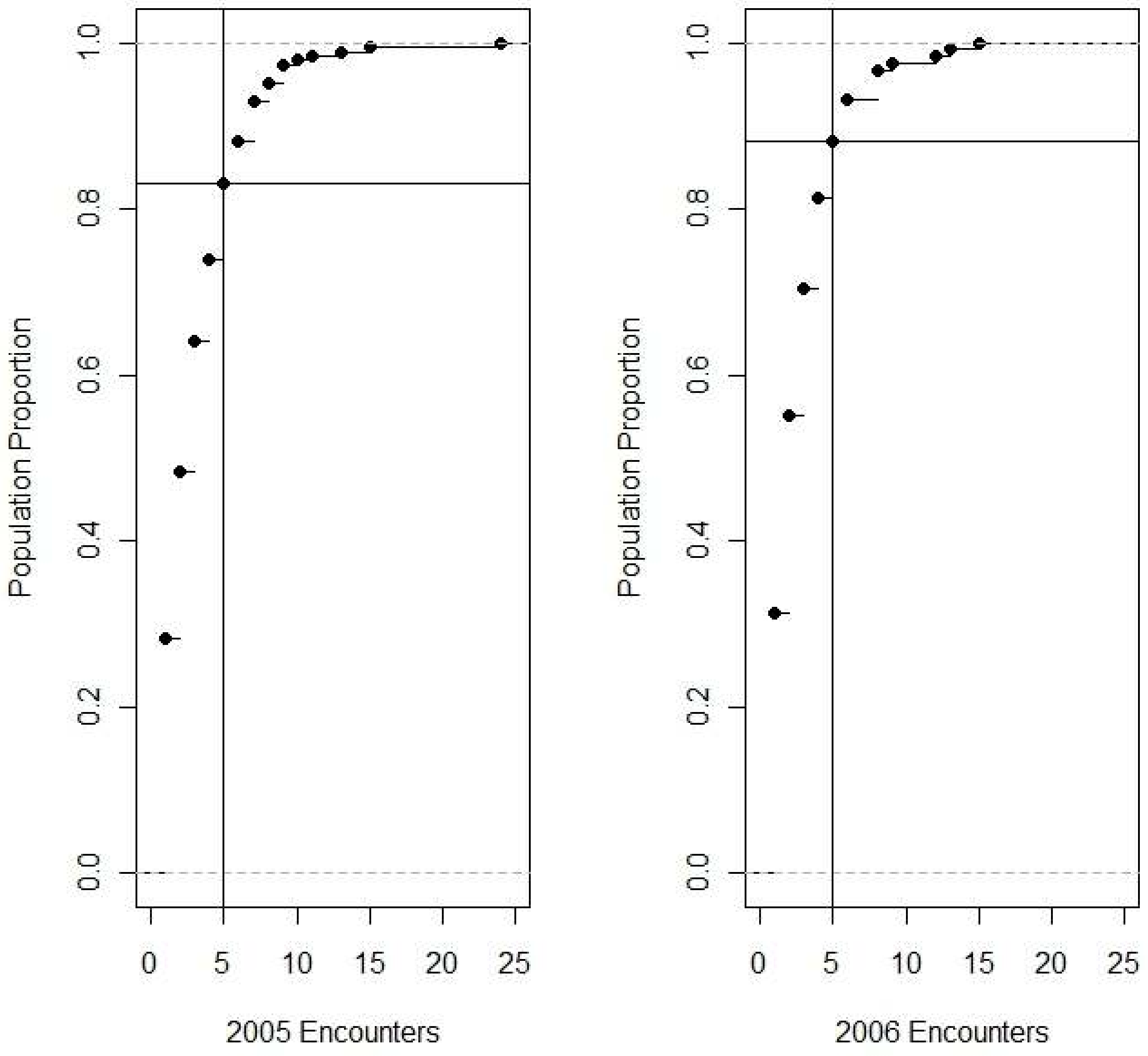

Figure 3-3: Empirical cumulative distribution function showing the proportion of the population versus the number of times the individual was observed encountering a scrape for identified adult male white-tailed deer at DeSoto National Wildlife Refuge in eastern Nebraska and western Iowa, 2005-2006

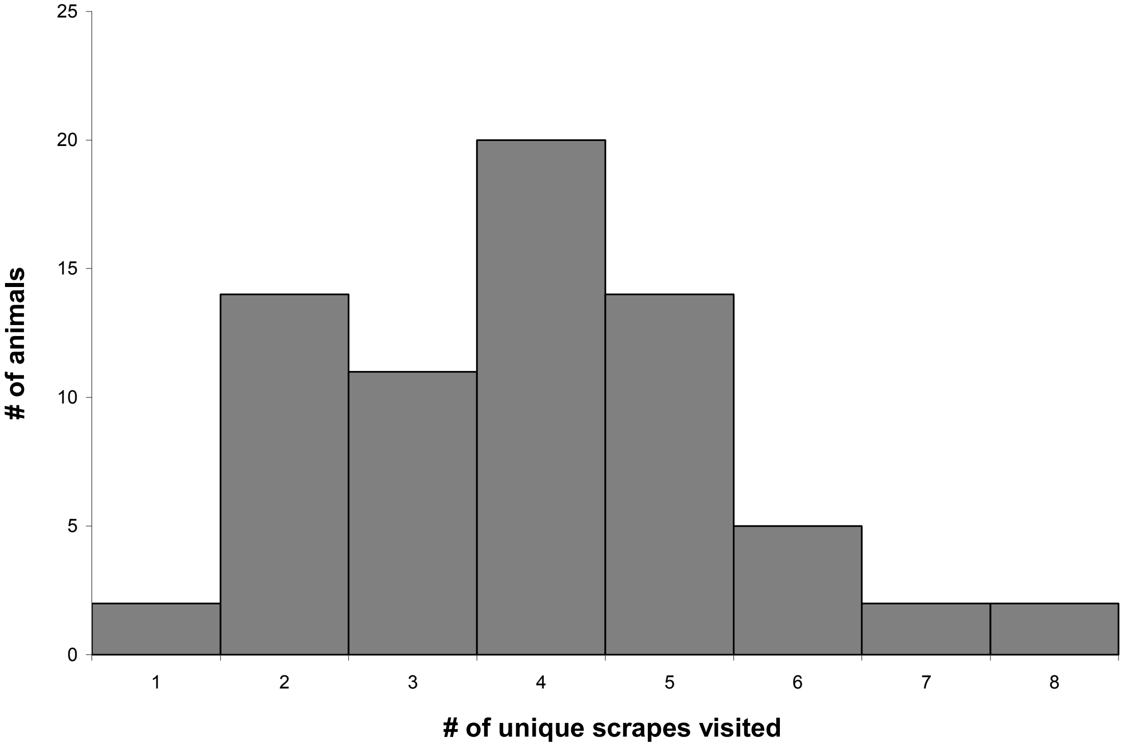

Figure 3-4: Number of unique scrapes visited by identified adult male white-tailed deer that were observed ≥5 times at DeSoto National Wildlife Refuge in eastern Nebraska and western Iowa, 2005-2006

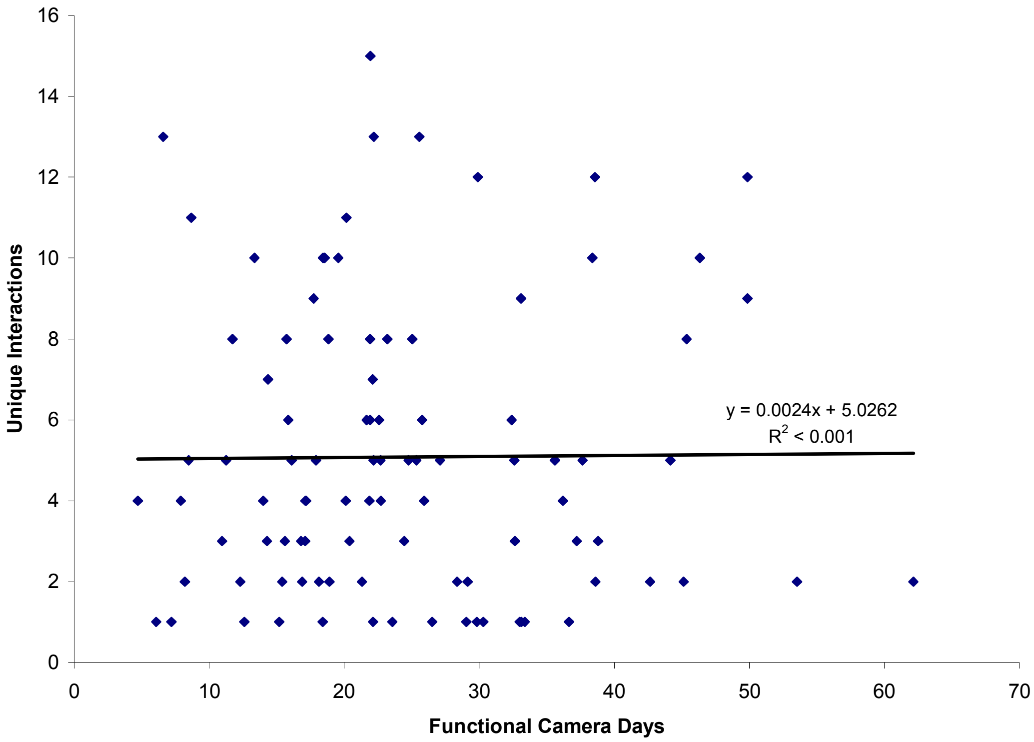

Figure 3-5: Number of unique individual adult male white-tailed deer interacting with a scrape (y) plotted against the functional camera days (x) at scrapes[a] at DeSoto National Wildlife Refuge in eastern Nebraska and western Iowa, 2005-2006

[a] Scrapes where at least 1 identifiable adult male was observed interacting with the scrape

CHAPTER 4 : THE POTENTIAL ROLE OF BEHAVIOR OF WHITE-TAILED DEER AT SCRAPES IN THE TRANSMISSION OF CHRONIC WASTING DISEASE

TRAVIS C. KINSELL*

School of Natural Resources, University of Nebraska-Lincoln

SCOTT E. HYGNSTROM

School of Natural Resources, University of Nebraska-Lincoln

GREG M. CLEMENTS

School of Natural Resources, University of Nebraska-Lincoln

CHARLES J. FROST

School of Natural Resources, University of Nebraska-Lincoln

KURT C. VERCAUTEREN

USDA, APHIS, WS, National Wildlife Research Center

*Corresponding Author: 244 Hardin Hall, University of Nebraska-Lincoln, Lincoln, NE 68583-0962. Phone: (402) 472-0508; Fax: (402) 472-2946; e-mail:tckinsell@huskers.unl.edu

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Abstract

High prevalence of chronic wasting disease (CWD) in older male white-tailed deer (*Odocoileus virginianus*) suggests that sex-specific social behavior may contribute to the spread of the disease among males. Scraping is a behavior performed by males during the breeding season in which a pawed depression in the soil is marked with urine, scent gland secretions and occasionally feces. An over-hanging branch typically is associated with each scrape and is marked with saliva and the pre-orbital gland. Scrapes serve as chemical signposts for deer in the area. We placed 71 and 35 motion-activated cameras on scrapes in DeSoto National Wildlife Refuge, in eastern Nebraska and western Iowa, from Oct. – Nov. 2005 and Sept. – Nov. 2006, respectively. Cameras were operational for 1495 and 1303 camera days in 2005 and 2006, resulting in 5009 encounters (deer came near the scrape) and 1830 interactions (deer performed a scrape-related behavior) with scrapes across all sex-age classes. We modeled Risk Values for contacting and shedding CWD prions at scrapes for sex-age classes of deer using the following parameters: frequency, duration, and Threat Rating of each behavior for contacting or shedding CWD. Adult males had the highest Risk Values for contacting CWD prions (114.1) and shedding CWD prions (59.4) among the sex-age groups. Adult male behaviors were 0.5-2 times more likely to facilitate contact with prions, and 2-3 times more likely to facilitate shedding of prions at scrapes than other sex-age classes. Adult males exhibited higher frequency of occurrence and longer duration of high-threat behaviors such as: grasp-lick branch, graze, and smell scrape (contacting 14.4-61.2%, 6-32 sec) and grasp-lick branch, defecate, and rub-urinate (shedding 5.7-44.2%, 6-8 sec). The grasp-lick branch behavior had the highest Risk Value for adult males for contacting and shedding prions (26.5 for both) because of higher frequency of behavior occurrence compared to other sex-age classes and high Threat Rating (10). Grazing in the vicinity of a scrape had high Risk Values for contacting prions by all sex-age groups (34.9-57.2). Grazing accounted for 62% of the contact risk, and 80% of the shedding risk for females, versus 32% and 15% for adult males, respectively. Understanding the role of scrape-related behavior in deer may facilitate the development of methods for control of reproduction or the spread of diseases such as chronic wasting disease.

Keywords

behavior, chronic wasting disease, disease transmission, *Odocoileus virginianus*, risk, scraping, white-tailed deer, wildlife disease.

INTRODUCTION

Chronic wasting disease (CWD) is a fatal transmissible spongiform encephalopathy (TSE) that affects free-ranging cervids (Williams and Young 1993; Spraker et al. 1997). Chronic wasting disease could have a significant impact on cervid populations if prevalence increases (Gross and Miller 2001). Cervid-related recreational opportunities (i.e. hunting, viewing) can make up a large portion of local and state revenue (as much as $1 billion in Wisconsin, Joly et al. 2003). Loss of this income due to CWD could have serious impacts on state and local economies (Joly et al. 2003).

The prevalence of CWD is >2 times higher in males than females in free-ranging mule deer (*Odocoileus hemionus*; Miller et al. 2000; Farnsworth et al. 2005; Miller and Conner 2005) and white-tailed deer (*Odocoileus virginianus*) and increases with age

(Grear et al. 2006; Osnas et al. 2009). Prevalence rates have been found to be 13% for 4.5- to 5.5-year-old male white-tailed deer in Wisconsin (Osnas et al. 2009). Sex-specific social behavior may be important to understanding why prevalence of CWD varies between the sexes (Miller and Conner 2005). Indirect transmission of CWD may occur through behavior associated with chemical communication such as scrapes and rubs (Skuldt et al. 2008).

Scrapes are chemical signposts made by male white-tailed deer to communicate with other deer in an area before and throughout the fall breeding season (Moore and Marchinton 1974; Hirth 1977). Scrapes are also thought to be a way for males to express dominance and establish a hierarchy (Hirth 1977; Miller et al. 1987; Moore and Marchinton 1974). Scraping is a behavior in which a male white-tailed deer typically paws a depression in the ground, marks the ground with urine and secretions from tarsal glands, and marks an over-hanging branch with secretions from scent glands and saliva (Hirth 1977; Kile and Marchinton 1977; Miller et al. 1987; Kinsell et al., [a] in review). Scrapes are thought to assist in the induction and synchronization of estrus in females (Moore and Marchinton 1974; Hirth 1977; Sawyer et al. 1989). Multiple males have been observed marking and inspecting a single scrape throughout the breeding season, and individual males have been observed marking multiple scrapes across the landscape (Alexy et al. 2001; Kinsell et al. [b] in prep).

Older male white-tailed deer make the majority of the scrapes (Ozoga and Verme 1985; Miller et al. 1987; Marchinton et al. 1990; Alexy et al. 2001; Kinsell et al. [a], in review). Adult males made 85% of the scrapes in a captive facility in Michigan and began scraping earlier than yearling males (Ozoga and Verme 1985). The degree of involvement in scraping by young males is still unclear. Yearling and 2.5-year-old males interacted with scrapes little or not at all in a captive facility in Georgia (Miller et al. 1987; Marchinton et al. 1990). Free-ranging yearling males created 42% of the scrapes in Georgia, however, and but marked scrapes less frequently than older males. Scraping activity of yearling males in that study was not delayed in relation to older males (Alexy et al. 2001). Scrape-related activity intensifies and peaks around late Oct. and declines around early Dec. (Kile and Marchinton 1977; Ozoga and Verme 1985; Ozoga 1989; Miller and Marchinton 1999; Alexy et al. 2001). Most scrape-related behavior occurs at night (Alexy et al. 2001; Kinsell et al. [b] in prep).

Transmission routes of CWD are relatively unknown. It is hypothesized that CWD prions are spread through feces, urine, direct contact with infected deer, and contaminated soil and water (Spraker et al. 1997; Miller et al. 1998; Gross and Miller 2001; Miller et al. 2004; Nichols et al. 2009). Prions can be passed through blood and saliva (Mathiason et al. 2006). Prions have been found in feces (Safar et al. 2008; Tamgüney 2009) and in low concentrations in urine (Haley et al. 2009). The nasal cavity is an efficient route of infection in hamsters (Kincaid and Bartz 2007). Prions have been shown to bond with soil particles, including some types of clay and quartz sand, enhancing their infectivity through oral exposure (Cooke et al. 2007; Johnson et al. 2006; 2007; Ma et al. 2007). Prions persist in the environment and remain infectious for years (Miller et al. 2004; Johnson et al. 2007; 2006; Mathiason et al. 2006; Seidel et al. 2007). Manganese oxides, however, may degrade prions in environments that are rich in manganese minerals (Russo et al. 2009). White et al. (2010) found that high manganese:magnesium concentrations in elk brain matter appeared to increase the risk of CWD infection.

Woolhouse et al. (1997, 2005) discussed the concept of the “20-80 rule,” whereby 80% of disease infections are caused by only 20% of the individuals. Adult male white-tailed deer in our study area make up an estimated ≤30% of the population (Hefley et al. 2010). Therefore, we predict that adult male white-tailed deer and scrape-related behavior may play an important role in the spread and persistence of CWD. The nature of scrape-related behaviors and proclivity of older males to interact with scrapes make scrapes likely hotspots for transmission of CWD among male white-tailed deer. Our objectives were to 1) identify the types of behaviors at scrapes that could contribute to the spread of CWD and 2) model the risk of contacting or shedding CWD prions at scrapes. We hypothesized that adult males would have the greatest risk of contacting and shedding CWD prions at scrapes, followed by yearling males, females, and fawns.

STUDY AREA

DeSoto National Wildlife Refuge (DNWR) is located in the flood plain of the Missouri River, about 32 km north of Omaha, Nebraska between Blair, Nebraska and Missouri Valley, Iowa, USA. The DNWR consists of a 3,384-ha patchwork of riparian hardwood forest, grassland, wetland, and cropland administered by the US Fish and Wildlife Service. The interspersion of habitat supports a diverse range of flora and fauna (US Fish and Wildlife Service 2009).

The soil on DNWR is quite variable because of past flooding and shifts of the Missouri river channel. The soil types are of Albaton-Haynie Associations. Albaton series soils are predominantly silty clay or clay in the Ap horizon, with 40-60% clay and 1-5% sand. Haynie series soils are predominantly silt loam, very fine sandy loam and silty clay loam in the Ap horizon, with 15-30% clay and 18-55% sand (Soil Survey Staff 2008). The topography is relatively flat with slopes of 0-2% (US Department of Agriculture 1976).

The forests of DNWR are dominated by mature eastern cottonwood (*Populus deltoides*), but also include black walnut (*Juglans nigra*), box elder (*Acer negundo*), American elm (*Ulmus americana*), eastern red cedar (*Juniperus virginiana*), black willow (*Salix nigra*), sandbar willow (*Salix interior*), and Chinese elm (*Ulmus parvifolia*). The understory includes hackberry (*Celtis occidentalis*), mulberry (*Morus rubra*), and green ash (*Fraxinus pennsylvanica*). Poison ivy (*Rhus radicans*) and common scouring-rush (*Equisetum hyemale*) dominate the ground layer (US Fish and Wildlife Service 2009). The grasslands of DNWR consist mostly of warm-season native species and to a lesser extent, cool-season species. Dominant native species include big bluestem (*Andropogon gerardii*), little bluestem (*Schizachyrium scoparium*), switchgrass (*Panicum virgatum*), Indian grass (*Sorghastrum nutans*), Canada wild rye (*Elymus canadensis*), and at least 160 species of native forbs and flowers. Cropland on DNWR includes corn (*Zea mays*), soybeans (*Glycine max*), and sweet clover (*Melilotus* spp.; US Fish and Wildlife Service 2009).

Estimates of pre-harvest densities of white-tailed deer at DNWR were 41-51 deer/km^2 from 2004–2007 (Hefley et al. 2010). Estimates of female:male ratios were 2.15:1 and 1.86:1 and fawn:doe ratios were 1.28:1 and 1.43:1 in 2005 and 2006, respectively (Clements et al. 2010). As part of other research efforts in the study area, 20-25 females and 20-30 males were radio-collared and ear-tagged on DNWR during the time of this study. An estimated 42 additional males and 17 females were marked with ear tags alone. We estimate that up to 24% of the males and 6% of the females were marked on DNWR during the study (Gilsdorf and Clements, pers. com.).

METHODS

We remotely monitored scrapes made by white-tailed deer during the fall breeding season from Oct - Nov., 2005 and Sept. - Nov., 2006. We located scrapes by walking forest-field edges, trails, and 2-track roads through the forest and geo-referenced them with a Global Positioning System (GPS, Garmin, Olathe, Kansas, USA). We selected scrapes if they were recently active (i.e., freshly disturbed soil in the depression or freshly broken over-hanging branches) and within 8 m of a tree that would support a camera. All monitored scrapes were associated with over-hanging branches. Trees with a circumference ≥30 cm were needed to support StumpCams (StumpCam^{TM} Inc., Tyler, Texas, USA), while trees with a circumference of ≥18 cm were sufficient for Reconyx cameras (Reconyx Silent Image, LaCrosse, Wisconsin, USA). We did not attempt to locate every scrape on the refuge, but rather searched for scrapes until all cameras were deployed in suitable locations (Figure 4-1). In 2005, we monitored 85 scrapes with 37 infrared motion-activated StumpCam video cameras and 34 motion-activated Reconyx digital camera systems. In 2006, we monitored 44 scrapes with 31 StumpCams and 4 Reconyx cameras. The majority of Reconyx units were unavailable in 2006 due to use on another study. Cameras were hung in trees 4-8 m from each scrape and 1-3 m aboveground and focused to provide a field of view that included a scrape, over-hanging branch, and ≤2-m radius of the surrounding area. We programmed StumpCams to record for 3 min when triggered, with a 10-sec lag between triggers and Reconyx digital cameras to take 1 frame per sec for 30 sec, with 1-sec between triggers. We moved cameras if scrapes were inactive for >1 week. We checked StumpCams once every 3-4 days, and Reconyx cameras once per week. We replaced batteries, videotapes and compact flash cards as needed. Each time cameras were checked, we recorded the camera identification code (ID), GPS location, date, time, and condition of the battery. We labeled each videotape with the camera ID, GPS location, and date and time of both insertion and removal from the camera. We reviewed StumpCam video tapes and digitized video of any interactions to a hard drive, and placed the digitized videos into a folder labeled with the camera ID, GPS location, and tape number for future reference. We labeled Reconyx media with the camera ID and downloaded images to a laptop at the end of each day when cameras were checked.

We defined an "encounter" with a scrape as an event in which a deer came within 2 adult body lengths (~2 m) of a scrape and could identify and interact with the scrape (i.e. a deer walks near a scrape versus running past). An "interaction" with a scrape occurred when a deer approached a scrape and performed ≥1 scrape-related behaviors. All interactions were also encounters, however, not all encounters resulted in interactions. Behavioral categories were: scrape ground, smell scrape, smell branch, grasp-lick branch, mark branch with pre-orbital gland, other branch interactions (i.e. rake antlers, and non-saliva or glandular contact with the branch), rub-urinate, urinate, defecate, and Flehmen. Each of these behaviors are described in detail in an ethogram by Kinsell et al. ([a] in review). We classified males as adult, yearling, or fawn, based on body size, body condition, and antler characteristics. We classified females as adult or fawn, based on body size, body condition, height, and length of rostrum. We did not classify yearling females due to their similar size and appearance to adults during Oct. - Nov. We examined the video images and still pictures frame by frame to identify behaviors associated with scrapes and over-hanging branches. We recorded length of time spent within 2 m of the scrape for each encounter and interaction. We recorded each behavior as present or absent during the time of an interaction. We recorded dates and times for the beginning and end of each encounter and used them to calculate elapsed time at the scrape. We analyzed time spent performing specific behaviors with the program JWatcher (Blumstein et al. 2006). We queried data out of Microsoft Access into a Microsoft Excel database (Microsoft Corporation, Redmond, Washington, USA) and formatted it for import into Program R (R Development Core Team, 2009) for statistical analysis. We used Program R, package chron (James and Hornik 2009) to analyze time data. We tested the percentage of occurrence for each behavior during interactions between 2005 and 2006 by testing a subset of the data during the peak of scraping activity from Oct. 15 - Nov. 15. We found no difference in behaviors of adult males between years (11-sample test for given proportions, X^2=88.8, 11 degrees of freedom, P<0.001). Therefore we combined data from the 2 years.

We ranked potential threat of behaviors on a scale of 0-10, where 0 was no likelihood and 10 was the absolute likelihood of contacting or shedding prions (Table 4-1 and Table 4-2, Appendix A). Behaviors with high Threat Ratings included contacting areas of a scrape with the nose, mouth, or eyes where other animals likely would have deposited any bodily secretions into a scrape, adjacent area within 2 m, or onto an over-hanging branch. Threat Rating was a qualitative number assigned to each behavior based on current knowledge of CWD transmission and what was found in this study about scrape-related behaviors (Table 4-1 and Table 4-2). We created an Exposure Index for each behavior by multiplying the average duration by the frequency of occurrence of the behavior, expressed as a percentage. We generated Risk Values for each behavior by multiplying the Exposure Index by the assigned Threat Rating of the behavior.

$\text{Risk Value} = (\text{Occurrence}_i * \text{Duration}_i)\text{Threat Rating}_i$

Where $i = 1$ of 11 scrape-related behaviors

We calculated Risk Values for contacting and shedding prions for adult males, yearling males, adult females (including yearlings), and fawns. Total Risk Value was the sum of the Risk Values for each behavior by sex-age class. We used Program R prop.test (R Development Core Team 2008), a test of equal or given proportions, to test for differences in occurrence of behaviors among the sex-age classes.

RESULTS

Cameras were operational for 1495 and 1303 camera days resulting in 41.0 and 30.2 hours of encounters/interactions in 2005 and 2006, respectively. We recorded 3106 and 1903 encounters with scrapes across all sex-age classes in 2005 and 2006, respectively (Table 4-3). Of those encounters, 39% (n=1218) and 32% (n=612) included interactions with scrapes. Adult males were the most likely to interact with a scrape during an encounter (60% of the time in both years) while fawns interacted the least (22% and 12% of the time) in 2005 and 2006, respectively (Table 4-3).

The scrape-related behavior that occurred most frequently in interactions by adult males was smell branch (64.7%, Table 4-4). Yearling males also frequently performed the smell branch behavior (60.4%). Smell branch occurred less often in interactions by females (42.3%) and fawns (22.5%) than in interactions by adult and yearling males. Smell branch, however, was the second most frequently occurring behavior for females and fawns. Smell scrape was exhibited most frequently by yearling males (66.2%), adult females (72.2%), and fawns (76.1%). Adult males (44.2%) and yearling males (30.7%) commonly performed the grasp-lick branch behavior, whereas it was rare for females (4.3%) and fawns (7.2%). Pre-orbital marking and"rub-urinating were almost exclusive to adult males. The occurrence of grazing (15-19%) and defecate (4.3-6.3%) was similar for all sex-age classes (Table 4-5).

Scrape-related behaviors of adult males tended to have longer average durations than other sex-age groups except for pre-orbital mark, graze, and defecate (Table 4-5). Fawns performed the pre-orbital marking longer (mean = 9 sec) but less frequently (1%, Table 4-4) than adult males. Mean grazing duration was longest (37 sec) for females and defecation was longest (8 sec) for yearling males. Grazing had the longest mean duration (27-37 sec) of any behavior for all sex-age classes. The shortest mean duration behavior was Flehmen (3 sec), which was only observed in adult males.

Total Risk Values for contacting CWD prions at scrapes (Risk Values$_c$) were highest for adult males (114.1, Table 4-6), followed by adult females (92.5), yearling males (79.1), and fawns (70.5, Figure 4-2). Adult males had the highest Risk Values$_c$ for all behaviors, with all contact Threat Ratings >0 except grazing. The Risk Values$_c$ for grazing was highest for adult females (57.2), which constituted 62% of their total Risk

Value$_c$, as opposed to 32% for adult males. Smell scrape had the second highest Risk Values$_c$ for all sex-age classes. Grasp-lick branch, which had the highest Threat Rating (10), had the highest Risk Values$_c$ for adult males (26.5) and yearling males (12.3) and were negligible for females (1.3) and fawns (2.2) (Table 4-6).

Total Risk Values for shedding CWD prions at scrapes (Risk Values$_s$) were highest for adult males (59.4), followed by yearling males (31.2), females (17.9), and fawns (15.5) (Figure 4-2). Adult males had the highest Risk Values$_s$ for all behaviors, with all shedding Threat Ratings >0 except for grazing and defecating (Table 4-7). The Risk Values$_s$ for grazing were highest for females (14.3) and fawns (10.3), which constituted 80% and 66% of their total Risk Values$_s$, respectively. Grazing accounted for 15% of the total Risk Value$_s$ for adult males. Grasp-lick branch, which had the highest Threat Rating (10), had the highest Risk Values$_s$ for adult (26.5) and yearling males (12.3), constituting 45% and 39% of their respective Total Risk Values$_s$ (Table 4-7).

DISCUSSION

Risk of Contacting Prions

We predicted the total Risk Values$_c$ would be highest for adult male white-tail deer, followed by yearling males, females, and fawns because adult males are more commonly seen interacting at scrapes than other sex-age classes (Miller et al. 1987; Marchinton et al. 1990; Alexy et al. 2001). Adult males had the highest total Risk Value$_c$ (114.1), which was 0.5 times higher than females (92.5), and nearly 2 times higher than yearling males (79.1) and fawns (70.5, Table 4-6). Females had a higher than expected Risk Value$_c$ due to slightly more frequent occurrence and longer duration of grazing, which had a high Threat Rating (8). Grazing resulted in the highest Risk Values$_c$ for all sex-age classes due to the long duration of grazing bouts. Since no statistical differences occurred among the sex-age classes for grazing (Table 4-4), we removed grazing from the total Risk Value$_c$ and the ranking changed (adult males > yearling males > females > fawns). All recorded grazing, urination, and defecation events occurred within 2 m of a scrape, however very little defecation and "normal" urination was observed (6% occurrence for both in males, and only 3 female urination events), and prion levels in urine and feces are thought to be very low (Haley et al. 2009, Safar et al. 2008, Tamgüney et al. 2009). Rub-urination typically was performed within the scrape depression. We believe that grazing near scrapes may still be a concern because prions bind with soil particles making them more infective (Cooke et al. 2007; Johnson et al. 2007; Ma et al. 2007), and deer are known to consume soil while grazing (Arthur and Alldrege 1979).

The three most risky behaviors for contacting prions for adult males were smell branch, smell scrape, and grasp-lick branch. Smell branch commonly resulted in direct nose contact with a branch and had the highest Risk Value$_c$ because of the high frequency of occurrence and a relatively long duration. Smell scrape had a relatively high Threat Rating (6), high frequency of occurrence, and long duration. We believe that smell scrape is a concern for contacting prions because the nasal cavity is an effective route of transmission in hamsters (Kincaid and Bartz 2007) and prions can bind to soil particles and become air-borne when scraping occurs. Smell scrape may be less of a concern for females because they do not paw at a scrape before smelling it. Grasp-lick branch was third in Risk Value$_c$ for adult males because it results in direct oral contact with the over-hanging branch, and had a moderate frequency of occurrence, and a high Threat Rating (10). The same three behaviors were the most risky for yearling males as well. Risk Values$_c$ for yearling males, however, were lower compared to values for adult males due to shorter duration and less frequent occurrence of high-threat behaviors. Other than grazing, smell scrape was the riskiest behavior for females and fawns due to high frequency of occurrence.

Risk of Shedding Prions

We predicted the risk of shedding prions would be highest for adult male white-tail deer, followed by yearling males, females, and fawns because adult males are more commonly seen interacting at scrapes than other sex-age classes (Miller et al. 1987; Marchinton et al. 1990; Alexy et al. 2001). The Risk Values$_s$ followed the expected progression (adult males > yearling males > females > fawns) because adult males exhibited high-threat behaviors more frequently and for longer duration than the other sex-age classes. The Risk Value$_s$ for adult males (59.4) was 2 times higher than yearling males (31.2), and 3 times higher than females (17.9), and fawns (15.5). Grasp-lick branch and rub-urinate posed the greatest risk of shedding prions by adult male white-tailed deer. The grasp-lick branch behavior in males received the highest Risk Value$_s$ because it occurred nearly 50% of the time and adult males manipulated the branch longer than other sex-age classes. Grasp-lick branch was followed by rub-urinate which received a higher Risk Value$_s$ due to receiving 1 of the highest Threat Ratings (6) for shedding. The behavior of greatest risk for yearling males was grasp-lick branch. Grazing was the only behavior with a high risk for shedding of prions from females and fawns, due to low occurrence or a lack of participation in other behaviors. Sawyer et al. (1982, 1989) indicated that it was common for females to urinate within 20 m of a scrape. We observed only 3 cases of urination by females near scrapes, which may be due to our focal area of a 2-m radius around the scrape.

Risk of Behaviors

Behaviors bring individuals into contact with various parts of their environment and other individuals of its species. Behaviors become a concern to disease biologists when those behaviors bring healthy individuals into contact with infected individuals or a contaminated environment. Scrapes made by male white-tailed deer may be focal points in transmission of CWD. While many scrapes may be distributed across the environment, each 1 is a specific point on the landscape in which individuals may visit and interact. A mean of 5 different individuals will visit a single scrape, and a single active male may visit at least 8 different scrapes that may be a mean minimum distance of 978 m apart (Kinsell et al. [b] in prep). If 1 male infected with CWD were to interact with a scrape and contaminate it with infectious prions, any animal subsequently interacting with that scrape may be at risk of contacting the disease agent and becoming infected.

Our study site was located in an area with high deer density (41-51/km^2) with female:male ratios near 2:1, which may influence breeding and scrap-related behavior. Areas with high deer density are likely to see increased scrape density, and increased sharing of scrapes among males, as home ranges are more likely to overlap. Lower female:male ratios may increase the chance that more than 1 male will interact with each scrape, as males may be inclined to expand their home range in the breeding season to maximize their chances of successfully mating. Males in areas with high female:male ratios may be less likely to roam due to an abundance of females. The age distribution in a given area may also have an effect on scrape use. Dominant adult males are more likely to interact with scrapes than younger males; therefore, populations that favor older males may facilitate more scraping activity and thus, more opportunity to spread disease.

We believe that scrape-related behavior may be a sex-specific social behavior that contributes to the spread of CWD in male white-tailed deer. Our study confirmed the hypothesis that adult male white-tailed deer are the sex-age class at highest risk for contacting and shedding CWD prions at a scrape. We found this to be consistent with a higher prevalence of CWD detected in male white-tailed deer and in older white-tailed deer (Grear et al. 2006; Osnas et al. 2009). Adult males are known to range more widely than females, especially during the breeding season (Nixon et al. 1991; Beier and McCollough 1990; Gavin et al. 1984; Marchinton and Hirth 1984; Nelson and Mech 1981) and this holds true in our study area (Clements et al. 2010). Up to 15 individual males may use a single scrape and some adult males may visit at least 8 different scrapes during a breeding season (Kinsell et al.[b] in prep). The deposition and inspection of many different secretions and excretions in the vicinity of a scrape lends credence to the possibility that scrapes are focal points for CWD transmission during the breeding season of white-tailed deer.

Management Implications

If scrape-related behavior by male white-tailed deer is indeed an effective route of transmission for chronic wasting disease, then management practices such as reducing deer density (especially density of older male deer) would be beneficial in reducing indirect contact between bucks at scrape sites. Areas that are managed for trophy animals could be of particular concern, since it is likely the older, high quality males are most likely to spread the disease through scrapes while in the pre-clinical or asymptomatic stages of the disease. Other management strategies to consider for reducing the spread of CWD through scrape-related behavior may be to decontaminate soils with manganese (Russo et al. 2009) or enzymes (Saunders et al. 2010), remove over-hanging branches along field edges, use scrapes as attractants to shoot deer, especially older aged bucks at night.

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TABLES AND FIGURES

Table 4-1: Threat Ratings and their rationale for contacting CWD prions based on scrape-related behaviors of white-tailed deer. Zero indicates no likelihood and 10 indicates absolute likelihood of contacting prions.

Behavior	Rating	Rationale	References
Smell branch	3	Branch contaminated with saliva & glandular secretions; some nose contact with branch; inhalation of scents with possible prion contamination	Mathiason et al. 2006; Kincaid and Bartz 2007
Smell scrape	6	Prions in feces and urine (at low levels) in scrape depression; prions bind with soil; scraping stirs up dust; inhalation of dust; possible nasal cavity infection route	Haley et al. 2009; Safar et al. 2008; Tamgüney et al. 2009; Spraker et al. 2009; Johnson et al. 2007; Miller et a. 2004; Kincaid and Bartz 2007; Williams and Young 1993
Grasp-lick branch	10	Known saliva transmission of prions; prions persist in the environment; oral contact with branch previously contacted orally by other individuals; over-hanging branch is integral to scraping	Miller et al. 2004; Johnson et al. 2006; Mathiason et al. 2006; Seidel et al. 2007; Hirth 1977; Kile and Marchinton 1977; Marchinton and Hirth 1984
Scrape ground	1	Little chance of infectious material contacting mucosal membranes; may stir up dust making it available for inhalation; possible secretions containing prions from inter-digital scent glands?	N/A[a]
Pre-orbital marking	2	Mucosal membrane (eye, glands) contact with branch; third eye-lid test for sheep scrapie; similarities between scrapie and CWD epidemiology	Sigurdson et al. 1999; O'Rourke et al. 2000
Rub-urinate	0	No mucosal membrane contact with potentially infectous material	N/A
Graze	8	Oral contact and ingestion of material near scrapes, possibly contaminated with urine, feces, glandular secretions, or dust from the scrape; prions found in urine and feces; ingestion of soil while grazing; prions bind with soil	Haley et al. 2009; Safar et al. 2008; Tamgüney et al. 2009; Arthur and Alldredge 1979; Johnson et al. 2007
Urinate	0	No mucosal membrane contact with potentially infectous material	N/A
Defecate	0	No mucosal membrane contact with potentially infectous material	N/A
Other branch	0	No mucosal membrane contact with potentially infectous material	N/A
Flehmen	4	Inspection of urine with the nasal cavity by males; prions found in urine at low levels	Haley et al. 2009

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[a] Not applicable

Table 4-2: Threat Ratings and their rationale for shedding CWD prions based on scrape-related behaviors of white-tailed deer. Zero indicates no likelihood and 10 indicates absolute likelihood of shedding prions.

Behavior	Rating	Rationale	References
Smell branch	0	No shedding of glandular secretions or bodily fluids	N/A[a]
Smell scrape	0	No shedding of glandular secretions or bodily fluids	N/A
Grasp-lick branch	10	Known transmission of prions in saliva; saliva depostion on branch; prions persist in the environment; over-hanging branch is integral to scraping	Miller et al. 2004; Johnson et al. 2006; Mathiason et al. 2006; Seidel et al. 2007; Hirth 1977; Kile and Marchinton 1977; Marchinton and Hirth 1984
Scrape ground	1	Inter-digital scent gland secretions may be deposited in scrape; no evidence of prion transmission through scent glands, however we believe the possibility exists	Moore and Marchinton 1974
Pre-orbital marking	3	Mucosal membrane (eye, glands) contact with branch; glandular deposition on branch; no evidence of prion transmission through scent glands, however we believe the possibility exists	N/A
Rub-urinate	6	Prions found at very low levels in urine; also deposits tarsal scent gland secretions; no evidence of prion transmission through scent glands, however we believe the possibility exists	Haley et al. 2009
Graze	2	Possible saliva contamination of forage materials; Saliva known to transmit prions	Mathiason et al. 2006
Urinate	5	Prions found at very low levels in urine	Haley et al. 2009
Defecate	7	Prions found in feces; rectal biopsies are an effective preclinical test for CWD	Safar et al. 2008; Tamgüney et al. 2009; Spraker et al. 2009
Other branch	0	No shedding of glandular secretions or bodily fluids	N/A
Flehmen	0	No shedding of glandular secretions or bodily fluids	N/A

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[a] Not Applicable

Table 4-3: Number of recorded encounters and interactions with scrapes by sex-age class of white-tailed deer at DeSoto National Wildlife Refuge in eastern Nebraska and western Iowa, 2005-2006.

	2005			2006		
	Encounters	**Interactions**	**Percent**	**Encounters**	**Interactions**	**Percent**
All	3106	1218	39%	1903	612	32%
Adult Male	936	566	60%	504	300	60%
Yearling Male	541	273	50%	375	154	41%
Adult Female	896	225	25%	549	101	18%
Fawn	691	153	22%	459	56	12%
Unknown adult	42	1	2%	16	1	6%

Table 4-4: Percent occurrence of scrape-related behaviors by white-tailed deer at DeSoto National Wildlife Refuge in eastern Nebraska and western Iowa, 2005-2006.

Percent Occurence of Interactions[a]				
Behavior	Adult male	Yearling male	Adult female	Fawn
Smell branch	64.7%[b]	60.4%[b]	42.3%[d]	22.5%[e]
Smell scrape	61.1%[b]	66.3%[bc]	72.7%[c]	76.1%[c]
Grasp-lick branch	44.2%[b]	30.7%[c]	4.3%[d]	7.2%[d]
Scrape	36.8%[b]	7.7%[c]	0.0%[d]	0.0%[d]
Pre-orbital mark	28.8%[b]	16.6%[c]	1.8%[d]	1.0%[d]
Rub-urinate	20.8%[b]	3.8%[c]	0.3%[d]	0.0%[d]
Graze	14.4%[b]	16.2%[b]	19.3%[b]	17.2%[b]
Urinate	5.9%[b]	8.4%[b]	0.9%[d]	1.0%[d]
Defecate	5.7%[b]	6.3%[b]	4.3%[b]	5.3%[b]
Other branch	3.1%[b]	0.9%[c]	0.3%[c]	1.0%[bc]
Flehmen	0.4%[b]	0.0%[b*]	0.0%[b*]	0.0%[b*]
Total interactions	866	427	326	209

[a] Percentages do not sum to 100% due to multiple behaviors within interactions.

[b, c, d, e] Differing letters between sex-age classes indicate difference at the 95% confidence level.

[*] Yearling males, adult females, and fawns did not peform Flehmen. No significant differences were observed, however, because of low occurrence by adult males.

Table 4-5: Average duration (sec) of each scrape-related behavior by sex-age group of white-tailed deer at DeSoto National Wildlife Refuge in eastern Nebraska and western Iowa, 2005-2006.

	Behavior Duration			
Behavior	**Adult male**	**Yearling male**	**Female**	**Fawns**
Smell branch	9	5	6	6
Smell scrape	7	5	6	5
Grasp-lick branch	6	4	3	3
Scrape	11	8	0	0
Pre-orbital mark	6	7	5	9
Rub-urinate	8	4	0	0
Graze	32	27	37	30
Urinate	7	4	4	4
Defecate	6	8	6	7
Other branch	8	4	0	0
Flehmen	3	0	0	0

Table 4-6: Risk Values$_c$ for contacting chronic wasting disease prions at scrapes for sex-age groups of white-tailed deer at DeSoto National Wildlife Refuge in eastern Nebraska and western Iowa, 2005-2006. Risk Value = (Occurrence$_i$ * Duration$_i$)Threat Rating$_i$, where i = 1 of 11 scrape-related behaviors.

	Contacting	**Risk Value**			
Behavior	**Threat Rating**	**Adult male**	**Yearling male**	**Adult female**	**Fawn**
Smell branch	3	17.5	9.1	7.6	4.0
Smell scrape	6	25.7	19.9	26.2	22.8
Grasp-lick branch	10	26.5	12.3	1.3	2.2
Scrape	1	4.0	0.6	0.0	0.0
Pre-orbital mark	2	3.5	2.3	0.2	0.2
Rub-urinate	0	0.0	0.0	0.0	0.0
Graze	8	36.9	34.9	57.2	41.3
Urinate	0	0.0	0.0	0.0	0.0
Defecate	0	0.0	0.0	0.0	0.0
Other branch	0	0.0	0.0	0.0	0.0
Flehmen	4	0.0	0.0	0.0	0.0
Total Risk Value		114.1	79.1	92.5	70.5

Table 4-7: Risk Values$_s$ for shedding chronic wasting disease prions at scrapes for sex-age classes of white-tailed deer at DeSoto National Wildlife Refuge in eastern Nebraska and western Iowa, 2005-2006. Risk Value = (Occurrence$_i$ * Duration$_i$)Threat Rating$_i$, where i = 1 of 11 scrape-related behaviors.

	Shedding	**Risk Value**			
Behavior	**Threat Rating**	**Adult male**	**Yearling male**	**Adult female**	**Fawn**
Smell branch	0	0.0	0.0	0.0	0.0
Smell scrape	0	0.0	0.0	0.0	0.0
Grasp-lick branch	10	26.5	12.3	1.3	2.2
Scrape	1	4.0	0.6	0.0	0.0
Pre-orbital mark	3	5.2	3.5	0.3	0.3
Rub-urinate	6	10.0	0.9	0.0	0.0
Graze	2	9.2	8.7	14.3	10.3
Urinate	5	2.1	1.7	0.2	0.2
Defecate	7	2.4	3.5	1.8	2.6
Other branch	0	0.0	0.0	0.0	0.0
Flehmen	0	0.0	0.0	0.0	0.0
Total Risk Value		59.4	31.2	17.9	15.5

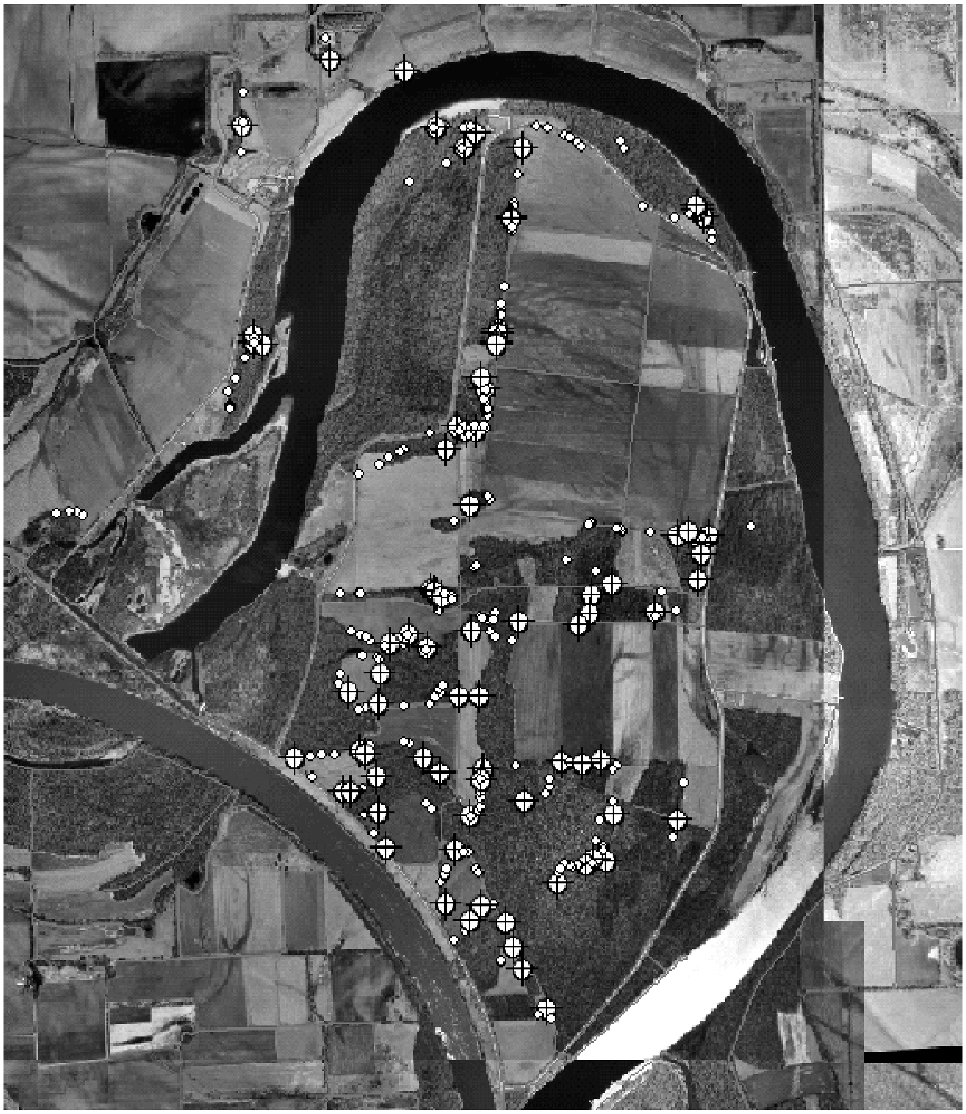

Figure 4-1 : Locations of scrapes (°) made by male white-tailed deer at DeSoto National Wildlife Refuge in eastern Nebraska and western Iowa, 2005. Twenty-seven percent of the observed scrapes were monitored with animal-activated cameras (⌖).

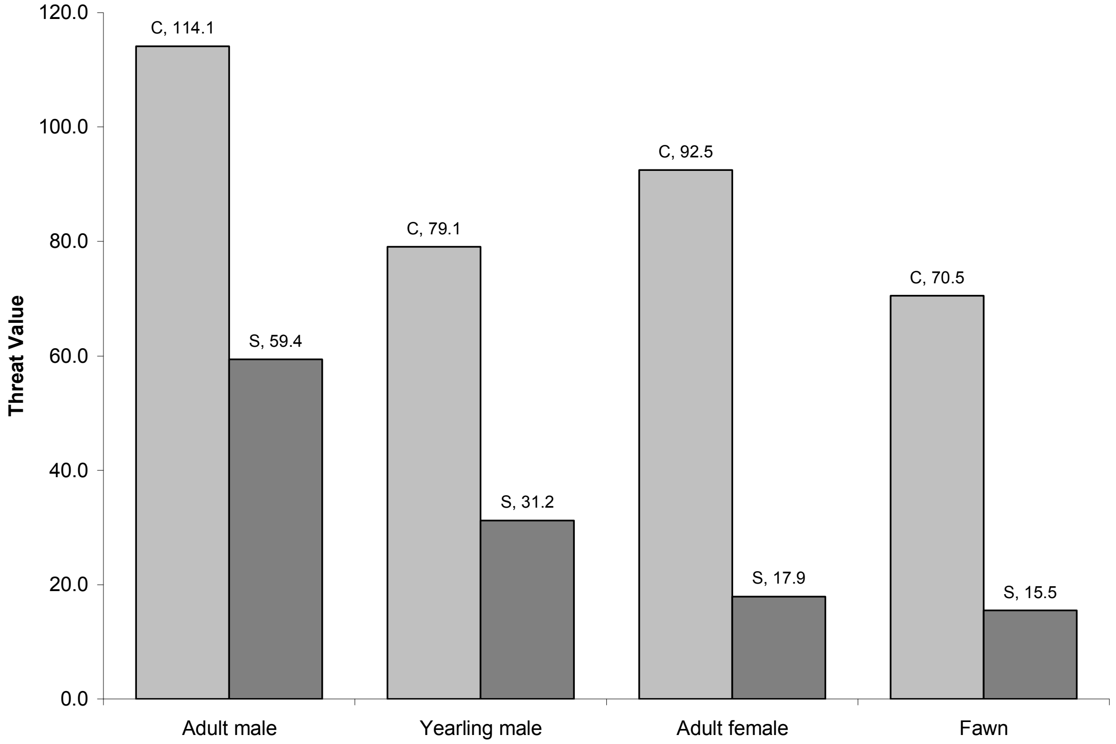

Figure 4-2: Total Risk Values[a] for contacting (C) and shedding prions (S) through scrape-related behaviors by adult male, yearling male, female, and fawn white-tailed deer at DeSoto National Wildlife Refuge in eastern Nebraska and western Iowa, 2005-2006.

[a] Total Risk Value = $\sum_{i=1-11}(Occurence_i * Duration_i)ThreatRating_i$, where $i = 1$ of 11 scrape-related behaviors.

APPENDIX A: THREAT RATING RATIONALE

This appendix is summarized in Table 4-1 and Table 4-2. In the following paragraphs, we will briefly describe how each behavior may bring an individual to come into contact with, or shed CWD prions at a scrape, and thus the reasoning for the Threat Ratings we assigned each behavior in Chapter 4.

Smell branch

We assigned "smell branch" a Threat Rating of 3 for contacting prions because it often involves a mucosal membrane (the nose) coming into contact with material that had previously been in contact with mucosal membranes of other deer (i.e. mouth, tongue, nose, pre-orbital glands). With evidence that CWD can be transmitted through saliva and the nasal cavity (Mathiason et al. 2006; Kincaid and Bartz 2007) we believe that this behavior has a moderate risk of shedding CWD. However, we assigned a Threat Rating of 0 for shedding prions because it does not involve directly depositing a substance on the branch. However, there may be a small chance of prion deposition due to mucosal membrane contact. Occurrence and duration of the smell branch behavior was higher in adult males than any other class which resulted in a much higher Risk Value for contacting prions for males than the other sex-age classes.

Smell scrape

We assigned "smell scrape" a Threat Rating of 6 for contacting prions because of evidence that animals may become infected through the nasal cavity and the likelihood that prions could be shed into the scrape depression via urine and feces. Prions have been found in feces and urine (Haley et al. 2009; Safar et al. 2008; Tamgüney et al. 2009), and rectal mucosa biopsies are an effective means of detecting preclinical CWD prions in elk (Spraker et al. 2009). Therefore, we believe urination, rub-urination and defecation may deposit CWD prions into the scrape depression if CWD is present in the area. Soil has been found to be an effective reservoir for prions, and bonds to some types of clay may increase infectivity (Cooke et al. 2007; Johnson et al. 2006; 2007; Ma et al. 2007). Prions remain infective in the environment for >2 years (Miller et al. 2004) and scrape sites are often re-used in subsequent years (we monitored 20 scrapes in 2006 that were also monitored in 2005 and only 1 was not re-used). The nasal cavity is an efficient means of CWD infection in hamsters (Kincaid and Bartz 2007). Severe lesions were found in the olfactory tubercle in a study of the central nervous system of CWD-infected mule deer and elk (Williams and Young 1993), which may suggest infection through the nasal cavity. We observed that male white-tailed deer often scraped the depression and immediately smelled the scrape, possibly inhaling dust particles that have been in contact with infected urine or feces. We believe that the risk of male white-tailed deer encountering environmental prions in this manner is high. We assigned smell scrape a Threat Rating of 0 for shedding prions because they are unlikely to be shed in this manner.

Lick/grasp branch

We assigned the “lick/grasp branch” behavior Risk Value of 10, for contacting and shedding prions, because it involves oral cavity contact with material that had previously been in contact with the oral cavity of other deer. Chronic wasting disease can be transmitted through saliva and CWD prions can survive in the environment for >2 years (Miller et al. 2004; Johnson et al. 2006; Mathiason et al. 2006; Seidel et al. 2007). We believe that this is the highest risk behavior performed by white-tailed deer at a scrape. Prions may be shed through saliva deposited on the over-hanging branch and subsequently other deer will also make oral contact with the contaminated branch. Threat Values (Table 4-6) for this behavior were higher for adult males (26.5) and yearling males (12.3) due to a much higher occurrence and longer duration compared to females (1.3) and fawns (2.2).

The over-hanging branch has been found to be an integral part of scraping activity and the association is highly significant (Hirth 1977; Kile and Marchinton 1977; Marchinton and Hirth 1984). All of our scrapes were associated with over-hanging branches.

Scrape ground

The “scrape ground” behavior received a low Threat Rating of 1 for both contacting and shedding prions because it involves little chance of potentially infectious material coming into contact with mucosal membranes of deer. It also poses little chance of shedding prions into a scrape depression. While scraping may stir up dust making dust particles available to be inhaled if the deer smells the scrape, scraping in and of itself is little threat. However, the possibility of secretions from the inter-digital scent glands containing CWD prions should not be ruled out.

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Pre-orbital marking

We assigned the low Threat Rating of 2 to "pre-orbital marking" for contacting because a mucosal membrane (eye and pre-orbital gland) may contact a previously infected branch. A Threat Rating of 3 was assigned for shedding because we were unable to find evidence that CWD prions are shed or transmitted through scent glands. However, Sigurdson et al. (1999) showed that CWD spreads throughout the body in a pattern similar to scrapie in sheep. O'Rourke et al. (2000) found that testing the third eyelid for scrapie prions in sheep is a practical live test for scrapie. We believe there is a small chance that CWD prions may be shed through membranes and glands near the eye, further research may be warranted. The Threat Rating for shedding is higher than that of contacting because it involves the deposition of scent gland secretions onto the over-hanging branch. However, we were unable to find evidence in the literature that suggests CWD prions are shed through scent glands.

Rub-urinate over scrape

We assigned a Threat Rating of 0 to "rub-urination" for contacting prions because there is little inherent risk of potentially infectious material coming into contact with the deer in a way that could cause infection. We rated it as 6 for shedding prions because it involves the deposition of urine and scent gland secretions into the scrape depression. Haley et al. (2009) detected CWD prions in urine by transgenic mouse bioassy, however at much lower concentrations than what is found in saliva. We were unable to find evidence in the literature that suggests CWD prions are shed through scent glands.

Graze

Grazing represents the biggest risk of transmission of CWD at scrapes to females and fawns. It was common for females and fawns to encounter a scrape while grazing, spend a few seconds inspecting the scrape, and then continue grazing in the area. We should also note that grazing occurred more frequently than is indicated by our interaction data. Grazing was considered an interaction if the deer also performed a scrape-related behavior. If no other scrape-related behavior was performed, grazing was considered an encounter and not included in the analysis. Greater than half of the Risk Values (Table 4-6 and Table 4-7) for contacting and shedding prions for females and fawns came from this behavior, due to long duration and high percentage of occurrence.

We assigned a Threat Rating of 8 to "grazing" for contacting prions because it involves oral contact and ingestion of vegetation in the vicinity of a scrape, which is likely to be contaminated with urine, feces, scent gland secretions, and/or dust from the scrape. Prions have been shown to exist in urine (Haley et al. 2009) and in the feces of infected hamsters and asymptomatic deer (Safar et al. 2008; Tamgüney et al. 2009). Mule deer in Colorado were found to ingest an average of 8-30 grams of soil per day while grazing, depending on the season (Arthur and Alldredge 1979). Deer that graze in the vicinity of a scrape may come into contact with grass or soil that has been contaminated with urine or feces from males that previously marked the scrape. We assigned a low rating of 2 for shedding prions due to the small chance that deer may leave saliva on grass that was not consumed.

Defecation and urination

We assigned a Threat Rating of 0 for contacting prions because these behaviors have little risk of bringing an animal into contact with environmental prions. We assigned moderate Threat Ratings of 7 for defecation and 5 for urination for shedding prions because of the evidence that prions exist in urine and feces. Urination received a lower rating because prion concentrations have been shown to be very low in urine (Haley et al. 2009). Defecation was given a higher rating because prions have been found in feces (Safar et al. 2008, Tamgüney et al. 2009), and rectal mucosa biopsies have been shown to be effective in preclinical CWD testing (Spraker et al. 2009), which may indicate a higher concentration of prions in feces than in urine. Risk Values for defecation and urination were low because of short duration and low occurrence.

Other branch contact

We assigned a Threat Rating of 0 to “other branch contact” for both contacting and shedding because these behaviors aren’t likely to be involved with shedding prions or making mucosal contact with potentially contaminated material at a scrape.

Flehmen

We assigned a Threat Rating of 4 to Flehmen for contacting prions because it involves inspection of urine with the nasal cavity. Prions have been found to exist in urine (Haley et al. 2009), but at low levels. The Flehmen behavior which was only observed 3 times in the vicinity of a scrape is the most likely way prions could be shed by females and transmitted to males near a scrape.

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