LITERATURE REVIEW OF MULE DEER AND WHITE-TAILED DEER MOVEMENTS IN WESTERN AND MIDWESTERN LANDSCAPES

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ABSTRACT—The relationships among seasonal change, population dynamics, social pressures, landscape dynamics, anthropologic disturbances, and behavioral ecology are complex. Therefore, migration and seasonal movements are poorly understood and dispersal continues to be one of the least understood aspects of animal ecology in North America. We reviewed scientific literature on movements of mule deer (*Odocoileus hemionus*) and white-tailed deer (*O. virginianus*) in western and midwestern landscapes to identify gaps in our knowledge and direct future research. We used electronic databases, library catalogs, Internet search engines, and peer-reviewed journals to conduct key word searches for pertinent articles. We found that deer disperse due to habitat conditions and social pressures that are based on seasonal influences. Dispersal rates and distances vary regionally and are influenced by landscape characteristics and competition for resources such as food, cover, and mates. Migration and dispersal may influence local population levels. Decisions to manipulate densities, sex ratios, and age structures should account for local deer movements.

Key Words: dispersal, migration, movements, mule deer, *Odocoileus hemionus*, *Odocoileus virginianus*, white-tailed deer

INTRODUCTION

Mule deer (*Odocoileus hemionus*) and white-tailed deer (*O. virginianus*) are two species of the family Cervidae that are endemic to the Great Plains of North America. Mule deer are found primarily between the West Coast and central Great Plains (Wallmo 1981), while white-tailed deer are widely distributed throughout North America (Halls 1984; Fig. 1). Many of the states within the central Great Plains support sympatric populations of mule deer and white-tailed deer. Although their geographic distributions overlap in some areas, both species are often segregated by habitat selection. Mule deer reside in pockets of vegetation in uplands adjacent to the wooded riparian areas that white-tailed deer prefer (Wood et al. 1989; Whittaker and Lindzey 2004). In addition, mule deer tend to orient spatially toward rangeland and areas of rough topography, while white-tailed deer tend more toward agricultural cropland.

Mule deer and white-tailed deer both serve a vital role in the economies of western and midwestern states, and

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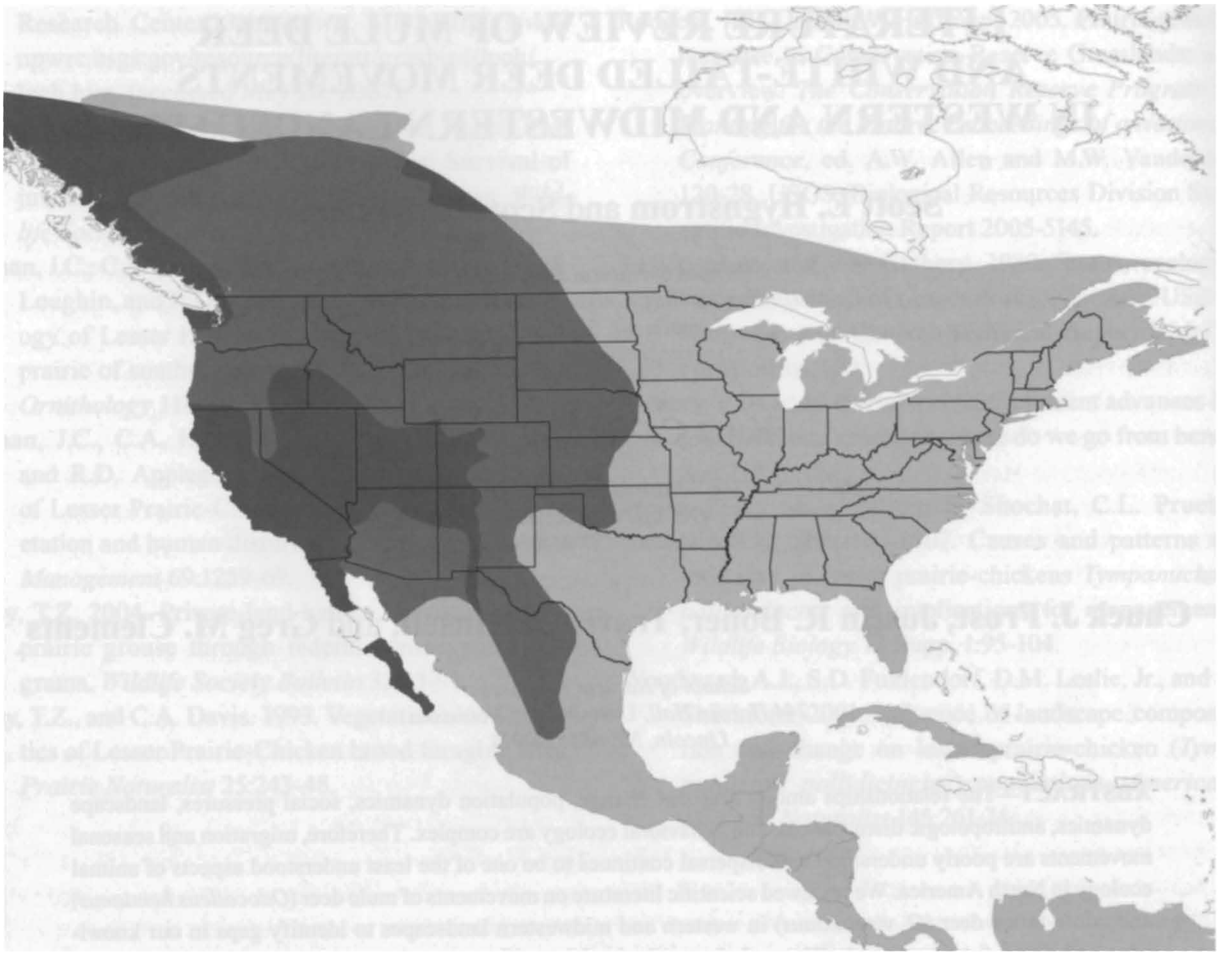

Figure 1. The distribution of mule deer and white-tailed deer in North America. The darkest shade of gray indicates the range of mule deer (*Odocoileus hemionus*), the lightest shade indicates the range of white-tailed deer (*O. virginianus*), and the medium shade indicates range overlap between the two species.

are considered an important resource. The U.S. Fish and Wildlife Service (2002) reported the economic impact of deer hunting nationwide to be $19.4 billion. Concern has been raised recently, however, because of wildlife diseases such as chronic wasting disease that threaten the health and viability of deer populations. Chronic wasting disease is a fatal transmissible spongiform encephalopathy in cervids and is caused by an abnormal, protease-resistant prion protein (Williams and Young 1980). Infected deer that move across the landscape have the potential to transmit diseases to uninfected deer or environments. The epidemic distribution of diseases like chronic wasting disease can reflect the movement patterns of the vector (Conner and Miller 2004). Since the year 2000, millions of dollars have been spent by state and federal agencies trying to determine the distribution, ecology, transmission, and impacts of chronic wasting disease. It is a major concern for wildlife agencies and hunters throughout North America because it affects the survival of deer and the dynamics of the disease are largely unknown. Hunters of cervids provide a large portion of state incomes (as much as $1 billion in Wisconsin), which if lost would have severe effects on local economies (Joly et al. 2003).

Our objective was to conduct an exhaustive review of the scientific literature on movements of mule deer and white-tailed deer in western and midwestern landscapes. Results will serve to identify gaps in our knowledge of deer movements and will direct future research. Knowledge of movements can provide insight into deer management and may help when formulating and evaluating plans to control deer populations or minimize the spread of wildlife diseases such as chronic wasting disease. Movements of deer vary across the United States, thus it is important for biologists and managers to evaluate movements regionally.

METHODS

We reviewed pertinent scientific literature on the movements of mule deer and white-tailed deer from the western and midwestern United States. Our methodology consisted of two components: (1) an assessment of the current literature on mule deer and white-tailed derived through electronic databases, library catalogs, Internet searches, and scientific journals, and (2) the collection of supplemental material through secondary searches of the literature cited in important articles.

We conducted a thorough search of the movements of deer using the interlibrary electronic databases accessed from the University of Nebraska–Lincoln (UNL) and the Nebraska State College System. We focused on biological databases available through the E-resource page of the UNL interlibrary system (http://www.unl.edu/libr/resources), searching each database using combinations of key words and linked words. We used the same combination of key words to search intercollegiate catalogs and various Internet search engines such as Google, Yahoo, MSN, and Excite. We used the electronic databases Biological Abstracts, BioOne, Ecology Abstracts, Science Citation Index (Web of Science), Wildlife and Ecology Studies Worldwide, and Zoological Record. We searched the peer-reviewed scientific periodicals *Journal of Wildlife Management*, *Wildlife Society Bulletin*, *Journal of Mammalogy*, *Canadian Journal of Zoology*, and the *Journal of Range Management* in conjunction with electronic databases. Key words were mule deer, white-tailed deer, deer, ungulate, movement, dispersal, migration, emigration, immigration, seasonal movement, temporary excursion, behavior, ecology, activity, distribution, spatial pattern, environmental factors, social organization, management, home range, radio-telemetry, Great Plains, Midwest, and Nebraska. We used three types of information for our review: peer-reviewed articles, theses and dissertations, and state- and government-reviewed documents. After information was gathered and read, we performed a secondary search of each "literature cited" section and cited references that we considered useful. All information was accessed between December 20, 2006, and March 13, 2008.

Definitions

We focus on two of the most prominent types of movement: dispersal and migration. "Dispersal," or "emigration," is defined as a process by which individuals are influenced to leave their natal range and establish a new, distinct home range (Halls 1984). An event or stimulus such as parturition may influence dispersal. Individuals usually continue along a path of dispersal until an area is found that fulfills their habitat needs. Once an individual's needs are met, a new home range is established. "Effective dispersal" refers to the movement of an individual to a new area where it produces offspring that subsequently breed (VerCauteren 1998). Effective dispersal is important since it is responsible for the continuation of lineages and may affect gene flow and genetic drift in a region (Smith et al. 1975; Anderson 1989).

"Migration" occurs when an individual moves from one home range to a different home range and then returns to the original. Generally, movement occurs between two ranges, summer and winter. Migration from winter to summer range is referred to as "spring migration" while migration from summer to winter is known as "fall migration." Migration commonly occurs in northern latitudes and mountainous areas where deer face inclement weather or where availability and quality of habitats change with the seasons (Gruell and Papez 1963; Siglin 1965; Nelson and Mech 1984; Garrott et al. 1987; Nixon et al. 1991). Deer in southern latitudes tend to be annual residents and generally do not migrate seasonally (Marchinton and Jeter 1966; Kammermeyer 1975). Some deer temporarily shift use of habitats within their ranges in response to fluctuating environmental conditions (Sparrowe and Springer 1970; Kucera 1976; Beier and McCullough 1990). Some deer do not migrate and occupy summer range year-round or briefly occupy a winter range when winters are mild (Drolet 1976; Blouch 1984; Nixon et al. 1991; Nelson 1995). Deer that fail to migrate to winter range or that migrate to winter range briefly and return to summer range are commonly referred to as "facultative migrators" (Nelson 1995; Sabine et al. 2002; Brinkman et al. 2005). Deer that routinely migrate to summer range in the spring and to winter range in early winter are commonly referred to as "obligate migrators" (Sabine et al. 2002).

"Temporary excursions" are local movements that occur when deer leave their home range for a short time and return without establishing a separate home range. Temporary excursions are generally longer than average daily movements and may be due to a variety of factors, such as human disturbance, feeding and bedding behavior, caring for fawns, breeding behavior, and weather (VerCauteren 1993). Temporary excursions may be viewed as adaptive since animals gain important information regarding the location, potential risks, and availability of resources surrounding their home range (Jeter and Marchinton

1964; Nelson and Mech 1984). Temporary excursions of white-tailed and mule deer have been up to 15 km from established home ranges (Inglis et al. 1979; Eberhardt et al. 1984). Sparrowe and Springer (1970) reported that anthropogenic influences, such as hunting, caused white-tailed deer to move up to 16 km. Although temporary excursions are an important movement of deer, they will only be briefly examined.

RESULTS AND DISCUSSION

Dispersal

Dispersal is an adaptive choice (Comins et al. 1980) that may result in increased fitness for individuals. Dispersal can offer better opportunities for reproduction and survival through access to higher quality habitat, increased reproduction, avoidance of competition or predators, increased gene flow, and a higher probability of offspring having desirable genotypic traits (Howard 1960; Lidicker 1962; Ricklefs 1973; Bekoff 1977). Parents may benefit from dispersing progeny through spread of the parents' genes to new areas, thereby increasing the parents' fitness (VerCauteren 1998). In unpredictable environments where local populations are in danger of extinction, dispersers help to restore and maintain the species (Levins 1968; Nixon et al. 1991). Benefits for individuals that choose to disperse may include increased availability of resources (Comins et al. 1980), decreased probability of inbreeding (Holzenbein and Marchinton 1992), and higher likelihood of surviving to reproduce (Horn 1983).

Dispersal should be viewed as a process rather than an incident, during which the mechanism is likely an accumulation and interaction of a variety of dynamic forces (Dobson and Jones 1985). The relationships among seasonal change, population demographics, social pressures, landscape dynamics, anthropogenic disturbances, and behavioral ecology are complex. Therefore, dispersal remains one of the least understood aspects of animal ecology (MacDonald and Johnson 2001).

Causative Factors

Seasonality plays an important role in the dispersal of mule deer and white-tailed deer. Important factors such as photoperiod, weather, plant phenology, agricultural activities, and protective cover change with each season. Many organisms that inhabit environments that vary seasonally have evolved circannual rhythms that optimize the timing of biological events (i.e., dispersal, migration, birth, and breeding). Most dispersal by deer occurs during the fawning period (Woodson et al. 1980; Eberhardt et al. 1984; Nixon et al. 1991; Brinkman et al. 2005) and breeding season (Ozoga and Verme 1986; McCoy et al. 2005; Shaw et al. 2006). The degree of seasonality fluctuates according to latitude and location, thus the timing of movements varies across time and space.

Spring Dispersal

As the fawning period approaches, many environmental, biological, and behavioral events change. The fawning season peaks between late May and early July for mule deer and white-tailed deer. Prior to the peak, pregnant females often separate and reduce their interactions with other deer (Fraser 1968; Bertrand et al. 1996). Pregnant does often search for isolated areas or specific fawning areas where they can give birth (Townsend and Smith 1933; White et al. 1972). To achieve separation, adult females exhibit aggressive behaviors toward their young from previous years to encourage them to disperse (Downing and McGinnes 1969; Hawkins and Klimstra 1970; Brinkman et al. 2005). Aggression by adult females may occur to reduce the potential for future inbreeding (Ozoga and Verme 1985; Harvey and Ralls 1986).

Maternal aggression is generally implicated as the sole reason for dispersal during fawning. In Texas, female white-tailed deer were harvested at a higher rate at one study site than at another, yet dispersal rates of yearling males did not change (McCoy et al. 2005). Other studies have presented alternative findings. In Illinois, no significant differences in dispersal behaviors were observed between orphan and non-orphan deer (Nixon et al. 1991; Shaw et al. 2006). In eastern Nebraska, spring dispersal of white-tailed deer occurred almost two months before the peak of parturition (VerCauteren 1993) and was associated with changes in photoperiod (VerCauteren 1998). Other factors such as food availability, competition, or social pressure from deer other than the dam may contribute to earlier spring dispersal (Holzenbein and Marchinton 1982).

Fall Dispersal

Fall dispersal occurs primarily in males and is related to the social pressures that arise during the breeding season (Hawkins et al. 1971; Kammermeyer and Marchinton 1976; Marchinton and Hirth 1984; Ozoga and Verme 1985; Tiersen et al. 1985; Ozoga and Verme 1986; Dusek et al. 1989; McCoy et al. 2005; Shaw et al. 2006). Female aggression is not presumed to be the proximate cause of fall dispersal (Shaw et al. 2006). The onset of breeding in deer is stimulated by the seasonal change in photoperiod (Verme and Ozoga 1987). During the breeding season, males compete for mates (Hawkins and Klimstra 1970; Kammermeyer and Marchinton 1976). The sexual competition hypothesis states that increased competition among breeding males during the fall promotes dispersal (Kammermeyer and Marchinton 1976; Marchinton 1982; Rosenberry et al. 2001; Shaw et al. 2006). In the fall, males separate from their summer bachelor groups to determine their rank within the social hierarchy. Status within the social hierarchy of males is thought to be linked to age and antler development (Townsend and Bailey 1981; McCoy et al. 2005), although exact relationships are still uncertain. Yearling males are considered to be the most subordinate (Hawkins et al. 1971; Greenwood 1980) and most likely to disperse during fall (Hawkins et al. 1971; Kammermeyer and Marchinton 1976; Nelson and Mech 1984; Tiersen et al. 1985; McCoy et al. 2005). Young adult males that cannot compete with older adult males for mates and suitable habitat and may have to travel long distances to satisfy these requirements (McCoy et al. 2005).

The relationship between antler size and social status remains uncertain. Dominance of male deer is thought to be related in part to antler size (Espmark 1964; Maylon and Healy 1994). Therefore, yearling deer with smaller antlers should be more subordinate and therefore more likely to disperse, but McCoy et al. (2005) reported lower dispersal rates in spike-antlered yearlings than branch-antlered yearlings. Also, males that are more sexually mature tend to have larger antlers (Wahlström 1994) and may participate in more behaviors associated with the breeding than nondispersers that are less sexually mature (McCoy et al. 2005).

Dispersal Rates

Rates of dispersal (per year) are important because of their role in the dynamics of populations and diseases (Rosenberry et al. 1999). The percentages of individuals that disperse during the spring or fall by state are as follows: eastern Colorado, 89% (Kufeld and Bowden 1995); central Colorado, 2% (Conner and Miller 2004); central Illinois, 51% (Nixon et al. 1991); southwestern Illinois, 80% (Hawkins et al. 1971); eastern Montana, 46% (Dusek et al. 1989); eastern Nebraska, 35% (VerCauteren 1993); and southern Texas, 26%-50% (McCoy et al. 2005).

The relationship between dispersal rates and high populations or densities of deer remains unclear. Nixon et al. (1991) suggested that pressures exerted by high densities of deer may contribute to increased dispersal. Dispersal may be density-dependent due to the increased probability of competition for resources, and dispersal rates may increase as densities increase (VerCauteren 1993). However, Long et al. (2005) found no correlation between density and dispersal rates. They suggest that density may have less of an influence on dispersal rates than previously suggested. The percentage of deer that disperse in a population can produce a significant exchange of individuals, influencing population size and composition within management areas (Rosenberry et al. 1999). Although the relationship between dispersal and density is not clear, high rates of dispersal could facilitate increased transmission of diseases across the landscape.

Distances Traveled during Dispersal

Distances traveled during dispersal can vary considerably. Maximum dispersal distances of mule deer in western states are as follows: 15 km in north-central Colorado (Conner and Miller 2004), 25–113 km in south-central Washington (Hedlund 1975; Eberhardt et al. 1984). Maximum emigration distances of white-tailed deer in the Midwest and Great Plains are 177 km in north-central Iowa (Zagata 1972), 168 km in northeastern Minnesota (Nelson 1993), 205 km in southwestern Minnesota (Brinkman et al. 2005), 87 km in eastern Nebraska (VerCauteren 1998), 224 km in eastern South Dakota (Sparrowe and Springer 1970), and 213 km in southeastern South Dakota (Kernohan et al. 1994).

Dispersal distances vary regionally and fluctuate depending on competition for resources, habitat availability, and landscape characteristics (Long et al. 2005). Dominant individuals typically establish themselves in the most optimal habitats. Dispersers generally have the lowest social rank, thus dispersal distances may reflect local competition. Individuals typically establish themselves in the first vacant or unchallenged home range where their needs can be met (Errington 1963; Waser 1985). When faced with highly fragmented agricultural landscapes or less productive habitats, white-tailed deer may move long distances (Nixon et al. 1991; VerCauteren 1993; Brinkman 2003). Frost et al. (n.d.) found over a 16-year study that sympatric herds of mule deer and white-tailed deer in western Nebraska dispersed longer distances than white-tailed deer in eastern Nebraska. In central Illinois and eastern Nebraska, dispersing female white-tailed deer selected routes from their natal range that offered protective cover (Nixon et al. 1991; VerCauteren 1993). Dispersal distances were positively correlated with the percentage of forest cover, and average dispersal distances were shorter in forested areas (Long et al. 2005). In contrast, differences in land cover (e.g., agricultural fields vs. forested areas) did not influence distances of seasonal movements for white-tailed deer in southwestern Minnesota (Brinkman et al. 2005). Further, they documented movements to temporary staging areas before deer dispersed to permanent ranges in intensive agricultural areas.

The ability for deer to disperse long distances has several implications. Dispersal distance is an important attribute because it constrains the ability of a species to colonize empty patches of habitat (Bowman et al. 2001). Effective dispersers that are able to move long distances carry genetic material that is unique to new locations. Introduction of such genetic material may reduce inbreeding and benefit regional gene flow among populations (Van Valen 1971; Hansson 1992). Deer that disperse may transmit infectious diseases, such as chronic wasting disease, long distances to habitats and other populations of deer that were previously uninfected. Jacques et al. (2003) suggested the possibility that white-tailed deer dispersing along river-bottom habitats could accelerate the spread of chronic wasting disease to new regions, further infecting populations.

Survival during Dispersal

As deer disperse, they often move through unfamiliar areas and may encounter challenges that threaten their survival. Dispersing deer may face increased energy expenditures and risk of mortality as they transition to areas where knowledge of food, water, and protection from weather and predators is unknown. Deer that disperse tend to have lower survival rates than philopatric individuals (Roseberry and Klimstra 1974; Nelson and Mech 1986; Holzenbein and Marchinton 1992; Nicholson et al. 1997). McCoy et al. (2005) observed higher nonhunting mortality rates for dispersers versus nondispersers. Male deer that dispersed in northern Minnesota were more susceptible to harvest, due to hunting-related pressures, which may be attributed to their lack of knowledge of protective cover (Nelson and Mech 1986). Mortality rates of deer that disperse may be related to a variety of factors that include predation risk, anthropomorphic influences, and unfavorable habitat conditions.

Migration

Throughout the northern portions of their distribution, white-tailed deer commonly migrate between summer and winter ranges (Severinghaus and Cheatum 1956; Zwank 1974; Nixon et al. 1991; Nelson 1995; Nelson 1998; Sabine et al. 2002). Mule deer in mountainous regions often migrate from low-elevation mature forests where they overwinter to more open, higher elevation habitat where they spend summers (Gruell and Papez 1963; Carpenter et al. 1979; Garrott et al. 1987; Conner and Miller 2004). In midlatitude regions, deer exhibit a mixture of migratory and nonmigratory behavior (Loft et al. 1984; Kufeld et al. 1989; Nelson and Mech 1991; Brown 1992; Nicholson et al. 1997).

Most hypotheses on migration focus primarily on reproductive success (Baker 1978; Nicholson et al. 1997). If migration provides better access to higher-quality resources, deer may be able to produce more or healthier young (Nicholson et al. 1997). Natural selection should favor deer that migrate if the risk associated with migration is minimal (Baker 1978). When the benefits of leaving one home range and its resources for part of the year are greater than the gains associated with staying, individuals should choose to migrate (Parker and Stuart 1976).

Migration is believed to be a learned behavior established early during social development (Nelson 1998; McCullough 1985) and may be passed from one generation to the next. As a result, orphaned deer may remain nonmigratory because they fail to learn the behavior from their mothers (Nelson 1995).

Spring Migration

The timing of spring migration can fluctuate annually, due to the dynamic forces acting on the seasonal environments and the response of each individual to the changing conditions. Average dates of departure associated with spring migration of white-tailed deer in the Great Plains and Midwest include March 9 through May 1 in central Illinois (Nixon et al. 1991), April 4-13 in northeastern Minnesota (Nelson et al. 2004), April 15 in eastern Nebraska (VerCauteren 1993), April 18 in southwestern Minnesota (Brinkman et al. 2005), and April 3 through May 30 in southeastern British Columbia (D'Eon and Serrouya 2005). Departure for mule deer in western Wyoming was April 1 through June 15 (Sawyer et al. 2005).

Environmental and biological cues associated with initiation of spring migration are variable. Photoperiod, plant development, temperature, snowmelt, relative humidity, preparturition, and precipitation have been suggested for initiating spring migration (Leopold et al. 1951; McCullough 1964; Ozoga et al. 1982; Loft et al. 1984; Garrott et al. 1987; Nixon et al. 1991; Nicholson et al. 1997; Sabine et al. 2002). Migration to summer range occurred when snow depths decreased to less than 9 cm in Minnesota (Nelson et al. 2004). Sabine et al. (2002) also observed that spring migrations coincided with the disappearance of snow cover.

Effects of climate on quality and quantity of available forage also may influence deer movements. Growth of seasonal crops such as corn, which provides an important source of food and cover, may play a role in migration (Nixon et al. 1991). Brinkman et al. (2005) refuted the relationship between crop phenology and timing of migration because deer residing in agriculturally dominated habitats completed spring migration before crop emergence.

Fall Migration

Similar to spring migration, timing of fall migration can vary seasonally according to individual preferences and fluctuating seasonal conditions. Mean departure dates or time periods associated with migration of white-tailed deer during the fall include September through January in central Illinois (Nixon et al. 1991), October 13 through December 8 in eastern Nebraska (VerCauteren 1993), November 3 through January 15 in northeastern Minnesota (Nelson et al. 2004), and November 28 in southwestern Minnesota (Brinkman et al. 2005). Mean departure dates and time periods for migration of mule deer during the fall include October 30 in southeastern British Columbia (D'Eon and Serrouya 2005) and October 15 through December 1 in western Wyoming (Sawyer et al. 2005).

Fall migration is believed to occur in response to several primary factors such as low temperatures, snow depth, photoperiod, and food availability (Verme 1968; Drolet 1976; Nelson and Mech 1981; Blouch 1984; Tiersen et al. 1985; Garrott et al. 1987; Nixon et al. 1991; Brown 1992; Nicholson et al. 1997; Sabine et al. 2002; Brinkman et al. 2005). Fall migration in New Brunswick began when snow depths reached 30–40 cm (Drolet 1976; Sabine et al. 2002). In central Colorado, mule deer progressively migrated to lower elevations as snow depths increased (Gilbert et al. 1970). Kelsall (1969) observed restricted movements of deer when snow depths exceeded 40 cm. Deer that attempt to migrate in deep snow experience increased energy expenditures and risk of mortality (Parker et al. 1984). Accumulations of snow may reduce quality of forage and availability of habitat (Garrott et al. 1987; Nixon et al. 1991; Brown 1992). Deer can afford to delay departure to winter range in areas where snow depth is not a limiting factor. Benefits from delayed departure may include increased abundance of food and reduced competition on summer range (Sabine et al. 2002). Tiersen et al. (1985) and Nelson (1995) reported cases of fall migration when temperatures dropped below -7°C, a critical point at which heat loss may exceed energy generated through regular metabolism and activity (McDonald et al. 1973). Migration may occur earlier in areas where excessive snowfall and abnormally low temperatures occur (Nelson 1995).

Migration Rates

The percentage of individuals within a population that migrate per year can vary regionally and seasonally. Brinkman et al. (2005) reported migration in 58%-76% of radio-collared white-tailed deer in southwestern Minnesota. Ninety-five percent of mule deer were migratory in western Wyoming (Sawyer et al. 2005). Although the average proportion of mule deer that migrated in north-central Colorado was 52%, rates of migration varied considerably by subpopulation (0%-100%), depending on the management unit being sampled (Conner and Miller 2004). Only 7% of female mule deer exhibited migratory behavior in the Rocky Mountain foothills of eastern Colorado (Kufeld et al. 1989).

Distances Traveled during Migration

Distances traveled during migration vary across western and midwestern states. Maximum migration distances by mule deer include 37 km in northwest Colorado (Siglin 1965), 115 km in southeastern Idaho (Thomas and Irby 1990), 130 km in Montana (Mackie 1998), 100 km in south-central Wyoming (Porter 1999), 28 km in north-central Colorado (Conner and Miller 2004), 13 km in southeastern British Columbia (D'Eon and Serrouya 2005), and 158 km in western Wyoming (Sawyer et al. 2005). Maximum migration distances by white-tailed deer included 13 km in Illinois (Nixon et al. 1991), 31 km in southwestern Minnesota (Brinkman et al. 2005), and 30 km in eastern Nebraska (VerCauteren 1998). Other studies have reported mean migration distances, which include 23 km in South Dakota (Sparrowe and Springer 1970), 21 km in Minnesota (Hoskinson and Mech 1976), and 11 km in southeastern Minnesota (Simon 1986). Although migration distances of mule deer and white-tailed deer differ across geographic location, no significant differences have been reported between sexes (Carpenter et al. 1979; Thomas and Irby 1990; Brown 1992). The relationship between migration distance and age is uncertain in white-tailed deer. In Illinois, yearling female white-tailed deer migrated almost three times the distance of adult females (Nixon et al. 1991).

In the Midwest, migration by white-tailed deer is usually completed within two weeks (Nelson and Mech 1981; Nixon et al. 1991; DePerno et al. 2002). Mule deer, however, have taken up to 90 days to complete their migration in western Wyoming (Sawyer et al. 2005). Migration generally occurs between noon and sunset when daily temperatures are the highest, allowing deer to conserve energy required for thermoregulation and traveling long distances (Nelson et al. 2004). During migration, white-tailed deer occasionally stop for short periods in areas known as transition ranges (Nelson and Mech 1981). Transition ranges can provide them with better foraging opportunities, allowing them to recover body condition earlier in the spring and maintain body condition later in the fall (Short 1981). Individuals with greater energy deficits may be more inclined to delay migration so they can continue foraging and resting before traveling again (Nelson et al. 2004). White-tailed deer may rest at transition areas for a few hours to several days before continuing migration (Nelson et al. 2004). In some cases, individuals that stop at transition ranges may be responding to immediate hunger or fatigue.

Fidelity to Seasonal Ranges

Both mule and white-tailed deer exhibit high fidelity to seasonal home ranges and may move long distances through suitable habitats or areas used by other deer when en-route to traditional seasonal ranges (Gruell and Papez 1963; Papez 1976; Carpenter et al. 1979; Tiersen et al. 1985; Garrott et al. 1987; Thomas and Irby 1990; Sawyer et al. 2005). White-tailed deer deviate very little from traditional migration corridors when traveling to and from seasonal ranges, suggesting natural selection has favored strong spatial awareness, navigational ability, and affinity for home range location (Nelson et al. 2004). Mule deer often show high fidelity to summer ranges (Gruell and Papez 1963; Wood et al. 1989; Brown 1992), and may have less attachment to winter range than summer range (Garrott et al. 1987; Brown 1992). Deer remained on summer ranges and did not move to traditional winter ranges when winters were less severe (Brown 1992; Sabine et al. 2002). High fidelity to summer ranges might reduce the expansion of summer populations into new habitats where densities of deer are below saturation levels (Brown 1992).

Survival during Migration

Although many studies have suggested migratory deer may have an increased risk of mortality, few have quantified the relationship. Deer may be subject to a greater risk of mortality as they leave their home ranges to move across less familiar areas (Holzenbein 1990). Deer that migrate may be less knowledgeable of the current distribution of escape habitat, hiding cover, and predators (Nicholson et al. 1997). Increased stress and energy expenditures associated with migrating long distances may increase vulnerability to predators and mortality (Nelson and Mech 1981). Nicholson et al. (1997) reported lower survival for migratory female white-tailed deer than resident females during periods of low precipitation.

CONCLUSIONS

Movements of mule deer and white-tailed deer are influenced most by social pressures and seasonal changes in the western and midwestern United States. Avoidance of inbreeding and sexual competition is postulated to be the ultimate mechanism of dispersal and is connected to the proximate mechanisms of dispersal, maternal-adult female aggression (Ozoga and Verme 1985; Nixon et al. 1991) and male breeding competition (Kammermeyer and Marchinton 1976; Rosenberry et al. 2001; McCoy et al. 2005). Annual variability in climate, particularly snow depths, may be responsible for mixed migration behavior (Nicholson et al. 1997; Sabine et al. 2002). Knowledge of regional dispersal and migration patterns may be important in understanding the suitability and effects of efforts to manage habitat and populations (Nelson and Mech 1992).

Populations that exhibit dispersal and migratory behavior may experience a significant exchange of individuals across state management zones (Rosenberry et al. 1999). Deer that exhibit seasonal movements during the fall may be more vulnerable to harvest, and movements should be incorporated into wildlife management plans (Shaw et al. 2006). Migration and dispersal have the potential to influence population dynamics, which can reduce accuracy of demographic estimates and influence decisions to manipulate densities, sex ratios, and age structures (Marchinton 1982). Better understanding of factors that influence dispersal may be achieved through long-term research. Future research should be directed toward studies that address the role of landscape dynamics in determining habitat selection after dispersal or migration has been initiated. Research involving movements of deer can provide insight into transmissible diseases, such as chronic wasting disease, that may spread across landscapes as a result of seasonal movements.

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