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A REVIEW OF WHITE-TAILED DEER MOVEMENTS IN THE GREAT PLAINS RELATIVE TO ENVIRONMENTAL CONDITIONS

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Abstract. *Movements of white-tailed deer (Odocoileus virginianus Rafinesque) in the eastern Great Plains and Midwest were examined. The proportion of deer that move between distinct summer and winter home ranges varies among different populations. Seasonal migration between home ranges is influenced primarily by phenological period, agricultural activities, and the availability of cover and food. Corn provides a nearly unlimited source of cover and food in summer and early fall. In late fall and early winter, deer move to areas of permanent cover, such as wooded river bottoms, draws, or slopes. Hunting, crop harvest, or seasonal change may influence deer movements and distribution, depending on the past experiences of individual deer and their situation. Emigration rates increase with deer population density because of increased social pressures, increases may or may not be proportional to the increase in overall populations. The ability of white-tailed deer to adapt to human activities has allowed them to thrive throughout the region, and current populations are stable to increasing. The availability of large tracts of secure winter cover and safe travel corridors between seasonal ranges are the primary factors limiting their populations.*

White-tailed deer movements have been evaluated at scattered sites throughout the United States and Canada, but the data is still incomplete. Deer in northern latitudes, where snow levels frequently impede deer movements, generally migrate to areas of secure cover prior to the onset of deep snow (Rongstad and Tester 1969; Nelson and Mech 1984). In southern latitudes, deer generally do not migrate seasonally (Kammermeyer 1975; Marchinton and Jeter 1966). In the eastern Great Plains, where deer are nonyarding and generally in good physical condition, the phenomena of migration and dispersal have adaptive advantages and disadvantages. The landscape in the eastern Great Plains and Midwest is a matrix of patchy

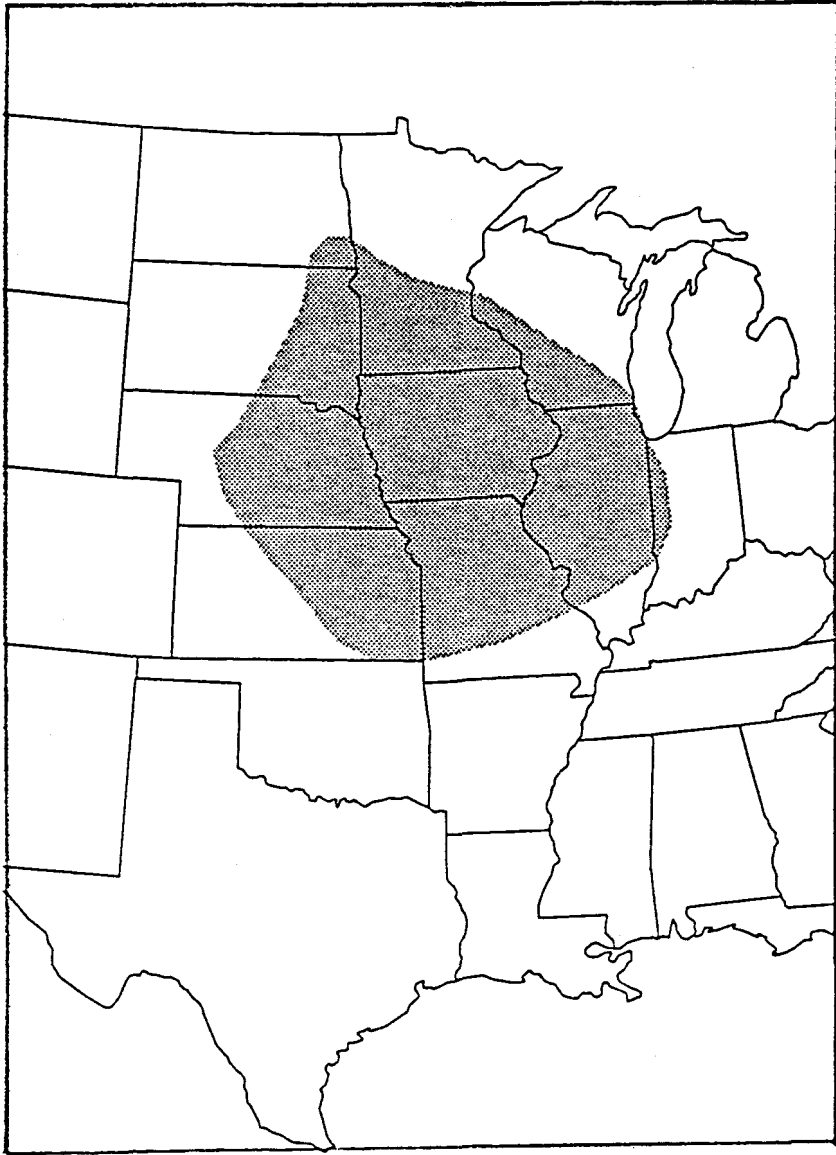


Figure 1. Portion of the eastern Great Plains and Midwest that is reviewed. The region is a matrix of patchy habitats dominated by agriculture.

habitats (Fig. 1). Row crops dominate the region and are subdivided by wooded riparian areas, brushy draws, grazed pastures, wetlands, forested ridges, and urban centers.

White-tailed deer were once abundant along the wooded waterways of the region (Thwaites 1905; Swenk 1907; Crane 1933; Cook 1945). Early settlers allowed woody vegetation to encroach into open areas by suppressing fire, planting trees, and establishing fencerows and windbreaks. They also reduced and eliminated populations of deer predators. As a result, white-tailed deer populations increased throughout the eastern Great Plains early in the nineteenth century. Populations then declined dramatically, however, between 1850 and 1900, because of overharvest by market and subsistence hunters and a series of severe winters (Leach 1909; Madson 1953). There were only about 50 deer, including both white-tailed and mule deer (*Odocoileus hemionus* Rafinesque), in Nebraska at the turn of the century (Bailey et al. 1957). During the early 1900s, deer repopulated the area through immigration and their numbers increased because of protection, controlled harvests (Pietsch 1954; Sanderson and Speaker 1954), and the conversion of rangeland to row crop agriculture. By 1940, populations had noticeably recovered, and deer were found in every county in Nebraska by 1957 (Bailey et al. 1957). Nebraska's current deer population is estimated to be about 210,000 (Hygnstrom and Baxter 1991).

Increased deer populations have provided increased hunting and viewing opportunities throughout the eastern Great Plains and Midwest. They have also caused problems for farmers, foresters, and motorists. Current population management strives to maintain deer populations at or below their natural carrying capacity, at levels that satisfy public demand, yet are tolerable to landowners (Gladfelter 1984).

White-tailed deer have adapted to the fragmented cover of the eastern Great Plains and have a nearly unlimited source of nutritious foods available throughout the year (Sparrowe and Springer 1970; Zagata 1972; Gladfelter 1978; Nixon et al. 1991). Total numbers are difficult to estimate, but populations are stable or increasing in most areas. Reported densities are highest in forested habitats and range between 5 to 80 deer/km² (Gladfelter 1984).

Definitions and Scope

We characterize deer movements as migration, emigration or dispersal, and immigration. A movement occurs whenever an animal leaves its established home range and forms a distinct new home range. Migration is a

seasonal movement away from an established home range and eventual return to the same area. Migrations are most common in areas where deer must cope with severe weather or where habitats change dramatically with the seasons, as in northern regions and in the intensively farmed Midwest (Schmautz 1949; Pietsch 1954; Dahlberg and Guettinger 1956; Rongstad and Tester 1969; Zagata 1972; Verme 1973; Masek 1979; Nelson and Mech 1984; Nixon et al. 1991).

Emigration refers to movement away from an established home range. An emigration movement has been completed when the individual establishes itself in a new home range entirely separate from a previous range. A subadult leaving its natal range to establish a new, distinct home range is an example of emigration. Immigration refers to movement into a new area. By definition, immigration into an area constitutes emigration from another area.

Prior to moving, a deer may leave its home range for a few days and return. This type of activity is defined as a temporary excursion. Local movements occur daily, seasonally, or annually within established home ranges. Although often regular and predictable, local movements can be influenced by many factors, including feeding and bedding behavior, human disturbance, fawn care, breeding behavior, and weather (Marchinton and Jeter 1966; Rongstad and Tester 1969; Sparrowe and Springer 1970; Zagata 1972; Gladfelter 1978). Local movements are a topic separate from migration and emigration movements and will not be discussed in this review.

Movement studies should emphasize an animal's specific needs and motivations (Sanderson 1966; Anderson 1989), however, most research studies have concentrated on distance moved, home range shape, or area covered by individual animals. An animal will usually stay in an area where all its needs are fulfilled until something forces it to move. Movement has been shown to be adaptive in both stable (Hamilton and May 1977; Comins et al. 1980) and variable (Cohen 1967; Levins 1968) environments and for both presumed r- (Gaines and McClenaghan 1980) and K- (McCullough 1979; Rogers 1987) selected species.

Both extrinsic and intrinsic stimuli influence deer movements, but studies have focussed on extrinsic stimuli and little attempt has been made to identify, or quantify intrinsic stimuli in free-ranging populations. Genetic traits, sensory acuteness, learning capacity, learned behaviors, and other intrinsic attributes may affect the movement characteristics of an individual. The fitness of an individual is contingent upon its ability to reproduce and pass on its genetic material. An individual deer may increase its fitness by

emigrating from a crowded habitat and colonizing an empty one (Ricklefs 1973). Further, by emigrating it serves to increase the fitness of deer that remain sedentary.

The decision to move, or not move, affects an individual's fitness as well as those it interacts with. Lineages ultimately persist only through the success of their disseminules (Anderson 1989). The perpetuation of an allele, gene combination, or chromosomal arrangement requires individuals to successfully transmit genetic material to new locations (Van Valen 1971). Genetic drift and microgeographical selection are thus effected (Smith et al. 1975).

Objectives

We review and discuss studies on deer movements in the eastern Great Plains in terms of important contributions to white-tailed deer management. Pertinent results from studies conducted in the Midwest are also considered because few researchers have studied deer movements in the eastern Great Plains and the geography, climate, topography, and land-use practices are similar in both regions.

White-tailed deer are one of the most economically important wildlife species in the region. Consolidating past deer movement studies will serve to advance our understanding of this very important species. Also, more efficient deer management may be facilitated through a review of the current literature.

Deer movements are influenced by seasonal weather variations, population and social pressures, agricultural activities, food availability, and the proximity of protective cover (Downing et al. 1969; Sparrowe and Springer 1970; Hawkins et al. 1971; Zwank et al. 1979; Murphy et al. 1985; Nixon et al. 1991). They are also influenced by hunting pressure and predators (Van Etten et al. 1965; Autry 1967; Marshall and Whittington 1968; Sparrowe and Springer 1970; Nelson and Mech 1981; Pilcher and Wampler 1982; Mech 1984; Nelson and Mech 1986; Root et al. 1988). The following discussion more closely examines these factors.

Seasonal Change

In several areas throughout the eastern Great Plains and Midwest, some deer routinely migrate between distinct summer and winter ranges (Dahlberg and Guettinger 1956; Zwank 1974; Gladfelter 1978; Nixon et al. 1988; Nixon et al. 1991). Nixon et al. (1991) found that 19.6% of marked yearling

and older does migrated an average of 13.0 ± 3.0 km ($n=10$) between summer and winter ranges. In Minnesota, 60% of marked subadult deer migrated (Rongstad and Tester 1969). The average migration distance of these deer, inferred from hunter kills, was 19.3 km ($n=5$).

Some deer move to specific winter sites in late fall because of changes in weather and food availability and remain there until the following spring. They may then migrate back to previously established spring and summer ranges or emigrate to distinct new ranges. More deer may move to traditionally used wintering sites during severe winters (Pietsch 1954; Sparrowe and Springer 1970; Zwank 1974; Nixon et al. 1991). Nixon et al. (1991) observed two Illinois does that did not leave their summer ranges during mild winters. Optimal winter habitat in the region consists of larger units of permanent cover found along waterways, which also function as travel corridors between winter and summer ranges.

Social Pressures

Social pressures occur when individuals compete for resources and may result in avoidance behavior and emigration of subordinate animals. Emigration rates are usually density dependent (Leopold 1933; Anderson 1989) because of the increased probability of competition or antagonistic interactions. Densities of 5 to 80 deer/km² occur in forested habitats in the eastern Great Plains and Midwest (Gladfelter 1984) and are highest in the winter. We hypothesize that emigration is greater in regional habitats with higher deer densities. In an east-central Illinois study, pressures due to high populations were suggested to have forced emigration of subadults, which composed nearly 43% of the prefawning spring population (Nixon et al. 1991). This percentage of subadults seemed to large to fit into the existing social structure because of limited forest cover. Deer that emigrate usually rank low in the social hierarchy and are most expendable in terms of population growth because they are immature (Hawkins et al. 1971).

Emigrations due to social pressures occur twice each year, and are often preceded by temporary excursions, usually in the direction of the eventual movement and residence (Nixon et al. 1991; Holzenbein and Marchinton 1992). Temporary excursions are adaptive because the animal gains information regarding the location, potential risks, and availability of resources (Jeter and Marchinton 1964). In addition, temporary excursions may reduce the risk of predation because the animal becomes familiar with the location of cover (Nelson and Mech 1984).

Female deer emigrate primarily in spring while males tend to emigrate in late summer and fall (Hawkins 1967; Kammermeyer and Marchinton 1976). Does are more active during spring, when looking for fawning areas (Gladfelter 1978) or habitats not occupied by other deer. Prior to fawning, adult does may be antagonistic toward their previous year's offspring, especially bucks, which often stimulates dispersal in younger deer (Downing et al. 1969; Hawkins and Klimstra 1970; McCullough 1979; Ozaga and Verme 1985; Holzenbein and Marchinton 1992). The majority of emigrating subadults presumably settle on ranges that are vacant due to the previous year's mortalities (Gladfelter 1978; Jackson 1990). The dam's fitness can be increased by the emigration of related males because of a reduced probability of inbreeding (Holzenbein and Marchinton 1992). Avoidance of inbreeding has been proposed as one cause for male emigration (Harvey and Ralls 1986; Ralls et al. 1986). In addition, by forcing progeny to emigrate from the natal site, a dam will likely reduce competition for resources (Hamilton and May 1977; Comins et al. 1980; Anderson 1989).

A maternally-based family group is a subdivision of a local deer population. A young doe will often remain associated with her dam for three or more years (Hawkins and Klimstra 1970; Nelson and Mech 1984; Nixon et al. 1991; Porter et al. 1991). The home range of such a doe is often adjacent to her dam's, and her movements may be influenced by social bonds between the two. Does in large family groups on winter ranges may migrate to separate summer ranges in the spring, regroup in the fall, and return to the winter range together, or regroup after returning to the winter range (Hawkins and Klimstra 1970; Nelson and Mech 1984). Does usually have high fidelity to their seasonal ranges throughout their lives (Hawkins and Klimstra 1970; Nelson and Mech 1984; Nixon et al. 1991).

A buck usually separates from its dam at one to three years of age (Hawkins et al. 1971; Kammermeyer and Marchinton 1976; Nelson and Mech 1984). Bucks often form bachelor groups and travel together throughout the summer (Hawkins and Klimstra 1970; Kammermeyer 1975; McCullough 1979; Nelson and Mech 1984). During the fall, bucks become more solitary and active due to the onset of the rut (Hawkins et al. 1971; Kammermeyer 1975; Kammermeyer and Marchinton 1976; Marchinton and Hirth 1984). Hawkins et al. (1971) found that 80% of yearling bucks dispersed in a southern Illinois refuge with a density of 31 deer/km², apparently due to social pressures. High dispersal rates may be typical for areas of refugia because the highest deer densities are found there (Gladfelter 1984).

Agricultural Activities

Spring and fall deer migrations are common in the eastern Great Plains and Midwest (Sparrowe and Springer 1970; Zwank 1974; Gladfelter 1978; Menzel 1984; Nixon et al. 1991). Permanent cover along riparian systems provides movement corridors through the mosaic of agricultural land and interspersed woodlands, which provides excellent habitat for deer. The annual growth of corn, which provides a nearly unlimited source of summer cover and food, may be a factor contributing to seasonal migration (Nixon et al. 1991). Corn is usually harvested at a time when deer need an abundance of high-energy, nutritious food to prepare themselves for winter. After crop harvest, deer movements are influenced primarily by the need for permanent cover and food (Sparrowe and Springer 1970; Zwank et al. 1979; Gladfelter 1978; Nixon et al. 1991). Moen (1968) stated that less protective winter cover is needed by deer if high-quality forage (waste grain or standing crops) is available. Waste corn is a key winter food throughout the Midwest (Nixon et al. 1970; Sparrowe and Springer 1970; Pils et al. 1981).

Annual crops, mainly corn, can serve as cover and allow deer to occupy summer ranges anchored on small, fragmented, linear strips of permanent cover. However, these areas lose their value as cover after crops are harvested and permanent cover loses its foliage. Deer are also negatively impacted by fall plowing, which buries waste grain, and clean farming, which eliminates valuable edge and travel corridors (Nixon et al. 1970; Gladfelter 1978; Murphy et al. 1985). These are common practices in the region.

Hunting

Deer movements and distributions are influenced somewhat by hunting activity (Sparrowe and Springer 1970; Pilcher and Wampler 1982; Root et al. 1988). Deer response to hunting pressure depends on the circumstances, habitat type, juxtaposition of refugia, and past experience. Sparrowe and Springer (1970) monitored deer that moved up to 16 km after being flushed by archers. They also observed two does that fled 3 and 6 km on one occasion, and yet remained in heavy cover while hunters walked within a few meters of them on another occasion.

During hunting season on a portion of the Deer Ridge Wildlife Area in Missouri, Root (1988) found deer movements from refugia were greater than movements to refugia. Does tend to move farther and more often than bucks when under intensive hunting pressure (Marchinton and Jeter 1966; Autry 1967; Root et al. 1988). Buck movements are variable and may increase

(Dasmann and Taber 1956), decrease (Autry 1967; Root et al. 1988), or not change in response to hunting pressure. This may be due to differences in experience, geographical location, habitat, vegetation type, and breeding activities. In Missouri (Root et al. 1988) and in Illinois (Nixon et al. 1991) deer that migrated from areas of refugia did not attempt to return during the hunting season. Conversely, Iowa deer were pushed to refugia by hunters (Zagata 1972). Deer often remain in refuge areas that provide winter food and cover until spring.

Legal harvest was the primary mortality factor of deer that dispersed from an Iowa refuge (Jackson 1990). Nixon (1991) found that 28 to 43% of the deer that were harvested from a surrounding county originally came from a 600-ha refuge.

Deer react to hunting in a variety of ways on both individual and population levels. Deer that migrate or emigrate are more susceptible to hunters. This differential mortality may select for individuals that do not move from refugia (Larson et al. 1978). Only movers, however, recolonize vacated habitats in areas where local populations are extirpated through hunting, thereby reestablishing and perpetuating the species (Levins 1968; Nixon et al. 1991).

Emigration and Migration Distances

Deer movement varies depending on the location and availability of habitat, food, population density, reproductive activity, and other factors (Sanderson 1966). For a mover to be successful, the benefits of moving must outweigh the costs involved in transition and establishment of a new home range (Hamilton and May 1977; Bengtsson 1978; Shields 1987; Anderson 1989). When moving, deer expend energy and increase risks of predation, accidents, and competition as they search for suitable habitat. Emigrating deer face a high risk of death and have difficulties associating with established residents (Holzenbein 1990).

Mean emigration distances were similar in Iowa (22 ± 5 km, $n=17$) and South Dakota (23 ± 2 km, $n=6$) (Gladfelter 1978; Sparrowe and Springer 1970, respectively). Emigration distances also ranged from 2 to 177 km ($n=5$) in Iowa (Zagata 1972). Illinois does emigrated an average of 49 ± 5 km ($n=84$), while bucks averaged 41 ± 5 km ($n=113$) (Nixon et al. 1991). Several researchers found distances between mark and recapture sites averaged less than 5 km (Hahn and Taylor 1950; Carlsen and Farnes 1957; Proguluske and Baskett 1958; Thomas et al. 1964; Hawkins and Klimstra 1970). Movements to new home ranges occur rapidly. Emigrating deer

usually complete a movement in less than 2 weeks (Nelson and Mech 1981; Tierson et al. 1985; Nixon et al. 1991).

Emigration rates of subadult bucks increase when they reach sexual maturity because of breeding competition and searching for mates (Hawkins and Klimstra 1970; Kammermeyer and Marchinton 1976; Shields 1987). In the fall, subadult bucks move farther than deer of other sex and age classes (Pietsch 1954; Montgomery 1963; Sparrowe and Springer 1970; Hawkins et al. 1971). Conversely, in the spring, subadult buck movements were shorter than those of subadult does (Gladfelter 1978; Jackson 1990; Nixon et al. 1991). Jackson (1990) stated that this difference in movement distance may be due to the higher percentage of bucks that are harvested, thus increasing the availability of vacant buck home ranges. Further, dispersing subadult does may have difficulty becoming socially accepted by unrelated adult does in adjacent habitats and may be forced to continue searching for suitable areas to establish permanent home ranges.

Conclusions

Winter refugia and forested corridors (which provide avenues for migration and dispersal) are the major factors that affect deer population dynamics in the Midwest (Nixon et al. 1991) and eastern Great Plains. They facilitate deer emigration and colonization after high mortality due to annual hunting. Agriculture, development, and hunting greatly affect deer habitat and movements. Deer, however, are an edge species, and their ability to adapt to human activity and human induced habitat changes has allowed them to thrive in the region.

Future research is needed to determine the factors and motivations that promote deer movement behaviors, the distance moved, the proportion of the population that moves, and the habitats they select. Research is also needed to determine the effect that intrinsic factors have on deer movements. Continued studies on deer movements will provide better information for managing and maintaining deer populations at levels that optimize environmental stability and human use and minimize conflicts with agricultural production and land use.

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