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## Diurnal activity and habitat associations of White-tailed deer in tallgrass prairie of eastern Kansas

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Diurnal and seasonal patterns of activity and habitat associations of white-tailed deer (*Odocoileus virginianus*) were assessed in a mosaic of grassland and woodland habitats on the Konza Prairie Biological Station, Kansas. We recorded deer seen during daylight hours in summer, autumn and winter periods from June 1997 through February 1998. Overall, diurnal activity increased from summer to winter and was largely crepuscular (i.e., early morning and late evening). Deer were observed primarily in lower uplands during summer and winter, and in lowlands during autumn. At a coarse scale (6.25 ha), white-tailed deer selected areas that had woody vegetation and avoided those that were dominated by grassy vegetation. In contrast, at a fine scale, groups of deer most often were observed foraging in the immediate vicinity of grassland vegetation, rather than in or by woody vegetation.

*Keywords: Flint Hills, grassland, Konza Prairie, Odocoileus virginianus, seasonal activity, topography, woodland, woody invasion*

### INTRODUCTION

White-tailed deer (*Odocoileus virginianus*) usually exhibit crepuscular activity (Michael 1970; Marchinton and Hirth 1984; Beier and McCullough 1990; Rouleau, Crête and Ouellet 2002) and are associated closely with wooded areas and edges (Melchior, Silker and Reeb 1985; Dusek 1987; Mooty, Karns and Fuller 1987; Compton, Mackie and Dusek 1988; Dusek, Wood and Mackie 1988; Plante et al. 2004). Historically, white-tailed deer were uncommon in the Great Plains and, when observed, were associated with riparian zones (Cook 1945; McCabe and McCabe 1984; Sexton, Hlavachick and van Zwoll 1985). However, many anthropogenic changes have occurred since European settlement of the region. These include conversion of native prairie to agricultural lands, livestock-grazed pastures and tree and shrub plantings; development of urban and suburban communities; and invasion of prairie by native and exotic trees and shrubs (Kaufman and

Kaufman 1997). Also, white-tailed deer in the region have increased in abundance while some other large mammals [e.g., bison (*Bos bison*), elk (*Cervus canadensis*) and mule deer (*O. hemionus*)] have been extirpated or have decreased in abundance (Sexton, Hlavachick and van Zwoll 1985; Kaufman and Kaufman 1997). Our goal was to assess habitat associations in a matrix of grassland and woodland habitats in the tallgrass prairie of the Flint Hills to better understand how white-tailed deer use the tallgrass prairie ecosystem currently.

The first objective was to describe the diurnal pattern of activity of white-tailed deer in summer, autumn and winter. We hypothesized that activity is greater in early morning and early evening than in midday in all seasons, but that midday activity, in response to ambient temperature, is proportionally greater in winter than summer and autumn. Our second objective was to determine whether habitat associations of the deer (e.g., type of vegetation and topographic features)

differed among seasons and among times of day. We examined these associations both at a fine scale, by recording the habitat in the immediate location of sightings, and at a coarse scale, by evaluating proportions of habitat within standard grid squares (6.25 ha) from an aerial photograph. We hypothesized that white-tailed deer would use lowland and upper lowland areas, which have a relatively high proportion of woody vegetation, more than upland areas, which have large amounts of open grassland. We expected this association to be strongest during summer, when deciduous vegetation offers maximal cover and forage and when hiding cover is most needed for rearing of fawns.

#### STUDY AREA AND METHODS

We observed white-tailed deer from June 1997 to February 1998 on the Konza Prairie Biological Station, a 3,487-ha experimental research site dominated by tallgrass prairie. Konza Prairie is located south of Manhattan in Riley and Geary counties in the Flint Hills region of eastern Kansas. This topographically diverse site consists of rolling hills that have substrata of Permian-age limestone and shale. Erosion of soils and substrata has resulted in relatively steep slopes separated by flat areas of prairie. These flat areas occurred at four general levels of elevation designated as: upland (about 425 to 440 m), lower upland (about 400 m), upper lowland (about 375 m) and lowland (about 350 m). Native tallgrass prairie occurred at all levels from lowland to upland and was dominated by big bluestem (*Andropogon gerardii*), little bluestem (*Schizachyrium scoparium*), indiagrass (*Sorghastrum nutans*) and switchgrass (*Panicum virgatum*). Common shrub species that occurred in scattered patches included rough-leaved dogwood (*Cornus drummondii*), wild plum (*Prunus americanus*) and smooth sumac (*Rhus glabra*). Gallery forest, which occurred in lowland and some upper lowland sites, was dominated by bur oak (*Quercus macrocarpa*),

hackberry (*Celtis occidentalis*) and chinkapin oak (*Q. muehlenbergii*; Freeman and Hulbert 1985). Lowland areas included about 50 ha of crop fields planted to wheat or soybeans and were located in the northwest corner of Konza Prairie.

Konza Prairie includes >50 experimental units that are burned in spring by prescribed fire at intervals of 1, 2, 4, 10 or 20 years and six units that are burned in other seasons (2 annually in fall, 2 annually in winter and 2 biennially in summer). Experimental burn units range in size from 10 to >200 ha and include any woodland habitat or gallery forest that occurs within the boundaries of the burn units. During the study, a herd of about 200 bison grazed year-round on a 900-ha experimental area whose fence was permeable to deer. Grazing impacts were minimal on most of the area because of a low stocking rate for bison. Our study encompassed most of Konza Prairie and included a range of landscape treatments of fire and bison grazing as well as a small portion of the cattle unit (300-ha), which was grazed by cattle (*Bos taurus*) from May to October. Hunting is not permitted on Konza Prairie.

Observations were made (MDV) by driving minimally developed gravel roads and fireguards on two different routes, a LOOP route and a NORTH/SOUTH (N/S) route. The LOOP route was a 13-km trail that circled through Konza Prairie, whereas the N/S route consisted of a 15-km north trail and a 20-km south trail that together covered the majority of Konza Prairie, including the area visible from the LOOP route. During a sampling period, a particular route was driven so that observed deer were counted and location, size and composition of groups recorded. Binoculars were used because deer often were seen at a hundred to several hundred m from the route.

About 2 h were required to drive and count deer from the LOOP route. During each

sampling day, the LOOP route was driven five times in both summer and autumn, but only four times in winter. The first sampling period started at dawn and the last ended at dusk; other sampling periods were spaced evenly throughout the day. Three permanent starting points, about equidistant from each other, were established along the route. Each LOOP survey consisted of a 3-day sampling set; each of three starting points (order of use chosen randomly) was used once during a sampling set. Direction of travel was chosen randomly for a sampling set, but was the same for all three days of the set. Two LOOP surveys were conducted during summer [13-26 June (13, 22, and 26 June) and 8-21 July (8, 15 and 21 July) 1997]; one during autumn [28 September-2 November (28 September, 25 October and 2 November) 1997] and two during winter [30 December 1997-26 January 1998 (30 December and 25 and 26 January) and 16-28 February (16, 22 and 28 February) 1998].

About 2.5 h were required to drive and count deer seen from each portion of the N/S route. Each N/S survey consisted of a 6-day sampling set. During each day, only the north or south trail was driven during dawn and midday, or during dawn and dusk or during midday and dusk. Order of the six route-time combinations (2 trails by 3 pairs of times) was selected randomly. Direction of travel was chosen randomly for each route-time combination during the first survey in a season and then reversed for the second survey. Three N/S surveys were completed during summer [29 June-6 July (29 and 30 June and 1, 2, 3 and 6 July), 7-14 July (7, 9, 10, 11, 13 and 14 July) and 16-31 July (16, 18, 20, 22, 23 and 31 July) 1997], two during autumn [29 September-16 October (29 September and 2, 4, 5, 6 and 16 October) and 18-29 October (18, 19, 20, 23, 26 and 29 October) 1997] and two during winter [31 December 1997-13 January 1998 (31 December and 2, 3, 11, 12 and 13 January) and 18 January-17 February (18 and 19 January and 4, 6, 13 and 17 February) 1998].

We counted number of active deer seen on LOOP and N/S routes. Neither bedded deer nor fawns were recorded as active deer. These groups were excluded because bedded deer were not up and moving and, thus, not active, whereas fawns were not counted to avoid inflating numbers of active deer in autumn and winter relative to summer.

Habitat associations were examined by plotting group locations from N/S surveys on a 1994 aerial photograph. A standard 250-m by 250-m grid system, overlaid on the aerial photograph, was established for Konza Prairie in 1981 to help maintain locality information for the site. Because this grid system produced identifiable 6.25-ha squares over the entire site, we used these squares to place deer location on a coarse habitat scale. For these habitat analyses, we included bedded groups of deer. Each group (the smallest cohesive unit of animals acting together) was recorded only once during a sampling period, but a specific group or individuals moving among groups might have been recorded in more than one sampling period within a single day. However, group sizes and locations suggested that the same groups were not recorded repeatedly in the same grid units. Furthermore, composition of groups likely changed between sampling periods because of the high mobility of individual deer on Konza Prairie.

Groups were assigned to one of four vegetation categories that were grassland, woodland, grassland-woodland and croplands. Grassland was mostly native prairie, but included small areas of planted grasses, whereas woodland contained gallery forest and patches of trees and shrubs. The grassland-woodland category was used for grassland habitats that were within 10 m of shrubs or trees, whereas cropland was comprised of cultivated fields only (< 1% of visible habitats). We also recorded whether a group was on a relatively level site or on a slope. Categories of level sites were upland, lower upland, upper lowland and lower lowland, as previously

Table 1. Number of diurnal surveys, average number of white-tailed deer (*Odocoileus virginianus*) observed per survey (D/S) and percent of observations in each daytime period for summer, autumn and winter on Konza Prairie Biological Station during June 1997 through February 1998. Deer were surveyed during five daylight periods in summer and autumn along the loop trail, but only four daylight periods in winter. Summer and autumn were summarized with the midday period excluded for comparison to winter. Deer were surveyed during only three daylight periods on the north/south trails.

			Percent				
	Surveys	D/S	Dawn	Morning	Midday	Afternoon	Dusk
<b>Loop trail</b>							
<b>Five periods</b>							
Summer	2	206	38	14	8	9	31
Autumn	1	349	26	16	8	18	32
<b>Four periods</b>							
Summer	2	191	41	15	--	10	33
Autumn	1	321	29	17	--	19	35
Winter	2	436	35	11	--	18	36
<b>North/south trails</b>							
Summer	3	182	47	--	9	--	44
Autumn	2	242	35	--	7	--	58
Winter	2	477	33	--	22	--	45

defined. Each group was assigned to only one habitat category and one landscape category based on the initial location of most individuals of the group, and this allowed us to analyze habitat association on a fine scale.

Furthermore, we characterized habitat conditions in each of the 464 grid squares (250 m by 250 m) in which deer could be seen from the N/S route. Field assessment indicated that we could see all or nearly all the surface of 422 grid units; the remaining 42 grid squares were excluded from further analysis. We then used field observations plus features visible in the aerial photograph to place each of the 422 grid squares into one of three categories based on woody cover. These categories were <1%, 1-30% and >30% woody vegetation, and this allowed us to analyze habitat association on a coarse scale.

We tested for differences in activity of white-tailed deer among diurnal periods and seasons and among vegetation and topographic categories by using log-likelihood ratio tests (G; Zar 1996). We expected equal numbers of observations in each diurnal period within a season if time of day had no effect on activity. To test for an association between deer and woody vegetation, we used the first two N/S surveys each season and performed G tests. These were done by using number of grid units with and without deer in each of the three coverage categories of woody vegetation. We used  $P < 0.05$  as the minimum level of significance for all statistical tests.

## RESULTS

### Activity

White-tailed deer observed during the LOOP

Table 2. Number of diurnal surveys, number of groups and percent of groups of white-tailed deer (*Odocoileus virginianus*) observed in upland (about 425 to 440 m in elevation), lower upland (about 400 m), upper lowland (about 375 m) and lowland (about 350 m) during summer, autumn and winter for surveys along north/south trails on Konza Prairie Biological Station during June 1997-February 1998.

Season	Surveys	Groups	Percent			
			Upland	Lower Upland	Upper Lowland	Lowland
Summer	3	410	7	52	19	23
Autumn	2	318	12	31	7	50
Winter	2	575	15	50	19	17

survey increased dramatically from summer to autumn to winter (four diurnal survey periods; Table 1). When five diurnal periods are considered, activity was significantly greater during dawn and dusk than in morning, midday and afternoon in summer ( $G = 155$ ,  $df = 4$ ,  $P < 0.001$ ) and in autumn ( $G = 68$ ,  $df = 4$ ,  $P < 0.001$ ). In winter, activity was significantly greater during dawn and dusk than during morning and afternoon ( $G = 172$ ,  $df = 3$ ,  $P < 0.001$ ). Activity during dawn, morning, afternoon and dusk differed significantly among seasons ( $G = 33$ ,  $df = 6$ ,  $P < 0.001$ ). This difference was due to proportionally higher activity during dawn in summer and lower activity both during afternoon in summer and dawn in autumn as compared to other times and seasons.

Similarly, active deer seen from the N/S route increased greatly from summer to autumn to winter (Table 1). Activity was significantly greater during dawn and dusk than midday in all three seasons (summer:  $G = 186$ ,  $df = 2$ ,  $P < 0.001$ ; autumn:  $G = 222$ ,  $df = 2$ ,  $P < 0.001$ ; winter:  $G = 74$ ,  $df = 2$ ,  $P < 0.001$ ). Deer were proportionally more active during dawn in summer than in autumn and winter, during dusk in autumn than in summer and winter and during midday in winter than in autumn and summer ( $G = 103$ ,  $df = 4$ ,  $P < 0.001$ ).

#### Use of habitat

A positive association of deer with flat sites as

compared to slopes during N/S surveys was stronger in autumn (85%) than in summer (60%) or winter (51%;  $G = 105$ ,  $df = 2$ ,  $P < 0.001$ ). Proportion of groups observed in upland, lower upland, upper lowland and lowland varied among seasons ( $G = 98$ ,  $df = 6$ ,  $P < 0.001$ ), but did not vary among diurnal periods within a season (summer:  $G = 11.3$ ,  $df = 6$ ,  $P > 0.05$ ; autumn:  $G = 12.2$ ,  $df = 6$ ,  $P > 0.05$ ; winter:  $G = 9.2$ ,  $df = 6$ ,  $P > 0.05$ ). Deer were associated more often with lower upland during summer and winter, but with lowland during autumn (Table 2).

For all N/S surveys, 57% of deer groups were observed in grassland as compared to grassland-woodland (22%), woodland (17%) and cropland (3%; Table 3). Because >80% of Konza Prairie is native tallgrass prairie, this observed habitat distribution of only 57% of groups in grassland suggests considerable under use of native prairie. However, in autumn, the proportion of deer was higher in grassland and lower in grassland-woodland than in these habitats in summer or winter ( $G = 24$ ,  $df = 6$ ,  $P < 0.01$ ). Also, type of woody vegetation used in autumn differed from that used in summer and winter. In autumn, 70% of the use of woodland habitat was by groups that used trees rather than shrubs as compared to only 3% in summer and 17% in winter. Furthermore, for groups recorded in grassland within 10 m of woodland, either trees or shrubs, 51% were observed beside trees

Table 3. Number of diurnal surveys, number of groups and percent of groups of white-tailed deer (*Odocoileus virginianus*) observed in open grassland (primarily native, but some planted grasses), grassland-woodland (grassland within 10 m of wooded vegetation), woodland (trees and/or shrubs) and cropland during summer, autumn and winter for surveys along north/south trails on Konza Prairie Biological Station during June 1997-February 1998.

Season	Surveys	Groups	Percent			
			Open Grassland	Grassland-Woodland	Woodland	Cropland
Summer	3	410	56	25	18	2
Autumn	2	318	65	15	15	5
Winter	2	575	53	26	19	2

during autumn as compared to 13% in summer and 5% in winter. During winter, deer had a higher association with woodland and a lower association with grassland in midday than at dawn or dusk ( $G = 33$ ,  $df = 6$ ,  $P < 0.001$ ). In contrast, vegetation association was similar among diurnal periods in summer ( $G = 6.6$ ,  $df = 6$ ,  $P > 0.10$ ) and in autumn ( $G = 10.6$ ,  $df = 6$ ,  $P = 0.10$ ).

During the first two N/S surveys each season, deer were observed at least once in 141, 120 and 163 of the 422 aerial map grid units in summer, autumn and winter, respectively. Presence of deer within grid squares differed from availability of coverage classes of woody vegetation [availability for <1% woody vegetation: 60 squares; 1-30% woody vegetation: 249 squares; >30% woody vegetation: 113 squares (only 3 of which had >60% woody vegetation)] in all seasons (summer:  $G = 33$ ,  $df = 2$ ,  $P < 0.001$ ; autumn:  $G = 18$ ,  $df = 2$ ,  $P < 0.001$ ; winter:  $G = 37$ ,  $df = 2$ ,  $P < 0.001$ ). Use of different categories, as measured by number of grid squares where deer were present per 10 grid squares available, was lowest in all seasons for sites with <1% woody vegetation (0.7, 1.0 and 1.2 for summer, autumn and winter, respectively), intermediate for sites with 1-30% woody vegetation (3.1, 2.4 and 3.8, respectively) and highest for sites with >30% woody vegetation (5.3, 4.8 and 5.5, respectively). This positive association with high levels of woody vegeta-

tion did not differ among seasons ( $G = 2.5$ ,  $df = 4$ ,  $P > 0.10$ ).

## DISCUSSION

### Activity

Observations of white-tailed deer on Konza Prairie increased more than two fold from summer to winter, which likely reflects a shift from nocturnal to diurnal activity (Montgomery 1963; Beier and McCullough 1990; Potvin, Boots and Dempster 2003) and increased overall activity during winter (Michael 1970). Seasonal differences in diurnal activity included relatively greater morning activity during summer and greater midday activity in winter. These patterns were congruent with the role of temperature in regulating seasonal activity. Furthermore, activity in autumn appeared to be transitional between summer and winter activity regimes.

Diurnal activity peaked near dawn and dusk in summer, autumn and winter, as expected for white-tailed deer (Marchinton and Hirth 1984; Beier and McCullough 1990). In summer, activity of deer was lowest during midday, when radiant energy is most direct, and during early evening, when temperature typically is highest. During winter when overall diurnal activity is high, activity of deer was elevated at dawn probably as a result of reduced nocturnal activity, although daily temperatures usually are lowest near dawn.

White-tailed deer on Konza Prairie might have been responding to solar radiation as well as ambient temperature as a means of regulating body temperature (Rogers, Moen and Sedd 1987).

A dramatic increase in activity from summer to winter on Konza Prairie is indicative of relatively mild winter conditions (Moen 1978) and has been observed for white-tailed deer in southern states (Michael 1970). Our observations contradict patterns in more northern populations where white-tailed deer have been reported to reduce activity (Beier and McCullough 1990) and either increase (Dusek et al. 1989), or, more commonly, reduce movement (Moen 1978; Murphy, Payne and Anderson 1985; Hölzenbein and Schwede 1989). Such observations usually are attributed to tradeoffs between forage intake and reduced energy expenditure associated with inactivity during extreme winter conditions (Holter et al. 1975; Moen 1976).

### Use of habitat

Seasonal changes in use of topography reported for more northern populations of white-tailed deer are tied closely to seasonal changes in use of vegetation ascribed to presumed or observed trade-offs between thermal cover and forage availability (Martinka 1968; Murphy, Payne and Anderson 1985; Dusek 1987; Pauley, Peek and Zager 1993; Morrison et al. 2003). In contrast, use of topography by white-tailed deer on Konza Prairie was similar during summer and winter; this pattern probably reflected type and availability of vegetation conditions. While we expected deer mostly to use lowland and upper lowland because of the relative abundance of woody vegetation, especially trees, all topographic positions on Konza Prairie provided grassland interspersed with wooded patches.

Contrary to our expectation of seasonal variation in use of topography, white-tailed deer did not use lowland and upper lowland

most often during fawning season. Fawns select bedsites with relatively heavy horizontal and vertical screening (Uresk et al. 1999). Does might consider hiding cover more important during fawning season when perceived predation risk is high (Bello, Gallina and Equihua 2001; DePerno, Jenks and Griffin 2003); coyotes (*Canis latrans*) and bobcats (*Lynx rufus*) are relatively common on Konza Prairie (Finck et al. 1986). Perhaps, use of wooded areas in lowland and upper lowland areas concealed bedded individuals effectively and thus number of deer was under represented in summer when trees and shrubs had leaves. Conversely, upper levels of topography might have had sufficient hiding and thermal cover for fawns as compared to lower levels of topography. Regardless of whether foliage reduced the number of inactive groups observed in summer, perusal of data suggested that defoliation of woody vegetation in winter did not account for the large seasonal increase in active deer observed.

At a coarse scale of habitat use (grid units of 6.25 ha), white-tailed deer chose areas that had a high proportion of woody vegetation and avoided those that were open grassland in all seasons. At a fine spatial habitat scale, in contrast, most foraging deer were observed in open grassland rather than in or beside wooded patches. These fine-scale responses generally agree with previous observations that white-tailed deer forage in open areas, although they bed in wooded cover (Montgomery 1963; Jageman 1984; Compton, Mackie and Dusek 1988; Beier and McCollough 1990), but at the same time, choose at a coarse scale those habitats dominated by woody vegetation.

White-tailed deer avoid sites grazed by cattle (Suring and Vohs 1979; Compton, Mackie and Dusek 1988; Dusek et al. 1989). On a coarse scale, our observations did not provide evidence that bison grazing negatively influenced habitat use by white-tailed deer;



deer were observed feeding near bison on many occasions. Furthermore, deer foraged regularly on grazing lawns, which are discrete areas that are repeatedly grazed by bison. This repeated grazing by bison results in continual new plant growth and a high ratio of forbs to grasses on grazing lawns. These grazing lawns likely are attractive to white-tailed deer because they selectively forage on forbs over  $C_4$  grasses (Anderson et al. 2005, 2006).

Use of grassland by white-tailed deer has varied from year-round avoidance (Dusek 1987; Dusek, Wood and Mackie 1988; Bell, Lauer and Peek 1992; DePerno et al. 2002) to use during spring through autumn (Murphy, Payne and Anderson 1985; Gould and Jenkins 1993) or increased relative use in winter (Beier and McCullough 1990). Implicit in avoidance of grassland by white-tailed deer is lack of thermal and hiding cover (DePerno et al. 2002). Suggested explanations for increased use of grassland by deer in various seasons usually are related to amount or quality of forage (Murphy, Payne and Anderson 1985; Beier and McCullough 1990) or a lack of alternative habitat patches because of snow cover (Keay and Peek 1980). Increased use of open grassland by deer in autumn on Konza Prairie likely was associated with increased growth of  $C_3$  plants in the prairie (Progulske and Duerre 1964; Bryant et al. 1996).

Deer were observed less often on slopes and more often in lowlands and open grassland during autumn than during summer and winter. Low use of slope during autumn probably was related to concentrated use of lowlands, which likely was related to the rut as well as changes in available forage, e.g., acorns and crop plants.

The extensive use of grassland, especially near woody vegetation, by white-tailed deer throughout Konza Prairie Biological Station is noteworthy. Because white-tailed deer tend

to use open areas more at night than day (Rouleau, Crête and Ouellet 2002), it is reasonable to expect that our diurnal observations of use of open grassland by deer under represent overall use of these areas, especially during summer. Frequent use of open areas also might be related to the lack of any hunting, regardless of season, on Konza Prairie. However, growing evidence suggests selective herbivory by white-tailed deer not only on browse (Strole and Anderson 1992) and forested understory species (Frankland and Nelson 2003), but also on grassland forbs in the tallgrass prairie region (Anderson et al. 2001, 2005). Our findings stress the importance of recognizing the presence and potential influence of deer in not only forested areas, but the entire mosaic of habitats present on Konza Prairie and other tallgrass prairie remnants.

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