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Charles M. Nixon  
Lonnie P. Hansen  
Paul A. Brewer  
James E. Chelsvig  
Joseph B. Sullivan  
Terry L. Esker  
Robert Koerkenmeier  
Dwayne R. Etter  
Jill Cline  
Jeanette A. Thomas

Illinois Natural History Survey, Lorin I. Nevling, Chief  
607 East Peabody Drive  
Champaign, Illinois 61820  
(217) 333-6880

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**Authors' addresses:**

Charles M. Nixon, Illinois Natural History Survey, 607 East  
Peabody Dr., Champaign, IL 61820; Lonnie P. Hansen,  
Missouri Department of Conservation, 1110 South College  
Ave., Columbia, MO 65201; Paul A. Brewer, Illinois Depart-  
ment of Conservation, Route 2, Box 108, Charleston, IL 61920;  
James E. Chelsvig, 1665 Sycamore, Hanover Park, IL 60103;  
Joseph B. Sullivan and Terry L. Esker, Illinois Natural History  
Survey, Box 56, Timewell, IL 62375; Robert Koerkenmeier,  
7602 Wayne Rd., Trenton, IL 62293; Dwayne R. Etter, 1001<sup>1</sup>/<sub>2</sub>  
Derry Ln., Macomb, IL 61455; Jill Cline, 509 South Main,  
Homer, IL 61849; Jeanette A. Thomas, Department of Biology,  
Western Illinois University, Macomb, IL 61455.

# Behavior, Dispersal, and Survival of Male White-Tailed Deer in Illinois

Charles M. Nixon<sup>1</sup>  
Lonnie P. Hansen<sup>2</sup>  
Paul A. Brewer<sup>3</sup>  
James E. Chelsvig  
Joseph B. Sullivan<sup>1</sup>  
Terry L. Esker<sup>1</sup>  
Robert Koerkenmeier<sup>1</sup>  
Dwayne R. Etter<sup>1</sup>  
Jill Cline<sup>5</sup>  
Jeanette A. Thomas<sup>4</sup>

**Abstract** — The behavior, dispersal, and survival of male white-tailed deer (*Odocoileus virginianus*) were studied during 1980–1992 at three widely separated sites in Illinois. Marked males (N = 267), including 43 that were radio marked, were used to determine male associations and seasonal movements, survival, and habitat selections. Between 55% and 75% of marked yearling males dispersed each year from the study areas, with 77% of these dispersals occurring in the spring. Dispersal behavior declined to < 14% for males between 18 and 24 months old and virtually ceased (< 4%) for males > 24 months old. Dispersal rates and distances moved differed significantly ( $P < 0.05$ ) among study areas and seasons, with spring dispersal distances being greater than those in the fall. Body size of fawns in midwinter, orphaning, and density of females  $\geq 1$  year old had no effect ( $P > 0.05$ ) on dispersal rates.

Nondispersing (in spring) yearlings associated with their female relatives until fall, when they moved away from their natal ranges or dispersed. Yearling males did not breed on the study areas and usually did not associate regularly with adult males until postbreeding. Survival of nondispersing yearlings and adult males during the nonbreeding season was high (> 80%) and similar among study areas. Dispersing yearlings died at higher rates ( $P < 0.05$ ) than nondispersers. Annual survival of males varied among study areas and ranged between 0.41 and 0.87, with hunting and associated wounding being the principal causes of death. Sexual segregation of adults occurred in summer but not winter. Adult males in summer in Illinois seek to maximize nutrient intake by exploiting landscapes avoided by females and yearling males, such as bottomland forests and areas with row crops. Genetic variability was measured using nine enzymes from yearlings in four adjacent counties in east-central Illinois. Only about 5.3% of the total genetic variability was attributable to spatial differences among sites within counties.

<sup>1</sup>Illinois Natural History Survey, Champaign

<sup>2</sup>Missouri Department of Conservation, Columbia

<sup>3</sup>Illinois Department of Conservation, Charleston

<sup>4</sup>Western Illinois University, Macomb

<sup>5</sup>University of Illinois, Urbana-Champaign

## INTRODUCTION

As noted by Clutton-Brock et al. (1982) in their landmark study of red deer (*Cervus elaphus*), the factors influencing reproductive success in the polygynous Cervidae differ between males and females, and these adaptations affect all phases of the life cycle, through physiological, social, and biochemical mechanisms. Females compete for resources to nurture offspring and perhaps for access to breeding males through solicitation of specific males (Geist 1981, Ozoga and Verme 1985, Bubenik 1982). Males compete for access to breeding females, with other forms of competition important only as they affect this competition (Trivers 1972). Breeding success is limited to those males that can gain and monopolize access to receptive females (Clutton-Brock et al. 1982). Thus, for males, factors such as body size, strength, and antler development directly affect reproductive success (Clutton-Brock et al. 1982, Geist 1971, Clutton-Brock et al. 1979).

Successful integration of male white-tailed deer as breeders following family breakup at age 11–12 months is often a long and difficult process (Holzenbein and Marchington 1992, McCullough 1979). To become a successful breeder, males must interact continually with other males to achieve a social position competitive with the mature males that constitute the annual breeding population (Ozoga and Verme 1985).

In addition to the challenge of socialization, males born within the intensively farmed region of the midwestern United States must adjust to a landscape with little permanent cover and dramatic seasonal changes in forage and cover as crops are planted, grow to maturity, and are harvested. Permanent cover (forests, marshes, prairies) exists only as small (< 100 ha), scattered parcels surrounded by row crops or urban development. Although dispersal of white-tailed females is rare in habitats with more cover (Nelson and Mech 1987, Teirson et al. 1985, Porter et al. 1991), extensive (> 50%) female dispersal is common in the fragmented ranges of the Midwest (Nixon et al. 1991, Gladfelter 1978). Within these fragmented landscapes, competition among individuals of both sexes for inclusion within the existing social structure is intense, as demonstrated by the extensive dispersal behavior of both sexes prior to 18 months of age and the seasonal migrations of some females living within these cover-deficient ranges

(Sparrowe and Springer 1970, Menzel 1984, Nixon et al. 1991). Our purpose was to examine male whitetail behavior and demographics within the intensively farmed landscape of Illinois, where hunting pressures on males are high, and foraging sites and protective covers are scattered and ephemeral.

## STUDY AREAS

Between 1980 and 1992, males were captured and marked using rocket nets on sites in northern (NO), west-central (WC), and east-central (EC) Illinois study areas (Figure 1). Each study area contained a mixture of public and private lands and included a wooded public park, which provided deer with abundant diurnal cover throughout the year, protection from severe winter weather, and refuge from firearm hunters. These core areas were surrounded by privately owned farms dominated by row crops. These farms provided relatively sparse diurnal cover in winter and were usually open to firearm deer hunting.

The 1,648-ha NO site was in DeKalb County, only 1.6% forested in 1985 (Hahn 1987). The study area included Shabbona Lake Recreation Area, a 479-ha public park surrounding a 128-ha lake. About 192 ha (40%) of the park was open to archery hunting during the study. The NO study area consisted of 59% row crops, either corn or soybeans, 14% second-growth hardwood forest, 7% reconstructed tallgrass prairie, 6% mixed species pine plantations, and 5% savanna; the remaining 9% consisted of a small suburban area, a golf course, and the lake. Most of the surrounding private farms were used by both firearm and archery hunters.

The 5,942-ha WC site straddled the boundary between Brown and Adams counties, which were about 20% forested in 1985 (Hahn 1987). The study area included Siloam Springs State Park, which covers 1,329 ha. The area was 52% forest (8% open canopy successional forest < 25 years old and 44% closed canopy forest > 50 years old), 39% row crops, 5% pasture or forage crops, and 3% tame hay fields or restored prairie. In 1990 and 1991, 79% (4,669 ha) of the study area was open to firearm hunting. In 1992, this increased to 91% (5,408 ha)



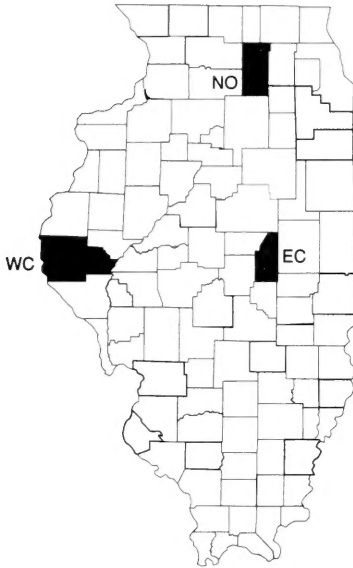


Figure 1. Illinois counties in which northern (NO), west-central (WC), and east-central (EC) study sites were located.

as more public land was opened to controlled firearm hunting. Archers hunted 88% and 91% of the study area during October and November-December, respectively. Archery hunting was intensive on the public area but lighter and more sporadic on the surrounding private farms.

The 2,953-ha EC site was in Piatt County, which was 2.7% forested in 1985. Land use on the study area was 64% row crops and 36% forest, with upland forest more abundant (22%) than bottomland forest (14%). There was a 600-ha refuge from all hunting in the center of this area. The remaining area was heavily used by both archers and firearm hunters each fall.

On all study areas, forests were understocked mixtures of previously pastured and cutover hardwoods. Younger uplands were mixtures of elms (*Ulmus* spp.), black walnut (*Juglans nigra*), honeylocust (*Gleditsia triacanthos*), black cherry (*Prunus serotina*), sassafras (*Sassafras albidum*), and shingle oak (*Quercus imbricaria*).

Older uplands were dominated by various oaks (*Q. alba*, *Q. velutina*, *Q. rubra*), and hickories (*Carya* spp.), with some sugar maple (*Acer saccharum*) and basswood (*Tilia americana*). The composition of the bottomland forests was dictated by flooding frequency. Frequently inundated stands were nearly a monotype of silver maple (*Acer saccharinum*). Better-drained sites supported mixtures of silver maple, elms, hackberry (*Celtis occidentalis*), honeylocust, sycamore (*Platanus occidentalis*), and bur oak (*Q. macrocarpa*). All natural cover supported a rich assemblage of forbs, grasses, and sedges.

Row crops were planted from April to early June depending on weather conditions. Soybean harvest began in late September, and corn harvest usually was completed by early November. Although most cornfields were disked or chisel- or deep-plowed each fall on the EC area, cornfields were usually left in stubble on the WC and NO areas. A few wheat and alfalfa-clover fields were present each year on each study area, and some areas were left in no till, providing deer with additional forage.

The climate of Illinois is temperate continental, with cold winters and warm summers. January, the coldest month, averages  $-3.1^{\circ}\text{C}$ , and July, the warmest, averages  $23.6^{\circ}\text{C}$  in central Illinois. Annual precipitation averages about 965 mm and is well-distributed throughout the year. Mean annual snowfall is about 84 cm in northern Illinois and 23 cm in the southern counties. In most years, snow seldom covers the ground for extended periods (Wendland 1987). As indicated by deer condition parameters such as yearling antler development in fall (antler beam diameters: EC =  $24.4 \pm 0.29$  mm, N = 132; WC =  $24.6 \pm 0.63$  mm, N = 38) and male fawn growth in mid-to-late winter on all three areas (chest girth: NO =  $82.7 \pm 0.7$  cm, N = 29; WC =  $80.9 \pm 0.6$  cm, N = 48; EC =  $81.2 \pm 0.8$  cm, N = 34), males were generally in good condition during our studies.

On each study area firearm hunters were issued county-specific permits, both "any sex" and "antlerless only" types. Because most hunters attempted to kill antlered males, hunting pressures were much heavier on antlered males than on antlerless deer, based on harvest levels of males compared with females in Illinois (Nixon et al. 1991, Roseberry and Woolf 1991).

## METHODS

Captured males were aged as fawn, yearling, or adult using tooth replacement and wear, and they were marked with numbered cattle-type plastic ear tags or with colored plastic streamers (NO = 47, WC = 94, EC = 126). A few males were also radio collared at each site (NO = 5, WC = 8, EC = 30).

The male year was divided into prebreeding, breeding, and postbreeding periods. The prebreeding period (15 April–30 September) was a time of weight gain and antlerogenesis. Males were ingesting large amounts of high-quality forages such as forage crops, perennial forbs and grasses, and row crops. Adult males were separated spatially from yearling males and females during most of this period. During the breeding period (1 October–15 January), males were searching for and defending access to estrous females. Human predation was high, and most of the annual mortality occurred during this period. Body weight and condition generally declined in adult males, but yearling males generally maintained their body weight and condition. During the postbreeding period (16 January–14 April), males attempted to regain body condition lost during breeding, antlers were shed, and social ties with other males were reestablished.

On all study areas, observations of marked males were obtained during routine field work, when spotlighting over fixed routes within each study area, and from reports provided by the general public. On the EC and WC study areas, radio-marked males were located using two truck-mounted, eight-element yagi antennas aligned in a null configuration. Each radio location was derived from two to five bearings taken from fixed locations scattered over both study areas. Accuracy was established using transmitters placed in known locations throughout each area. Locations produced by radio fixes were validated using the computer program LOCATE II (Nams 1990) and an unpublished program for the APPLE II (L.P. Hansen, Illinois Natural History Survey) for the WC and EC areas, respectively. The small amount and scattered nature of cover on the NO site enabled males to be located within a 1-ha grid using only a single antenna, a close approach, and direct observation. All acceptable male locations were placed within the appropriate hectare on each study area.

Seasonal core areas of home ranges, arithmetic centers of activity, and distance moved between radio locations (considered the center of a grid) were calculated using the computer program HOME RANGE (Ackerman et al. 1990). The Harmonic Mean Estimator was used to calculate core areas of seasonal use because it produced the least bias (Boulanger and White 1990). Means of home range sizes were log transformed and compared among age classes and seasons using one-way ANOVA.

All 1-ha grids on each study area were cover-mapped as to principal plant species and placed into one of nine cover types: upland oak-hickory, pasture and forage, row crops, bottomland hardwoods, early successional upland forest (< 30 years), late successional upland forest (30–60 years), pine plantations, upland savanna, and restored prairie. Using chi-square analysis, we compared these proportions with the seasonal locations of a combined sample of radio-marked yearlings and a combined sample of adults separately for each study area.

Survival and cause-specific mortality were calculated for marked males on each study area using the MICROMORT procedure (Heisey and Fuller 1985). All marked males whose fate was known (EC = 114/140 marked males, 81%; WC = 73/83, 88%; NO = 41/45, 91%) were used to determine survival. For yearling males, seasonal mortality was divided between males that remained sedentary after family breakup and those that dispersed from their natal areas. Seasonal and annual survival rates were compared among years and study areas using a Z-statistic (Heisey and Fuller 1985).

In 1990, blood sera and samples of muscle and heart (if available) were collected from yearling males shot by hunters in four counties (Champaign, Piatt, McLean, and Macon) surrounding the EC site in an effort to ascertain spatial-genetic variation in yearling males adjacent to one of our study areas (Figure 2). Samples from three of these counties were subdivided further by watersheds that were separated by intensively farmed or urban areas devoid of cover for deer. Two watersheds (Sangamon and Vermilion) were selected in Champaign County, three (Lake Decatur area, North Macon, and South Macon along the Sangamon River) in Macon County, and three (Mackinaw, Kickapoo, and Sugar Creek) in McLean County (Figure 2). At least six samples were available

from each watershed. Nine enzymes were examined for polymorphisms using starch gel electrophoresis. The enzymes were esterases (EST-1 & 2), aspartate amino transferase (AAT-A & M), mannosephosphate isomerase (MPI-1), 6-phosphogluconate dehydrogenase (6PGHD),  $\alpha$ -glycerophosphate dehydrogenase (GPDH), and malic enzyme (ME 1 & 2). Allele frequencies and estimates of single and multiple locus heterozygosities, deviation from the Hardy-Weinberg equilibrium, and dendrogram construction were calculated using the 1.7 version of the BIOSYS-1 program for the IBM PC (Swofford and Selander 1981).

We used marked females  $\geq 1$  year old rather than marked males to estimate trends in prehunt deer abundance on our study areas because (1) males were more difficult to observe during most of the year than

were females (see McCullough and Hirth 1982); (2) males frequently lost marking devices on the EC site, where we used a different marking method than on the other areas; and (3) for some years, too few marked males (< 10–12) were present on the study areas in late summer and fall to estimate male numbers. Although there are serious biases in spotlight counts (McCullough and Hirth 1982), prehunt estimates of females derived from spotlight counts provided reasonable estimates of female abundance comparable to those generated by a computer model of the EC deer population (Nixon et al. 1991). We knew the location (whether on or off of the spotlight routes) for > 92% of the marked females on each area.

Yearling and older females were counted periodically from late August to early October along fixed routes on each study area using spotlights. We used a weighted

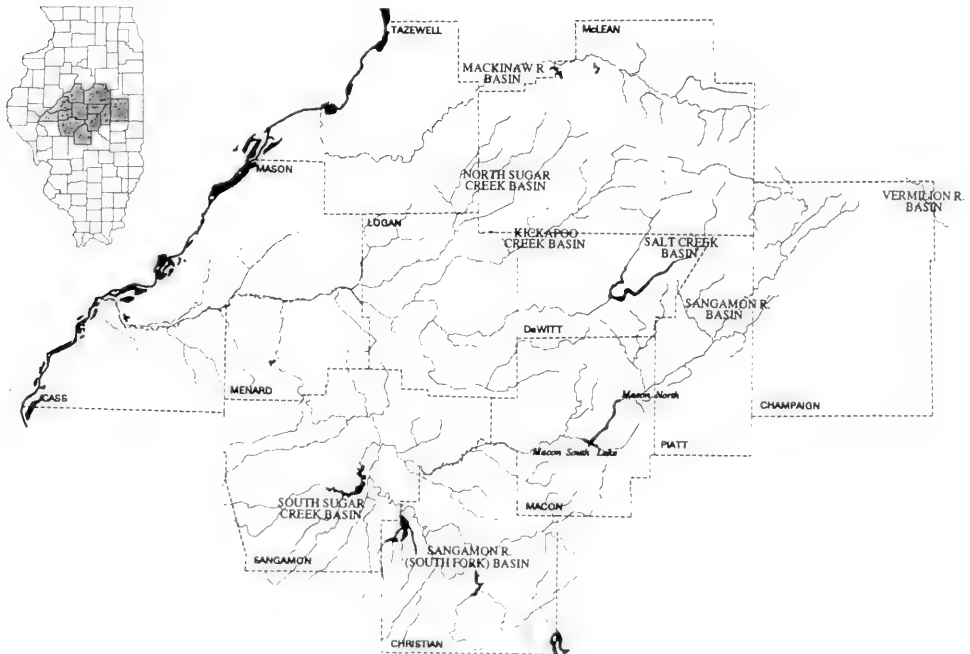


Figure 2. The principal watersheds and counties of east-central Illinois in which genetic variation in yearling males was examined using starch gel electrophoresis.

Table 1. Late-summer estimates of abundance for females  $\geq 1$  year old on three study areas in Illinois.

Study area	Land area (km <sup>2</sup> )	Year	No. counts	No. females				
				Peterson-Lincoln method		Schnabel procedure		
				Mean $\pm$ SE	Per km <sup>2</sup>	Mean	95% CI	Per km <sup>2</sup>
West-central	10.2	1990	5	72.7 $\pm$ 16.4	7.1	65.7	40.9–108.1	6.4
		1991	8	71.0 $\pm$ 2.7	7.0	73.4	46.2–92.5	7.2
		1992	7	78.8 $\pm$ 4.5	7.7	80.1	61.3–136.2	7.9
North	16.7	1990	4	65.5 $\pm$ 13.9	3.9	66.8	36.5–127.7	4.0
		1991	8	76.7 $\pm$ 8.2	4.6	80.9	57.3–115.4	4.8
		1992	7	89.6 $\pm$ 4.4	5.4	90.7	66.2–132.5	5.4
East-central	12.0	1981	3	33.3 $\pm$ 1.4	2.8	37.7	17.6–70.8	3.1
		1983	5	51.5 $\pm$ 2.4	4.3	54.8	37.1–77.2	4.6
		1984	8	63.5 $\pm$ 5.3	5.3	64.3	47.2–84.3	5.4
		1985	7	58.3 $\pm$ 2.7	4.9	59.3	47.5–105.6	4.9

average of the Peterson-Lincoln method (McCullough and Hirth 1982) and the Schnabel procedure (Chapman and Overton 1966) to estimate female numbers each year (Table 1).

## RESULTS

### LOCAL MOVEMENTS

Tertiary sex ratios favor males in Illinois (Roseberry and Wolf 1991, Nixon et al. 1991), and male fawns still predominate at the time of family breakup in late May (Hawkins and Klimstra 1970). Once separated from daily contact with their mothers, yearling males began to move over larger home ranges, whether they remained close to their natal ranges or dispersed to new home ranges.

For five radio-marked yearlings that remained on the EC area, core harmonic mean home ranges increased sixfold after family breakup, from 37 ha as fawns to 226 ha as yearlings (Table 2). The mean distance between centers of activity before and after family breakup for these yearlings was 972 m, ranging from 0 (for yearling 618, which associated with his mother as soon as she would permit it after parturition) to 2.7 km (Table 2). Sibling brothers (624 and 625) established prebreeding ranges of about the same size (367 and 396 ha), but the

arithmetic center of activity for male 625 was three times closer to the center of activity of the natal range than that of his brother (Table 2).

Average harmonic mean core areas for nondispersing yearlings and adult males were similar ( $P > 0.05$ ) during the prebreeding and breeding periods, but yearlings were more sedentary than adults during the postbreeding period ( $P < 0.05$ ) (Table 3). Home ranges of nondispersing yearlings were somewhat larger during the prebreeding period than during the remainder of the year, likely a reflection of wandering behavior immediately after family breakup. For example, yearling 334 wandered southward from the EC area for about 18 km during June but returned to a site near his natal range and remained there until death. Three other yearlings on the EC area (624, 625, and 556) temporarily ( $< 2$  weeks) wandered between 5 and 6 km from their natal ranges during May and June, then returned and selected a home range that included part of their natal ranges. Dusek et al. (1989) found that yearling males in eastern Montana did not establish a "traditional" home range until their second winter (during postbreeding at 19–21 months of age).

Yearlings traveled shorter distances between radio fixes than did older males throughout the year, whether activity was measured by the distance moved between radio locations on consecutive days or from 30-minute changes in movements between consecutive nocturnal radio locations (Figure 3). However, the differences were significant only during the breeding period (Figure 3). Less activity in yearling males during breeding is re-

Table 2. Harmonic mean home range (ha) and mean distance (m) between arithmetic centers of activity for males as fawns prior to family breakup and as yearlings after family breakup, east-central study area.

Deer no.	As fawns		As yearlings		Mean distance between centers of activity (m)
	No. loc.	Home range core area (ha)	No. loc.	Home range core area (ha)	
334	52	34.5	31	147	2,675
624 <sup>a</sup>	23	25.3	53	396	699
625 <sup>a</sup>	23	25.3	53	367	200
618	11	55.7	37	42	0
559	12	44.1	36	180	1,276
Mean		36.9		226	972
SE		5.8		67	479

<sup>a</sup> Brothers

flected by a lower frequency of scraping and marking signposts (Fudge et al. 1992). Ozoga and Verme (1985) also found yearlings were less active than mature males and remained close to their natal ranges during the prebreeding period. Distance moved (between sequential radio locations) was greater in fall than summer for males in northwestern Georgia (Kammermeyer and Marchinton 1977).

Yearling movements from diurnal resting/bedding sites to nocturnal feeding sites during prebreeding varied somewhat but not significantly depending on the habitats. Yearling movements within wooded habitats averaged  $748 \pm 168$  m ( $N = 23$  yearlings), from wooded sites into crop fields  $878 \pm 98$  m ( $N = 23$ ), and among crop fields  $726 \pm 105$  m ( $N = 19$ ). Yearling movements among crop fields were significantly greater ( $P < 0.05$ ) than similar movements by adult males in the same general area ( $458 \pm 53$  m,  $N = 6$ ).

During the breeding period, centers of activity for yearlings ( $N = 5$ ) shifted an average of  $742 \pm 249$  m from their prebreeding centers of activity on the EC area (Table 4), and yearlings averaged about the same home range size as older males (Table 3).

Shifts in range between breeding and postbreeding periods for yearlings appear to be less than those between other periods. Two yearlings on the EC area moved their postbreeding centers of activity an average of  $442 \pm 142$  m from the center of their breeding ranges (Table 4).

Table 3. Harmonic mean home ranges (km<sup>2</sup>) for sedentary yearling and older males radio marked in Illinois.

Age	Prebreed		Breed		Postbreed	
	No. deer	Mean $\pm$ SE	No. deer	Mean $\pm$ SE	No. deer	Mean $\pm$ SE
Yearling	7	$2.3 \pm 0.5$	7	$1.8 \pm 0.3$	6	$1.8 \pm 0.5$
Adult	15	$2.0 \pm 0.4$	8	$2.0 \pm 0.5$	11	$2.7 \pm 0.6$

During the postbreeding period, nocturnal movements were shorter on average for yearlings than for adult males in wooded habitats and in moving from woods to crop fields. Yearlings also had smaller home ranges (Table 3) and showed somewhat less movement between radio locations than adult males (Figure 3). Dusek et al. (1989) found that yearling males were more mobile than other deer from June through November but less mobile from December through May. On an annual basis, Dusek et al. (1989) found that travel between wooded and nonwooded habitats along the Yellowstone River remained within 500 m, which was shorter than averages for Illinois males. Beir and McCullough (1990) found yearling males were less active than adult males during the prebreeding and breeding periods and about equally as active as adults during the postbreeding period.

There was no significant correlation between age and size of home range during each season ( $r$  values between  $-0.05$  and  $0.29$ ,  $P > 0.10$ ). Nelson and Mech (1981) found home ranges of adult males to be significantly larger than those of yearlings during both early summer and fall in an extensively forested area of northern Minnesota.

Adults were most active at night during the prebreeding period. Based upon the distance between diurnal bedding sites on consecutive days, adults also moved farther than yearlings during the breeding and postbreeding periods.

Seasonal shifts in centers of activity among adults were greatest between the postbreeding and prebreeding periods, when males spatially separated from females and fawns. For six adults on the EC area and three on the NO site, these movements averaged 1.2 and 0.65 km, respectively; for 22 adult males radio tracked during 24 spring seasons, two moved to a summer range in late

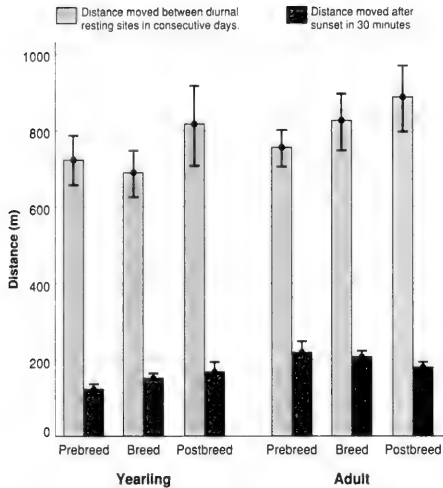


Figure 3. Mean ( $\pm 1$  SE) distance moved (m) by yearling and adult males between diurnal resting sites on consecutive days and average 30-minute distance moved by males after sunset by season in Illinois.

February, one moved in March, seven moved in April, five in May, four in June, and three in July. Two males on the WC area remained on their winter range throughout the year. Male 366 moved to his summer range in May during two consecutive years. Male 302 moved to a summer range in April when 2 years old and in February when 5 years old. Forty-five percent of these movements (10/22) occurred before antler growth began, and 55% after antlerogenesis was well under way. These males usually returned to their breeding range in wooded habitat in late September (an exception was male 209, which remained on his summer range on the NO area in unharvested corn until killed in mid-November).

A comparison of centers of activity for the same adult male in successive years indicates the stability of seasonal home ranges of adult males from year to year. For male 366 on the EC study area at age 3 and again at age 4, the centers of his two postbreeding ranges were 555 m apart, and the centers of his two prebreeding ranges were 1.9 km apart. For male 127 on the NO area at ages 3 and 4, the centers of his two prebreeding

Table 4. Distance (m) between seasonal arithmetic centers of activity for yearling and adult males on an east-central Illinois study area.

Seasons	Yearling		Adult	
	No.	Mean $\pm$ SE	No.	Mean $\pm$ SE
Prebreed-breed	5	742 $\pm$ 249	5	882 $\pm$ 116
Breed-postbreed	2	442 $\pm$ 142	4	803 $\pm$ 186
Postbreed-prebreed	2	704 $\pm$ 342	6	1,174 $\pm$ 285

ranges were 800 m apart. Male 302 was radio tracked on the EC area at ages 1, 2, and 5. This male's three prebreeding ranges were 1.1 km, 699 m, and 1.5 km apart between ages 1 and 2, 2 and 5, and 1 and 5, respectively. The three breeding ranges were 333 m, 777 m, and 1.01 km apart for the same three age comparisons, and the postbreeding ranges at age 1 and and at age 5 were 800 m apart. These data suggest that annual shifts in centers of activity were generally < 1.5 km within seasons for these males and indicate considerable site fidelity once a permanent range was selected, usually prior to age 2. Observations, radio locations, and/or hunter kill reports for 52 males that dispersed from our study areas and survived > 1 year after marking indicated that they also remained close to the sites selected after dispersal movements stopped. Dusek et al. (1989) found that most adult males in the northern Great Plains established a permanent range by their second winter after leaving the family groups. Gavin et al. (1984) reported that shifts in centers of activity averaged < 302 m between years for an insular population of Columbian white-tails (*O. v. leucurus*). Beir and McCullough (1990) found that about one-third of the males in the George Reserve occupied distinct summer and winter ranges; the remaining males occupied overlapping winter and summer ranges. Ranges were < 1.0 km apart in this confined population. Nelson and Mech (1981) found that radio-marked males in northern Minnesota demonstrated high fidelity to specific winter and summer ranges.

Daily movements differed between yearlings and adults only during the postbreeding period (Figure 3). There was no significant sex difference in average distance moved from bed sites to crop fields ( $F = 1.1$ , 7, 39 df,  $P > 0.35$ ), with females averaging 565  $\pm$  40 m and males 721  $\pm$  164 m. Males penetrated farther into crop fields from woodland borders than females (males = 285

$\pm 56$  m,  $N = 8$ ; females =  $179 \pm 17$  m,  $N = 15$ ,  $P < 0.05$ ). On the EC area, yearling and adult males typically used sites for diurnal resting that were farther from areas of potential human disturbance than were sites used by females. Distances from diurnal resting sites to areas of potential disturbance were as follows: yearlings = 251 m in winter,  $N = 7$  males, 264 m in summer,  $N = 6$ ; adults = 205 m in winter,  $N = 8$ , 303 m in summer,  $N = 9$ . For values for females, see an earlier report by Nixon et al. (1991).

Adult males did not shift their centers of activity in response to hunting on our study areas. Radio-marked adult males ( $N = 8$  for EC area, 4 for NO area) moved onto and away from the refuge portion of each study area throughout each hunting season, apparently responding to the demands of breeding rather than moving in response to hunting (no consistent movements away from hunters while being radio located). Root (1986) also found that males did not change their movement activities in response to hunting in northeast Missouri.

## ASSOCIATIONS

We obtained simultaneous locations for several pairs of radio-marked does and their yearling male offspring on the EC area. Centers of activity for siblings 624 and 625 during prebreeding averaged 755 and 222 m, respectively, from their mother's center of activity. During prebreeding, 624 was never located with his mother when they were simultaneously radio located, and 625 was radio located with his mother only once (Table 5). Nonetheless, consideration of all marked yearlings located after family breakup shows that nondispersing yearling males continued to associate at least occasionally with their immediate relatives during the prebreeding period. When yearling males were observed during the prebreeding period, they were with immediate relatives (mother, siblings) in nearly one-third of instances, with other yearling males during 22% of the observations, with unrelated does and fawns in 22% of cases, alone on 20% of occasions, and with mature males in < 5% of instances (Figure 4). Hawkins and Klimstra (1970) also observed a continued high association of siblings into the summer. Hardin et al. (1976) found that yearling male key deer (*O.v. clavium*) spent as much time with their dams after

family breakup as did yearling females (17–19%). Brown (1974) used the name "subdominant floaters" to denote yearlings that associated with a variety of groups, both male- and female-dominated, after family breakup. Nelson and Mech (1981) observed that male offspring associated at least occasionally with their mothers for up to 24 months in northern Minnesota.

During the breeding period, yearling males associated less often with their female relatives than they did at other times. They were most often observed alone (34% of observed associations) or with unrelated females and fawns (33%); they were only occasionally observed with other yearling males (15%) or adult males (14%) (Figure 4). During the breeding season, the centers of activity for four yearlings averaged  $455 \pm 142$  m from their mother's center of activity (Table 5). All four males spent brief visits (5.3–16.7% of simultaneous radio locations) with their mothers, but these visits were of short duration during evening feeding and often provoked aggression from their mothers. Brown (1974), Hawkins and Klimstra (1970), and Hardin et al. (1976) observed males to be most solitary during the breeding season in south Texas, southern Illinois, and the Florida Keys, respectively. As noted by others (Ozoga and Verme 1985, Holzenbein and Marchinton 1992), yearlings on our study areas avoided their relatives during the breeding season, often dispersing or temporarily ranging into new areas. Five radio-marked males in EC Illinois moved their breeding centers of activity an average of  $742 \pm 25$  m (range = 100 m–1.3 km) from their prebreeding centers of activity (Table 4).

During the postbreeding period, one of two radio-monitored yearlings reestablished an association with female relatives. Yearling 625 began traveling with his mother in early January and remained with her until parturition in late May ( $N = 17$  simultaneous radio locations) (Table 5). However, male 438 had no contact with his mother while being radio located ( $N = 15$  radio locations), and his center of activity averaged 955 m from his mother's center of activity.

During postbreeding, yearlings were less often alone (15%), were frequently seen with females and fawns (37%), and spent more time in association with yearling (21%) or adult males (18%) (Figure 4). Ivey and Causey (1988), Hawkins and Klimstra (1970), and Brown (1974) also observed that antlered males regrouped after the breeding period.

Table 5. Mother-yearling son association on the east-central Illinois study area based upon simultaneous radio locations.

Deer no.		Season	No. loc.	Distance between arithmetic centers of activity (m)	Home range (ha)		Times together
Mother	Son				Mother	Son	
342	625	Prebreed	44	222	54	264	1
342	624	Prebreed	24	755	54	411	0
442	438	Breed	11	744	5	25	1
372	382	Breed	18	633	37	88	3
342	624	Breed	19	311	16	64	1
342	625	Breed	30	132	16	109	4
442	438	Postbreed	15	955	24	128	0
342	625	Postbreed	17	0	11	11	17

Brown (1974) found that males often remained part of the maternal family group for up to two years in south Texas. In contrast, Hawkins and Klimstra (1970) found that males permanently left the family group at one year in southern Illinois and that the frequency of association between mothers and sons declined from 75% before family breakup to only 3% after breakup. Our observations were similar to those of Ozoga and Verme (1985), with nondispersing yearlings remaining close to their family group until fall.

During prebreeding, adult males were usually alone (47% of observations) or with other males (37%); during breeding they were either alone (44%) or with females (38%); and during postbreeding they were with other adult males (43%) or with females in mixed groups (24%) (Figure 4). Males more than 2 years old were abundant on all three study areas, so associations should not have been influenced by a lack of other adult males. On the EC area, group sizes for antlered males were lowest in June and November and highest in February-March (Nixon et al. 1991). Whitetail males in the Florida Keys were mostly solitary throughout the year except during breeding, with fraternal associations most prevalent in June (Hardin et al. 1976). Brown (1974) observed that in south Texas adult males associated in fraternal groups throughout the year except during the breeding season, with each group formed around a core of two to four dominant males. Within these groups, intraspecific strife was low, reducing the likelihood of serious injuries. Ivey and Causey (1988) found that 93% of the males were solitary during the breeding period in Alabama, with males regrouping during postbreeding. Gavin et al.

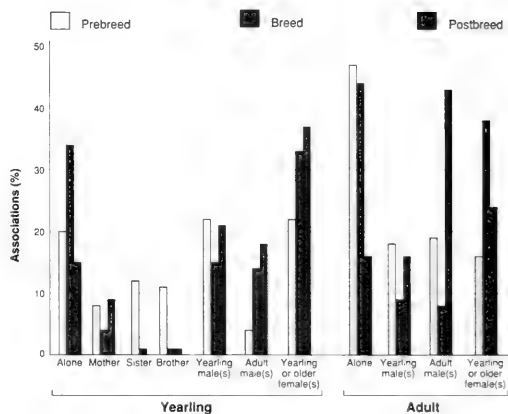


Figure 4. Associations of yearling and adult males throughout the year in Illinois based upon observations of males marked on three study areas.

(1984) observed that Columbian whitetail males were least social during late summer and autumn, similar to our observations. Nelson and Mech (1981) found males most likely to associate during December-March (postbreeding) and least likely to associate during the breeding period.

Nondispersing adult males occasionally were seen near their mothers or siblings within feeding or resting groups throughout the year but paid little attention to their relatives. An exception was male 516, which



traveled with his mother during his fourth winter on the EC area. He was not seen with her during the following prebreeding period (when he was alive) or during subsequent winters.

### DISPERSAL

Dispersal among yearlings occurred during two periods: the prebreeding period in May-June immediately following family breakup and the breeding period in October-November. Prebreeding dispersal was more important in terms of numbers of males. For marked males dispersing from our study areas, 94/122 (77%) dispersed in the spring (Table 6). There was no difference among years ( $P > 0.05$ ) in dispersal rates within our three study areas, but we found overall (spring and fall combined) dispersal rates differed among our study areas, averaging 55% (EC area), 71% (WC area), and 75% (NO area) of those marked each year ( $G = 13.88$ , 4 df,  $P < 0.01$ ). There also was a significant difference in the extent of fall dispersal among the three study areas, ranging from 13% on the EC area to 36% on the WC site ( $G = 7.53$ , 2 df,  $P < 0.025$ ).

Fall dispersers moved shorter distances than spring dispersers, with spring movements averaging  $38.1 \pm 3.7$  km ( $N = 56$ ) and fall movements only  $18.6 \pm 3.2$  km ( $N = 22$ ) ( $F = 9.52$ , 1,76 df,  $P < 0.01$ ). This difference may have been at least partially the result of death from hunting prior to completion of the dispersal movement in the fall. Yearlings on the WC area dispersed shorter distances (spring and fall combined) than males on the other two areas (WC =  $19 \pm 3.8$  km,  $N = 30$ ; EC =  $38 \pm 4.4$  km,  $N = 46$ ; NO =  $36 \pm 4.2$  km,  $N = 13$ ;  $F = 5.98$ , 2,86 df,  $P < 0.01$ ), perhaps reflecting the greater amount of nonagricultural cover available in west-central Illinois compared with the EC and NO areas. Male dispersal movements beyond 50 km were more common on the NO and EC areas than on the WC site (Figure 5). Yearling male 270 was killed 161 km north of the EC area in fall 1981, thus far the record dispersal movement for Illinois deer. Only Nelson (1993) reported a longer dispersal movement for white-tailed deer, that being 168 km for a female marked in northeast Minnesota.

On the EC and NO study areas, most males (31/43, 72%) dispersed toward the nearest boundary of each

Table 6. Dispersal of yearling males marked on three study areas in Illinois, 1980–1992.

Area	Year	No. of males		
		Sedentary	Dispersal	
			Spring	Fall
Northern	1990	1	3	2
	1991	2	9	1
	1992	5	7	2
	Total	8	19	5
	%	25	59	16
West-central	1990	7	7	3
	1991	4	6	8
	1992	7	15	5
	Total	18	28	16
	%	29	45	26
East-central	1980	2	2	3
	1981	3	7	0
	1982	7	6	1
	1983	7	8	0
	1984	9	14	1
	1985	15	10	2
	Total	43	47	7
	%	44	48	7

study area, not across the area in the opposite direction. This pattern was less apparent on the more forested WC area. Distance moved in relation to the quadrant of dispersal did not differ ( $P > 0.05$ ) on the NO and WC areas, but on the EC area, dispersal distance in the southwest quadrant was significantly less than dispersal distance in the northeast quadrant ( $F = 5.26$ , 1,29 df,  $P < 0.01$ ) (Figure 6). This difference may have been due to landscape differences between quadrants, with a large city (Decatur) and reservoir blocking deer movements to the southeast of the EC area. More deer dispersed northeast or southwest than northwest or southeast from the EC area, a reflection of the orientation of the riverine forests along the Sangamon River (Figure 6).

Of 22 pairs of male and female siblings in which one or both members dispersed, 15 pairs demonstrated dispersal behavior in the spring and seven in the fall. In the spring, three pairs dispersed together; in five pairs only the male dispersed, in four pairs both members dispersed at different times and in different directions,

and in three pairs only the female dispersed. In the fall, only the male dispersed from each of the seven pairs.

For 20 pairs of male siblings in which one or both members dispersed in the spring, nine pairs dispersed together; in eight pairs only one male dispersed, and in three pairs both members dispersed at different times and in different directions. For nine pairs of male siblings still associating at least occasionally in the fall at age 16–17 months, one pair dispersed together; in five pairs only one male dispersed, and in three pairs both males dispersed separately. Dispersal behavior evidenced by siblings together may be more common in the cover-deficient midwestern United States than reported for whitetails in more northern ranges, where Nelson and Mech (1992) found only one instance of male-female siblings dispersing together ( $N = 7/35$  marked females dispersed). Woodson et al. (1980) found that four of five pairs of orphaned sibling males dispersed together, whereas male-female pairs of siblings remained sedentary.

Siblings were more likely to disperse together in the spring (34%) than in fall (6.2%) ( $G = 3.57$ ; 1 df;  $P < 0.10$ ), perhaps because they had been together constantly since birth at the time of spring dispersal. In the fall, most sibling associations were more infrequent, and close associations were less likely to occur at the time dispersal behavior was initiated.

Holzenbein and Marchinton (1992) presented evidence that orphaned yearling males were significantly more likely to remain on their natal ranges than non-orphans. However, we found no significant difference in dispersal behavior between orphans and non-orphans for a sample of marked yearlings. For 16 males orphaned after weaning, nine (56%) dispersed and seven were sedentary. Of 125 non-orphans, 68 (54%) dispersed and 57 were sedentary ( $P > 0.75$ ). The disparity in sample size makes a significance test suspect in this case, but our orphaned sample dispersed at a higher rate than was reported for orphaned males in Virginia (9.1%) (Holzenbein and Marchinton 1992). Woodson et al. (1980) orphaned 21 fawns in the fall in Virginia and observed dispersal rates between orphans and a control group of fawns with living mothers. They also found a higher dispersal rate among orphans compared with males with a living mother (24% of orphaned males and 6% of males with a living mother dispersed).

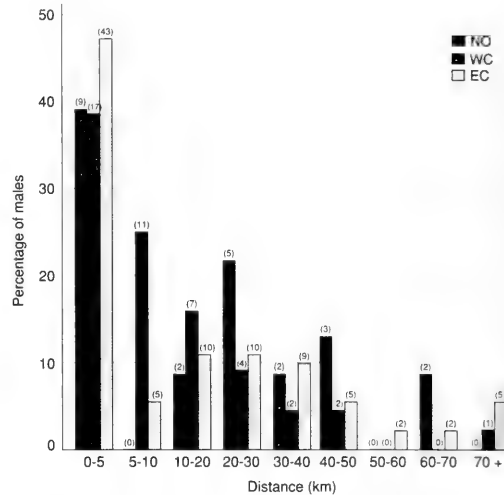


Figure 5. Distribution of dispersal distance (km) for dispersing yearling male deer in Illinois. Numbers above each column are the number of males in each distance interval.

In Illinois, there is a segment ( $\geq 20\%$ ) of the female population that seasonally migrates to and from forested areas used as wintering sites after crop harvest. Migratory behavior was noted among females on all three of our study areas, and these movements affected subsequent movements of some marked yearling males after family breakup. Males 264 and 2201 migrated with their mothers to a winter range at age 6 months and subsequently dispersed from the winter range to a new summer range separate from their mother's range. Males 290 and 557, however, returned to their mother's summer range with their mother in April-May at age 10-11 months and subsequently dispersed to a new home range during June.

Forest cover per se does not appear to be important in initiating dispersal behavior among yearling males. Dispersal rates were similar in NO (forest covers  $< 2\%$  of the landscape) and WC Illinois (forest covers  $> 19\%$  of the landscape). Deer abundance and the degree of crowding among family groups may be more important than available forest cover in initiating male dispersal.

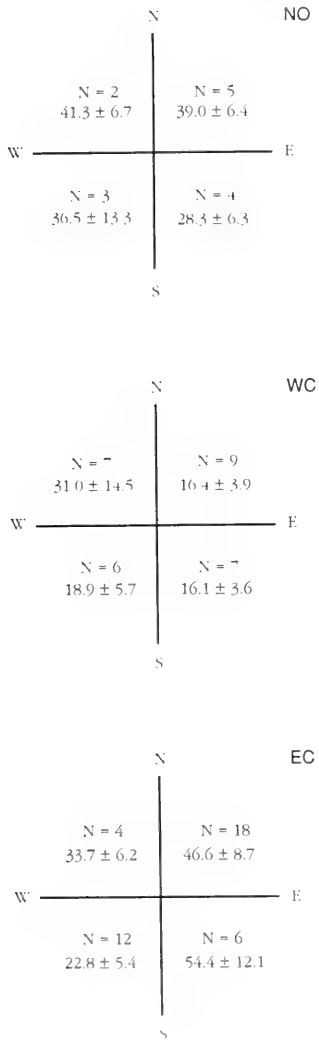


Figure 6. Directional distribution of dispersing yearling males and mean distance moved (km  $\pm$  1 SE) in each quadrant surrounding three marking sites in Illinois.

However, we were unable to demonstrate a significant correlation ( $P > 0.05$ ) between the proportion of males dispersing in spring and estimated densities of adult females in early fall on our study areas (Table 1).

We found no significant difference in dispersal rates from our study areas for fawns that were above and below mean chest girth, which was used as an indicator of size prior to initiation of spring dispersal.

Dispersal was not evident in winter in Illinois, though winter dispersal has been observed in northeast Missouri (Root 1986). Some investigators have suggested that dispersal behavior may be more prevalent during winters with little snow (Rongstad and Tester 1969). Nonetheless, although winters in Illinois were mostly snow-free during our studies (except for the winter of 1982-1983), no marked yearling males dispersed during the postbreeding period.

Of 54 marked males known to survive to age 2 years on our study areas, only seven (13%) dispersed after age 18 months and only two moved after age 24 months. Male 168 dispersed or migrated from the NO area in May 1992 at age 35 months. He remained on a new range 6.6 km south of his 1991-1992 winter range through the peak of the breeding period until he was killed by a hunter in December. However, because he was marked only three months before he left his postbreeding range and because he did not survive into the following postbreeding period when he could have migrated back to his marking site, we were not certain his movement was a true dispersal (no return). Male 120 did disperse in fall 1991 from the WC area at age 27 months and moved 41 km southwest of his last sighting on the study area. The distance moved indicates this movement was a true dispersal, not a migration, because marked deer in Illinois have never returned from such long-distance movements. Prior to dispersal, he had remained on the WC area for 23 months since tagging.

The five remaining males dispersed at ages 22-24 months and settled an average of  $16.7 \pm 6.9$  km from their previous ranges (range 4.5-36 km). Teirson et al. (1985) reported an identical percentage of adult male dispersals (7/52, 13%) after marking in the central Adirondacks of New York. In southern Illinois, 3 of 44 adult males (7%) dispersed or shifted home range after becoming adults (Hawkins and Klimstra 1970). Nelson (1993) reported that 9% (2/22) of a marked sample of

2-year-old males dispersed and that all six males that survived to 3–5 years of age continued to use home ranges selected as yearlings. Kammermeyer and Marchinton (1976) found fall dispersals of 50% (5/10) for males 1.5–2.5 years old in a refuge in Georgia.

### **SURVIVAL**

Yearling survival rates were calculated separately for males that dispersed and those that remained on or close (< 2 km) to their natal ranges. Survival was high and similar ( $P > 0.10$ ) for males marked on all three study areas during the prebreeding (> 95%) and postbreeding (> 81%) periods (Table 7). Survival during the breeding period was lower ( $P < 0.01$ ) for males dispersing from our WC and EC study areas than for sedentary males, but survival of these two groups was not different on the NO area (Table 7). Annual survival of dispersing males was significantly lower than that of sedentary males ( $P < 0.02$ ) on all study areas.

Hunting was the principal cause of mortality for yearling males in Illinois (Table 7). For nondispersing yearlings, archery kills were important because archery hunting was widespread on all three study areas. For dispersing males, firearm hunting and autos were important causes of death. Nondispersing yearlings were more vulnerable to archery hunting compared with firearm hunting whereas dispersing males were more vulnerable to firearms (Table 7). During the closed season, highway accidents were the principal cause of death, with only a few yearlings dying each year from poaching and fence collisions. Yearlings were about equally vulnerable to archers as to firearm hunters and were less likely to die from firearm- or archery-caused wounding than were older males (Tables 7 and 8).

Dispersal movements might be expected to increase the risk of death for yearling males as they traverse unknown landscapes. For yearlings dispersing from the NO area, 3 of 13 (23%) fall mortalities of marked yearling males occurred during dispersal movements based on the short time between initiation of dispersal and death. Two of these males were killed by archers and one by a firearm hunter. Only one death occurred among our marked yearlings in spring from the NO study area, and he died from an auto collision during dispersal. On the

EC area, 4 of 48 (8.3%) fall deaths (one firearm, one archery, one archery wounding, and one auto) and three of five spring deaths (one poaching, two highway deaths) of marked yearlings occurred during dispersal. On the WC area, 7 of 20 (35%) fall deaths of marked yearlings occurred during a dispersal movement (one archery, six firearm hunting). Only one marked yearling male died in the spring, and he was killed by an automobile while dispersing from the WC area. Yearlings appeared particularly vulnerable to highway accidents during spring dispersal in Illinois, as they must traverse landscapes crisscrossed with unfamiliar, high-speed highways. Highway accidents were less likely during fall, perhaps because yearlings were older and had more experience avoiding vehicular traffic. However, in fall, yearlings were dispersing during the archery and firearm hunting seasons, and movements through strange areas at this time apparently increased vulnerability to hunting, particularly from firearms. Nelson and Mech (1986) found a disproportionate number of deer killed by wolves in Minnesota while the deer migrated between seasonal ranges during the fall, in contrast to the spring.

Size of males at 7–9 months of age did not affect subsequent survival. We used chest girths taken from male fawns captured in winter as a measure of potential size and weight of these deer in future years and compared survival to breeding age ( $\geq 2$  years) of males above and below the mean chest girth. There was no significant difference in the proportion of males reaching breeding age whether above or below mean values (above mean chest girth survival = 50.9%,  $N = 59$  fawns; below mean chest girth survival = 56.3%,  $N = 55$  fawns).

Survival of males  $\geq 2$  years old was significantly higher ( $P < 0.05$ ) than that of yearling males that dispersed from the EC and NO study areas, but it was similar ( $P > 0.10$ ) to survival of dispersing yearlings on the WC area and sedentary yearlings on all three areas (Tables 7 and 8). Annual survival of adult males was significantly higher ( $P < 0.001$ ) on the NO area than on the WC and EC areas (Table 8). We believe the survival rate for adult males on the NO area to be much higher than the norm for adult males in much of northern Illinois. This may be an artifact of the relatively small numbers of marked males available, eastward dispersal tendencies that placed several males into the metro-

Table 7. Survival and cause-specific mortality rates of yearling (11–24 months) males marked in northern (NO) (1990–1992), west-central (WC) (1990–1992), and east-central (EC) (1980–1985) Illinois. Sedentary males remained on their natal range, and dispersers moved to a new range.

Site	Movement behavior	Season	Interval (days)	Deer days	No. deaths	Survival	95% CI	Cause of death					
								Auto	Archery	Firearm	Archery wounding	Firearm wounding	Misc.
NO	Sedentary	Prebreed	153	2,601	0	1.00	—	—	—	—	—	—	—
WC				5,661	0	1.00	—	—	—	—	—	—	—
EC				10,098	1	0.984	0.95–1.00	0.02	—	—	—	—	—
NO				Breed	107	1,712	5	0.724	0.55–0.96	—	0.16	—	0.05
WC	3,959	9	0.783			0.67–0.92	0.02	0.07	0.04	0.04	0.02	—	
EC				6,741	19	0.737	0.64–0.84	—	0.12	0.07	0.04	0.01	0.01
NO				Postbreed	105	1,155	2	0.827	0.64–1.00	0.16	—	—	—
WC	2,940	0	1.00			—	—	—	—	—	—	—	
EC				4,725	3	0.934	0.86–1.00	0.04	—	—	—	—	0.02
NO				Annual		5,468	7	0.626	0.44–0.88	0.10	0.16	—	0.05
WC	12,560	9	0.769			0.64–0.91	0.02	0.07	0.05	0.05	0.02	—	
EC				21,564	23	0.677	0.57–0.79	0.04	0.12	0.07	0.04	0.01	0.02
NO				Dispersed	Prebreed	153	3,825	1	0.960	0.88–1.00	0.04	—	—
WC	5,508	1	0.972				0.92–1.00	0.02	—	—	—	—	—
EC				6,885	1	0.977	0.93–1.00	0.02	—	—	—	—	—
NO				Breed	107	2,568	8	0.711	0.56–0.90	0.03	0.07	0.14	—
WC	3,745	20	0.559			0.43–0.72	0.04	0.15	0.15	0.02	0.04	0.02	
EC				4,173	28	0.482	0.37–0.63	0.05	0.18	0.20	0.01	0.03	0.01
NO				Postbreed	105	11,680	0	1.00	—	—	—	—	—
WC	2,205	0	1.00			—	—	—	—	—	—	—	
EC				1,260	1	0.916	0.78–1.00	0.08	—	—	—	—	—
NO				Annual		8,073	9	0.511	0.38–0.68	0.07	0.16	0.16	0.02
WC	11,458	21	0.665			0.51–0.86	0.07	0.07	0.14	—	0.03	—	
EC				12,318	30	0.410	0.29–0.56	0.09	0.19	0.21	0.01	0.03	0.01

Chicago area that was closed to firearm hunting, and poor hunting success of archery hunters on or adjacent to the NO area.

Males older than 24 months suffered little mortality during the pre- and postbreeding seasons (survival > 96%) (Table 8). During the breeding season, hunting accounted for most of the annual loss. Even poaching seemed to be concentrated within the breeding period. In contrast to yearlings, mature males appear somewhat more vulnerable to firearm hunting compared with archery hunting (Table 8). Wounding losses among adult males as a proportion of firearm- and archery-caused mortality were higher than for yearling males, perhaps a result of the greater strength of the adults when wounded which enabled them to escape capture (Table 8).

Gavin et al. (1984) found male mortality to be higher than female mortality in winter but similar in summer for a population of Columbian whitetails. On the EC area, annual male survival was significantly less than that of yearling and older females (Nixon et al. 1991). Dusek et al. (1989) found the average annual mortality of males to be more than twice that of females in eastern Montana. Males in Illinois survived at considerably higher rates than males in north-central and northeast Minnesota, which are exposed to wolves and severe winters (survival of 0.46 for all males in north-central Minnesota [Fuller 1990]; survival of 0.41 for yearlings and 0.47 adults in northeast Minnesota [Nelson and Mech 1986]). DeYoung (1989) reported annual survival of 0.71 for males  $\geq$  2 years old exposed to mountain lion (*Felis*

Table 8. Survival and cause-specific mortality rates calculated from adult males &gt; 2 years old marked in northern (NO) (1990–1992), west-central (WC) (1990–1992), and east-central (EC) (1980–1985) Illinois.

Site	Season	Interval (days)	Deer days	No. deaths	Survival	95% CI	Cause of death				
							Auto	Archery	Firearm	Archery wounding	Firearm wounding
NO	Prebreed	153	4,590	0	1.000	—	—	—	—	—	—
WC			7,497	0	1.000	—	—	—	—	—	—
EC			13,311	2	0.977	0.94–1.00	0.01	—	—	—	0.01
NO	Breed	107	3,210	4	0.873	0.76–0.99	—	—	0.093	0.03	—
WC			5,243	18	0.689	0.58–0.82	—	0.13	0.08	—	0.06
EC			8,774	30	0.691	0.60–0.79	—	0.04	0.19	0.04	0.02
NO	Postbreed	105	2,730	0	1.00	—	—	—	—	—	—
WC			3,255	0	1.00	—	—	—	—	—	—
EC			5,460	0	1.00	—	—	—	—	—	—
NO	Annual		10,530	4	0.873 <sup>b</sup>	0.75–0.99	—	—	0.09	0.03	—
WC			15,995	18	0.662	0.55–0.80	—	0.14	0.09	—	0.07
EC			27,545	32	0.645	0.55–0.74	0.02	0.04	0.20	0.04	0.02

<sup>a</sup> Includes drowning, poaching, fence, collisions, canine predation.

<sup>b</sup> Significantly different from WC and EC survival ( $P < 0.001$ ).

*concolor*) and coyote (*Canis latrans*) predation on two ranches in south Texas.

We calculated survival of an average 100 males born on each study area (Table 9). Male fawn mortality was based on repeated observations of marked does from early postpartum to family breakup a year later. Survival was calculated separately for sedentary and dispersing yearlings (Table 7). Because adult survival on the NO area was considered to be higher than average for most of northern Illinois, we used a value of 0.65 for annual adult survival on this area. This was the mean of annual survival of adult males on the WC (0.66) and EC (0.64) areas.

Less than 20% of those born on the study areas survived to 5 years old; survival to this age ranged from 9% for dispersing males in EC Illinois to 18% for sedentary males in WC Illinois (Table 9).

### HABITAT USE

Nondispersing yearling males in Illinois did not occupy habitats separate from does and fawns during the prebreeding period, as occurred with adult males, but continued to frequent habitats favored as parturition sites by resident females, including their dams. Six of 7 and 12 of 14 radio-marked yearling males remained on summer

ranges that overlapped those of several nursing females on the EC and NO study areas, respectively. On the EC area, prebreeding yearlings selected oak-hickory forest and avoided row crops in summer, with other habitats used in accordance with abundance, a pattern similar to that observed for females (Table 10) (Nixon et al. 1991).

During the breeding season in EC Illinois, yearling males selected both upland and bottomland forest and avoided crop fields, again frequenting areas favored by females and fawns in the fall (Nixon et al. 1991). During postbreeding and after crop harvesting and fall tillage, yearlings avoided crop fields and selected upland successional forest and bottomland forest where cover was abundant (Table 10). Dusek et al. (1989) found that yearling males and females occupied similar habitats in summer and autumn, but yearling habitats more closely resembled those of adult males in winter and spring, a pattern similar to that observed in Illinois.

In late spring, adult males moved from postbreeding ranges shared with does, fawns, and yearling males to areas dominated by agricultural crops or bottomland forests. Habitat selection also changed at this time (Table 10). On the EC area, postbreeding adults selected successional forests and avoided crop fields, similar to habitat selections made by yearling males. Adult males selected bottomland forests and used other habitats in

Table 9. Survival of 100 sedentary (S) and dispersing (D) males on east-central (EC), west-central (WC), and northern (NO) Illinois study areas.

Year class	EC		WC		NO <sup>a</sup>	
	S	D	S	D	S	D
0-1	100	100	100	100	100	100
1-2	87	87	80	80	80	80
2-3	59	36	61	53	50	41
3-4	38	23	41	35	33	27
4-5	24	15	27	23	21	17
5+	16	9	18	15	14	11

<sup>a</sup> Adult survival for NO = mean of EC and WC males.

proportion to their occurrence on the study area during the prebreeding period. Row crops made up 59% of the EC area, and only adult males used crop fields in proportion to their occurrence on the EC area, resulting in considerable use of these habitats. Females and yearling males spent considerably less time in row crops in summer. Prebreeding adults in NO Illinois selected upland and bottomland forests, with no preference for remaining landscape features. Postbreeding adults avoided row crops and selected upland forests (Table 10). In WC Illinois, adults selected forage crops and pastures during the prebreeding period, avoided row crops and selected pastures and Conservation Reserve Program "set aside" fields during breeding, and selected forage crops during postbreeding. Remaining landscapes were used in proportion to availability during each season (Table 10). Prior to crop maturation, adult males often moved from their postbreeding ranges to the edges of the wooded uplands or to bottomland forests offering open understories and rich feeding areas, unoccupied by breeding females and yearling males.

Adult males often remained in crop fields for extended periods during the summer (Nixon et al. 1991). On the EC area, adult male 500 remained away from woody cover in a complex of row crops and forage for over four weeks; adult male 366 spent 21 and 22 hours in a cornfield during two 24-hour tracking sessions during July 1982. On the NO area, male 209 remained within a single large cornfield for about six weeks in late summer. Without the constraints of fawn nurturing imposed on females, males were not required to make periodic returns to permanent cover. Of eight adult males

radio tracked on the EC site, five averaged > 70% of their summer ranges in row crops, mainly tall corn. In contrast, on the same study area, 58 females averaged < 36% of their summer ranges in row crops.

During breeding and postbreeding, males occupied habitats similar to those occupied by females. On the EC area, male 366 spent > 50% of 18 hours of continuous tracking in woodlands in February, 100% of 12 hours in April in woodlands, and 100% of 13 hours in woodlands in January. Male 464 spent 20 of 22 hours in woodlands in winter.

The seasonal separation of adult males from females with fawns in summer is a common behavior in whitetails and other ungulates (Main and Coblenz 1990). One theory is that males separate from females in order to seek sites offering open understories to avoid damaging their growing antlers as well as to interact with other males prior to the breeding period (Verme 1988). We examined a sample of adult and yearling males brought to check stations in EC Illinois in 1992 and compared antler damage thought to be the result of accidents that occurred during antler growth, that is, before calcification. We found damaged antlers to be more common in yearlings (no. damaged = 45/158, 28.5%) than in adult males (no. damaged = 16/95, 16.8%) ( $G = 3.90, 1 \text{ df}, P < 0.05$ ). Whether this difference in damage was the result of movements through different habitats is unknown, but in summer, yearlings remained on sites with denser understories than did adults (Nixon et al. 1991).

### BREEDING SUCCESS

On the EC area, 119 captured males were released alive. The average age of these males at death was  $2.49 \pm 0.11$  years, indicating that the average male participated in breeding activities for only one breeding season before death (yearlings rarely breed successfully in Illinois, and only one instance of a possible successful breeding by a yearling male was observed during our study). Thirty-one of these males (26%) reached at least 3 years of age on the EC area before dying, and they likely participated in at least one breeding season. Male captures on the WC and NO study areas have been too recent (as of March 1994) to estimate average male life span, but 53 (77 (69%)) and 27 (41 (66%)) of the males surviving capture on the

Table 10. Seasonal habitat selection by yearling and older male white-tailed deer in Illinois. Use of habitats was determined on the basis of averages of radio locations of individual males summarized for each period.

Age	Season	No. of deer	No. of radio locations	Habitat type							
				A	B	C	D	E	F	G	H
				EAST-CENTRAL <sup>a</sup>							
Yearling	Prebreed	7	292	0 <sup>b</sup>	+ <sup>b</sup>	0	0	0	- <sup>b</sup>	0	
	Breed	7	241	0	+	+	+	0	-	0	
	Postbreed	5	146	0	0	+	0	0	-	+	
Adult	Prebreed	10	492	0	0	0	0	0	0	+	
	Breed	7	194	0	0	+	0	0	-	+	
	Postbreed	6	210	0	0	+	0	0	-	+	
				NORTHERN <sup>c</sup>							
Adult	Prebreed	3	117	0	0	0	0	+	+	0	0
	Postbreed	3	62	-	0	+	0	+	0	0	0
				WEST-CENTRAL <sup>d</sup>							
Adult	Prebreed	7	143	0	+	+	0	0	0	0	0
	Breed	5	53	-	0	+	0	0	0	0	0
	Postbreed	2	30	0	+	0	0	0	0	0	0

<sup>a</sup> East-central: A = pasture-forage; B = oak-hickory; C = successional forest < 60 years old; D = silver maple; E = conifer plantations; F = row crops; G = bottomland hardwoods.

<sup>b</sup> 0 = Use and availability of habitat not significantly different; + = more use of habitat than was available within each composite home range; - = less use of habitat than was available.

<sup>c</sup> Northern: A = row crops; B = restored prairie; C = successional forest; D = savanna forest; E = oak-hickory; F = bottomland forest; G = mixed mesophytic forest; H = conifer plantations.

<sup>d</sup> West-central: A = row crops; B = forage crops; C = pasture and Conservation Reserve Program; D = old fields and restored prairie; E = early successional forest; F = oak-hickory forest; G = bottomland hardwoods; H = conifer plantations.

WC and NO areas, respectively, reached 2 years of age and were potential breeders. From a hypothetical 100 males at birth, 14%, 16%, and 18% would still be alive at age 5 for the NO, EC, and WC areas, respectively, based on the average survival rates of sedentary marked males (Table 9). These survival rates are higher than those indicated from harvested deer in Illinois, where an average of only 13% and 18% of the antlered harvest was  $\geq 3$  years old when killed during 1985–1988 in the NO-EC and WC regions, respectively. This age discrepancy may have been the result of mis-aging of older deer into younger age classes by inexperienced agers at check stations (Illinois uses university students with minimal training as deer checkers, and annual changes in personnel are frequent). We also marked deer on or adjacent to refuges present on each study area, and although refuges exist throughout Illinois on un hunted farmland, our refuges may have offered marked males some extra protection compared with males on more heavily hunted ranges.

## GENETIC VARIATION

Reintroductions of deer into east-central Illinois date from the late 1940s, or about 13–15 generations ago (assuming 2.5–3 years/generation, Karlin et al. 1989). The origin of this stock is not well defined. Deer reintroduced into east-central Illinois were from southern Illinois, but the origin of the southern Illinois stock was mainly from northern sources (Pietsch 1954). Based upon current deer dispersal behavior, it is likely that these reintroductions were augmented by immigrants from existing populations in west-central and southwestern Illinois, sites also originally stocked by a mix of deer of northern origins. Oral histories of older residents of the NO and EC study areas indicate that deer dispersals and/or migrations from wooded refuges used in winter were common from the earliest years of reintroduction. These dispersals likely resulted in a considerable mix of genetic material during each generation (Pietsch 1954).

Allele frequencies (Table 11) and measures of genetic variability (Table 12) indicate high heterozygosity



among our samples of yearling males from east-central Illinois. Analysis of allelic frequencies indicated that three loci (6PGDH, EST-2, and GPDH) accounted for most of the genetic variability among groups (Table 13). However, positive  $F(IT)$  and  $F(IS)$  mean values indicated more homozygous individuals than expected from Hardy-Weinberg equilibrium (Table 12). There were significant  $F(ST)$  values for the enzymes EST-2 and GPDH, indicating a significant differentiation among populations at these two loci. Overall, 5.3% ( $F(ST) = 0.053$ ) of the total genetic variability ( $F(ST)$  averaged across all loci) is attributable to differences among sampled sites.

A cluster analysis determined by an unweighted pair group method (Swofford and Sealander 1981) showed overall genetic similarity among adjacent watersheds and counties (Figure 2). The modified Roger's distance indicated that similarities with deer from Piatt County were greatest for samples from the Champaign-Sangamon watershed and McLean-Mackinaw, followed by all three Macon areas (North, South, Lake) and McLean-Kickapoo. The Cavalli-Sforza and Edwards chord distance provided similar groupings and indicated the deer in Macon-South and Macon-Lake to be most similar, followed by McLean-Mackinaw compared with McLean-Kickapoo, the three Macon sites together, and Champaign-Sangamon compared with deer in Piatt County. Of interest was the segregation of samples from the Vermilion River in Champaign County, which drains eastward into the Wabash River, from the remaining watersheds draining west or southwest into the Sangamon River or directly into the Illinois River (Figure 2). Marked yearling males were known to have dispersed from the EC area in Piatt County to all but two of the sites used in this analysis, Macon-South and Champaign-Vermilion. Among deer of both sexes dispersing from the EC area between 1980 and 1985, 24 marked deer dispersed to the Champaign-Sangamon area, five remained in Piatt County, 10 settled in Macon-North and five in Macon-Lake, and five dispersed to McLean-Kickapoo, one to McLean-Sugar Creek, and one to McLean-Mackinaw.

Wright (1978) developed a model to determine the distance that dispersers must travel to reach a new breeding subpopulation. He considered an area that included 86% of the parents of individuals based on the standard deviation of normally distributed dispersal distances to define the radius of a subpopulation.

Because dispersal data are usually kurtotic, Nelson (1993) used as a radius the distance from birth sites within which 86% of individuals breed. Our natal dispersal distances (including nondispersers = 0 distance) averaged 23 km ( $SD = 19$ ,  $N = 23$ ) in northern Illinois, 16 km ( $SD = 18$ ,  $N = 44$ ) in west-central Illinois, and 29 km ( $SD = 25$ ,  $N = 91$ ) in east-central Illinois. The 86th percentile distances for these males were 43 km, 25 km, and 28 km for the NO, WC, and EC areas, respectively. Three males on the NO area, six on the WC area, and 13 on the EC area moved beyond the 86th percentile distance and became potential breeders in new subpopulations. However, only 0/3 (NO), 3/6 (WC), and 4/13 (EC) of these males survived to at least age 2 years, the likely breeding age in Illinois.

Several studies have demonstrated a positive association between genetic heterozygosity and several life history traits (fetal growth rate, maternal and paternal weight, the number of does with more than two fetuses, and antler points) (Smith et al. 1982, Johns et al. 1977, Cothran et al. 1985). Both the number of yearling male antler points (range 5.9 [Piatt] to 6.9 [Macon]) and antler beam diameters (range 23.8 mm [Macon] to 25.0 mm [Champaign]) were similar among sample sites ( $P > 0.05$ ).

## DISCUSSION

For male white-tailed deer in Illinois, hunting is the only important source of mortality currently affecting their population dynamics. Yearlings are more vulnerable to hunting than are older males because they generally are socially subordinate to older males and to their female relatives (Ozoga and Verme 1985), and they move through strange habitats during the hunting season. Fall-dispersing yearlings appear to be particularly vulnerable to hunting mortality when occupying these transient ranges (Roseberry and Woolf 1988, this paper). Annual mortality of yearlings in Illinois averages at least about 30–35% for sedentary males (with at least some refuge protection) and 45–50% for dispersing males. Older males average 30–35% annual mortality throughout the state. High harvest rates for antlered males have little impact on the deer herd size in Illinois, as compared with the harvest levels for antlerless deer (Nixon and

Table 11. Allele frequencies of nine variable loci for yearling male white-tailed deer sampled from four counties in east-central Illinois.

Locus	Population (N) <sup>a</sup>								
	1 (25)	2 (7)	3 (16)	4 (9)	5 (8)	6 (14)	7 (24)	8 (6)	9 (29)
6PGDH									
1	.040	.000	.000	.000	.000	.000	.000	.000	.000
2	.960	1.000	1.000	1.000	1.000	1.000	.979	1.000	1.000
3	.000	.000	.000	.000	.000	.000	.021	.000	.000
AAT-A									
1	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
AAT-M									
1	.060	.214	.031	.111	.063	.036	.083	.000	.000
2	.940	.786	.969	.889	.938	.964	.917	1.000	1.000
MPI-1									
1	.500	.286	.469	.389	.500	.571	.583	.667	.431
2	.500	.714	.531	.611	.500	.429	.417	.333	.569
EST-1									
1	.880	.714	.813	.944	.813	.821	.750	.667	.724
2	.120	.286	.188	.056	.188	.179	.250	.333	.276
EST-2									
1	.060	.000	.031	.056	.063	.071	.021	.000	.052
2	.800	.929	.531	.667	.500	.821	.813	.917	.810
3	.140	.071	.438	.278	.438	.107	.167	.083	.138
GPDH									
1	.820	.643	.688	.722	.875	.929	.729	.917	.759
2	.180	.357	.313	.278	.125	.071	.271	.083	.241
ME-1									
1	1.000	1.000	1.000	.944	.938	.964	.896	.917	.966
2	.000	.000	.000	.056	.063	.036	.104	.083	.034
ME-2									
1	.740	.714	.813	.722	.688	.857	.792	.833	.707
2	.260	.286	.188	.278	.313	.143	.208	.167	.293

<sup>a</sup> 1 = Champaign-Sangamon, 2 = Champaign-Vermilion, 3 = Macon-North, 4 = Macon-South, 5 = Macon-Lake, 6 = McLean-Mackinaw, 7 = McLean-Kickapoo, 8 = McLean-Sugar Creek, 9 = Piatt County.

Table 12. Levels of genetic variability among yearling male white-tailed deer sampled from four counties in east-central Illinois.

County	Watershed	Hardy-Weinberg Mean $\pm$ SE	Alleles per locus	Proportion polymorphic <sup>a</sup>	No. deer
Champaign	Sangamon	0.217 $\pm$ 0.061	1.89	0.667	25
	Vermilion	0.258 $\pm$ 0.073	1.67	0.667	7
Macon	North	0.244 $\pm$ 0.077	1.78	0.556	16
	South	0.254 $\pm$ 0.070	1.89	0.778	9
	Lake	0.266 $\pm$ 0.075	1.89	0.778	8
McLean	Mackinaw	0.185 $\pm$ 0.057	1.89	0.556	14
	Kickapoo	0.258 $\pm$ 0.057	2.00	0.778	24
	Sugar Creek	0.197 $\pm$ 0.064	1.67	0.667	6
Piatt	Sangamon	0.233 $\pm$ 0.070	1.78	0.556	29

<sup>a</sup> A locus is considered polymorphic if the frequency of the most common allele is  $\leq$  0.95.

Table 13. Wright's F-statistics for each locus from a sample of yearling white-tailed deer collected in four counties of east-central Illinois.

Locus	F(IS)	F(IT)	F(ST)
6PGDH	-0.033	-0.007	0.26
AAT-M	-0.064	-0.003	0.057
MPI-1	-0.095	-0.049	0.041
EST-1	0.157	0.189	0.038
EST-2	0.159	0.253	0.112 **
GPDH	0.174	0.229	0.067 *
ME-1	0.144	0.172	0.033
ME-2	0.108	0.124	0.018
Mean	0.076	0.125	0.053

\*  $P < 0.05$

\*\*  $P < 0.01$

Hansen 1986). Simulation modeling of the Illinois deer herd under various levels of male harvest indicates that harvests must approach 65% of yearling males and 55% of older males for subsequent numbers of older males to decline.

Because male survival is less than that of females, sex ratios favor females following age 18 months in Illinois (Nixon et al. 1991), and this tendency increases as deer grow older, with females constituting 70–80% of deer  $\geq$  4 years old.

Hunting could be either a compensatory or a noncompensatory type of mortality in whitetails depending on population status in relation to carrying capacity

(McCullough 1992). For marked yearlings, nonhunting mortality was somewhat lower for sedentary (0.06) than dispersing (0.09) males but was too low to indicate whether hunting mortality is additive or compensatory at current population levels in Illinois. Density-dependent mortality factors such as severe winter weather or nutritional deprivation are not currently important sources of mortality among males in Illinois. This is partially a function of the near absence of males  $>$  5 years old in these populations. Males  $\geq$  5 years old were rarely reported at hunter check stations or captured on our study areas. Thus, our mortality rates were derived from marked samples of males in or approaching their prime years. Mackie et al. (1990) found that density-dependent compensation of survival and/or recruitment rates did not occur among mule and white-tailed deer populations in Montana. Most free-ranging deer populations do not occupy stable environments, the situation necessary to meet the assumptions of current population regulation theory (Mackie et al. 1990), and this is particularly true for deer in the highly fragmented landscapes of the midwestern United States. Connally (1981) felt that hunting was noncompensatory mortality in mule deer (*Odocoileus hemionus*) populations below range carrying capacity, the situation in much of Illinois at present.

Male ungulates have a shorter average life span than females (McCullough 1979, Clutton-Brock et al. 1982, Dusek et al. 1989) because of the stresses associated with breeding activities and higher losses to predators (human and natural) compared with females (Hornocker 1970,

Pimlott et al. 1969, Mech and Frenzel 1971). Dusek et al. (1992) reported a similar conclusion for adult whitetails in Montana, and experimental evidence suggests that density effects in ungulates are expressed as changes in juvenile, not adult, survival (Bartmann et al. 1992, Skogland 1985).

Dominance and breeding success in males are affected by antler size and body weight (Townsend and Bailey 1981, Fudge et al. 1992, Miller et al. 1987). We were unable to measure breeding success (as number of live births and rearing success of offspring) among our marked males. Based upon our observations, breeding success among yearlings appeared to be low, but observations indicated that 2-year-old males were frequently successful breeders on our study areas. However, the combination of increasing deer numbers and the compressed nature of the female breeding period may be providing yearlings with an enhanced opportunity to breed in Illinois. Tending of individual does approaching estrus by mature males may take up so much time during the short breeding season that yearling males may successfully court and breed females, although such behavior was not common on our study areas.

### *DISPERSAL BEHAVIOR*

Historically, seasonal dispersals and migrations evolved as adaptive responses by white-tailed deer to efficient predators, variable climates, and dynamic vegetational patterns in North America after the retreat of the ice sheets. Activities of both aboriginal humans and European settlers increased the opportunities for deer to exploit many new and dynamic situations as the landscape was changed from wilderness to a fragmented landscape offering abundant forage and sufficient cover. Once exploitation of deer by humans was controlled, these movement behaviors allowed deer to adapt fairly easily throughout their continental range to the intensively farmed and fragmented landscapes created by human activities.

Behavioral differences between the sexes begin as early as four weeks postpartum, when males begin to move about more frequently and farther than females (Schwede et al. 1992). Male fawns are also more independent of their mothers earlier and show more curiosity

about other deer than do females, a means of preparing males for interactions with strangers and unfamiliar areas when dispersing (Schwede and Hendrichs 1989). From one-half to three-fourths of the males reaching 10 months of age in Illinois disperse prior to reaching breeding age, a behavior typical of the male whitetail throughout its continental range (Holzenbein and Marchinton 1992, Nelson and Mech 1984, Kammermeyer and Marchinton 1976). Male fawns on more northern ranges, where winter yarding behavior is necessary for survival, learn a winter-summer migration pattern from their older relatives and tend to use these ranges throughout life (Nelson and Mech 1981, Teirson et al. 1985). In the fragmented landscapes of the Midwest, however, where winter conditions are more benign, most males disperse to new postnatal ranges without kin support (except siblings). At present we do not know how dispersing deer select a new range, whether landscape features, social factors (aggression by resident adults, particularly females), or internal factors such as fatigue or hunger (Nelson and Mech 1992) stop a dispersal movement. Once home ranges are selected and dispersal movements stop, males remain close to the new site (within 3–5 km) throughout their remaining life. Breeding opportunity for surviving immigrant males is likely enhanced on hunted sites, at least at age 2, because the average life span of males on these sites is < 3 years (Nixon et al. 1991). However, dispersal behavior carries an increased risk of dying, with risk during both spring (highway collisions) and fall (hunting) being highest during the actual dispersal movement, as males search unfamiliar landscapes for permanent homes. The few dispersing males that succeed in surviving to breeding age may raise overall reproductive success of dispersers above that of nondispersers and may have thus led to the evolution of dispersal behavior by individual selection (McCullough 1979).

Whether external or internal stimuli are responsible for initiating dispersal movements is not well defined in white-tailed deer (Nelson and Mech 1992, Nixon et al. 1991). The external impetus for initiating dispersal behavior in yearlings during both spring and fall is more likely to be resident female aggression than aggression from adult males. We base this assumption on several arguments. First, in late spring and early summer when most male dispersal occurs in Illinois (Table 6), adult males are segregated spatially from most yearling males

(Nixon et al. 1991, McCullough et al. 1989), and yearling male-female aggressive interactions are common (Holzenbein and Marchinton 1992) (Figure 4). Second, Ozoga and Verme (1985) observed yearling dispersal in the fall in the absence of adult males. Yearlings are frequently subordinate to their female relatives (Ozoga and Verme 1985, this study), and nearly all the nondispersing yearling males on our study areas left their natal ranges in the fall. Fall movements also prevent incestuous matings (Holzenbein and Marchinton 1992), with most breeding groups composed of related females and unrelated males (Teirson et al. 1985). Third, interactions of yearlings with older males are most prevalent on a continuing basis (as opposed to the short-term interactions observed during the breeding period) during postbreeding, yet dispersals did not occur at this time. Increased interactions among males at this time may be adaptive, reducing the risk of serious injury when antlers are loose or absent and new social hierarchies are forming among the survivors of the breeding period. For example, red deer males showed more aggressive threats in winter after antlers were cast than in summer and fall (Clutton-Brock et al. 1982). Dusek et al. (1989) also observed that yearling male dispersal behavior may have resulted from social interactions with related females and not older males.

In east-central Illinois, birth order and body condition (as measured by chest girth) did not affect male dispersal rates (Nixon et al. 1991). Males born near the boundary of the study area, where there was less permanent cover, dispersed at higher rates ( $P < 0.05$ ) than males born near the center, suggesting that the amount of permanent cover (excluding row crops) may affect dispersal behavior.

### **SEXUAL SEGREGATION**

Sexual segregation is common among ungulates outside the breeding season (Clutton-Brock et al. 1982, McCullough et al. 1989, Main and Coblentz 1990). In Illinois, adult males separate spatially from females and yearling males each spring and summer. These movements may commence as early as February and as late as July. About half of our marked males moved to their summer range prior to the onset of antlerogenesis and

half after antler growth was well under way (one-half to three-fourths grown).

Of the nine hypotheses and associated behavioral adaptations proposed to explain sexual segregation in ungulates by Miquelle et al. (1992:12), two may characterize some of the behaviors observed in male whitetails during the prebreeding period in Illinois. Hypothesis 1 suggests that spring and summer segregation occurs because females with young select habitats to reduce predation on neonates and males select habitats to maximize nutrient intake. Five of six predictions associated with this hypothesis appear to be true in Illinois (females with young segregate from males, females should be solitary for some of the postpartum period, female sociality should increase as neonates mature or die and male sociality should remain constant, females with young should select forested habitats more than males, and males should select habitats offering high forage biomass). One prediction, that barren females and males should select similar summer habitats, does not seem to occur in Illinois. Barren (nonbreeding) females, few in number in EC and NO Illinois, more abundant in WC Illinois, were radio located on all three study areas in habitats favored by females with young and not on ranges favored by adult males. These barren females began associating with their older female relatives as soon as these breeders would permit the association after parturition.

Hypothesis 2 suggests that males are segregated from females in summer because they select habitats that provide opportunities for social interactions, that reduce the risk of antler damage, and that provide cover from predators. In Illinois, only two of four associated predictions seem to occur (segregation occurs during both the parturition and postpartum periods and males should select, relative to females, more open habitats). Two predictions, that all males segregate from females and that social interactions among males should be more common in summer than in winter, were not observed in Illinois. Yearling males remained either within or between home ranges of adult females in summer and interacted with females on a daily basis. Adult males were more likely to be alone in summer than in winter on our study areas even though males  $> 2$  years old were abundant on all study areas in summer (Figure 4). In addition, about half our radio-marked males did not

move to a summer range until antler growth was well under way.

Because of differences in habitat availability between winter and summer in Illinois, we cannot assess the applicability of the remaining seven hypotheses proposed by Miquelle et al. (1992) to explain winter segregation of the sexes. Males are forced to remain with females in limited upland cover during winter because habitats favored by males in summer are unacceptable or unavailable in winter (crop fields are tilled and bottom-land forests are often flooded or ice-covered). For sexual segregation to occur, landscapes must be heterogeneous and contain a mix of those elements of importance to both sexes (Miquelle et al. 1992). In winter, when crop fields are fallow, landscapes in Illinois tend more toward homogeneity.

The relationships between the sexes in winter were not always clear to us. We observed males close to females and fawns in both feeding and resting groups during daylight hours. These groupings often were stable in winter, at least on feeding sites, as marked members of both sexes were often observed together for several weeks in winter on both the EC and NO study areas. Mature males were often seen intermixed with females (not grouped along the edges) of these feeding groups. Males usually associated with one or more other males in fraternal groupings (Linsdale and Tomich 1953, Hirth 1977) within these larger groups of mixed sex. Intermingling of maternal and all-male groups was reported as common in southern Illinois in winter but was considered "temporary" because the deer did not move together as a herd (Hawkins and Klimstra 1970). Deer drives and aerial counts on our study areas in winter indicated both sexes were close together during daylight hours (bed association unknown in most cases; when observed, all were running together).

Association with females during late winter also allowed males to breed those females that entered estrus late, either because of an unsuccessful conception during one or more estrous periods in yearlings or older females or because of a delayed first estrus in fawn females. We believe late estrus occurred on all our study areas each year, based on annual observations of small spotted fawns on these areas during September and October.

Bouckhout (1972) observed mature male mule deer associating in large herds with females in winter on the

Canadian prairies. In Alabama, mixed-sex groups of white-tailed deer varied from 7% of observations during postbreeding to 15% during prebreeding (Ivey and Causey 1988). Hirth (1977) and Dasmann and Taber (1956) observed mixed groups of whitetails and mule deer, respectively, throughout the year, but these were considered temporary associations, formed to exploit forage or limited available cover.

Hirth (1977) found that males associated more with females on the more open Welder area in southern Texas than on the more wooded George Reserve area in Michigan. This grouping behavior on more open sites may be an adaptation for predator avoidance (Mech 1984) as well as for optimizing feeding efficiency (Hirth 1977), and this behavior was observed frequently on all three study areas in Illinois. Groups of 40–80 deer of both sexes and composed of several family and buck groups fed, traveled, and bedded together in winter on these generally open sites.

Winter segregation of the sexes may, however, occur in whitetails where landscapes remain relatively stable throughout the year. Kolenosky (1972) and Laramie and White (1964) found that males tended to remain apart from does and fawns in winter yards in Ontario and New Hampshire, respectively.

Yearling males may pay a price for their habitat selection through increased incidence of antler damage while in velvet, but antler configuration and condition may be less important than body size to social position among yearlings (Townsend and Bailey 1981). Verme (1988) also noted that yearling antlers were much more likely to be malformed compared with adult antlers in Michigan. Yearling aggression seems to pose less of a threat of serious injury among combatants than aggression among adult males.

Even in the relatively benign climate of Illinois, with abundant and accessible winter foods, male whitetails must replenish body resources depleted by breeding activities and environmental conditions. Although their condition is generally not life-threatening, our observations of marked males (> 2 years old) in Illinois indicate a marked deterioration in body condition between the beginning of breeding and its conclusion. Adult males compete with females and younger males for forage gleaned from crop fields and woodlots during late winter and early spring. Beginning in late spring on into

summer, they move to bottomland forests and row crop fields to continue to feed on nutritious diets free from competition with females. Bottomland forests are frequently devoid of understory cover because of frequent flooding and are probably avoided by females because they provide poor cover for fawns (Nixon et al. 1992). Females also avoid deep penetration into crop fields because parturition and nursing demands require them to remain close to the permanent cover selected for fawn rearing before crops are mature enough to hide neonates. Male ungulates appear to be less adaptable to food competition than females (Clutton-Brock et al. 1982, Clutton-Brock et al. 1987), and their growth patterns appear to be more habitat-specific than the growth patterns of females (Leberg et al. 1992). Leberg and Smith (1993) found there was no threshold for density-dependent effects on year-to-year growth rates of adult males (female growth was not related to density) within the Savanna River site in South Carolina. These authors concluded that growth patterns of adult males were more responsive to density effects either because they were less competitive than females for available nutrition or that the energetic costs of male competition for mates (specifically the almost total depletion of fat reserves at the conclusion of breeding each year) affected subsequent growth regardless of deer density. Thus, males may have to separate from females to maximize intake of quality forage during the prebreeding period when growth and antlerogenesis demand quality nutrients. Most females in Illinois nurse one or more fawns each summer, and selection of a site for birthing, rearing, and protecting fawns may be more important than maximizing foraging opportunities (Lent 1974). Clutton-Brock et al. (1987) concluded that red deer males avoided areas supporting low forage biomass and could be excluded from areas as a result of passive competition for forage with females. LaGory et al. (1991) observed more males than females feeding on areas with higher quality forage on Ossabaw Island, Georgia, a site offering both sexes generally very low forage availability and quality.

McCullough (1979) found that recruitment for the enclosed deer population on the George Reserve area was negatively correlated with female but not male numbers, with competition for resources more direct among females. Because intersex competition is reduced by sexual segregation, female competition seems to drive

density-dependent effects such as productivity and recruitment (McCullough et al. 1989).

Pronounced differences in feeding behavior exist in many ungulates, including red deer (Clutton-Brock et al. 1987), fallow deer (*Dama dama*) (Putman et al. 1993), sitka deer (*Cervus nippon*) (Takatsuki 1980), and whitetails (McCullough 1979). These dietary differences are most pronounced in dimorphic species, with the larger males feeding on different plant species or concentrating on bulk feeding at the expense of forage quality (Staines et al. 1982, Clutton-Brock et al. 1982).

In summer in Illinois, we believe adult male whitetails seek to maximize nutrient intake by exploiting landscapes avoided by other sex-age classes. There is no evidence that these landscapes in Illinois provide a less nutritious diet for males than is available to females, but such sites are free of female competition. Miquelle et al. (1992) calls this behavior ecological dimorphism, where females seek to reduce risk of predation on neonates and males seek to maximize nutrient intake. In EC Illinois, females most often selected successional upland forest (< 60 years) for parturition (Nixon et al. 1992). Thus, male and female survival strategies are based on different selective pressures; females must successfully raise young and males must grow a large body and antlers to compete successfully for females (Townsend and Bailey 1981, Clutton-Brock et al. 1982). Until crops are high enough to protect them, females must remain close to a forested area used to hide neonates. Once these parturition sites are selected, females then remain close to them throughout the summer, avoiding the deep penetration into crop fields that typically characterizes the behavior of mature males. Although we do not believe these habitats are specifically selected to protect growing antlers from damage, they are more open than habitats used in fall and winter and usually result in damage-free antler growth (Nixon et al. 1991).

## GENETIC VARIATION

Most males do not disperse beyond about 70 km in Illinois (Figure 5); the 95th percentile dispersal distance ranged between +0 and 50 km in NO and WC Illinois and between 60 and 70 km in EC Illinois. These distances exceed those documented for dispersing deer in

Minnesota, New York, and southern Illinois, and they are likely a reflection of deer adjustment to the fragmented landscapes of Illinois (Nelson 1993, Hawkins and Klimstra 1970, Teirson et al. 1985).

Given the high rate of dispersal for both sexes in EC Illinois, it is not surprising that gene flow or "genetic migration" (Chepko-Sade and Shields 1987) is extensive among yearling male subpopulations located along the major watersheds in EC Illinois. Only the Vermilion River watershed in Champaign County (Figure 2) appeared to represent a distinct breeding subpopulation of deer. This area lies about 72 km from the EC area, well beyond the average dispersal distance of this population and farther than the other watersheds examined during the study (Figure 2). Deer breed and winter along each of the watersheds examined, and gene flow should homogenize allele frequencies among these sites. Unlike the delayed breeding of females characteristic of deer on more northern ranges (Nelson 1993, Verme and Ozoga 1987), precocious females in Illinois usually breed on their natal range at 6–8 months old. Thus, dispersing females do not contribute genetically on their new range until age 18 months. Breeding usually occurs on the summer ranges, based on the timing of return migrations of females to a wintering site (occurring both during and after peak breeding dates [Nixon et al. 1991]) in EC and NO Illinois. This arrangement allows for extensive genetic mixing of deer from separate wintering sites on the summer ranges.

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