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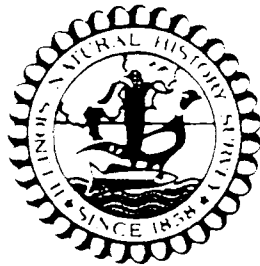
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Cooperative Forest Wildlife Research
Illinois Deer Investigations

W-87-R-16

Annual Job Progress Report

by

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Illinois Natural History Survey

1 July 1993 through 30 June 1994

State: Illinois
Project No: W-87-R-16

Project Type: Research

Project Title: Cooperative Forest Wildlife Research

Sub-project: Illinois Deer Investigations

Period Covered: 1 July 1993 through 30 June 1994

Study No. 1; Title: Population dynamics and ecology of white-tailed deer in Illinois.

Study Objectives:
1. To access the amount, distribution, and quality of white-tailed deer habitat in Illinois.

2. To relate spatial aspects of deer habitat to other important attributes such as hunter access, proximity to human habitation, and agricultural patterns.

3. To complete ongoing studies describing current natality rates, fawn recruitment, seasonal movements, and seasonal and annual mortality rates for previously marked deer in west-central and northern Illinois.

4. To develop interactive, menue driven, portable computer models and software packages to facilitate analysis of harvest data, predict effects of alternative harvest regimes, and help select appropriate strategies to achieve specific goals and objectives.

Job No. A; Title: Habitat inventory, classification, and analysis.
Objectives: (1) To investigate alternative techniques for classifying white-tailed deer habitat from remote sensing data; (2) To use these techniques and data sources to inventory deer habitat in Illinois; (3) To describe the habitat characteristics of sites selected by dispersing deer

and to compare these characteristics with the habitats available within the boundaries of known dispersals from marking sites in northern, west-central, and east-central Illinois; (4) To develop HSI models for the purpose of assessing the relative quality of deer habitat using digital land use classifications from remotely sensed data and; (5) To integrate information relating to spatial distribution of habitat with other pertinent attributes relating to hunter success, human habitation, and agricultural patterns.

(a) Activity: Job and reporting assigned to Dr. A. Woolf and J. Roseberry, Southern Illinois University, Carbondale.

(b) Target date of Achievement: 1 September 1995.

(c) Date of Accomplishment: On schedule.

(d) Significant Deviations: None.

(e) Remarks: None.

(f) Recommendations: None.

(g) INHS Costs: Federal--$9,035; State--$3,012; Total--$12,047.

Job No. B; Title: Deer ecology and life history in west-central and northern Illinois.

This report constitutes the final report for this job and includes all written material generated to date by the results of this study. Any additional scientific and popular reports generated by the results of this study will be reported as part of Job No. D, Analysis and Reporting, under the W-87-R-17 segment of the study.

Objectives: (1) To determine age specific natality and seasonal and annual survival rates of deer marked in west-central and northern Illinois; (2) To determine seasonal movement patterns and habitat selection of marked deer in west-central and northern Illinois; (3) To integrate these

natality and survival data collected from this study within new population models of the Illinois deer herd.

(a) Activity:

Study areas

All study areas 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 winters, and refuge from firearm hunters. These core areas were surrounded by privately owned farms dominated by row crops. These farms provided relatively sparse winter cover and were usually open to archery and firearm hunting.

The 1,648-ha northern area (NOA) 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. The study area consisted of 59% row crops, 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. Deer densities averaged 10-12 per km^2 in late winter during our study.

The 5,942-ha west-central area (WCA) 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 study area consisted of 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) as more public land was opened to controlled firearm hunting. Late winter deer densities varied from 12-25 deer per km^2 over the study area, averaging about 13 per km^2 on the state park and up to 25 per km^2 on the private farms.

For comparative purposes, we also include data collected 1980-85 on the Piatt County Study Area, east-central Illinois. This 2,953-ha area consisted of 64% row crops and 36% forest (22% upland and 14% bottomland forest). There was a 600-ha refuge from all hunting in the

center of this area. Deer numbers averaged 4-6 per km^2 in late winter during our study (see Nixon et al. 1991 for more complete description of the Piatt County Study Area).

Capture and marking

Deer were livetrapped and marked using rocket propelled nets on the WCA (N = 230) and NOA (N = 122) between 1989 and 1993 (see APPENDIX 1 & 2 for a complete listing of all captures). All deer were aged as fawn, yearling, or adult using tooth replacement and wear, and were marked with numbered cattle-type plastic ear tags. A total of 60 deer (8 males, 52 females) and 32 deer (5 males, 27 females) were radio marked on the WC and NO areas, respectively. Females without radios were marked with plastic collars bearing fluorescent numbers.

Radio marked deer were located on the WCA using 2 truck-mounted, 8-element yagi antennas aligned in a null configuration. Each radio location was derived from 2 to 5 bearings taken from fixed locations scattered over the study area. Accuracy was established using transmitters placed in known locations throughout the area. Locations produced by radio fixes were validated using the computer program LOCATE 11 (Nams 1990). The small size and scattered nature of cover on the NO Illinois study area enabled deer to be radio located within the standard 1-ha grid used for locating deer on our study areas using only a single antenna, a close approach, and direct observation.

Natality

On the WCA only, blood samples were collected from all does captured in 1990 and 1991 (68 does) and for fawn does only in 1992 and 1993 (25 does). Progesterone levels indicated that breeding activity among fawn does was low all 4 years and apparently declining (Table 1). Progesterone levels also indicated that all yearling and older does (N = 40) were pregnant when bled in 1990 and 1991.

Repeated observations of marked does allowed us to access annual breeding rates and fawn production by age class for marked does on both study areas. Breeding rates for fawn does differed among sites, from an average of 21% for west-central fawns to 70% for east-central fawn does (G = 36.6, P<0.001). As demonstrated by progesterone levels, observed

breeding rates of fawns declined as the study progressed, from 50% (N = 4) in 1989 to 6% (N = 17) in 1992 (Table 2). Breeding rates of yearling and adult does did not differ among areas (P>0.05) (Table 2).

As described in a previous report(final report W-87-R-12,13,14), we do not believe natality rates found among fawn does on the WC study areas are typical of the WC region (Nixon et al. 1992). Grubaugh et al. (1988) found that 85% of fawns killed in highway accidents (N = 20) in west-central Illinois were pregnant. Their sample size was not large and it is likely their estimate of fawn breeding is too high for the region as a whole because this rate exceeds that of fawn does in both northern and east-central Illinois, where nutrition is optimum. It is true that dressed body weights of fawn does (29.6 kg) shot in west-central Illinois in 1991 were significantly lower (F = 6.96, 1,82 df, P<0.01) than doe fawn dressed weights in east-central Illinois (31.0 kg). Average weights from both areas were below the 36 kg body weight thought to be necessary for estrous to occur in fawn does (Verme and Ullrey 1984), yet nearly 70% of the doe fawns attain estrous at 6-7 months old in east-central Illinois. Blood protein levels were actually higher (P<0.05) in west-central Illinois fawn does (mean = 6.0 ± 0.39 gm/dl) compared to east-central fawn does (mean = 5.1 ± 0.36 gm/dl) in the fall of 1991. We believe the reduced incidence of fawn breeding on our WC study area to be a physiological response to the higher number of yearling and older females present on this area compared to our other study areas. Average deer densities in winter were 3-4 times higher on the WCA compared with the ECA. Verme (1987) presented evidence of reduced breeding among doe fawns as deer numbers have increased in Ohio and Michigan, due to social domination of the fawns by their older female relatives. As noted in a previous report (Nixon et al. 1992), reductions in the incidence of fawn breeding have also been documented within several other refuge protected herds in Illinois.

We were able to estimate age specific fawn production and survival for each year based upon repeated observations of marked known-aged does and their fawns on each study area. Fawn recruitment to 1 year old was highest among does in east-central Illinois and lowest for does from west-central Illinois (Table 3). Adult breeders contributed most to fawn production each year, as a result of their greater numbers in the population and their higher individual production. The number of fawns

seen per marked doe was significantly lower for west-central Illinois yearling (F = 8.09, 2,117 df, P<0.01) and adult (F = 33.6, 2,320 df, P<0.001) does compared with females in northern and east-central Illinois (Table 3). This reduction is not due to a reduced incidence of breeding among yearlings or adult does, but an apparent reduction in the number of live births per female as postpartum fawn survival appears to be comparable among regions (Table 3). Based on these data, there should be an average of 1.09, 1.10, and 1.35 fawns per doe present between January and late May on the NO, WC, and EC areas, respectively. These are the fawns that recruit into the yearling population each June.

Postpartum fawn losses were significantly higher for fawns born to 2-year old does 24%, (G = 5.6, 4 df, P<0.025) compared to those born to younger or older mothers. Surprisingly, primaparous yearling mothers experienced the lowest loss of fawns (<10%) of the age classes examined. Older does (>3 years) lost an average of 15.8% of their fawns in the west-central area, 19.7% on the northern area, and 13.8% on the east-central area before age 1.

Preweaned fawn losses (<4 months old) were higher than postweaning losses on the west-central (preweaned fawn loss = 61%) and northern (67%) areas but were lower compared with postweaning losses on the east-central area (preweaned fawn loss = 21%) (G = 14.0, 2 df, P<0.01). Fawn losses before weaning were not significantly different (G = 2.4, 4 df, P>0.60) among age classes of does (yearlings = 25%, 2-year = 43%, 3-year = 46%, 4-year = 56%, and 5-year = 30%) but were different among years (G = 18.2, 7 df, P<0.02), ranging between 11 and 82% of the total annual fawn mortality.

The loss of 1 or more fawns was not indicative of a higher probability that a doe would loss fawns in subsequent years (X^2 = 0.01, 1 df, P>0.95). On the northern study area, 2 of 13 does lost fawns in consecutive years, 9 of 13 lost 1 or more fawns during 1 of the 3 years of study, and 2 does lost no fawns during the study. Of 33 does monitored more than 1 year on the east-central area, only 3 does lost fawns in consecutive years, 18 lost fawns in at least 1 year, and 12 does lost no fawns during the 6-year study. On the west-central area, 5 does lost fawns in consecutive years, 15 lost at least 1 fawn during 1 year, and 13 raised all their fawns to 1 year of age during the 3-year study.

Fawn deaths prior to weaning were likely the result of predation, nutritional failures early postpartum, or if the doe was <3 years old and socially subordinate, the inability to rescue fawns that strayed into parturition areas of older, more dominant females (Mech 1984, Verme 1969, Ozoga et al. 1982). Fawn deaths after weaning were almost entirely harvest-related or the result of highway accidents. Fawn deaths due to severe winter weather are almost unknown in Illinois (Nixon et al. 1991).

Daughters usually move farther away from their mother's parturition range at age 22-24 months to give birth and for the first time since birth must protect themselves and their offspring without kin support (Ozoga et al. 1982). Based on observations from all 3 study areas (N = 1,225), the frequency of association (number of times seen together / sum of all observations of both individuals [Hawkins and Klimstra 1970]) of mothers and daughters declined from 42% when daughters were yearlings to 24% when daughters were 2 years old (G = 44.0, 1 df, P<0.001). Year-to-year overlap of parturition ranges for the same doe increased from an average of 27 ± 3.9% (N = 15 does) between yearling and 2 years of age to an average of 43 ± 3.7% (N = 22) overlap of parturition ranges for does between 2 and 3 years old (F = 7.8, 1,35 df, P<0.01), as does settled on a permanent parturition range.

The higher mortality for fawns born to 2-year old mothers appears to relate more to social behaviors relating to loss of support by matriarchal does than to differences in habitat selection or in movement to areas where the hazard to fawns from hunting and highway accidents would be higher (see APPENDIX 3 for more discussion of maternal age and fawn survival).

Survival

Survival rates and cause specific mortality were calculated using the program MICROMORT (Heisey and Fuller 1985). All marked deer whose fate was known (>90% of all marked deer that survived capture) were used to determine survival. Seasonal and annual survival rates were compared among years and areas using a Z-statistic.

For purposes of analyzing annual survival patterns of both sexes, the year was divided into periods bounded by important behavioral or physiological changes that potentially affect survival. 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. During breeding (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 time. 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. The female year was divided into parturition and early postpartum (16 May-15 July), prebreeding (16 July-30 September), breeding (1 October-15 January), and postbreeding (16 January-15 May) periods.

Yearling females averaged lower annual survival ($P<0.05$) compared to adults each year of study (Tables 4 & 5). Adult females survived better ($P<0.05$) during 1992 on the NOA and on the WCA during 1993 (Table 5). Yearling females survived better than yearling males on the NOA, but not on the WCA. Adult females survived better ($P<0.01$) than adult males on both study areas. Hunting and associated wounding contributed most to annual mortality among females and yearlings were more vulnerable to both archery and firearm hunting and also to auto accidents compared to adult does (Tables 4 & 5). Both study areas showed higher annual survival ($P<0.05$) for both yearlings (averages were NO = 0.74; WC = 0.0.73) and adults (NO = 0.85; WC = 0.87) during 1990-92 compared with females marked during 1980-85 in east-central Illinois (averages were yearlings = 0.62; adults = 0.71) (Nixon et al. 1991). This difference was due to higher harvest related mortality of does in east-central Illinois. Annual survival was not significantly reduced ($P>0.10$) for dispersing females compared with females that remained as residents on either study area.

Male survival rates are reported in more detail in APPENDIX 4. For yearling males, seasonal and annual survival rates were calculated separately for males that dispersed and those that remained on or close to their natal range in EC, WC, and NO Illinois (APPENDIX 4, Table 7). Survival was high and similar ($P>0.10$) for males marked on all study areas during the prebreeding (>95%) and postbreeding (>81%) periods. Survival during the breeding period was reduced ($P<0.01$) for males dispersing from our WC and EC study areas, but was not different for males marked on the NO study area. Annual survival of dispersing males was significantly reduced

(P<0.02) compared to the annual survival of sedentary yearling males on all study areas (APPENDIX 4, Table 7).

More recent data available from the NOA have indicated that average annual adult male survival was overestimated as 0.87 in Table 8, Appendix 4. The corrected average annual survival of adult males marked on the NOA averaged 0.68 for 1990-93, close to annual averages reported in Appendix 4 for the WC (average = 0.66) and EC (0.65) areas.

Survival of males $\geq$2 years old was significantly better (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 yearling males on the WC study area and sedentary yearlings on all 3 areas (APPENDIX 4, Tables 7 & 8). Mature males were somewhat more vulnerable to firearm hunting than archery hunting, the reverse of yearling males (APPENDIX 4, Tables 7 & 8).

These data indicate that survival of both sexes is quite high in EC, WC, and NO Illinois. Yearling females averaged >70% and adult females >80% annual survival during 1990-93. Yearling males that remained on or close to their natal ranges averaged >65% annual survival while dispersing yearling males averaged better than 50% annual survival. Adult males ($\geq$2 years old) averaged about 65% survival per year during the study. Because hunting related deaths accounted for >90% of the annual mortality, current hunting pressures appear to be cropping about 20% of the adult females, 30% of the yearling females, 35-50% of the yearling males, and about 35% of the adult males. For males, current survival rates indicate that , for each 100 yearlings alive 1 October, <10 will reach the age of 5 years.

Our marking studies have allowed us to estimate the extent of deer deaths due to wounding by archery and firearm hunters. For archery hunters the ratio of wounding losses to legally reported deaths were: Yearling males = 8 wounded and killed for 28 legally reported (28.5%); Yearling females = 4 wounded for 8 reported taken (50%); Adult males = 5 wounded for 12 taken (42%); Adult females = 10 wounded for 12 reported killed (83%). The archery hunter ratios of wounded to legally taken deer would be about 3:1 for yearling males, 2:1 for yearling females, nearly 2:1 for adult males, and nearly 1:1 for adult females.

Firearm hunters wounded and lost a lower proportion of the deer hit by gunfire; Yearling males = 8 wounded and killed for 29 reported killed (28%); Yearling females = 5 wounded for 17 killed (29%); Adult males = 6

wounded for 27 killed (22%); Adult females = 9 wounded for 26 reported killed (35%). For firearm hunters a ratio of 1 wounded deer lost for 3 legally taken appears to hold for yearlings of both sexes and adult females. For adult males, the ratio falls to about 1 wounded for 4 legally taken, perhaps the result of a more intensive search by hunters for the large antlered adult males.

Dispersal

Dispersal behavior of both sexes was extensive on both study areas. The data summarizing male dispersal from our study areas is presented in APPENDIX 4, Pages 11-14, and will not be repeated here.

For females, dispersal behavior usually occurred in the spring at age 10-12 months and coincided with family breakup and the search for a parturition site if the fawn/yearling was pregnant or, if barren, a search for a site to minimize harassment from older females (Table 6). An average of 44% (15/34) marked yearling females dispersed from the NO study area and 22% (11/49) from the WC area (G = 3.36, P<0.10). Overall, male dispersal from these areas was significantly higher than female dispersal (G = 24.24, P<0.001).

Females marked on the NO study area dispersed an average of 38 ± 3.6 km (N = 15). All but 3 of these deer traveled east toward the metro-Chicago area, for no apparent reason as more forests were located south and west of the study area. Fourteen females dispersing from the WC area also averaged 38 ± 7.8 km and also tended to travel eastward (9 of 14). Proportionally more females dispersed from the ECA (50%) compared with the WCA (31%) or the NOA (42%) (Table 6). The proportion of female fawns dispersing from each area was not correlated (P>0.10) with the number of yearling and older females present on each area but may instead relate to the amount of permanent cover available in the spring before field crops mature and provide cover. Females need cover to protect fawns from predators and other deer and such cover was relatively scarce in northern and EC Illinois (<5% of the landscape). The reproductive state of the fawn (whether pregnant or barren in the spring) also did not influence dispersals from our study areas (P>0.05).

A few females dispersed from our study areas at age 22-23 months. On the ECA 9 of 43 (21%), on the WCA 3 of 19 (16%), and on the NOA 3 of

12 (25%) marked yearling females either migrated seasonally or dispersed away from the study areas. All these females were pregnant when they dispersed and may have moved to locate a parturition site away from their mother for either their first (if barren as fawn) or second pregnancy. Two-year old females usually separate from their mother for the parturition and early fawn rearing periods (Ozoga et al. 1982).

Yearling males were more likely to die during a dispersal movement than were yearling females because males often dispersed in the fall during the hunting season while females only dispersed in the spring. For yearling females marked on both study areas (N = 30), only 3 (10%) died during a dispersal. For yearling males, 12 died during dispersal (N = 50), with most of these deaths occurring in the fall from hunting related causes (10/12). Annual survival was similar (P>0.10) for females that dispersed and those that remained sedentary on or close to their natal ranges after family breakup.

The effects of orphaning on dispersal movements, local movements, and survival were examined for 14 females (13 fawns, 1 yearling), either accidentally or intentionally orphaned, and compared with similar statistics for 108 non-orphaned females. Dispersal rates were higher (P = 0.006) for female orphans than for non-orphans. Ten of 14 (71%) orphans dispersed in spring or early summer. In contrast, only 36 of 108 (33%) non-orphans dispersed away from their natal range. The results of this study are more extensively discussed in APPENDIX 3, " Emigration and Survival of Orphaned Female Deer in Illinois".

Local movements

Northern Illinois--Seasonal home ranges were calculated for radio marked deer on both study areas using computer programs HOME RANGE (Ackerman et al. 1990) and RANGES IV (Nams 1990). Seasonal core areas were determined for each deer with a minimum of 19-20 acceptable radio fixes using the Harmonic Mean Estimator (Boulanger and White 1990). Home ranges and other local movements of males are summarized in APPENDIX 4, Pages 6-9.

Core home range size of females in northern Illinois varied considerably throughout the year (F = 13.07, 3,99 df, P<0.01), being larger during the postbreeding season and smallest during the parturition period

(Table 7). The mean distance from the arithmetic center of activity to each radio fix (a measure of daily movement) summarized for all does each season also varied by season (F = 12.9, 3,99 df, P<0.01) in a similar fashion. Females were most active during postbreeding (516.5 ± 33.5 m) and least active during parturition and early postpartum (241.6 ± 14.3 m). The postbreeding period of midwinter-early spring for females is a time of stable social relationships, with related females associating together in clans and sharing the home ranges of the females in the group. Without the responsibilities of protecting and nurturing fawns, and the need to stabilize or gain weight to support a pregnancy 3-4 months into the gestation period, females are free to wander more freely than at other periods during the year. In contrast, females are restricted in movements during the parturition-early postpartum period, protecting neonates from predators and other deer.

West-central-- As demonstrated for does in northern Illinois, home range size varied (P<0.01) among seasons in west-central Illinois. Average parturition and prebreeding home ranges were nearly identical for the 2 regions (Table 7). Breeding status (whether pregnant or barren) did not influence home range size (P>0.05) during the parturition-early postpartum period although barren does did have somewhat larger ranges (barren = 31 ha; pregnant = 23 ha).

The west-central study area provided an opportunity to examine the importance of farm crops to deer in Illinois. One portion of the study area included Siloam Springs State Park, a forested area with few farm fields. Park does averaged larger ranges than does marked off the Park (Park = 46 ± 4 ha; Farmland = 32 ± 4 ha P<0.02). This difference may be attributed to the distances Park does had to travel to reach farm fields compared to farmland dwelling does. Park deer often bedded during the day in the Park forests and then traveled up to 1-2 km outside the Park to farm fields at night.

Analysis of variance for distances measured between arithmetic centers of activity (a measure of site fidelity between years for individual does) found no significant difference (P>0.05) among age classes (between 1 and 2, 2 and 3 etc.) or seasons. In general, these distances declined somewhat with age (for example, from an average of 188 ± 111 m between ages 1 and 2 years to 165 ± 176 m between ages 3

and 4 years for the parturition period) as does became more faithful to their home ranges.

Another measure of site fidelity involves measurement of the percent overlap of home ranges among seasons for individual does using the 100% harmonic mean calculation of home range size. Overlap differed among seasons (F = 8.01, 2,275 df, P<0.001) for all does and within seasons for related does (P<0.001) (Table 8). The postbreeding period exhibited the greatest overlap, a time of intermingling of both related and strange deer on localized feeding sites, and parturition the least overlap, when does are alone with their fawns. Among years, home range overlap differed for individual years for the breeding and postbreeding periods (P<0.04) (Table 8).

Ranges of barren yearling does overlapped more with relatives (78%, N = 14) than did ranges of pregnant adults (60%, N = 31). This difference was due to larger ranges of barren does during the parturition period compared to does with fawns (more likely to include more of the ranges of relatives), and the sharing of parturition ranges by mothers and daughters during parturition.

Habitat preference

Habitat preferences were compared for radio marked deer on each area. A 1-ha grid overlay of these areas was mapped into 1 of 7 (northern) or 1 of 6 (WC) vegetative types. Radio locations of each deer were placed within 1-ha grids overlaying the study areas and compared with the total home range (available habitat) encompassed by each deer during the life of the radio or deer. Habitat selections were compared with available habitat for each deer and tested for independence using chi-square analysis. 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. 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 yearling males selected oak-hickory forest and avoided row crops in summer, with other habitats used in accordance with abundance, a pattern similar to females.

During the breeding season in EC Illinois, yearling males selected both upland and bottomland forest and avoided crop fields , again areas favored by does and fawns in the fall. During postbreeding, yearlings avoided crop fields and selected upland successional forest (<60 years old) and bottomland forest where cover was abundant.

In late spring into summer, adult males on the EC and NO areas moved from postbreeding ranges shared with does, fawns, and yearling males to areas dominated by agricultural crops or bottomland forests. 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. For 6 adults on the ECA and 3 on the NOA, these movements averaged 1.2 and 0.65 km, respectively. Adult males often remained in crop fields for extended periods during summer. Without the constraints of fawn nurturing imposed on females, males were not required to make periodic returns to permanent cover. Of 8 adult males radio- tracked on the EC site, 5 averaged >70% of their summer ranges in row crops, mainly maturing corn. During fall breeding and winter postbreeding, males occupied habitats similar to those occupied by females.

In summer in Illinois, we believe adult male whitetails seek to maximize nutrient intake by exploiting landscapes avoided by other sex-age classes. Males are apparently 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 growth patterns of females (Leberg et al. 1992). There is no evidence that the landscapes selected by males in summer in Illinois provide a less nutritious diet than is available to females, but such sites are free of female competition. This segregation by habitat allows males to rapidly gain weight and develop large, damage free antlers and females to locate where there was less risk of predation to neonates. See APPENDIX 4, for further discussion of seasonal habitat selections among males.

Northern Illinois--On the northern area, only diurnal selection or avoidance of habitats (P<0.05) were determined for radio-marked females (N = 11) as little radio tracking occurred at night. For the parturition and early postpartum period, females selected restored prairie (5 of 11), successional forest (<60 years) (7 of 11), and oak-hickory forest (4 of 11)

and avoided row crops (7 of 11). For the prebreeding period, females also avoided row crops (7 of 11), selected successional forest (8 of 11), as well as prairie and oak-hickory forest (both 3 of 11). During the breeding and postbreeding periods, does selected oak-hickory forest (4 of 11), prairie (3 of 11), successional forest (3 of 11), pine plantations (2 of 11), and avoided crops (4 of 11).

West-central--During postbreeding, 6 of 13 does differed (P<0.05) in habitat use, four of 13 selected grassland, 3 avoided row crops, 2 selected row crops, and single does selected or avoided early successional forest and oak-hickory. During parturition, 13 of 29 does showed a significant difference from the available habitat, with 6 avoiding early successional forest, 5 selecting early successional forest, 5 selecting grassland, 4 selecting oak-hickory forest, 4 avoiding grassland, and 2 avoiding oak-hickory forest. During summer, 10 of 25 does selected row crops, usually corn, 8 does avoided grassland, and 5 avoided early successional forest. Two adult does that selected grassland for parturition avoided grassland during the postpartum period. The use of corn away from forest cover may provide deer with some relief from biting insects that are very abundant in forest understories (Nixon et al. 1991). Fourteen of 31 does with fawns and 2 of 4 barren yearling does differed from expected frequencies of available habitats during breeding. Six selected grassland, 5 avoided grassland, 4 selected row crops and 4 avoided row crops, 3 selected successional forest and 3 avoided this same habitat, 3 avoided oak-hickory forest, and 2 selected oak-hickory.

These often contradictory selections and avoidance of particular habitats are not unexpected given the generalist nature of habitat selection by white-tailed deer throughout it's continental range. Selection or avoidance of a particular habitat probably depends as much on social relationships and social position in the dominance hierarchy as on selection or avoidance decisions based on nutrition or cover needs. Whitetails in Illinois can locate a nutritious diet in nearly all habitats available, winter or summer. The effect of habitat on fawn rearing success as affected by maternal age also seems to be contradictory, with does seemingly using all available habitats as parturition sites (see

APPENDIX 3 for a more complete discussion of habitat selection pre- and postpartum by doe age class).

(b) Target date of Achievement: 1 September 1994.

(c) Date of Accomplishment: On schedule.

(d) Significant Deviations: None.

(e) Remarks: We have met the objectives of this job: to determine age specific natality and seasonal and annual survival rates, to determine habitat selections and movement patterns of both sexes for deer in WC and NO Illinois, and to provide these data to the IDOC and others for use in population models of the Illinois deer herd. Natality and survival data generated by these marking studies are currently being used in the new population computer model developed for the Illinois deer herd under Job NO. C, of this study.

(f) Recommendations: Current survival rates for marked deer in west-central and northern Illinois indicate females are still being underharvested in the 1990's if the management goal includes stabilizing or reducing the size of the Illinois deer herd. Current mortality rates of adult females are generally <25% per year, far below the >30% level needed to slow the rate of increase in deer numbers. Statewide, prehunt deer numbers appear to be near 600,000 and farmer dissatisfaction with concurrent deer damage to crops is growing statewide.

Because of the growing deer population, density dependent effects are becoming more evident on overcrowded public lands and some private refuges. Natality rates are declining on these areas, the result of high survival of females and the formation of extended families of does on these areas. Nutrition continues to be adequate on these areas as demonstrated by the continued high natality of yearling and older does because deer in Illinois derive much of their foods from farm fields. Maternal domination of fawn does apparently depresses reproductive activity through increased biosocial interactions caused by high doe densities (Verme 1987). This effect was present on the WC study area

throughout our study and similar observations have been noted at several other sites in Illinois. Only removal of a higher proportion of females will improve doe fawn natality on these areas.

Future research efforts should include a determination of optimum deer population levels for public lands in Illinois. Deer numbers must be held at levels that minimize farmer complaints and damage to vegetation, while at the same time providing for the opportunity to view deer in a natural setting, providing deer for hunting recreation, and, because of the importance of dispersing deer to hunting opportunities on surrounding private lands, protecting enough does to ensure sufficient dispersing fawns to restock hunted areas. It will not be easy to determine what optimum levels are or how they can be realistically maintained. Regulation of deer numbers will depend on management flexibility as the methods used to manage deer will likely vary from area to area , and it will be impossible to completely satisfy all the often conflicting viewpoints generated by deer throughout Illinois. But such research would certainly help the IDOC to manage the deer based on research data, not opinion, the only position that can hope to reconcile groups as diverse as PETA and the Illinois sportsman alliance.

(g) INHS Costs: Federal--$42,166; State--$14,055; Total--$56,221.

Job No. C.; Title: Population Analysis

Objectives: (1) To develop interactive, menue-driven, portable computer models and software packages to analyze population data, model herd performance, and predict outcome of alternative harvest strategies on herd size, herd composition, and hunter behavior and success; and (2) To assist the IDOC in integrating this system into their deer management program.

(a) Activity: Job and reporting assigned to Dr. A. Woolf and J. Roseberry, Cooperative Wildlife Lab, Southern Illinois University, Carbondale.

(b) Target Date of Accomplishment: 1 September 1995.

(c) Date of Accomplishment: On Schedule.

(d) Significant Deviations: None.

(e) Remarks: None.

(f) Recommendations: None.

(g) INHS Costs: Federal--$6,025; State--$2,008; Total--$8,033.

Job No. D ; **Title:** Analyze and Report.

Objectives: (1) To analyze results and prepare products from Jobs A-C; and (2) To report and discuss findings and present products in a timely manner.

(a) Activity: Project summaries, an annual report of progress, and quarterly reports of progress were submitted to the funding agencies as required. Various topics dealing with deer hunting and life history and ecology were reported to the IDOC as requested.

Presentations discussing deer ecology in Illinois were given before various groups during the segment. Numerous queries from the press regarding deer ecology and life history were answered and ongoing discussions were held with IDOC personnel regarding deer herd management.

The following manuscripts were prepared for publication by the Illinois Natural History Staff as a part of this study:

Nixon, C.M., L.P. Hansen, P.A. Brewer, and J.E. Chelsvig. 1992. Stability of white-tailed doe parturition ranges on a refuge in east-central Illinois. Canadian J. Zoology 70:968-973.

_____, and _____. 1992. Habitat relationships and population dynamics of deer in the intensively farmed midwestern United States. Pages 22-29, in R.D. Brown, Editor. The biology of deer. Springer-Verlag, New York. 596pp.

Morgan, G.W., C.M. Nixon, J.C. Van Es, and J.H. Kube. 1992. Attitudes of Illinois farmers regarding deer and deer hunters, 1990. Tech. Bull. 6. Ill. Dept. Conservation, Springfield. 24pp.

Nixon, C.M., L.P. Hansen, P.A. Brewer, J.E. Chelsvig, J.B. Sullivan, T. Esker, R. Koerkenmeier, D.R. Etter, J. Cline, and J. A. Thomas. 1994. Behavior, dispersal, and survival of male white-tailed deer in Illinois. Biological Note 139. Illinois Natural History Survey, Champaign. 30pp (APPENDIX 4).

_____, and D.R. Etter. 1994. Maternal age and fawn rearing success for white-tailed deer in Illinois. Submitted to Amer. Midl. Naturalist (APPENDIX 3).

Etter, D.R., and C.M. Nixon. 1994. Emigration and survival of orphaned female deer in Illinois. Manuscript under review (APPENDIX 5).

(b) Target Date of Achievement: 1 September 1995.

(c) Date of Accomplishment: On Schedule.

(d) Significant Deviations: None.

(e) Remarks: None.

(f) Recommendations: None.

(g) INHS Costs: Federal--$3,012; State--$1,004; Total--$4,016.

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Table 1. Number of fawn does breeding on the west-central study
area based on progesterone levels in blood sera
collected from does captured in January-March 1990-1993

Year	No. Does Examined	No. Does Breeding	Percent Breeding
1990	8	3	38
1991	20	3	15
1992	17	1	6
1993	7	0	0
Total	52	7	13

Table 2. Fawn production on 3 study areas in Illinois based on repeated observations of marked does postpartum. Number of does and number of fawns shown in parenthesis.

| | Breeding Age | | | | | |
| | 6-8 Months | | 18 Months | | 30+ Months | |
Year	Percent Breeding	No. Fawns/ Breeding Doe	Percent Breeding	No. Fawns/ Breeding Doe	Percent Breeding	No. Fawns/ Breeding Doe
			NORTHERN			
1989	100	1.0	100	2.0	100	1.67
	(3)	(3)	(2)	(4)	(3)	(5)
1990	25	1.0	100	1.33	100	1.83
	(4)	(1)	(6)	(8)	(6)	(11)
1991	78	1.0	100	2.00	100	1.77
	(9)	(7)	(7)	(14)	(13)	(23)
1992	70	1.0	100	1.80	100	1.63
	(10)	(7)	(10)	(18)	(19)	(31)
1993	--	--	0.88	1.71	0.96	1.91
			(8)	(12)	(24)	(44)
Means	69	1.0	0.97	1.75	0.98	1.78
	(26)	(18)	(33)	(56)	(65)	(114)
			WEST-CENTRAL			
1989	50	1.0	100	1.20	0.91	1.40
	(4)	(2)	(5)	(6)	(11)	(14)
1990	43	1.16	0.85	1.00	0.92	1.67
	(14)	(7)	(7)	(6)	(26)	(40)
1991	15	1.00	100	1.40	0.97	1.62
	(26)	(4)	(15)	(21)	(41)	(65)
1992	6	1.00	100	1.55	0.97	1.64
	(17)	(1)	(9)	(14)	(32)	(51)
1993	--	--	100	1.62	100	1.70
			(8)	(13)	(30)	(51)
Means	21	1.08	0.98	1.39	0.96	1.64
	(61)	(14)	(44)	(60)	(140)	(221)

Continued.

Table 2. Page 2.

			EAST-CENTRAL			
1980	83	1.00	100	1.33	100	1.80
	(6)	(5)	(3)	(4)	(5)	(9)
1981	92	1.18	100	1.83	100	2.17
	(12)	(13)	(6)	(11)	(6)	(13)
1982	64	1.14	100	1.87	100	2.08
	(11)	(8)	(8)	(15)	(13)	(27)
1983	78	1.00	100	1.78	100	2.11
	(9)	(7)	(9)	(16)	(26)	(55)
1984	60	1.11	100	1.71	100	1.96
	(15)	(10)	(7)	(12)	(27)	(53)
1985	58	1.14	100	1.71	100	1.97
	(12)	(8)	(7)	(12)	(32)	(63)
1986	--	--	100	1.75	100	2.00
			(4)	(7)	(15)	(30)
Means	70	1.09	100	1.75	100	2.02
	(65)	(46)	(51)	(77)	(124)	(250)

Table 3. Fawn production and recruitment to 1 year postpartum on 3 sites in Illinois.

| | BREEDING AGE IN MONTHS | | | | | | | | |
| | 5-8 | | | 16-18 | | | 28+ | | |
	NO	WC	EC	NO	WC	EC	NO	WC	EC
No. Does	32 [a]	33	37	20	20	20	48	47	43
% Breeding	69	85 [b]	76	97	98	100	98	96	100
Does Breeding	22	28	28	19	20	20	47	45	43
Fawns/doe	1.0	1.08	1.13	1.75	1.39	1.82	1.78	1.64	2.1
Total Fawns	22	30	32	33	28	36	84	74	90
Fawn deaths to 1 year	2	-- [c]	3	10	7	7	17	12	13
Fawns Recruited	20	--	29	23	21	29	67	62	77
Recruited Fawns/doe	0.62	--	0.78	1.15	1.05	1.45	1.39	1.32	1.79

[a] Regional age structure on 1 June provided by J. Roseberry, SIU-Carbondale.

[b] Fawn breeding rate for WC region from Grabaugh et al.(1988).

[c] No data.

Table 4. Survival and cause specific mortality rates of yearling females marked in Northern (NO) and West-central (WC) Illinois, 1990-92.

Year	Season	Location	Deer Days	No. Deaths	Survival	95% C.I.	Cause of Death					
							Auto	Archery	Firearm	Archery Cripple	Firearm Cripple	Misc. b
1990	Postbreed a (119 days)	WC	732	0	1.00	—	—	—	—	—	—	—
		NO	714	0	1.00	—	—	—	—	—	—	—
1991		WC	1,064	1	0.89	0.72-1.00	—	—	—	—	—	0.11
		NO	714	0	1.00	—	—	—	—	—	—	—
1992		WC	2,739	1	0.96	0.88-1.00	0.04	—	—	—	—	—
		NO	1,309	0	1.00	—	—	—	—	—	—	—
1993		WC	1,666	0	1.00	—	—	—	—	—	—	—
		NO	1,547	1	0.92	0.79-1.00	0.08	—	—	—	—	—
1990	Parturition (60 days)	WC	496	0	1.00	—	—	—	—	—	—	—
		NO	420	0	1.00	—	—	—	—	—	—	—
1991		WC	1,364	0	1.00	—	—	—	—	—	—	—
		NO	720	0	1.00	—	—	—	—	—	—	—
1992		WC	1,245	1	0.95	0.86-1.00	—	—	—	—	—	0.05
		NO	1,020	2	0.89	0.75-1.00	0.11	—	—	—	—	—
1990	Prebreed (77 days)	WC	616	0	1.00	—	—	—	—	—	—	—
		NO	539	0	1.00	—	—	—	—	—	—	—
1991		WC	1,694	0	1.00	—	—	—	—	—	—	—
		NO	924	1	0.93	0.82-1.00	0.06	—	—	—	—	—
1992	Prebreed	WC	1,540	0	1.00	—	—	—	—	—	—	—
		NO	1,155	0	1.00	—	—	—	—	—	—	—

Continued.

Table 4. Page 2.

Year	Period		N		Survival	CI					
1990	Breed (107 days)	WC	905	2	0.79	0.57-1.00	—	—	0.21	—	—
		NO	749	2	0.75	0.50-1.00	—	0.12	0.13	—	—
1991		WC	2,106	4	0.82	0.67-1.00	—	0.05	0.09	0.04	—
		NO	1,177	2	0.83	0.65-1.00	—	0.08	—	0.09	—
1992		WC	1,824	6	0.70	0.53-0.93	0.05	0.05	0.20	—	—
		NO	1,605	1	0.93	0.82-1.00	0.07	—	—	—	—
1990	Annual	WC	2,749	2	0.77	0.53-1.00	—	—	0.23	—	—
		NO	2,422	2	0.74	0.48-1.00	—	0.13	0.13	—	—
1991		WC	6,228	5	0.75	0.58-0.96	—	0.10	0.10	0.05	—
		NO	3,535	3	0.73	0.52-1.00	0.09	0.09	—	0.09	—
1992		WC	7,352	8	0.67	0.51-0.88	0.08	0.04	0.17	—	0.04
		NO	5,089	4	0.75	0.56-0.99	0.25	—	—	—	—

[a] Postbreed - 16 January-15 May; Parturition - 15 May-15 July; Prebreed - 16 July-30 September; Breed - 1 October-15 January.

[b] Includes drowning, poaching, fences, trains, canine predation, and nuisance removal.

Table 5. Survival and cause specific mortality rates for adult females marked in Northern (NO) and West-central (WC) Illinois, 1990-92.

Year	Season	Location	Deer Days	No. Deaths	Survival	95% C.I.	Cause of Death					
							Auto	Archery	Firearm	Archery Cripple	Firearm Cripple	Misc.
1990	Postbreed	WC	1,536	0	1.00	–	–	–	–	–	–	–
	(119 days)	NO	595	0	1.00	–	–	–	–	–	–	–
1991		WC	4,359	1	0.97	0.92-1.00	–	–	–	–	–	0.03
		NO	1,119	0	1.00	–	–	–	–	–	–	–
1992		WC	6,181	1	0.98	0.94-1.00	0.02	–	–	–	–	–
		NO	2,380	0	1.00	–	–	–	–	–	–	–
1993		WC	7,731	1	0.99	0.96-1.00	–	–	–	–	–	0.01
		NO	2,499	1	0.95	0.87-1.00	0.05	–	–	–	–	–
1990	Parturition	WC	1,550	0	1.00	–	–	–	–	–	–	–
	(60 days)	NO	600	0	1.00	–	–	–	–	–	–	–
1991		WC	2,728	0	1.00	–	–	–	–	–	–	–
		NO	780	0	1.00	–	–	–	–	–	–	–
1992		WC	4,999	2	0.98	0.94-1.00	0.01	–	–	–	–	0.01
		NO	2,100	0	1.00	–	–	–	–	–	–	–
1993		WC	4,680	0	1.00	–	–	–	–	–	–	–
		NO	2,700	2	0.96	0.90-1.00	0.02	–	–	–	–	0.02
1990	Prebreed	WC	1,925	0	1.00	–	–	–	–	–	–	–
	(77 days)	NO	770	0	1.00	–	–	–	–	–	–	–

Continued.

Table 5. Page 2.

Year		N	n	Est.	95% CI							
1991	WC	3,453	1	0.98	0.93–1.00	0.02	–	–	–	–	–	–
	NO	1,771	0	1.00	–	–	–	–	–	–	–	–
1992	WC	6,079	1	0.99	0.96–1.00	–	–	–	–	–	–	0.01
	NO	2,695	0	1.00	–	–	–	–	–	–	–	–
1993	WC	6,006	0	1.00	–	–	–	–	–	–	–	–
	NO	3,311	0	1.00	–	–	–	–	–	–	–	–
1990 Breed (107 days)	WC	2,644	2	0.92	0.82–1.00	–	–	–	0.04	–	–	0.04
	NO	1,070	1	0.90	0.74–1.00	–	–	0.10	–	–	–	–
1991	WC	4,463	4	0.91	0.83–1.00	–	–	0.05	0.02	–	–	0.02
	NO	2,568	3	0.88	0.77–1.00	–	0.04	0.04	0.04	–	–	–
1992	WC	7,664	12	0.85	0.77–0.93	–	0.09	0.04	0.01	0.01	–	–
	NO	3,745	2	0.94	0.87–1.00	–	0.03	–	0.03	–	–	–
1993	WC	8,396	6	0.92	0.87–0.98	–	0.04	0.04	–	–	–	–
	NO	4,601	8	0.83	0.73–0.94	0.02	0.11	–	0.04	–	–	–
1990 Annual	WC	7,655	2	0.91	0.80–1.00	–	–	0.05	–	–	–	0.04
	NO	3,035	1	0.89	0.70–1.00	–	–	0.11	–	–	–	–
1991	WC	15,003	6	0.86	0.77–0.97	0.03	–	0.05	0.03	–	–	0.05
	NO	6,309	3	0.84	0.69–1.00	–	0.05	0.05	0.06	–	–	–
1992	WC	24,923	16	0.79	0.70–0.88	0.03	0.09	0.04	0.01	–	–	0.03
	NO	10,920	2	0.93	0.85–1.00	–	0.03	–	0.04	0.01	–	–
1993	WC	26,813	7	0.91	0.84–0.97	–	0.04	0.04	–	–	–	0.01
	NO	13,111	11	0.73	0.61–0.88	0.07	0.12	–	0.05	–	–	0.03

[a] Seasonal intervals = see Table 4.

Table 6. Dispersal of yearling females marked on 3 study areas in
Illinois, 1980-92.

Area	Year	No. of Females		
		Sedentary	Disperse	% Dispersing
Northern	1990	4	3	43
	1991	5	6	55
	1992	10	5	33
	Total	19	14	42
West-Central	1990	7	4	36
	1991	14	7	33
	1992	14	5	26
	Total	35	16	31
East-Central	1980	4	4	50
	1981	5	9	64
	1982	14	3	18
	1983	8	10	56
	1984	10	8	44
	1985	11	8	42
	Total	42	42	50

Table 7. Seasonal harmonic mean core areas (mean ± S.E.) for females radio marked on the northern and west-central study areas, 1990-93.

Area	Seasons			
	Postbreed	Parturition	Prebreed	Breed
	HOME RANGE (HA)			
Northern	86.2 ± 11.4 (N = 27)	23.5 ± 3.7 (N = 25)	41.6 ± 6.9 (N = 28)	36.1 ± 5.2 (N = 23)
West- Central	50 ± 8 (N = 14)	22 ± 5 (N = 38)	41 ± 5 (N = 31)	51 ± 5 (N = 37)

Table 8. Mean percentage overlap of 100% harmonic mean home ranges among seasons for all does and within seasons for related does on the west-central area, 1990-1994.

Season	Within Seasons		Among Seasons	
	No.	% Overlap ± S.E.	No.	% Overlap ± S.E.
Postbreed	16	89 ± 5	42	78 ± 3
Parturition	52	67 ± 3	94	58 ± 2
Prebreed	38	71 ± 3	78	63 ± 3
Breed	34	75 ± 3	65	66 ± 3

APPENDIX 1. Age, sex, date of capture, and disposition of deer
   marked on the Western Central Study Area, Brown and Adams
            counties, from January 1990 - March 1994.

Appendix 1. Age, sex, date of capture, and disposition of
deer marked on the Western Central Study Area. Brown and
Adams counties, from Jan. 1990 - Mar. 1994.

EAR TAG #	COLLAR # OR FREQUENCY	SEX	AGE	DATE MARKED	DISPOSITION	
2	2	F	A	01-09-90	FOUND DEAD	12-14-90
3	3	F	A	01-08-90	HARVESTED	11-29-92
4	4	F	F	01-08-90	HARVESTED	12-16-90
5	165.430	F	A	01-14-90		
6	6	F	F	01-16-90		
7	7	F	A	01-22-90		
8	8	F	A	01-16-90		
9	9	F	A	01-22-90	HARVESTED	11-16-91
10	10	F	A	01-24-90		
11	11	F	A	01-24-90		
12	12	F	A	02-04-90		
13	13	F	F	02-09-90	DEAD	02-07-91
14	14	F	F	02-02-90	HARVESTED (IOWA)	12-90
16	165.200	F	A	02-08-90		
17	165.030	F	F	02-13-90	MISSING	
18	165.110	F	A	02-06-90		
19	---	M	F	02-20-90	HARVESTED	11-15-91
20	---	M	F	01-09-90	HARVESTED	11-15-91
21	---	M	F	01-14-90	HARVESTED	11-14-92
22	---	M	F	01-14-90		
23	---	M	F	01-17-90		
24	---	M	F	01-22-90	HARVESTED	11-17-90
25	---	M	F	01-24-90	HARVESTED	10-09-91
26	---	M	F	02-02-90		
27	---	M	F	02-06-90	HARVESTED	10-09-91
28	---	M	F	02-06-90	FOUND DEAD	12-90
29	---	M	F	02-16-90		
30	---	M	F	02-13-90	CAPTURE MORTALITY	
31	---	M	F	02-20-90	FOUND DEAD	04-23-92
32	---	M	F	02-20-90	HARVESTED	11-15-90
33	---	M	F	01-17-90	HARVESTED	10-19-91
34	165.480	M	A	02-18-90	HARVESTED	11-05-90
35	165.820	F	F	02-20-90		
36	---	M	F	02-22-90		
37	---	M	F	03-03-90		
38	---	M	F	03-27-90	FOUND DEAD	03-05-92
39	---	M	F	03-07-90	KILLED	11-11-90
40	165.270	F	A	02-13-90		
41	165.658	F	A	03-20-90	FOUND DEAD	03-19-91
42	165.835	F	F	03-20-90	HARVESTED	12-15-91
43	165.230	F	A	03-21-90	FOUND DEAD	02-24-94
44	44	F	F	03-22-90		
45	45	F	F	02-22-90		
46	165.780	F	A	02-16-90		
47	165.250	F	A	02-13-90		
48	165.352	F	Y	02-20-90	HARVESTED	11-06-92

EAR TAG #	COLLAR # OR FREQUENCY	SEX	AGE	DATE MARKED	DISPOSITION	
49	165.500	F	A	03-15-90		
50	165.368	F	A	02-20-90		
51	165.090	F	A	02-20-90	CRIPPLING LOSS	
52	165.450	F	A	03-15-90		
53	165.412	F	Y	03-21-90	FOUND DEAD	07-11-92
54	166.428	F	A	01-14-91	HARVESTED	11-02-92
55	55	F	F	01-14-91		
56	56	F	A	01-14-91	HARVESTED	11-06-92
57	57	F	F	02-26-90	HARVESTED	11-16-91
58	58	F	A	02-26-90	HARVESTED	11-19-93
59	59	F	F	01-13-91		
60	165.480	M	A	12-18-90	LOST COLLAR	01-13-92
61	165.310	M	A	03-25-90	FOUND DEAD	11-02-90
62	--	M	F	03-18-90	CRIPPLING LOSS	
63	--	M	F	12-20-90		
64	--	M	F	01-04-91	HARVESTED	10-05-91
65	--	M	F	01-03-91		
66	--	M	F	01-08-91		
68	--	M	F	01-07-91		
69	--	M	F	01-07-91		
70	--	M	F	03-03-90		
71	165.290	F	Y	03-27-90		
72	72	F	Y	01-04-91		
73	73	F	Y	12-20-90		
74	165.130	F	F	03-21-90		
75	75	F	F	12-28-90		
76	76	F	Y	12-28-90	HARVESTED	01-01-93
77	77	F	A	01-04-91	FOUND DEAD	10-02-91
78	165.130	F	A	01-18-91		
79	79	F	Y	01-14-91	HARVESTED	10-10-92
80	80	F	A	01-07-91		
81	81	F	A	01-14-91	CAPTURE RELATED	
82	82	F	F	01-18-91		
83	83	F	F	01-21-91		
84	84	F	F	01-21-91		
85	85	F	A	01-21-91		
86	86	F	A	01-30-91		
87	87	F	F	01-30-91	HARVESTED	11-09-91
88	88	F	A	01-30-91		
89	89	F	A	01-30-91	HARVESTED	11-21-92
90	90	F	A	01-31-91		
91	91	F	F	01-31-91		
92	92	F	F	01-31-91	HARVESTED	12-02-93
93	93	F	Y	02-08-91	FOUND DEAD	05-11-93
94	94	F	A	02-10-91		
95	95	F	A	03-08-91		
96	96	F	F	03-15-91		
97	97	F	F	03-15-91		
98	98	F	A	03-24-91		

EAR TAG #	COLLAR # OR FREQUENCY	SEX	AGE	DATE MARKED	DISPOSITION	
99	99	F	F	03-24-91		
100	--	M	F	01-13-91	ROAD KILL	04-25-91
101	--	M	F	01-13-91	HARVESTED	11-16-91
102	--	M	F	01-18-91	FOUND DEAD	04-28-92
103	--	M	F	01-18-91	HARVESTED	11-20-92
104	--	M	F	01-30-91		
105	--	M	F	01-30-91		
106	--	M	F	02-08-91		
107	165.310	M	A	01-23-91	LOST COLLAR	11-24-91
108	--	M	F	02-08-91	HARVESTED	11-16-91
109	165.892	F	F	01-13-91	HARVESTED	12-05-93
110	165.850	F	F	01-08-91		
111	165.580	F	F	01-08-91	CRIPPLING LOSS	
112	165.750	F	A	01-08-91		
113	165.070	F	F	01-13-91		
114	165.328	F	A	09-13-91		
115	165.990	F	Y	01-13-91		
116	165.835	F	A	01-13-91	CAPTURE MORTALITY	
117	165.702	F	F	01-23-91	HARVESTED	11-16-91
118	118	F	F	03-24-91		
119	119	F	Y	01-14-92		
120	--	M	F	02-10-91	HARVESTED	12-04-92
121	--	M	F	02-10-91		
122	--	M	F	02-26-91	CRIPPLING LOSS	
123	--	M	F	02-26-91	HARVESTED	11-10-91
124	--	M	F	03-08-91	CAPTURE MORTALITY	
125	--	M	F	03-08-91		
126	--	M	Y	03-13-91	HARVESTED	11-20-92
127	165.270	M	Y	03-13-91	HARVESTED	11-01-92
128	--	M	F	03-13-91	HARVESTED	12-02-93
129	--	M	Y	03-15-91	HARVESTED	12-04-93
130	--	M	F	03-26-91	CRIPPLING LOSS	
131	--	M	F	03-29-91	HARVEST	11-16-91
132	--	M	F	01-10-92		
133	--	M	F	12-22-91	HARVEST	11-20-92
134	--	M	F	01-08-92		
135	--	M	F	01-08-92	ROAD KILL	10-26-92
136	165.680	F	A	03-29-91		
137	165.050	F	A	03-07-91	ROAD KILL	08-19-91
138	165.644	F	F	03-07-91	CRIPPLING LOSS	
139	165.390	F	F	03-07-91	ROAD KILL	01-19-92
140	140	F	F	12-20-91		
141	141	F	F	12-20-91	FOUND DEAD	06-25-92
142	166.390	F	F	03-21-91		
143	165.212	F	A	03-21-91		
144	144	F	F	01-14-92	HARVEST	10-03-93
145	145	F	A	01-23-92	CRIPPLING LOSS	
146	46	F	A	01-29-92		
147	165.970	F	A	03-21-91		

EAR TAG #	COLLAR # OR FREQUENCY	SEX	AGE	DATE MARKED	DISPOSITION	
148	148	F	A	01-16-92	HARVESTED	12-04-92
149	-	M	F	01-10-92	HARVESTED	11-19-93
150	165.702	M	Y	01-10-92	HARVESTED	11-13-93
151	51	F	Y	01-24-92		
152	-	M	F	01-08-92		
153	53	F	A	01-24-92	HARVESTED	11-16-92
154	54	F	F	01-29-92	HARVESTED	11-23-93
155	55	F	Y	01-29-92		
156	-	M	F	01-16-92	HARVESTED	11-20-92
157	57	F	A	01-31-92		
158	58	F	A	01-30-92		
159	165.010	F	F	01-30-92		
161	61	F	A	02-07-92		
162	62	F	F	02-08-92		
163	63	F	F	02-11-92	HARVESTED	12-03-92
164	64	F	F	02-13-92	FOUND DEAD	05-24-92
165	65	F	F	02-13-92		
166	66	F	F	02-17-92	HARVESTED	12-05-92
167	67	F	F	02-19-92	HARVESTED	12-04-92
168	68	F	A	03-10-92	HARVESTED	09-27-92
169	-	M	F	01-10-92		
170	-	M	Y	01-10-92		
171	71	F	A	02-20-92		
172	-	M	F	01-30-92	HARVESTED	11-13-93
173	73	F	Y	02-25-92		
174	74	F	A	02-25-92	HARVESTED	11-20-92
175	75	F	A	02-28-92		
176	76	F	A	02-28-92		
177	77	F	F	03-11-92		
178	78	F	F	03-11-92		
179	79	F	A	03-11-92		
180	80	F	Y	03-11-92	HARVESTED	10-23-93
181	81	F	A	03-12-92		
182	82	F	F	03-21-92		
185	-	M	F	01-31-92	HARVESTED	11-07-93
186	165.580	M	Y	01-06-92		
187	166.850	F	F	01-17-92	HARVESTED	11-04-92
188	-	M	F	01-13-92		
189	-	M	F	01-13-92		
190	-	M	F	01-23-92		
191	-	F	A	01-20-92	CAPTURE RELATED	
192	165.160	F	F	01-20-92		
193	-	M	F	01-20-92		
194	166.990	F	F	01-16-92		
195	166.670	F	A	01-16-92	ROAD KILL	02-12-92
196	-	M	F	01-24-92	HARVESTED	11-22-92
197	165.658	F	A	01-22-92		
198	166.410	F	F	01-22-92		
199	166.488	F	F	01-22-92		

EAR TAG #	COLLAR # OR FREQUENCY	SEX	AGE	DATE MARKED	DISPOSITION	
200	165.480	M	A	01-25-92	HARVESTED	11-01-92
201	--	M	F	01-28-92		
202	--	M	F	01-28-92	HARVESTED	11-19-93
203	--	M	F	02-04-92	HARVESTED	12-06-92
204	--	M	F	02-04-92	HARVESTED	11-03-92
205	--	M	Y	02-04-92	HARVESTED	10-02-92
206	--	M	F	02-07-92	HARVESTED	11-17-93
207	166.550	F	F	02-08-92		
208	--	M	F	02-08-92	HARVESTED	11-21-93
209	--	M	F	02-12-92		
210	--	M	F	02-11-92		
211	--	M	Y	02-17-92	HARVESTED	12-03-92
212	--	M	F	02-25-92	DISPATCHED	02-25-92
213	--	M	Y	02-26-92		
214	--	M	F	02-28-92		
215	--	M	F	03-08-92		
216	--	M	A	03-10-92	HARVESTED	11-21-92
217	--	M	F	03-10-92		
218	--	M	F	03-10-92	HARVESTED	11-21-92
219	--	F	F	03-17-92	CRIPPLING LOSS	
220	166.251	F	F	03-08-92		
221	166.670	F	Y	03-08-92		
222	166.788	F	Y	03-08-92		
224	--	M	F	03-12-92	ROAD KILL	11-05-92
225	--	M	F	03-12-92	HARVESTED	11-19-93
226	26	F	Y	03-23-92	ROAD KILL	06-28-92
227	27	F	F	03-23-92	ROAD KILL	11-05-92
228	28	F	Y	03-23-92		
231	--	M	F	03-21-92		
232	165.050	F	A	03-17-92	FOUND DEAD	11-07-92
233	--	M	F	03-21-92		
234	165.310	F	A	03-19-92		
235	165.390	F	F	03-19-92	HARVESTED	12-05-92
236	--	M	A	03-15-92		
237	--	M	F	03-22-92	HARVESTED	12-06-92
239	--	M	F	03-26-92	ROAD KILL	12-20-92
301	165.390	F	F	01-13-93	HARVESTED	11-19-93
302	165.050	F	F	01-13-93		
304	--	M	F	01-13-93		
305	165.850	F	F	01-30-93	FOUND DEAD	04-25-93
306	--	M	F	01-30-93		
307	--	M	F	01-30-93		
308	166.040	F	Y	02-13-93		
309	--	M	F	02-13-93		
310	165.480	F	A	02-13-93		
311	166.428	F	Y	02-13-93		
313	--	M	F	02-13-93		
314	--	M	F	02-20-93		
315	165.282	F	A	02-20-93	POACHED	05-07-93

EAR TAG #	COLLAR # OR FREQUENCY	SEX	AGE	DATE MARKED	DISPOSITION
316	165.348	F	F	02-26-93	
317	-	M	F	02-26-93	HARVESTED 11-19-93
318	-	M	Y	02-26-93	HARVESTED 11-19-93
319	-	M	F	03-15-93	HARVESTED 11-19-93
320	-	M	F	03-15-93	
321	165.412	F	F	03-16-93	
322	-	M	F	03-16-93	HARVESTED 11-20-93
323	165.808	F	A	03-17-93	
324	166.360	F	F	03-17-93	BROKEN LEG 10-03-93
325	166.272	F	F	03-26-93	
326	166.797	F	A	03-17-93	HARVESTED 12-02-93
331	-	M	F	03-25-93	
332	-	M	F	03-25-93	HARVESTED 11-10-93
335	-	M	F	03-26-93	HARVESTED 11-06-93
336	166.562	F	Y	03-28-93	HARVESTED 11-20-93
338	166.100	F	F	03-24-93	HARVESTED 11-01-93
339	-	M	F	03-24-93	
340	165.910	F	A	03-24-93	
342	166.212	F	F	04-03-93	
343	166.650	F	F	04-03-93	
401	-	F	A	01-13-93	DISPATCHED! ORPHAN
402	-	F	A	01-13-93	DISPATCHED! ORPHAN
405	-	F	Y	01-30-93	DISPATCHED! ORPHAN

APPENDIX 2. DEER MARKED AT SHABBONA LAKE STATE PARK,
1990-1992.

DEER MARKED AT SHABBONA LAKE STATE PARK 1990 - 1992.

EAR TAG NO.	PLASTIC OR RADIO COLLAR NO.	SEX	AGE	DATE MARKED	KNOWN FATE
102	#1	Female	Yearling	1-22-90	On park
103	--	Male	Fawn	1-22-90	Dead
109	--	Male	Fawn	2-13-90	Dead
108	#2 (Removed) Radio 165.430	Female	Fawn Recapture	2-13-90 2-6-91	On park
110	#4	Female	Adult	2-13-90	On park
104	#5	Female	Fawn	2-21-90	Left park
105	--	Male	Yearling	2-21-90	Left park
106	--	Male	Fawn	2-21-90	Dead
112	--	Male	Fawn	2-27-90	Dead
113	#7	Female	Adult	2-27-90	On park
114	#6	Female	Fawn	2-27-90	Dead
107	#84	Female	Adult	2-28-90	On park
111	#3 or E	Female	Yearling	2-28-90	Left park
116	#8	Female	Yearling	2-28-90	Dead
117	#12	Female	Yearling	3-7-90	On park
119	--	Male	Fawn	3-7-90	Left park
120	#11	Female	Yearling Recapture	3-7-90 3-20-92	On park
Radio	165.010	Female	Yearling	3-15-90	Dead

Continued.

EAR TAG NO.	PLASTIC OR RADIO COLLAR NO.	SEX	AGE	DATE MARKED	KNOWN FATE
115	--	Male	Fawn	3-15-90	Dead
Radio	165.162	Female	Yearling	3-15-90	On park
Radio	165.050	Female	Adult	3-15-90	Dead
118	--	Female	Fawn	3-27-90	Dead
121 Radio	165.680	Female	Adult Recapture	3-27-90 3-19-91	On park
122 Radio	165.750	Female	Fawn	3-27-90	Dead
123	#14	Female	Fawn Recapture	3-28-90 1-25-91	On park
124	#17	Female	Fawn	12-5-90	Dead
125	#8	Female	Yearling Recapture	12-5-90 3-24-92	On park
129	#21	Female	Fawn Recapture	12-10-90 1-30-91	Dead
127	165.070	Male	Yearling	12-10-90	Dead
126	165.010	Male	Adult	12-20-90	On park
128	--	Male	Fawn	1-3-91	On park
130	--	Male	Yearling	1-3-91	Dead
131	--	Male	Fawn	1-3-91	Left park
132	--	Male	Yearling	1-17-91	On park
133	#31	Female	Fawn	1-17-91	Dead

Continued.

EAR TAG NO.	PLASTIC OR RADIO COLLAR NO.	SEX	AGE	DATE MARKED	KNOWN FATE
134	--	Male	Adult	1-17-91	On park
135	--	Male	Adult	1-17-91	On park
136	#36	Female	Fawn	1-25-91	Left park
137	--	Male	Fawn	1-25-91	Dead
138	#39	Female	Adult	1-25-91	Dead
139	#38	Female	Fawn	1-30-91	On park
140	--	Male	Fawn	1-30-91	Left park
141	#13	Female	Fawn	1-30-91	On park
142	#25	Female	Adult	1-30-91	Dead
143	--	Male	Fawn	1-30-91	Dead
144	--	Female	Fawn	1-30-91	On park
146	--	Male	Fawn	2-6-91	Left park
145	165.860	Female	Fawn	2-6-91	On park
147	165.580	Female	Adult Recapture	3-6-91 3-10-92	On park
149	--	Male	Fawn	3-6-91	Left park
150	--	Male	Fawn Recapture	3-6-91 3-14-91	Dead
148	--	Male	Yearling	3-6-91	Dead

Continued.

EAR TAG NO.	PLASTIC OR RADIO COLLAR NO.	SEX	AGE	DATE MARKED	KNOWN FATE
151	#37	Female	Adult	3-14-91	On park
152	165.390	Female	Fawn	3-14-91	Dead
153	165.697	Female	Fawn	3-14-91	Left park
154	#2	Female	Yearling	3-14-91	On park
155	166.132	Female	Fawn	3-19-91	Left park
156	--	Male	Fawn	3-19-91	On park
	165.010		Yearling Recapture	11-21-91 12-18-91	
157	--	Male	Fawn	3-26-91	Dead
158	--	Male	Fawn	3-26-91	Left park
159	166.012	Female	Fawn	3-26-91	Left park
160	--	Male	Fawn	3-26-91	Left park
161	166.072	Female	Adult	3-26-91	Dead
162	17	Female	Fawn	11-21-91	Alive
163	24	Female	Fawn	11-26-91	Alive
164	--	Male	Fawn	11-26-91	Alive
165	23	Female	Fawn	11-26-91	Alive
166	10	Female	Fawn	11-26-91	Alive

Continued.

EAR TAG NO.	PLASTIC OR RADIO COLLAR NO.	SEX	AGE	DATE MARKED	KNOWN FATE
167	Radio 166.072	Female	Adult	11-26-91	Alive
168	Radio 165.070	Male	Adult	12-4-91	Alive
169	--	Male	Fawn Recapture	12-10-91 12-18-91	Alive
170	--	Male	Fawn	12-18-91	Alive
171	--	Male	Fawn	12-18-91	Alive
172	--	Male	Fawn	1-17-92	Alive
173	Radio 165.312	Female	Fawn	1-21-92	Alive
174	--	Male	Fawn	1-21-92	Alive
176	Radio 166.162	Female	Adult	1-21-92	Alive
177	Radio 166.192	Female	Fawn	1-28-92	Alive
178	Radio 166.103	Female	Adult	1-28-92	Alive
179	--	Male	Fawn	1-31-92	Alive
180	30	Female	Adult	1-31-92	Alive
181	Radio 166.040	Female	Fawn	2-5-92	Dead
182	--	Male	Fawn	2-11-92	Alive
183	--	M	Fawn	2-11-92	Alive
184	--	M	Fawn Recapture (Ear Tag Replaced as #204)	2-11-92 3-10-92	Alive Alive

Continued.

EAR TAG NO.	PLASTIC OR RADIO COLLAR NO.	SEX	AGE	DATE MARKED	KNOWN FATE
185	--	Female	Adult	2-11-92	Alive
186	Radio 165.970	Female	Fawn	2-19-92	Alive
187	Radio 165.260	Female	Fawn	2-19-92	Alive
188	--	Male	Fawn	2-19-92	Alive
189	--	Male	Fawn	2-19-92	Alive
190	57	Female	Yearling	2-25-92	Alive
191	Radio 166.040	Female	Fawn	2-25-92	Dead
192	--	Male	Fawn	2-25-92	Alive
193	Radio 165.050	Female	Fawn	2-19-92	Alive
194	--	Male	Fawn	2-19-92	Alive
195	Radio 165.390	Female	Fawn	2-19-92	Alive
196	Radio 165.644	Female	Adult	2-19-92	Alive
197	35	Female	Adult	2-25-92	Alive
198	Radio 165.240	Female	Yearling	2-25-92	Alive
199	--	Male	Fawn	2-28-92	Alive
200	40	Female	Fawn	2-28-92	Alive
201	26	Female	Yearling	3-6-92	Alive
202	46	Female	Fawn	3-6-92	Alive

Continued.

EAR TAG NO.	PLASTIC OR RADIO COLLAR NO.	SEX	AGE	DATE MARKED	KNOWN FATE
203	28	Female	Fawn	3-6-92	Alive
205	25	Female	Fawn	3-10-92	Alive
206	31	Female	Fawn	3-10-92	Alive
207	22	Female	Adult	3-10-92	Alive
208	--	Male	Fawn	3-13-92	Alive
209	Radio 165.282	Male	Adult	3-13-92	Alive
210	--	Male	Fawn	3-20-92	Alive
211	51	Female	Adult	3-24-92	Alive
212	Radio 166.040	Female	Fawn	3-24-92	Alive
213	21	Female	Fawn	3-24-92	Alive
314	--	Male	Yearling	3-27-92	Alive
215	--	Male	Yearling	3-27-92	Alive

APPENDIX 3. MATERNAL AGE AND FAWN REARING SUCCESS
        FOR WHITE-TAILED DEER IN ILLINOIS.

MATERNAL AGE AND FAWN REARING SUCCESS FOR WHITE-TAILED DEER IN ILLINOIS

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ABSTRACT

Fawn survival during the first year postpartum was determined for marked white-tailed does (Odocoileus virginianus) of known ages at 3 locations in Illinois. Fawns born to 2-year old does died at significantly higher annual rates (24%, $P<0.02$) than fawns born to younger (<10%) or older does (15%). Losses of fawns before weaning were not different ($P>0.50$) among dam age classes but differed ($P<0.01$) among years, ranging from 11 to 82% of total annual fawn mortality. Higher mortality for fawns born to 2-year-old dams appears to relate more to social behaviors relating to loss of support by matriarchal does than to differences in habitat selection or in movement to areas where the hazard to fawns from hunting and highway accidents would be higher.

INTRODUCTION

Maternal age and reproductive experience have been reported to affect the ability of white-tailed deer females to successfully rear offspring. Fawns born to does ≥ 4 years old have been reported to survive at significantly higher rates than fawns born to younger and less experienced does (Ozoga and Verme 1986, Mech and McRoberts 1990). Unlike fawn does on more northern ranges that rarely breed at 6-7 months old (Verme and Ullrey 1984), as many as 70-80% of the fawn does and virtually all does ≥ 1 year old breed each year in the intensively farmed regions of the

Midwest (Haugen 1975, Stoll and Parker 1986, Graubaugh et al. 1988, Nixon et al. 1991).

Although fawn mortality rates have been reported for deer in the Midwest (Bryan 1980, Huegel et al. 1985, Nelson and Woolf 1987), they have not been linked to the age and experience of the dam on these ranges. Our objective was to document fawn survival in relation to age of dam from 3 sites in Illinois, based upon repeated observations of marked females and their fawns (marked and unmarked) throughout their first year of life.

METHODS

Does (N = 140) were captured using rocket-propelled nets on sites in northern (DeKalb County), west-central (Brown and Adams counties), and east-central (Piatt County) Illinois. These sites were dominated by croplands (>50%), with permanent cover consisting of a mosaic of upland and bottomland forest, restored prairie, pine plantations, and old fields. Wheat and hayfields, often used as sites of parturition by deer when available, were not consistently available on our study areas. Each study area had mixtures of both public and private lands and included a wooded refuge that provided deer with diurnal cover, protection from severe weather, and refuge from firearm hunters. Does were marked with radio collars or plastic collars marked with fluorescent numbers, aged as fawn (<12 months), yearling (13-24 months), or adult (>25 months) based on tooth replacement and wear, ear tagged, and released.

Our mortality rates must be considered conservative because they do not include fawn loses that may have occurred within 48 hours of birth. Because fawns counts on our study areas approached those of fetal counts

reported for farmland does in the Midwest (Haugen 1975, Grubaugh et al. 1988), such early postpartum losses must be low (Nixon et al. 1991).

Evaluation of fawn mortality was based upon repeated observations of marked does and their fawns from shortly after parturition through family breakup at 1 year for 6-year (east-central) and 3-year (northern and west-central) periods. Does were observed by project personnel during the course of routine field work and radio tracking and spotlight surveys. Each observation included the age and sex of any companions of the marked doe and the behavior of the group while under observation. Radio tracking was used to locate several less readily observed does during daylight hours in fall and winter. They were deliberately forced to move into open areas where any fawns present could be observed. Many fawns (N = 210, 24 when <1 week old) of marked does also were captured and marked at some time during their first year, enhancing the opportunity to locate and observe them.

Habitat preferences were compared for radio marked yearling, 2-year-old, and $\geq$3-year-old does between birth and midsummer period (15 May-15 July) on each area. A 1-ha grid overlay of these study areas was mapped into 1 of 8 (east-central), 1 of 7 (northern), or 1 of 5 (west-central) vegetative types. Radio locations of does were placed within the 1-ha grids overlaying the study areas for the parturition period and compared with the total home range (available habitat) encompassed by each female during the life of each radio or deer. Habitat selections were compared with available habitat for each individual doe and tested for independence using chi-square analysis.

Primaparous does reportedly give birth within or immediately adjacent to their mother's parturition range and then move away from

their mother's range for subsequent births (Ozoga et al. 1982). We used 2 methods to measure the magnitude of this movement; (1) The overlap of consecutive parturition sites for the same radio marked doe was compared at 2 intervals, between 12 months and 24 months, when does move away from their mother, and between 24 and 36 months, when the doe should have established a permanent site (Ozoga et al. 1982, Dusek et al. 1989, Nixon et al. 1992); (2) The average distance moved between home range centers of activity was compared for the same 2 intervals. We also compared the size of the parturition and early fawn rearing home ranges between yearlings and 2-year-old does using a 100% convex polygon calculated using the programs HOME RANGE and RANGERSIV (Akerman et al. 1990, Kenwood 1990). These measurements were compared among age classes using one-way ANOVA.

RESULTS

Surprisingly, primaparous yearling mothers experienced the lowest loss of fawns for the age classes examined, with an average of <10% of their fawns dying before age 1. Significantly more fawns born to 2-year-old mothers died on our study areas compared with those born to younger or older mothers (G = 5.6, df = 4, P<0.025). Older ($\geq$3 years) does lost an average of 15.8 % of their fawns in the west-central area, 19.7% on the northern area, and 13.8% on the east-central area before age 1 (Table 1).

Preweaning fawn losses (<4 months old) were higher than postweaning losses on the west-central (preweaned fawn loss = 61%) and northern (67%) areas but were lower compared with postweaning losses on the east-central area (preweaned fawn loss = 21%) (G = 14.0, df = 2, P<0.01). Fawn losses before weaning were not significantly different (G =

2.4, df = 4, P>0.60) among age classes of does (yearlings = 25%, 2-year = 43%, 3-year = 46%, 4-year = 56%, and 5-year = 30% of the annual fawn loss) but were different among years (G = 18.2; df = 7; P<0.02), ranging between 11 and 82% of the total annual fawn mortality.

For our sample of 24 fawns marked when $\leq$1 week old (17 on the east-central area and 7 on the northern area), 2 died before weaning, (both to does 3+ years-old), 10 died during the postweaning period (4 to does 2 years old, 6 to does 3+ years old), and 12 survived to 1 year old. A unique aspect of our fawn tagging effort was the marking of quadruplets belonging to an unmarked doe on the northern study area. She lost 1 fawn during preweaning and 2 during postweaning when she was also killed. The remaining fawn soon joined a group of unmarked does and fawns and remained with them throughout the winter months.

The loss of 1 or more fawns was not indicative of a higher probability that a doe would lose fawns in subsequent years (X^2 = 0.01; df = 1; P>0.95). On the northern study area, 2 of 13 does lost fawns in consecutive years, 9 of 13 lost 1 or more fawns during 1 of the 3 years of study, and 2 does lost no fawns during the study. Of 33 does monitored more than 1 year on the east-central area, only 3 does lost fawns in consecutive years, 18 lost fawns in at least 1 year, and 12 does lost no fawns during the 6-year study. On the west-central area, 5 does lost fawns in consecutive years, 15 lost at least 1 fawn during 1 year, and 13 raised all their fawns to 1 year of age during the 3-year study.

Daughters usually move farther away from their mother's parturition range at age 22-24 months to give birth and for the first time since birth must protect themselves and their offspring without kin support (Ozoga et al. 1982). Based on observations from all 3 study areas (N = 1,225), the

frequency of association (number of times seen together/ sum of all observations of both individuals [Hawkins and Klimstra 1970]) of mothers and daughters declined from 42% when daughters were yearlings to 24% when daughters were 2 years old (G = 44.0; df =1; P< 0.001). Year-to-year overlap of parturition ranges for the same doe increased from an average of 27 $\pm$ 3.9% (N = 15 does) between yearling and 2 years of age to an average of 43 $\pm$ 3.7% (N = 22) overlap of parturition ranges for does between 2 and 3 years old (F = 7.8; df = 1,35; P<0.01).

The average distance between arithmetic centers of activity for pre- and early postpartum ranges in successive years declined from 192 $\pm$ 49 m between 12 and 24 months for 7 does to 149 $\pm$ 22 m for between 24 and 36 months for 9 does (all study areas) (P>0.05). The distance between the arithmetic centers of activity for mother and daughters on the east-central area averaged 172 $\pm$ 42 m (N = 4 pairs) when the daughters were yearlings and 518 $\pm$ 71 m when the daughters were 3 years old (N = 3 pairs).

The average distance between arithmetic centers of activity for parturition and early postpartum ranges in successive years declined from 192 $\pm$ 49 m between 12 and 24 months (N = 7 does) to 149 $\pm$ 22 m between 24 and 36 months (N = 9) on the study areas (P>0.10). On the west-central area, the center of activity for 6 does moved an average of 330 $\pm$ 103.8 m between 12 and 24 months. For 2 of these does, the distance between centers of activity declined to an average of 183 $\pm$ 39 m between 24 and 36 months.

Parturition home ranges (100% convex polygon) were similar (P>0.05) in size for yearling mothers (average = 35.2 $\pm$ 10.3 ha, N = 6), 2-

year-old does (average = 36.0 ± 5.5 ha, N = 21), and ≥3-year-old does (average = 35.0 ± 2.1 ha, N = 40).

Habitat selection among yearling, 2-year-old, and ≥3 year old does differed somewhat on each area, but habitat selection often overlapped among age classes. All age classes avoided row crop fields during the parturition period, probably because growth of row crops was insufficient in June and early July to hide mother and fawn(s). Three of 5 yearling females on the east-central area selected oak-hickory forest (P<0.05), and the other 2 does selected successional forest (30-60 years old) for parturition. On the west-central area, 5 of 7 yearlings showed no selection of habitat, 1 doe selected grassland and 1 selected successional forest.

Three of 5 2-year-old does on the northern area (N = 5) also selected oak-hickory forest, and the remaining 2 does selected successional forest. On the east-central area, 4 of 6 2-year-old does selected oak-hickory forest, the remainder successional forest. On the west-central area, only 2 does showed any selection, and they used grassland for parturition.

For older does on the northern area (N = 8), 4 of 8 selected restored tallgrass prairie, 1 selected mixed pines and grassland, and 3 selected successional forest for parturition. On the east-central area (N = 14), 12 older does selected either early successional (<30 years old) or older successional forest (30-60 years), 1 selected pasture and bottomland forest, and 1 selected oak-hickory forest. On the west-central area (N = 8), only 3 does showed any selection, and they selected successional forest as a parturition site.

Habitat selection for the prebreeding and breeding periods was similar to that for parturition as does tended to remain close to their

parturition site throughout the year. We were also unable to consistently relate location of a home range among does to increased environmental hazards for fawns such as hunting or highway accidents. We did not find more 2-year old does located closer to hunted areas or high speed highways.

DISCUSSION

Fawn deaths prior to weaning were likely the result of predation, nutritional failures early postpartum, or, if the doe was <3 years old and socially subordinate, the inability to rescue fawns that strayed into the parturition areas of older, more dominant females (Mech 1984, Verme 1969, Ozoga et al. 1982). Fawn deaths after weaning were almost entirely harvest-related or the result of highway accidents. Deaths due to severe winter weather are almost unknown in Illinois (Nixon et al. 1991).

Illinois does seldom lost fawns in consecutive years. Differences among areas and years in the proportion of fawn deaths before weaning also suggest that the extent of these deaths are variable in both space and time, a product of predator abundance and learned searching behavior, doe maternal experience, and the quality of the habitats available for doe parturition. Dusek et al. (1989) also found that fawn losses were rare in consecutive years (<15% of pregnancies) among individual whitetails in Montana.

Nondispersing yearling does established a home range close to their mother whether they were pregnant (east-central and northern areas) or were barren (most west-central does). This sharing of a parturition range with their mother may account in part for the high survival of fawns born to yearling mothers on our study areas (Table 1). These primaparous

females usually conceive only a single fawn, which may render fawn surveillance and protection somewhat easier. For their second pregnancy, these does usually moved away from their mother, selecting the site they typically occupied each spring until death (Dusek et al. 1989, Nixon et al. 1992). Higher fawn mortality is often associated with this shift in parturition range regardless of reproductive experience (whether as a 2 year old [northern and east-central areas, this paper] or as a 3 year old (many west-central females) suggesting that increased fawn mortality was the result of selecting a new parturition site and not doe age per se (Ozoga et al. 1982). There is also the possibility that parental behavior by the mother includes not only sharing a portion of her home range with a yearling daughter but perhaps also assisting in active defense of the fawn against predation or incursion into the parturition range by other females (Ozoga and Verme 1986). Most nursing does respond to distress calls by fawns (Richardson et al. 1983), and yearling does may benefit from the anti-predator strategies of the more experienced mother. Nixon et al. (1991) observed that daughters sharing their mother's home range tended to remain downwind of their mother during the postpartum period, perhaps as a means of locating her in case of danger. Active defense of fawns by related does has been reported among black-tailed does (O. hemionus columbianus) (Miller 1974, Dasmann and Taber 1956).

Often the majority of fawn deaths occurred after weaning from hunting or highway accidents. For 2-year old mothers, the lack of guidance by more experienced does and their own inexperience in avoiding these hazards on less well known home ranges may account for higher fawn mortality (Ozoga et al. 1982). Yearling mothers were usually traveling

with their mother during the postweaning period and could benefit from her experience at avoiding potentially dangerous situations.

Does >3 years old often selected habitats with dense understory cover during parturition and the early postpartum period, using habitats such as restored prairie and young pine plantations on the northern area and successional forest <30 years old on all 3 areas. Two-year old does often gave birth in oak-hickory forests and bottomland forests that did not offer fawns the dense overhead cover important for concealment during the early weeks postpartum (Huegel et al. 1985, Ozoga and Verme 1986, Lent 1974). We are not convinced, however, that differences in habitat selection alone accounted for the higher fawn deaths for 2-year old females. A combination of selecting somewhat more risk associated habitats, and their subordinate position in the female society while settling on a new home range only a short time before giving birth resulted in the higher fawn mortality associated with 2-year old mothers. Dusek et al. (1989) observed that older females selected habitats offering more diversity and interspersion compared with younger does along the Yellowstone River in Montana.

Fawn survival improved after age 2 for most marked does (Table 1). Even though does often suffered higher fawn losses during their second pregnancy, there were reproductive benefits to the individual doe in moving away from her dam for later conceptions. Ozoga and Verme (1984), for deer held captive and supplementally fed, found that isolated (mothers removed) 3-year old does (age at parturition and undergoing a second pregnancy) were more successful mothers (breeding earlier, conceiving larger litters with higher weaning success) than social 3-year-old does whose mothers were present during conception and parturition. They

associated these differences in fawn-rearing success with the more sedentary behavior of isolated does that remained on the range of the absent mother. In contrast, the social doe had to fight for a new parturition site that was frequently located in poor fawn-rearing habitat. Differences in fawn survival disappeared after these social does became familiar with their new range, with fawn rearing success equal to that of isolated does in subsequent years as does grew older and moved higher in the social hierarchy (Ozoga and Verme 1984).

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Table 1. Maternal age and percent mortality of fawns between birth and 1 year of age for west-central (WC), northern (NO), and east-central (EC) study areas in Illinois. The numbers of fawns observed are in parenthesis.

Doe Age	Percent Mortality (N)			
	WC	NO	EC	Total
1	0.0 (3)	11.1 (9)	10.7 (29)	9.7 (41)
2	26.0(50)	29.6 (28)	20.0 (50)	24.2(128)
3	16.7(60)	18.2 (33)	12.7 (63)	15.4(156)
4	17.1(64)	11.1 (18)	13.3 (45)	14.9(127)
5+	13.7(51)	30.0 (10)	15.4 (52)	15.9(113)

APPENDIX 4.   BEHAVIOR, DISPERSAL, AND SURVIVAL OF
       MALE WHITE-TAILED DEER IN ILLINOIS

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

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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 ≥ 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.

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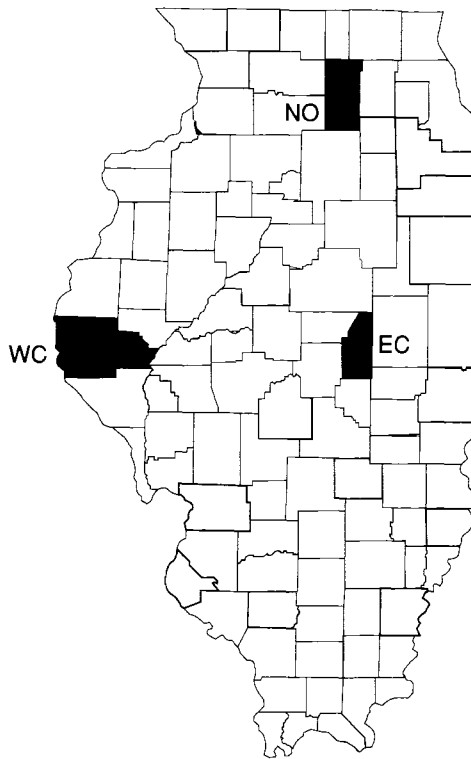
Figure 1. Illinois counties in which northern (NO), west-central (WC), and east-central (EC) study sites were located.

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°C, and July, the warmest, averages 23.6°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 ± 0.29 mm, N = 132; WC = 24.6 ± 0.63 mm, N = 38) and male fawn growth in mid-to-late winter on all three areas (chest girth: NO = 82.7 ± 0.7 cm, N = 29; WC = 80.9 ± 0.6 cm, N = 48; EC = 81.2 ± 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), asparate amino transferase (AAT-A & M), mannosephosphate isomerase (MPI-1), 6-phosphogluconate dehydrogenase (6PGHD), α-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 ≥ 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
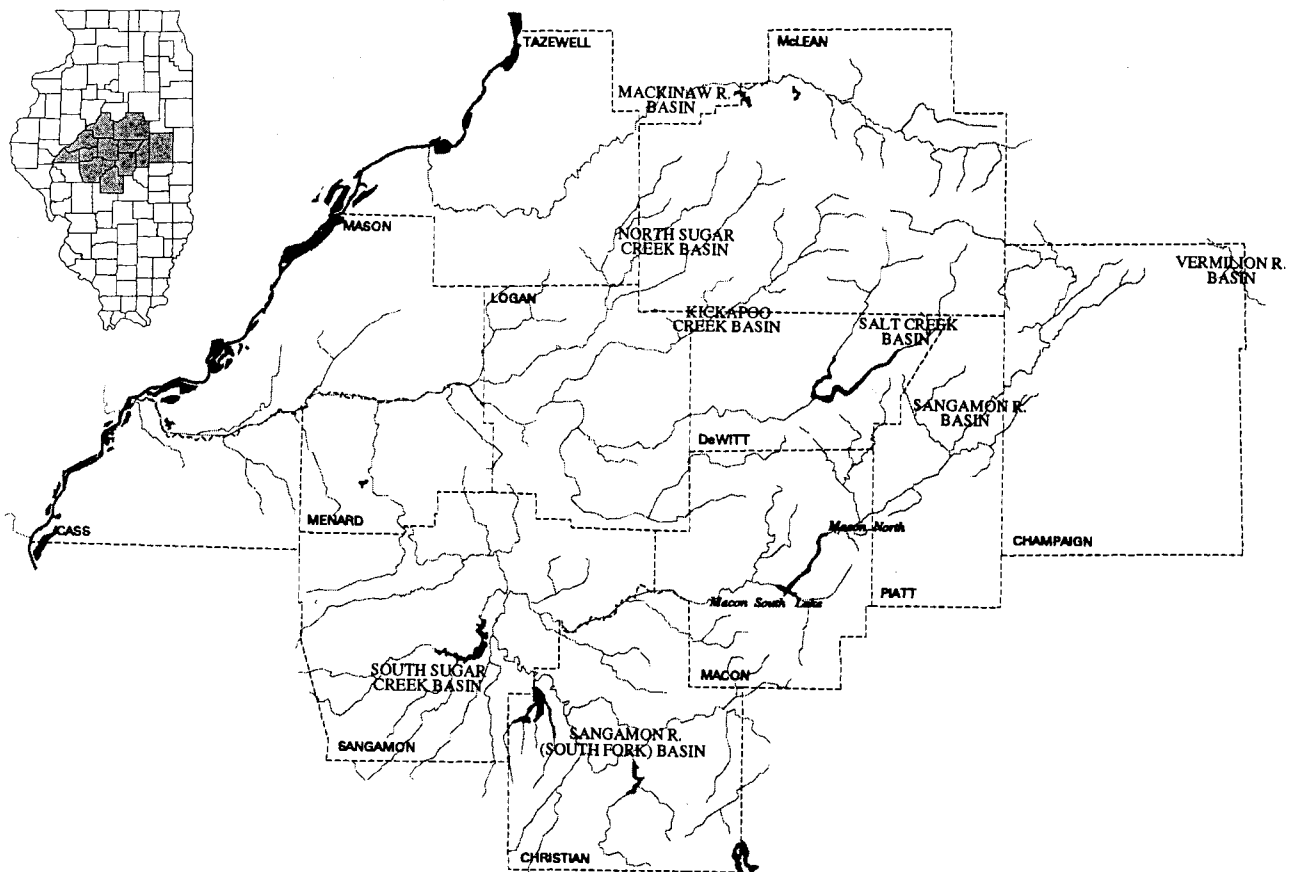
Figure 2. The principal watersheds and counties of east-central Illinois in which genetic variation in yearling males was examined using starch gel electrophoresis.

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

Study area	Land area (km²)	Year	No. counts	No. females Peterson-Lincoln method Mean ± SE	Per km²	Schnabel procedure Mean	95% CI	Per km²
West-central	10.2	1990	5	72.7 ± 16.4	7.1	65.7	40.9–108.1	6.4
		1991	8	71.0 ± 2.7	7.0	73.4	46.2–92.5	7.2
		1992	7	78.8 ± 4.5	7.7	80.1	61.3–136.2	7.9
North	16.7	1990	4	65.5 ± 13.9	3.9	66.8	36.5–127.7	4.0
		1991	8	76.7 ± 8.2	4.6	80.9	57.3–115.4	4.8
		1992	7	89.6 ± 4.4	5.4	90.7	66.2–132.5	5.4
East-central	12.0	1981	3	33.3 ± 1.4	2.8	37.7	17.6–70.8	3.1
		1983	5	51.5 ± 2.4	4.3	54.8	37.1–77.2	4.6
		1984	8	63.5 ± 5.3	5.3	64.3	47.2–84.3	5.4
		1985	7	58.3 ± 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 southwestward 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[a]	23	25.3	53	396	699
625[a]	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

[a] Brothers

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

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

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 pre-breeding 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 ± 168 m (N = 23 yearlings), from wooded sites into crop fields 878 ± 98 m (N = 23), and among crop fields 726 ± 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 ± 53 m, N = 6).

During the breeding period, centers of activity for yearlings (N = 5) shifted an average of 742 ± 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 ± 142 m from the center of their breeding ranges (Table 4).

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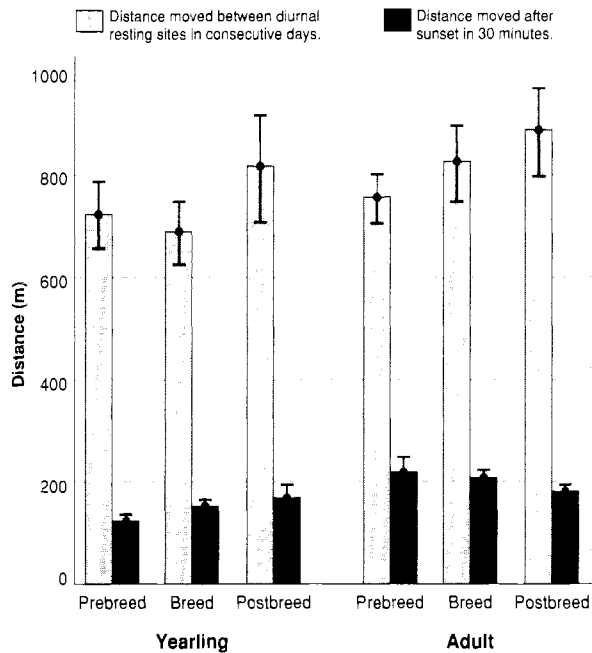
Figure 3. Mean (± 1 SE) distance moved (m) by yearling and adult males between diurnal resting sites on consecutive days and average 30-minute distance moved by males after sunset by season in Illinois.

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

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

ranges were 800 m apart. Male 302 was radio tracked on the EC area at ages 1, 2, and 5. This male's three pre-breeding 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 whitetails (*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 $565 ± 40$ m and males $721 ± 164$ m. Males penetrated farther into crop fields from woodland borders than females (males = 285

± 56 m , N = 8; females = 179 ± 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 ± 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 ± 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.			No.	Distance between arithmetic centers	Home range (ha)		Times
Mother	Son	Season	loc.	of activity (m)	Mother	Son	together
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.
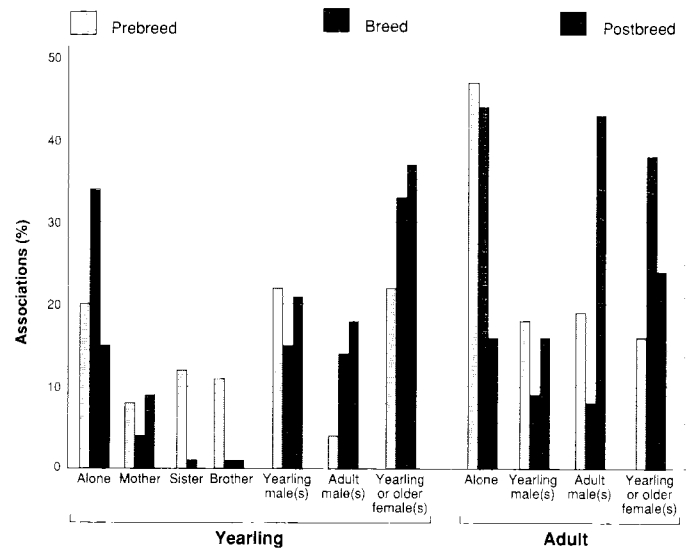
Figure 4. Associations of yearling and adult males throughout the year in Illinois based upon observations of males marked on three study areas.

(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 differ-ence 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 ± 3.7 km (N = 56) and fall movements only 18.6 ± 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 ± 3.8 km, N = 30; EC = 38 ± 4.4 km, N = 46; NO = 36 ± 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 | | |
| | | | Dispersal | |
		Sedentary	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 southest 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).
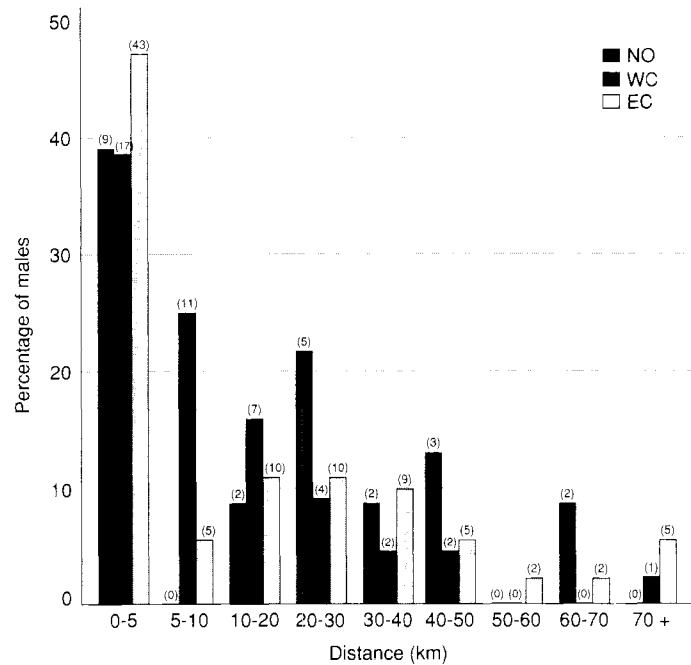
Figure 5. Distribution of dispersal distance (km) for dispersing yearling male deer in Illinois. Numbers above each column are the number of males in each distance interval.

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.
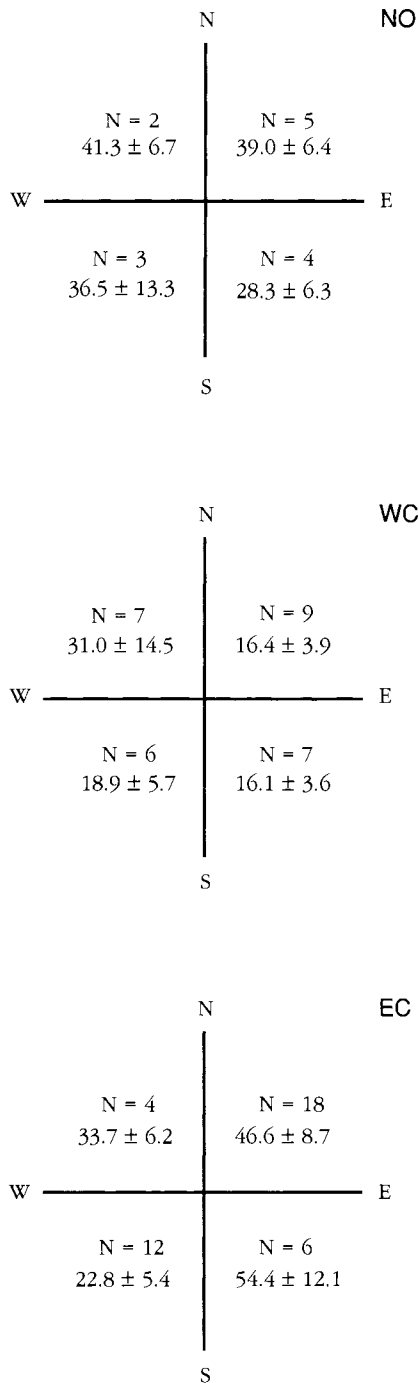
N   NO

N = 2	N = 5
41.3 ± 6.7	39.0 ± 6.4
N = 3	N = 4
36.5 ± 13.3	28.3 ± 6.3

W —————————— E

S

N   WC

N = 7	N = 9
31.0 ± 14.5	16.4 ± 3.9
N = 6	N = 7
18.9 ± 5.7	16.1 ± 3.6

W —————————— E

S

N   EC

N = 4	N = 18
33.7 ± 6.2	46.6 ± 8.7
N = 12	N = 6
22.8 ± 5.4	54.4 ± 12.1

W —————————— E

S

Figure 6. Directional distribution of dispersing yearling males and mean distance moved (km ± 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 a 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 ± 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 (≥ 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 ≥ 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	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	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	—	0.03	—
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	0.04	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 ≥ 2 years old exposed to mountain lion (*Felix*

Table 8. Survival and cause-specific mortality rates calculated from adult males > 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	Misc.[a]
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	0.01
EC			8,774	30	0.691	0.60–0.79	—	0.04	0.19	0.04	0.02	0.01
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[b]	0.75–0.99	—	—	0.09	0.03	—	—
WC			15,995	18	0.662	0.55–0.80	—	0.14	0.09	—	0.07	0.01
EC			27,545	32	0.645	0.55–0.74	0.02	0.04	0.20	0.04	0.02	0.02

[a] Includes drowning, poaching, fence, collisions, canine predation.

[b] 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[a]	
	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

[a] 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 understo-ries 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 Coblentz 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 calcifica-tion. 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 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 ± 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[a]							
Yearling	Prebreed	7	292	0[b]	+[b]	0	0	0	−[b]	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[c]							
Adult	Prebreed	3	117	0	0	0	0	+	+	0	0
	Postbreed	3	62	−	0	+	0	+	0	0	0
				WEST-CENTRAL[d]							
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

[a] 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.

[b] 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.

[c] 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.

[d] 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 ≥ 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 unhunted 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. 1983). 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)[a]								
	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

[a] 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 ± SE	Alleles per locus	Proportion polymorphic [a]	No. deer
Champaign	Sangamon	0.217 ± 0.061	1.89	0.667	25
	Vermilion	0.258 ± 0.073	1.67	0.667	7
Macon	North	0.244 ± 0.077	1.78	0.556	16
	South	0.254 ± 0.070	1.89	0.778	9
	Lake	0.266 ± 0.075	1.89	0.778	8
McLean	Mackinaw	0.185 ± 0.057	1.89	0.556	14
	Kickapoo	0.258 ± 0.057	2.00	0.778	24
	Sugar Creek	0.197 ± 0.064	1.67	0.667	6
Piatt	Sangamon	0.233 ± 0.070	1.78	0.556	29

[a] 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 hemoionus*) 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, 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 Coblenz 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 40 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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APPENDIX 5. EMIGRATION AND SURVIVAL OF ORPHANED FEMALE DEER
IN ILLINOIS

Emigration and Survival of Orphaned Female Deer in Illinois

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ABSTRACT

Emigration and survival were examined for 14 orphaned and 108 nonorphaned female white-tailed deer (Odocoileus virginianus) captured at <22 months of age from free-ranging populations in Illinois. Emigration rates were higher (P = 0.006) for female orphans than for nonorphans. Ten of 14 (71%) orphans emigrated in spring through early summer. In contrast, only 36 of 108 (33%) nonorphans emigrated. Annual survival rates for all females from three Illinois study areas were 0.60 (east-central) and 0.79 (west-central and northern) study areas. Possible stimuli for emigration among orphaned female white-tailed deer include pregnancy, low social position, and loss of maternal support.

INTRODUCTION

Harvest of female deer as a means of population control has become accepted in most states (Blouch, 1984; Wishart, 1984). An increasing white-tailed deer (Odocoileus virginianus) population in Illinois prompted the Illinois Department of Conservation (IDOC) to target female deer for harvest by increasing "antlerless only" hunting permits. Little is known, however, about how this relatively recent change in harvest strategy affects the behavior and composition of matrilineal groups, particularly the associations, seasonal movements, and survival of orphan females. Removal of the matriarch from a group may move some does into a higher position in the hierarchy but isolate others (Ozoga and Verme, 1984). Hawkins (1967) reported that sibling orphan fawns in southern Illinois remained together and formed family groups with other relatives.

Holzenbein and Marchinton (1992a) examined dispersal of orphaned male white-tailed deer in Virginia and concluded that orphans had a significantly higher affinity for their natal range than nonorphans. They also reported an overall higher 2-year survival rate for orphans (46.2%) than for nonorphans (6.7%). In contrast, Nixon et al. (1994) found no difference in emigration rates between orphaned and nonorphaned male fawns in Illinois. Woodson et al. (1980) observed low emigration rates for both male and female orphans (N = 21) and nonorphans (N = 37) and reported only one death (a nonorphan) through the first winter in an 826-ha enclosure in Virginia.

In this study, 14 females (13 fawns, 1 yearling) were either accidentally or intentionally orphaned. Home range, emigration behavior,

and survival of these orphans were compared with those of 108 female fawn and yearling nonorphans.

METHODS

We captured 122 female deer <22 months old with rocket-powered nets on three sites in Illinois (west-central [WCA]= 53, northern [NOA] = 17, east-central [ECA] = 52) from December through March 1980-85 on the ECA, and 1989-93 on the WC and NO study areas (Fig. 1). Deer were aged by tooth replacement and wear as either fawn ($\leq$ 12 months), yearling (13-24 months), or adult (> 24 months) (Severinghaus, 1949). All deer were ear tagged. Selected females (55 fawns, 8 yearlings) were fitted with radio collars (Wildlife Materials, Carbondale, IL.; Telonics, Inc., Mesa, AZ.; or Advanced Telemetry Systems, Isanti, MN.) operating at 165-166 MHz, and equipped with a motion-sensitive mortality signal. All other females (52 fawns, 7 yearlings) were marked with 7.5-cm wide plastic collars bearing reflective numbers. Our observations of social relationships among these deer were based on capture history (sex and age of capture group) and subsequent field observations of the marked females with other marked and unmarked deer.

Each study area included private lands in a rural agricultural setting and a public park, including areas open to hunting and a restricted (from firearm hunting) refuge area. The NO and EC study areas were located within some of the world's most intensively farmed areas. Forests consisting of small, isolated woodlots and narrow, forested corridors were found along railways, streams and roadways (Nixon et al. 1991).

Blood samples were collected on the WCA from all female deer in 1989-91 (N = 68), and from fawn does only in 1992-93 (N = 34) and

examined for pregnancy using progesterone assays (Wood et al. 1986). Field observations after parturition were used to confirm successful pregnancy for marked does on the other two study areas.

Nine females (8 fawns, 1 yearling) were accidentally orphaned (vehicle collisions or capture-related mortality) on the WC (4) (1990-92), NO (1) (1991), and EC (4) (1980-85) areas, respectively. In addition, in 1993 on the WCA, the dams (N = 4) of 5 female fawns were euthanized by gunshot to the head as set forth in the American Veterinary Medical Association guidelines, <u>1993 DRAFT REPORT OF THE AVMA PANEL ON EUTHANASIA</u> (Amer. Vet. Med. Assoc., 1992). In addition, the study was reviewed and approved by Western Illinois University Animal Use Protocol Committee. Dispatched deer were processed and donated to underprivileged families in west-central Illinois. After these removals, orphaned and nonorphaned does <22 months of age totaled 14 (WCA = 9, NOA = 1, ECA = 4), and 108 (WCA = 44, NOA = 16, ECA = 48), respectively.

Seasonal movements of marked does were documented by radio-location from a tracking truck or fixed-wing aircraft, observations by study personnel, and reported observations by the general public. Observations by the public were confirmed by study personnel whenever possible.

In 1993, home range size and distance moved between consecutive radio locations were examined for several months after capture (postbreeding period) for 4 fawn does (2 orphaned sisters and 2 nonorphans) on the WCA. Deer were tracked using two truck-mounted, four-element yagi antennas aligned in a null configuration. Radio tracking included one daytime radio-location followed by 3 to 4 hours of more intensive nighttime tracking (locations every 45-60 min.). Deer locations

were confirmed by use of the program LOCATE II (Nams, 1990). Home range area was defined by the minimum convex-polygon (Mohr, 1947) with at least 17 acceptable locations per deer using the program Ranges IV (Kenward, 1990). The harmonic mean (HM) estimator (Boulanger and White 1990) of home range was used for comparative purposes with other range estimates.

One-way ANOVA was used to test for significant differences ($P \leq 0.05$) between orphans and nonorphans in home range sizes and distance moved. Differences in emigration rates between orphans and nonorphans were determined for combined samples using chi-square contingency analysis ($P \leq 0.05$). For similar tests on the WCA only, where more than 1/5 of the cells were sparse (9 orphans, 44 nonorphans), Yates-corrected chi-square was employed (Wilkinson 1990). Chi-square contingency analysis was also used to compare emigration rates between pregnant and barren fawns.

The MICROMORT program was used to calculate seasonal and annual cause-specific mortality (using deer days per interval) for all female fawns and yearlings through their first (fawns) and second (yearlings) hunting season (Heisey and Fuller, 1985). The female year was divided into four seasons based on important behavioral or physiological changes that potentially affect survival and movement patterns (Holzenbein 1990, Nixon et al. 1991): postbreeding (16 Jan-15 May), parturition and early postpartum (16 May-15 July), postfawn (16 July-30 Sept), and breeding (1 Oct-15 Jan).

In this study, emigration was defined as severance of all matrilineal social ties (Moore and Ali, 1984), except social ties with siblings. This definition of emigration included dispersal and annual migration away

from the matrilineal group and natal range. We feel justified in using this definition of emigration for female deer in Illinois because 1) siblings were about as likely to disperse together (12 of 21 pairs) as to move separately (9 of 21 pairs) from ECA (Nixon et al., 1991) and sibling dispersal has been documented by others (Nelson and Mech, 1992; and Woodson et al., 1980); 2) only four cases of migration from the WCA occurred during the 4-year study and each migrating individual was an orphan (e.g., this population was non-migratory); 3) social organization in female white-tailed deer is based on a family group centered around a matriarchal hierarchy (Hawkins and Klimstra, 1970) with the matriarchal doe providing leadership to the family group (Coe et al., 1980; Hawkins and Klimstra, 1970; Nelson and Mech, 1984; Ozoga and Verme, 1984; Woodson et al., 1980).

RESULTS AND DISCUSSION

Chi-square contingency analysis on a pooled sample of female fawns and yearlings from the three study areas yielded significant effects of orphaning ($P = 0.006$) on emigration rates. Ten of 14 (71%) females orphaned when <22 months of age, and 36 of 108 nonorphans emigrated. On the WCA only, six of 9 (66%) orphans either dispersed (no returns) ($n = 2$) or migrated (left and returned) ($n = 4$), whereas only 7 of 44 (16%) nonorphans dispersed ($P = 0.005$). All emigration occurred in spring prior to (1 orphan and 1 nonorphan in April from the WCA) or during family breakup in May. Aggression towards young females during the fawning season may account for emigration during this period (Hirth, 1977; Nelson and Mech, 1992; Ozoga et al., 1982) and should have the same effect on orphans and nonorphans alike (Holzenbein and Marchinton, 1992b).

During spring of 1993, we documented wandering behavior for 3 of 5 orphans on WCA, and 2 of these 3 eventually emigrated. Wanderings occurred frequently (4 or 5 documented movements per individual over a 3-to-4-week period) and always in the same direction. Holzenbein and Marchinton (1992a) reported similar behavior for dispersing male fawns in Virginia. Two orphaned sisters (301 and 302) always wandered together, although simultaneous radio tracking and observations confirmed they were not always together on their winter-spring range. Female 302 eventually migrated in May 1993, but 301 remained on her natal range. Wandering behavior ceased in orphan 301 after her sister dispersed, suggesting the wandering behavior displayed by this set of twins was influenced by orphan 302. In contrast, Woodson et al. (1980) found orphan yearling male twins usually traveled and dispersed together, suggesting that neither twin would disperse unless both were so inclined. Nelson and Mech (1992) documented a case of brother-sister dispersal and concluded social relationships, such as various social interactions with relatives might influence or prevent dispersal from occurring in siblings. We documented two cases of orphaned siblings emigrating together from WCA. A brother-sister group (<10 months old) dispersed and a sister-sister group (1 <10 months of age, and 1 <22 months of age) migrated from WCA.

Wandering behavior also was observed in 3 of 44 nonorphans on WCA (1 in 1992 and 2 in 1993) during the fawning season. Two nonorphans eventually returned to their natal ranges and became sedentary, but one continued to wander for 10 months between her natal range and a range 3 km away. These wanderings between the two ranges increased during hunting season, particularly after the harvest of her dispersal mate and

twin brother. Nixon et al. (1994) and Woodson et al. (1980) reported that some yearling males and females displayed wandering behavior during family breakup, but later returned and settled on a range that included a portion of their natal range.

Home range size varied between orphans and nonorphans for 2 of the 3 HM estimators used (HM 50%, $P > 0.1$; HM 75%, $P = 0.04$; HM 95%, $P = 0.004$) (Table 1). Holzenbein and Marchinton (1992a) also found orphaned males <18 months of age had larger winter-early spring ranges than nonorphans. The distance moved did not vary ($P > 0.10$) for orphans and nonorphans from presumed bed location during the day to presumed evening feeding location, for consecutive evening locations ($P > 0.4$), and for all day and evening locations combined ($P > 0.7$) (Table 1).

Two mothers captured as adults on ECA were never observed associating with other deer, and we suspected they were immigrants. Two of their female offspring subsequently emigrated, behavior consistent with what might be expected for young females with mothers that hold a low rank in the social hierarchy. During a study of behavior and ecology of red deer (Cervus elaphus) in Rhum, Scotland, Clutton-Brock et al. (1982) observed that daughters of dominant mothers spent more time with their mothers than did daughters of subordinate mothers.

Samples were not sufficient to examine the effects of pregnancy on subsequent movements by orphaned and nonorphaned fawns. When orphans and nonorphans were combined, breeding condition had no effect on emigration rates on the three study areas combined ($X^2 = 0.317, 1$, $P > 0.5$).

Survival rates were high for both orphans and nonorphans (Fig. 2). Only 8 deaths among 122 female fawns and yearlings (three study areas combined and orphans and nonorphans combined) occurred outside breeding

and the coinciding hunting season. Samples, therefore, were too small to test for differences in seasonal survival among study areas for orphans and nonorphans. Likewise, samples of orphans on WCA (8), NOA (1), and ECA (4) were too small to test for differences in annual survival between orphans and nonorphans on individual study areas.

A two-way ANOVA of combined annual orphan and nonorphan survival approached significance (P = 0.06) among study areas and reflected the higher hunting mortality associated with the ECA (survival = 0.60 for ECA compared to 0.79 for both WCA and NOA).

No difference (X^2 = 0.001, df = 1, $P \geq$ 0.95) was found in annual survival between orphans and nonorphans for the three study areas combined. However, when annual survival was compared between all emigrants and sedentary females (orphans and nonorphans, from all study areas), sedentary females were more likely to survive (X^2 = 5.483, df = 1, P = 0.019) than emigrants.

Increased emigration by orphaned female fawns and yearlings in Illinois may be explained by the loss of social status due to the death of the dam. Because a doe's social position depends largely on her age (Clutton-Brock et al., 1982; Townsend and Bailey, 1981; and Ozoga and Verme, 1984), the social rank of an orphaned fawn may be reduced. Clutton-Brock et al. (1982) observed that threats among hinds in red deer were more common and more intense towards nonrelatives than relatives. They also observed that some (but not all) orphans in the population were regularly threatened by hinds and that orphaned females spent more time moving and standing than nonorphans and were forced to exist on the periphery of the group. Threatened individuals may be denied access to a food source and forced to spend time and energy moving away from the

attacker, always risking injury from more physical threats (Clutton-Brock et al., 1982). This type of "social outcasting" of orphans may serve as a stimulus for emigration, because individuals forced to emigrate are frequently the socially subordinate, younger and weaker members of the group (Archer, 1970; Lidicker, 1975; Watson and Moss, 1970).

If we consider the factors note above, the impetus to emigrate would likely be greater during parturition when parous females increase aggressive threats toward other deer, including offspring (Ozoga et al., 1982, Schwede et al. 1993). In most instances, emigration in this study was limited to the fawning season, a finding similar to previously reported patterns in female emigration (Nelson and Mech, 1992; Woodson et al., 1980). Repeated aggressive threats from adult does during fawning may cause yearling does to leave their mother's range permanently (Robinette, 1966), or to wander and eventually return to their mother's range when she becomes more tractable (Robinette, 1966; Dasmann and Taber, 1956). This behavior raises the following question: if orphans and nonorphans are under the same social pressure from adult does during fawning, why are orphans more likely to emigrate than nonorphans? Nelson and Mech (1992) concluded that a yearling needed to move only a short distance to escape threats from her mother whose movements were confined to her parturition range. Aggression therefore, cannot be the sole initiator for dispersal. Scent may play a role in maintaining a nonvisual bond between mothers and daughters in densely vegetated ranges during parturition. Nixon et al. (1991) obtained simultaneous locations from two pairs of mother-daughters in May-July on ECA and found that these daughters were more likely to be downwind of their mothers (21 of 34 locations). Downing and McGinnes (1976) also found 15 instances of

similar mother-daughter behavior within a Virginia enclosure. Scent may allow daughters to verify the location of their mothers and may act to reinforce the matrilineal bond without a physical confrontation. Orphans would not have this reassurance and as a result may increase their wandering behavior (Nelson and Mech, 1992) and home range size (Woodson et al., 1980; and this study) in an attempt to locate an area devoid of aggressive adult does. Finding such an area may be difficult in the intensively farmed regions of Illinois where competition for parturition ranges is intense (Nixon et al. 1992).

Missouri Dept. Conservation, Dr. R.E. Warner, University of Illinois, R. Stoll, Ohio Dept. of Natural Resources, Dr. S.K. Robinson, Illinois Natural History Survey, and the editorial office, Illinois Natural History Survey, reviewed the manuscript.

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Figure 1.--Location of study areas. Numbers at each site indicate female captures.

Figure 2.--Seasonal and annual survival for marked orphaned and nonorphaned female deer <22 months of age in Illinois. Results were produced by the MICROMORT program using deer days per interval (Heisey and Fuller, 1985). Numbers on each bar represent number of marked deer alive at the beginning of the interval.

Table 1.   Harmonic mean (HM) home range area ± SE (ha) and mean
distance ± SE (m) moved between consecutive locations for 2
orphans and 2 nonorphans during postbreeding period on the
WCA.

Estimator	Orphans	Nonorphans
50% HM	80 ± 9	52 ± 8
75% HM	140 ± 6	81 ± 11[a]
95% HM	194 ± 3	117 ± 4[b]
Day bed to feeding area movement	626 ± 174	402 ± 212
Consecutive evening locations	265 ± 127	336 ± 261
All movements combined	385 ± 186	360 ± 278

[a] Orphan and nonorphan means significantly different (F = 22.172; 2; 2 df; P = 0.042).

[b] Orphan and nonorphan means significantly different (F = 282.647; 2; 2 df; P = 0.004).
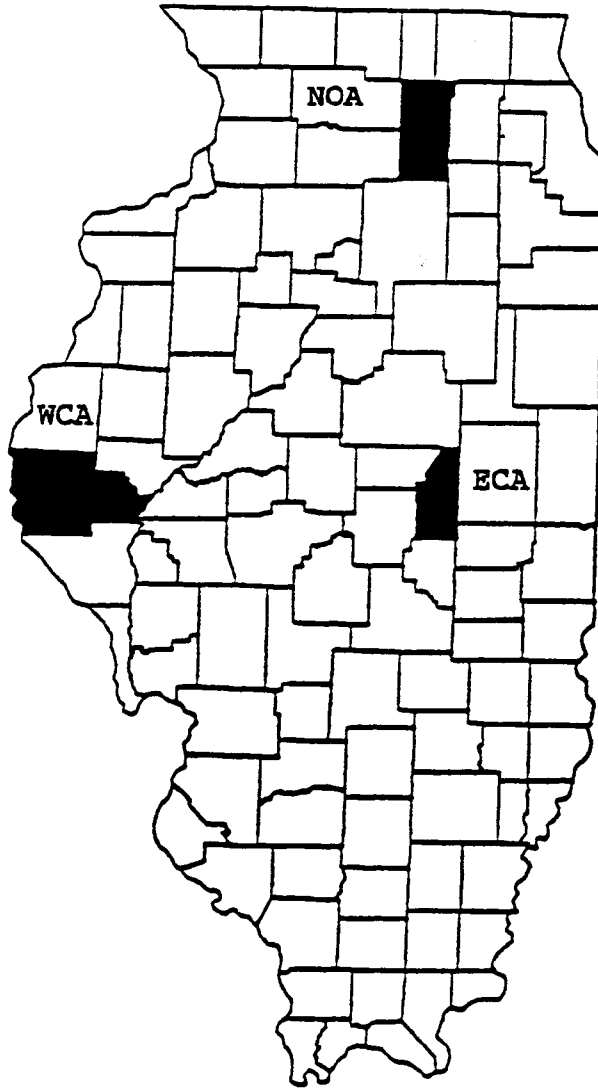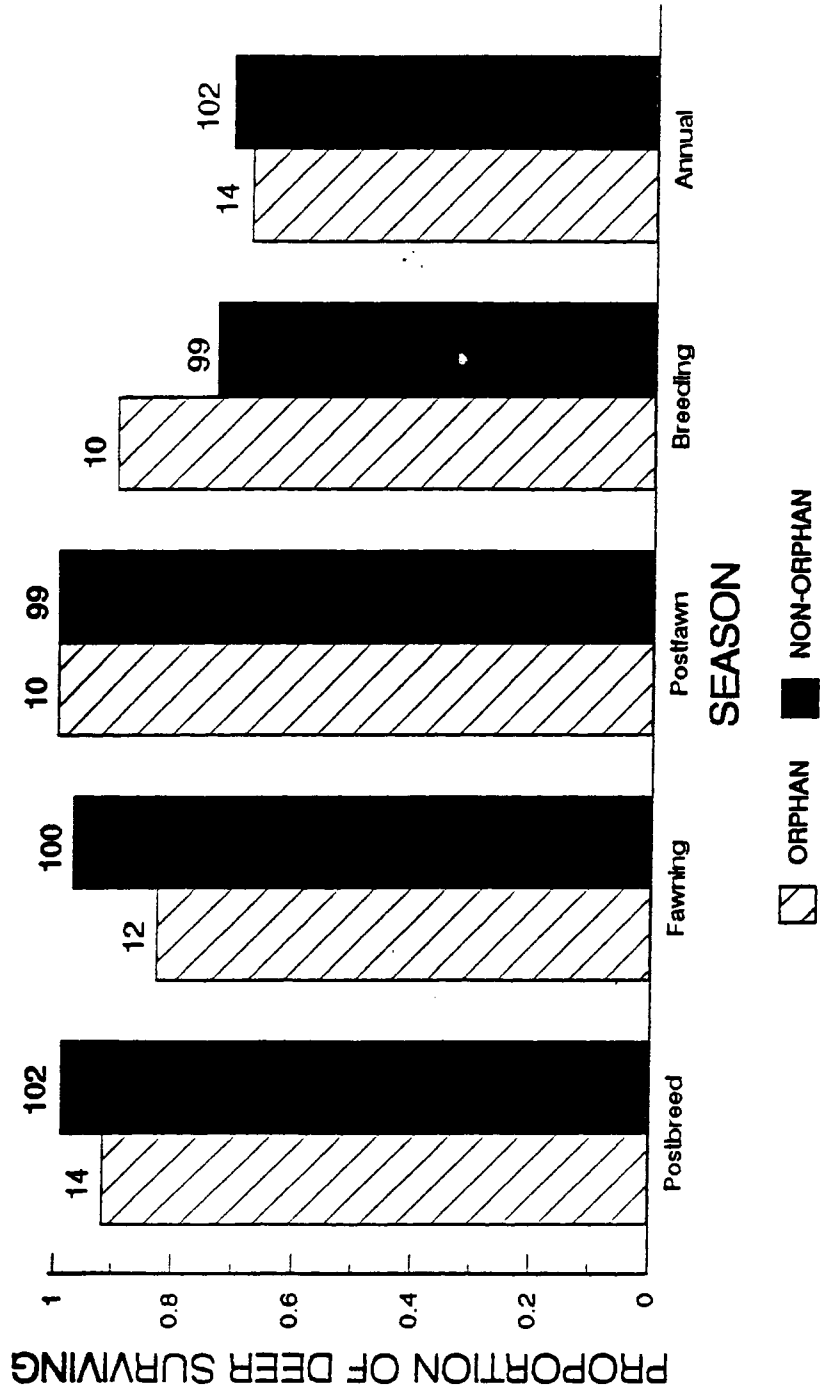
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