

DISPERSAL BY YEARLING MALE WHITE-TAILED DEER AND IMPLICATIONS FOR MANAGEMENT

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Abstract: The scale at which populations use the landscape influences ecological processes and management decisions. Dispersal and home-range size define the scale of landscape use for many large-mammal species. We measured dispersal and home-range size of yearling male white-tailed deer (*Odocoileus virginianus*) in southern Texas, and compared our results to values from the literature to understand the implications of dispersal in management of deer populations. We used radiotelemetry to monitor 22 yearling deer on one study site from October 1998 to October 1999, and 27 yearling deer on a second study site from October 1999 to October 2000. On the 2 study sites, 68% and 44% of yearling deer established new areas of use 4.4 ± 1.0 km and 8.2 ± 4.3 km, respectively, from the center of their autumn home range. Yearling males with spike antlers (2 points) were less likely to disperse than yearlings with fork antlers (>2 points) on 1 study site. Computer simulation showed that the scale at which deer use the landscape is large compared to property sizes in southern Texas and probably in other areas of the white-tailed deer's range. Differences in scale between land ownership patterns and landscape use by deer may result in a failure to meet management objectives and conflict among managers. High harvest rates for male deer occur in part because deer movements are large relative to property size, creating a "tragedy of the commons." Cooperative management groups are beneficial if all landowners in an area agree on management objectives. Otherwise, deer-proof fences often are erected to reduce conflicts among property owners.

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The scale at which populations use the landscape influences ecological processes and management decisions. Dispersal and home-range size define the scale of landscape use for nonmigratory populations of large mammals. For intensively managed populations of white-tailed deer, understanding dispersal and movements within home ranges is important for effective management. Yearling male white-tailed deer are more likely to disperse from their natal home range than other sex and age classes, and dispersal often is the greatest movement of any individual in the population (Hawkins et al. 1971, Nelson and Mech 1984, Tierson et al. 1985). Dispersal is an important contributor to gene flow across the landscape (Nelson 1993), and it can result in movement of deer from source to sink populations (Nixon et al. 1991), thus complicating the formulation of management plans and interpretation of harvest data (Rosenberry et al. 1999). Dispersal also may affect the rate at which disease moves across the landscape (Gross and Miller 2001).

Individuals in a population that disperse generally are younger and weaker members that main-

tain a subordinate social status (Greenwood 1980). Antler dimensions of yearling males are influenced strongly by environmental and maternal factors (e.g., mothering ability, milk production, and health; Lukefahr and Jacobson 1998, Scribner et al. 1989) and may serve as an index to fitness. Furthermore, dominance in male cervids is related in part to antler size (Espmark 1964, Barrette and Vandal 1986, Maylon and Healy 1994). These relationships suggest that yearling male deer with small antlers may be less fit, more subordinate, and therefore more likely to disperse. This dispersal pattern may be important to managers because yearling antler characteristics can predict antler size at older ages (Ott et al. 1997), thus providing an indication of whether deer with the potential to develop into economically valuable animals are dispersing from the property. Knowledge of which animals are likely to disperse may be beneficial because, in many species, dispersing individuals may have lower survival rates than philopatric individuals (Holzenbein and Marchington 1992, Petersburg et al. 2000).

Our objectives were to estimate survival, home-range size, and dispersal distances of male white-tailed deer for 1 year beginning in October of their yearling year. We then used dispersal dis-

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tances and home-range sizes from our study and those from the literature in a simulation model to assess the impact of dispersal and home-range size on the scale of white-tailed deer management. Finally, we compared dispersal rates between spike- and fork-antlered yearlings to test the hypothesis that males with ≤ 2 antler points would be more likely to disperse due to their presumed lower fitness and subordinate social status compared to males with > 2 points.

STUDY AREA

Our study was conducted on the Callaghan Ranch from October 1998 to October 1999 and on the Laureles Division of the King Ranch from October 1999 to October 2000. The Callaghan Ranch was located in the western Rio Grande Plains region, 43.4 km northeast of Laredo in Webb County, Texas, USA. The ranch consisted of 34,400 ha of mesquite (*Prosopis glandulosa*) dominated rangeland. There were no deer-proof fences within or on the border of the study area. Some properties in the vicinity were enclosed by deer-proof fences, and one study animal was located within 400 m of a deer-proof fence. The ranch was stocked with domestic cattle at a rate of 1 animal unit/21 ha, and deer density was estimated at 1 deer/9.7 ha (A. Bisbey, Callaghan Ranch, unpublished data). Free water was distributed across the ranch through earthen water catchments and ephemeral creeks. Supplemental feed was available at feeding stations at various locations on the study area at approximately 1 feeder/365 ha. Corn was provided as bait at the hunters' discretion during the hunting season. Webb County has an average daily maximum temperature in July of 36.8 °C, an average daily minimum in January of 6.3 °C, and receives a mean annual rainfall of 50.3 cm (Sanders and Gabriel 1985). The area received approximately 48 and 42 cm of rainfall in 1998 and 1999, respectively (A. Bisbey, Callaghan Ranch, unpublished data). The Laureles Division of the King Ranch is in the eastern Rio Grande Plains region, 4 km east of Kingsville in Kleberg County, Texas. The entire division consists of 103,691 ha, which includes 28,329 ha of crop land. There were no deer-proof fences on the study area or in areas where our study animals were located during the project. The area was a mixed shrub rangeland dominated by mesquite and huisache (*Acacia farnesiana*). The Laureles Division was stocked with domestic cattle at an average rate of 1 animal unit/10 ha. Deer density was estimated at 1 deer/

17.2 ha (M. W. Hellickson, King Ranch, unpublished data). Water was available from both ephemeral and permanent creeks, stock watering tanks, and earthen water catchments. Corn was provided as bait during the hunting season. Kleberg County has an average daily maximum temperature in July of 35.0 °C, an average daily minimum in January of 7.7 °C (Griffiths and Bryan 1987), and an average annual rainfall of 70 cm (National Climatic Data Center 1999). The Laureles Division of the King Ranch received approximately 76 and 48 cm of rainfall during 1999 and 2000, respectively (M. W. Hellickson, unpublished data).

METHODS

A net-gun fired from a helicopter (Barrett et al. 1982) was used to capture 23 and 28 yearling male white-tailed deer on the Callaghan and King ranches during October 1998 and October 1999, respectively. Deer age was determined by tooth replacement and wear (Severinghaus 1949). All deer were fitted with radiocollars (Advanced Telemetry Systems, Isanti, Minnesota, USA) equipped with mortality sensors. Coordinates of the site of capture were identified with a differentially corrected Global Positioning System (DGPS). Deer were released at the site of capture.

Locations of radiocollared deer were estimated by triangulation and biangulation from the ground using a radio-receiver and H-antenna (Telonics, Mesa, Arizona, USA). For each position, ≥ 2 bearings were taken from stations located throughout the study area. The location of each station was determined with DGPS. We attempted to locate each deer ≥ 2 times/week until after the post-rut period (Feb–Mar), and once/week thereafter, except for short periods of time when some deer that left initial home ranges could not be found. Additional positions were collected for deer that made large movements (> 3 km) or displayed dispersal behavior after the post-rut period. Visual observations also were recorded and identified by DGPS and contributed to final home-range estimates. Aerial locations were taken for deer that could not be found from the ground and also contributed to home-range estimates.

Deer locations were estimated from telemetry data using LOAS (Location Of A Signal) software (Ecological Software Solutions™, Sacramento, California, USA). Locations derived from ≥ 3 bearings were estimated by the Maximum Likelihood Estimator and those derived from 2 bearings were calculated by Best Biangulation. Loca-

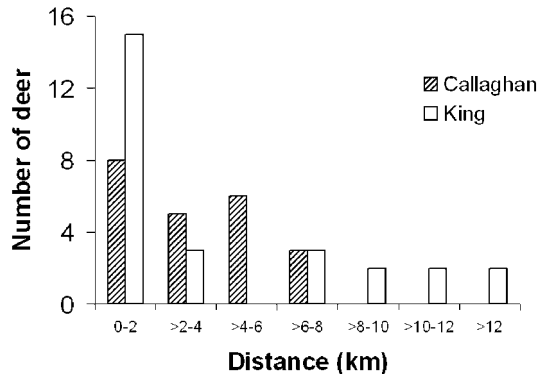


Fig. 1. Dispersal distances of yearling male white-tailed deer on the Callaghan and King Ranches in southern Texas, USA, 1998–2000.

tions were converted to a Geographic Information System (GIS) overlay for use in Arc-View software (Hutchinson and Daniel 1997). Average (\pm SD) telemetry error was 127.6 ± 54.2 m for biangulation and 128.2 ± 40.5 m for triangulation ($n = 5$ for each; McCoy 2001).

Home ranges were estimated using the kernel home-range estimator with the Animal Movement extension (Hooge and Eichenlaub 1997) in Arc-View software. Initially the default smoothing parameter (H) was used with a 95% probability polygon for all location points of an individual deer. For deer that dispersed, the same kernel analysis was then repeated separately for points in the initial and final home range. The initial home range was the area used from the time of capture until the deer exhibited dispersal or wandering movements and generally was a distinct area of utilization. Different areas of utilization also were analyzed separately for wanderers. This follow-up process was performed because analysis including all locations resulted in excessive buffering around locations that could not be corrected by smoothing parameter adjustments.

We defined dispersal as any movement that was made out of the initial home range without return. Deer that used areas outside of their initial home range but continued to return to their initial home range were defined as wanderers. Nondispersers were deer that remained in their initial home range throughout the study period, although they may have had ≤ 6 exploratory movements outside of their home range. Initial, final, and total home-range sizes were calculated. Initial home ranges are presented only for wanderers and dispersers. We defined final home range as the range that a deer settled in or where

it spent most of its time. Estimates for final home range are given for all groups. Total home range is the estimate of total area used by deer, calculated by adding initial and final home ranges.

Dispersal distances were estimated from the centers of initial and final home ranges using the arithmetic mean of the points in each home range calculated by the spider distance analysis tool in the Animal Movement extension. Dates of dispersal and departure of wanderers out of initial home ranges were estimated by taking the midpoint between the dates of the last location in the original home range and the first location after dispersal or departure occurred.

We compared dispersal dates relative to breeding season based on conception dates of Texas white-tailed deer in the western (year 1) and eastern (year 2) Rio Grande Plains (Williams et al. 1995). We defined the onset of breeding as the date of first conception and the peak of breeding as the average conception date. Dispersal of deer captured in 1998 and 1999 was analyzed separately.

A chi-square analysis was used to compare, separately by ranch, the proportion of spike-antlered deer with the proportion of fork-antlered deer that left their home range (both dispersers and wanderers). We defined antler points as points ≥ 2.5 cm in length. Wanderers were included in the dispersal group because they, like dispersers, moved out of their initial home range. A chi-square analysis was also used to compare the proportion of dispersers that died with the proportion of nondispersers that died. We used the lifetest analysis (Allison 1995) to determine the mortality rate of deer on each ranch. All means are reported ± 1 SD.

Modeling Scale of Landscape Use

We wrote a program in SAS (SAS Institute 1989) to model the landscape scale used by dispersing male white-tailed deer. For each simulation, 100 deer were randomly located on a square-shaped property of given size by generating x and y coordinates from a uniform random distribution. The location assigned to each deer represented the center of that deer's predispersal home range. The distribution of dispersal distances observed in our study (Fig. 1) was used to determine how far each deer moved during dispersal or wandering movements. The appropriate proportion of all deer in the simulation was assigned to each dispersal distance interval. The exact distance each deer dispersed within its respective interval (e.g., 2–3.9 km or 4–6 km) was

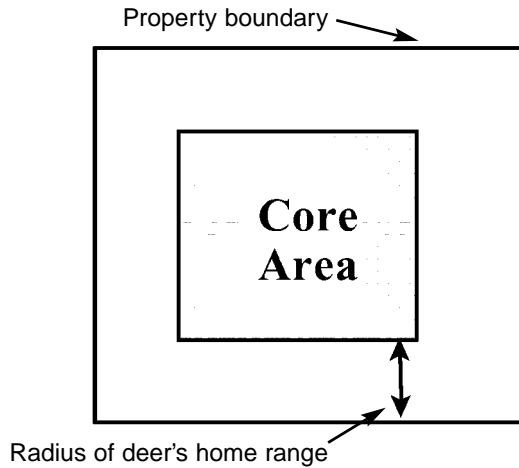


Fig. 2. The core area of a property, as defined in our simulations of deer dispersal, was that portion of a property beyond the radius of a deer's home range from the property boundary.

chosen randomly from a uniform distribution. The direction of dispersal was chosen randomly and used with dispersal distance to calculate the center of the deer's postdispersal home range. This procedure was repeated 10 times each for property sizes ranging from 500 to 100,000 ha, and we calculated the average proportion of deer whose final home range was within the property boundaries.

To incorporate the fact that a deer's movements within its home range could take it off the property, we placed a buffer equaling the radius of an average deer's home range, assuming a circular home range, within the boundaries of the property. We used the average final home range of all deer on a given ranch to calculate the buffer size. The area contained within this buffer was defined as the property core (Fig. 2), and represented an area in which deer would not be

subject to the management practices of neighboring properties. The variable reported in this simulation was the proportion of deer whose home ranges were in the core area after dispersal.

To compare the scale of landscape use by yearling deer in southern Texas to yearling white-tailed deer elsewhere in North America, we used values from the literature (Table 1) to repeat our computer simulation. For studies in which only average dispersal distance was reported, the proportion of deer dispersing was used to determine which deer moved, and dispersal distance of each deer that moved was determined as a random normal variable. When variance was not reported, a value was assumed that resulted in maximum dispersal distances approaching the maximum reported. Dispersal distances >1 km were set equal to 1 km to keep from inflating the proportion of nondispersing deer. For studies in which home-range size was not reported, we assumed either a home-range radius of 1,000 m or equal to the radius of home ranges reported by another study conducted in the same state.

RESULTS

Callaghan Ranch

We captured 14 and 9 yearling male white-tailed deer on 16 October and 1 November, 1998, respectively. Seventeen (73.9%) were spike-antlered (2 points) and 6 (26.1%) were fork-antlered (>2 points). One male was censored when it could not be located until late in the study period; therefore, all calculations (except mortality estimates) were made using 22 deer. A minimum of 40 and a maximum of 58 locations were taken for deer that survived throughout the study period. Sixty-nine percent of locations were derived from ≥3 bearings, 26% from 2 bearings,

Table 1. Studies and data used in simulation of landscape scale of dispersal movements and home-range (HR) size of yearling white-tailed deer.

Location	Habitat	Data used for dispersal distance	HR radius	Reference
Texas-Callaghan	Thornshrub rangeland	Distribution in Fig. 1	948 m	This study
Texas-King	Thornshrub rangeland and agriculture	Distribution in Fig. 1	1,166 m	This study
Maryland	Agriculture and forest	Distribution in Fig. 3 of cited study	1,000 m ^a	Rosenberry et al. 1999
Minnesota	Forest	Distribution in Fig. 1 of cited study	1,000 m ^a	Nelson 1993
Illinois	Agriculture and forest	80% disperse, \bar{x} = 8.0 km, SD ^b = 6.0	1,249 m ^c	Hawkins et al. 1971
Illinois	Agriculture and forest	51% disperse, \bar{x} = 40.9 km, SD = 38.1	1,249 m	Nixon et al. 1991
Montana	Riparian forest and agriculture	46% disperse, \bar{x} = 18.5 km, SD ^b = 15.0	970 m	Dusek et al. 1989

^a Not reported in cited study. Rounded value representative of home-range radii of yearling deer from other studies.

^b No measure of variation reported in cited study. Value chosen to result in range of dispersal distances similar to those in cited study.

^c Not reported in cited study. Taken from Nixon et al. (1991).

Table 2. Number and percent of spike and fork antlered yearling male white-tailed deer classified as nondispersers, dispersers, and wanderers on the Callaghan and King Ranches, southern Texas, USA, 1998–2000.

Study site Dispersal status	Spike		Fork		Total	
	<i>n</i>	%	<i>n</i>	%	<i>n</i>	%
Callaghan						
Nondispersers	5	31	2	33	7	32
Dispersers	8	50	3	50	11	50
Wanderers	3	19	1	17	4	18
Total	16		6		22	
King						
Nondispersers	4	100	11	48	15	56
Dispersers	0	0	7	30	7	26
Wanderers	0	0	5	22	5	18
Total	4		23		27	

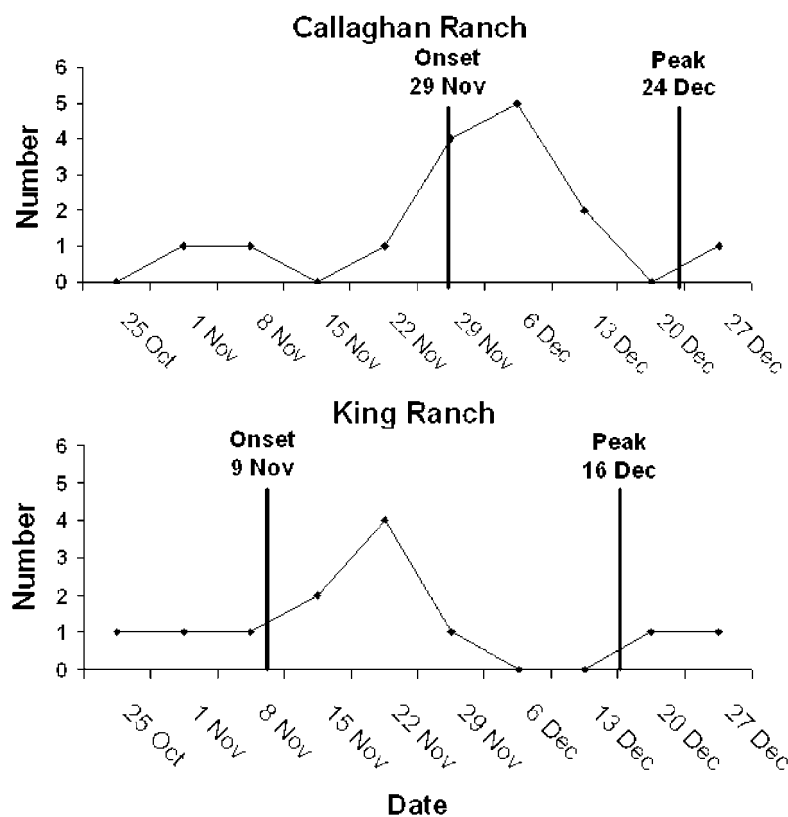


Fig. 3. Number of yearling male white-tailed deer moving out of initial home ranges by week relative to the onset and peak of breeding activity on 2 ranches in southern Texas, USA, 1998–2000.

4% were aerial locations, and 1% were visuals. Twenty-three and 27 locations were taken for deer that died or could not be located until late in the study, respectively.

Fifty percent of the deer dispersed, 18% were wanderers, and 32% were nondispersers (Table 2). Average dispersal date was 2 December \pm 15 days, which was 3 days past the onset (29 Nov) and 22

days prior to the peak of breeding (24 Dec) for this region. The average date of movement outside of the initial home range by both dispersers and wanderers was 4 December \pm 14 days with a range from 5 November to 2 January (Fig. 3).

Dispersers moved an average of 4.25 ± 1.76 km from their initial home range, with a minimum distance of 1.9 km and a maximum distance of 7.3 km. Wanderers moved 4.77 ± 1.02 km with a range of 3.3 to 5.7 km. The combined average between both groups was 4.39 ± 1.57 km. The rate of dispersal between spike-antlered (69%) and fork-antlered (66%) yearlings was not different ($\chi^2 = 0.009$, $df = 1$, $P = 0.926$; Table 2). Initial, final, and total home-range size averaged 143 ± 93 , 282 ± 148 , and 380 ± 173 ha, respectively, for all deer on the Callaghan Ranch (Table 3).

Annual nonhunting mortality of yearling bucks on the Callaghan Ranch was 4.5%. No deer were lost to hunting because hunters were instructed not to harvest radio-collared deer. The 1 mortality that occurred was a disperser. On 16 January, 41 days after dispersal,

hunters released the deer from a fence in which it had become entangled. The deer was found dead <24 hrs later. Too few mortalities occurred to test for the effect of dispersal on mortality.

King Ranch

We captured 19, 5, and 4 yearling male white-tailed deer on 13, 14, and 15 October 1999, respec-

Table 3. Initial, final, and total home-range sizes (ha) of yearling male white-tailed deer, by dispersal status on the Callaghan and King Ranches, southern Texas, USA, 1998–2000.

Ranch	n	Initial		Final		Total	
		\bar{x}	SD	\bar{x}	SD	\bar{x}	SD
Callaghan							
Nondispersers	7	–	–	–	–	294	155
Dispersers	11	132	102	281	159	413	196
Wanderers	4	173	61	264	138	437	86
King							
Nondispersers	15	–	–	–	–	525	342
Dispersers	6	160 ^a	90	265	95	345	142
Wanderers	5	679	544	330	229	1,009	602

^a n = 3 for this mean because 3 deer dispersed shortly after capture and we did not obtain an estimate of initial home-range size.

tively. There were 5 (17.9%) spike- and 23 (82.1%) fork-antlered deer. Of the 28 deer, 1 was censored when it died from capture-related injuries. A minimum of 42 and a maximum of 55 locations were taken for deer that survived throughout the study period. A range of 12 to 43 locations were taken for males that died or could not be located until late in the study. Fifty-three percent of locations were derived from ≥ 3 bearings, 37% from 2 bearings, <1% were aerial locations, and 10% were visual observations.

One deer was not located until reported hit by a vehicle off the study area 38 days after capture. Only capture and mortality locations were known for this deer, although it was considered a disperser because of the distance moved (14.9 km). Three other deer on the King Ranch that moved greater than the average dispersal distance from their capture sites and never returned within 3 km of the capture site also were classified as dispersers. We believe these deer satisfied our definition of dispersers based on the average distance (0.70 ± 1.7 km for both ranches) of initial home ranges from capture sites for all deer. Most deer (55%) were captured within their initial home range while 77% of all deer were captured <0.40 km from the edge of their initial home range.

Twenty-six percent of deer dispersed, 18% were wanderers, and 56% were nondispersers (Table 2). The average dispersal date was 21 November ± 21 days which is 12 days past the onset (9 Nov) and 25 days prior to the peak of breeding for this region (16 Dec). The average date of the first movement outside of the initial home range by both dispersers and wanderers was 24 November ± 19 days with a range from 26 October to 30 December (Fig. 3).

Dispersers moved an average of 7.86 ± 4.56 km with a range of 2.1 to 14.9 km. Wanderers moved

an average of 8.66 ± 4.17 km with a range of 3.4 to 13.8 km. The combined average was 8.20×4.29 km. The King Ranch had 0% of spike- and 52% of fork- antlered deer disperse (Table 2), suggesting a difference ($\chi^2 = 3.76$, $df = 1$, $P = 0.053$) in dispersal rates between the 2 groups. Initial, final, and total home-range size averaged 484 ± 494 , $427 \pm$

299, and 576 ± 423 ha, respectively, for all deer on the King Ranch (Table 3).

Five deer were harvested and 5 died of non-hunting causes on the King Ranch, resulting in a 22.1% nonhunting mortality rate. Of the 5 non-hunting mortalities, 1 was hit by a vehicle, 1 was entangled in a fence, and 3 were of unknown causes. Nonhunting mortality rate was higher for dispersers (41.7%) than nondispersers (0.0%; $\chi^2 = 5.39$, $df = 1$, $P = 0.02$), although this test may not be valid because of insufficient sample size.

Modeling Scale of Landscape Use

The relationship between property size and percent yearling male deer that remained on the property after dispersal was asymptotic (Fig. 4A), with the greatest effect of property size in populations with a high percentage of the population dispersing. On small properties (<1,000 ha), the proportion of deer remaining on the property after dispersal varied from 9 to 56% (Fig. 4A). On larger properties, 62 to 89% of yearlings remained on the property after dispersal. On property sizes >10,000 ha, a greater percent of deer remained on the property after dispersal in Texas than in other states.

Incorporating a buffer within the property boundary representing the radius of a yearling deer's home range resulted in $\leq 8\%$ of the deer remaining entirely on the property after dispersal for properties <1,000 ha (Fig. 4B). All other deer either left the property or were close enough to the boundary to have a portion of their home-range overlap an adjoining property. Properties of 12,000–25,000 ha were necessary in Texas studies to ensure 50% of yearling deer were maintained within the core of the property, whereas properties of 25,000–70,000 ha were necessary outside Texas. Even on properties of 100,000 ha, 17 to

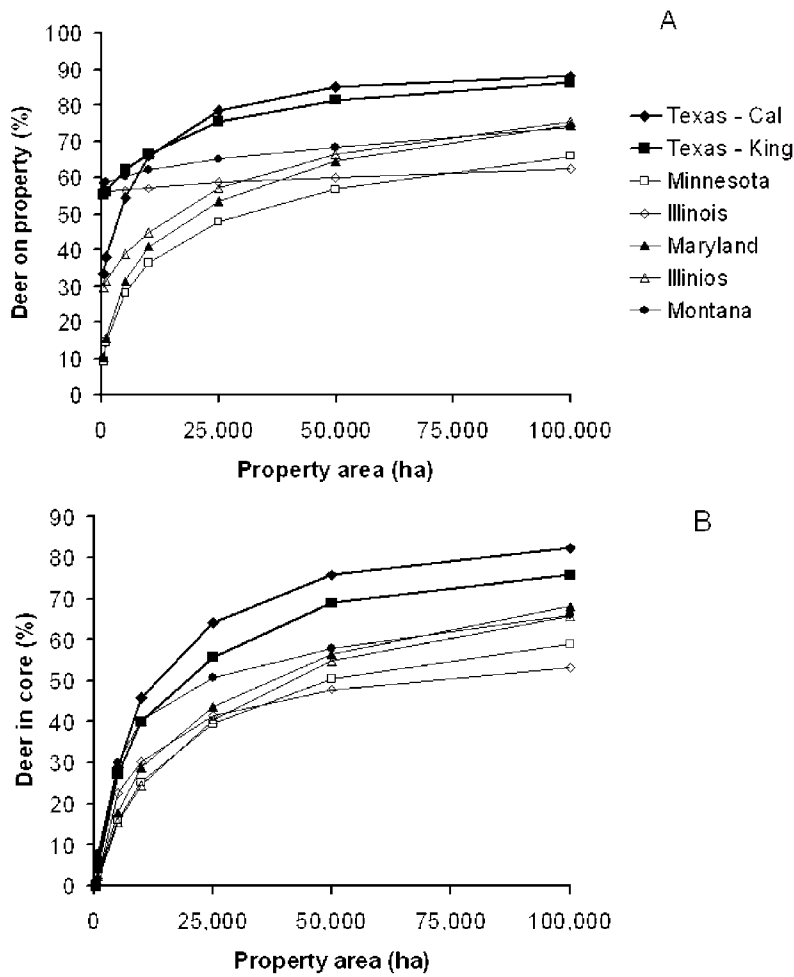


Fig. 4. The proportion of yearling male white-tailed deer remaining (A) on a property or (B) within the core of a property (Fig. 2) after the autumn dispersal period as a function of property size, using data from the literature (Table 1).

47% of yearling deer left the property or had home ranges overlapping a neighbor's property.

DISCUSSION

Dispersal

Percentage of deer dispersing in our study was similar to that in Georgia (50%; Kammermyer and Marchington 1976), Illinois (51%; Nixon et al. 1991), and Montana (46%; Dusek et al. 1989), but less than those reported in another site in Illinois (80%, Hawkins et al. 1971). A larger percentage of males (68%) on the Callaghan Ranch left their initial home ranges either through dispersal or wandering movements than on the King Ranch (44%). If the proximate reason for dispersal is aggression from maternal females (Holzen-

bein and Marchington 1992), differences in dispersal rates between our 2 study areas could be explained by differences in female harvest rates. However, females were harvested at an average rate of 20% of the number of females seen during pre-hunting season helicopter surveys on the Callaghan Ranch from 1995–1999 (A. Bisbey, Callaghan Ranch, unpublished data), while no females were harvested on the King Ranch during 1998 in the pastures where our study occurred (M. W. Hellickson, King Ranch, personal communication). Thus, the likelihood of dams surviving to their male fawn's dispersal age would be greater on the King Ranch, and a higher rate of dispersal would be expected. Because this was not observed, the presence of the dam may not be the sole mechanism triggering dispersal. Instead, the myriad of other factors

that differed between the 2 study sites apparently had a greater effect on the likelihood of a yearling male leaving his autumn home range.

Our data do not support the hypothesis that smaller-antlered males would be more likely to disperse because of nutritional or social inferiority. On the King Ranch, fork-antlered deer were more likely to disperse, while on the Callaghan Ranch an even percentage of spike- and fork-antlered deer dispersed. One possible explanation for this contradiction could be that larger-antlered males reach sexual maturity earlier than spikes and are triggered to disperse by sexual competition or mate searching. Ozoga and Verme (1985) found that dominant yearling males spent less time in natal ranges as the breeding season began, and subordinate yearlings

increased their association with related females as the breeding season progressed. In roe deer (*Capreolus capreolus*), larger-antlered yearlings, which are more sexually mature than small-antlered yearlings, are more likely to disperse because of aggression from mature males (Wahlström 1994). Furthermore, dispersing roe deer are heavier than philopatrics, which may also be an index of earlier sexual development (Wahlström and Liberg 1995). Rosenberry et al. (2001) examined behavior of yearling white-tailed deer males in Maryland and found that the majority of agonistic behavior (e.g., hard look, ear drop, sidle) was among yearlings as opposed to interactions with adult deer and that dispersers tended to participate more in breeding-season behaviors (e.g., antler threat, sparring). They also stated that dispersers and nondispersers were equally subordinate to adult males and females and correlated dispersal with sexual competition among yearlings. Although no indication of sexual maturity (e.g., antler size, body mass) was discussed, dispersing yearlings participating in breeding behavior would logically be more sexually mature than nondispersers that showed no participation. In the same Maryland study site, Shaw et al. (2003) noted that yearling males with large antlers were more likely to disperse than yearling males with small antlers when the deer herd was managed for older age classes.

Most movements out of initial home ranges by dispersers and wanderers occurred before the peak of the breeding season on both ranches. Average dispersal dates for both ranches were between the onset and peak of breeding, consistent with other studies reporting that dispersal occurs at the same time as breeding activity (Hawkins et al. 1971, Kammermeyer and Marchington 1976, Ozoga and Verme 1985). During this time, yearling males probably received aggressive pressure from related females and dominant males. An alternate hypothesis is that yearling males were sexually mature and moved either in search of receptive females or in an attempt to avoid inbreeding. Nelson and Mech (1984) reported yearling males separating from their mothers and making exploratory trips at 12 months of age, but most began dispersing during their first potential breeding season at 17 months. An exception to breeding season dispersal occurred in Illinois where most male dispersal took place during summer (Nixon et al. 1991).

The timing of dispersal movements is important in managing deer populations. If movement

occurs after annual population censuses, then the number of yearling males on a property may change dramatically after the census. If dispersal occurs during the hunting season, then harvest of yearling males may increase, particularly if deer are likely to cross property boundaries during dispersal. Both of these conditions are true in southern Texas, making population and harvest projections difficult.

Home-range Size

Final home-range sizes of yearling males in our study were considerably larger than those of male deer in other southern regions (Michael 1965, Kammermyer and Marchington 1976, Inglis et al. 1979), although comparisons are confounded by different home-range estimators used in other studies. Studies conducted in more northern regions reported larger home ranges (Nelson and Mech 1984, Nixon et al. 1991), probably because of movements between summer and winter ranges.

Mortality

Nonhunting mortality on the King Ranch (22.1%) was comparable to that reported by Nelson and Mech (1986; 21%) and Van Deelen et al. (1997; 16%). The Callaghan Ranch had lower nonhunting mortality rates (4.5%) than expected. Half of nonhunting mortalities were caused by human changes in the landscape (fences and roads). Dispersing deer may be more susceptible to these landscape changes because they are moving long distances through unfamiliar areas. The deer that made the greatest movement (14.9 km) moved off the King Ranch and was struck by a vehicle. All other mortalities were found in areas occupied for ≥ 1.8 months.

Nonhunting mortality was not concentrated in any season, but 4 of 5 males that died on the King Ranch did so after the breeding season ended (18 Jan). One deer died soon after the breeding season ended, another died in March, while the other 2 mortalities occurred during summer (Jun and Aug). Summer is often a period of nutritional and environmental stress in southern Texas due to high temperatures and poor forage conditions as a result of sporadic rainfall (Meyer et al. 1984).

Mortality rates differed on the King Ranch between deer that left initial ranges and nondispersers, with all nonhunting mortalities being dispersers and wanderers. Although there was no significant relationship on the Callaghan Ranch, the one mortality that occurred was a disperser. It

might be predicted that mortality would be higher for yearlings on the Callaghan Ranch because a larger proportion of deer dispersed. However, mortality rates can vary geographically due to a number of factors such as predation risks and habitat conditions. If mortality rates are greater for deer that depart natal ranges due to the exploration of novel areas and associated energy costs, then wanderers should be more susceptible to mortality risks than dispersers who apparently settle more efficiently. Future research should investigate this relationship with larger sample sizes. Hunting mortality varied between our study sites because of differences in harvest guidelines on each site. All deer harvested were shot after the average date of dispersal and within the home range they used initially after their capture. Other studies (Roseberry and Klimstra 1974, Nelson and Mech 1986) reported dispersing deer were more susceptible to harvest.

Scale of Landscape Use

Movements made by yearling male deer, both within their home range and those associated with dispersal, help define the scale at which white-tailed deer management should occur. Our results show that on properties <10,000 ha in size, >50% of the yearling males present on a property in October will either leave the property entirely or be susceptible to management by neighbors. In central and northern portions of the United States, properties need to be over 25,000 ha to ensure >50% of yearling deer will be maintained entirely on the property. These results are conservative because they assume square-shaped properties. As length and width axes of a property become more disparate (i.e., more elongated or rectangular in shape), the size of the core will shrink.

Most properties in Texas are small relative to the scale at which deer use the landscape. Eighty percent of properties in rural Texas are <200 ha. Even in southern Texas, where property sizes tend to be large, average rural property size ranges from 250 to 6,000 ha, depending on county (Wilkins et al. 2000). Property leased for deer hunting in southern Texas averaged 2,067 ha (Hanselka et al. 1991). Therefore, most property owners in southern Texas are managing deer with their neighbors and this is likely true of many areas of private land within the white-tailed deer's range.

Dispersal limits inbreeding in cervids and is one of the main contributors to gene flow and maintenance of genetic diversity (Greenwood

1980, Lidicker and Patton 1987). Antler size, body mass, and fat levels of cervids are positively correlated with heterozygosity (Scribner and Smith 1990). Inbreeding has been linked to higher juvenile mortality in ungulates (Ralls et al. 1979). Habitat fragmentation may restrict gene flow in a population and is a concern in the conservation of many species (Soule 1983, Demarais et al. 2002). Landscape features or management practices prohibiting dispersal may reduce genetic exchange and increase homozygosity. However, dispersal patterns in white-tailed deer suggest that even severe fragmentation from agriculture, such as described by Nixon et al. (1991), is not sufficient to cause isolation. In fact, dispersal distances appear to be greater in landscapes fragmented by agriculture. The impact of other forms of fragmentation, such as urban development and deer-proof fences, on dispersal and gene flow in white-tailed deer is not clear (Demarais et al. 2002).

MANAGEMENT IMPLICATIONS

Our results support the observations of Rosenberry et al. (1999) that yearling dispersal can complicate interpretation of harvest data. Characteristics of yearling male deer often are used to assess herd health because they often are the most common age and sex class in the harvest and are sensitive to nutritional conditions (Harder and Kirkpatrick 1994). Yearling deer harvested on a small landholding after the beginning of the breeding season may reflect range conditions of some place other than the harvest site. Interpreting harvest data may be even more difficult if larger-antlered yearlings are more likely to disperse, as suggested from our King Ranch data.

When deer use the landscape at a scale less than the average size of management units, then population management is possible. Our results indicate that for management involving yearling male deer, the size of a viable management unit may be >25,000 ha as suggested by the reduction in the slope of curves in Fig. 4B. As management units become small relative to the scale of deer landscape use, then some deer management objectives will become difficult to achieve. The results of our simulation study show that the scale at which deer use the landscape is large compared to the average size of private landholdings in Texas and probably elsewhere in the white-tailed deer's range. A predictable outcome of this disparity is that in many instances, male deer will be harvested at first opportunity, because if they are not, they are likely to be harvested on another

er property. This tragedy of the commons (Hardin 1968) means there is little opportunity for male deer to mature and the natural social system determining which males breed (Hirth 1977, Marchinton and Hirth 1984) may be disrupted. To avoid the highly skewed age ratios resulting from heavy harvest of yearling male deer, managers in areas composed of small landholdings can either increase the effective size of their property (that is move to the right on the x -axis of Fig. 4) or restrict deer movements. Property size can effectively be increased through management cooperatives in which many small landholdings are managed as a unit (Rollins and Higginbotham 1997, Harper et al. 1999). If managers are unable to agree on management objectives, a necessary prerequisite of management cooperatives, then restricting deer movements through the use of deer-proof fences may occur. In southern Texas, 61% of respondents to a deer management survey had properties entirely (26%) or partially (35%) enclosed by deer-proof fences (Bryant et al. 1999). Confining deer with fences has both positive and negative biological and social implications (Demarais et al. 2002).

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