



Management and Conservation Article

Influence of Roads, Rivers, and Mountains on Natal Dispersal of White-Tailed Deer

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ABSTRACT Natural and anthropogenic landscape features, such as rivers, mountain ranges, and roads can alter animal dispersal paths and movement patterns. Consequently landscape, through its effects on dispersal, may influence many ecological processes, including disease transmission, invasion dynamics, and gene flow. To investigate influences of landscape features on dispersal patterns of a large mammal, we captured and radiomarked 363 juvenile male white-tailed deer (*Odocoileus virginianus*), including 212 confirmed dispersers, in 2 topographically dissimilar study areas in Pennsylvania, USA. Dispersal azimuths were uniformly distributed in the western study area (WSA), where there was irregular, hilly topography. Mean dispersal azimuths paralleled ridge direction in the eastern study area, where long parallel ridges were aligned northeast–southwest. Major roads in both areas and a large river in the WSA were semipermeable barriers to dispersal of juvenile males; dispersal paths were less likely to intersect these linear features. Dispersal movements were direct and brief, typically lasting <12 hours. For all dispersers, we found no evidence for preference or avoidance of establishing adult, postdispersal ranges in proximity to roads; however, deer that encountered roads near the terminus of their dispersal path were more likely to stop on the near side. Further, for deer that established postdispersal home ranges near major roads, these features influenced range placement such that locations were typically clustered on one side of the road. The influence of roads, rivers, and mountains on dispersal paths and postdispersal locations of white-tailed deer suggest that landscape-specific features should be considered in conservation and management of this and possibly other species of large mammals.

KEY WORDS barriers, disease spread, dispersal direction, dispersal pathway, emigration, movement, *Odocoileus virginianus*, path analysis, Pennsylvania, white-tailed deer.

Dispersal, or permanent movement away from source, influences many ecological processes, such as gene flow, disease transmission, and range expansion (Nathan 2001). Recently there has been interest in better understanding the patterns, processes, and consequences of dispersal (Bullock et al. 2001, Clobert et al. 2001). During the transfer phase of dispersal, landscape features such as mountains, rivers, and roads can alter dispersal paths and function as complete or semipermeable barriers, thereby influencing individual behavior and population dynamics (Mader 1984, Forman and Alexander 1998, Wiens 2001, Andreassen et al. 2002).

Anthropogenic habitat alteration, including construction of roads and urban centers, has increased dispersal-related mortality or prematurely terminated dispersal (Beier 1995, Trombulak and Frissell 2000, Shine et al. 2004). Dispersal barriers represent special conservation concerns, and populations may become genetically isolated as gene flow is limited by urbanization and habitat fragmentation (Ernest et al. 2003, Dixon et al. 2007). Recent efforts to mitigate the negative effects of these barriers have included restoring population connectivity via corridor construction (Beier 1993, Mech and Hallett 2001, Haddad et al. 2003) and translocation (Hedrick 1995, Westemeier et al. 1998, Matthee and Robinson 1999).

Landscape features may also influence dispersal direction. In simplified dispersal models movements are assumed to be nondirected, thereby maximizing outbreeding (Slatkin 1973,

Porter and Dooley 1993). However, asymmetrical, directionally biased dispersal can result from landscape formations such as mountain ranges (Matics 2003, Rueness et al. 2003), large bodies of water (Ayres and Clutton-Brock 1992, Hayes and Sewlal 2004, Blanco et al. 2005, Blanchong et al. 2007), and unsuitable habitat patches (Desrochers and Hannon 1997, Berry et al. 2005). Deviation from random, directional dispersal has implications for many ecological processes, including gene flow (Slatkin 1987), population spread and persistence (Lutscher et al. 2005, Pachepsky et al. 2005), pathogen transmission (Xu and Ridout 2001), and invasion dynamics (Sallam et al. 2001, Cook and Crisp 2005).

We studied dispersal paths of radiomarked white-tailed deer (*Odocoileus virginianus*) associated with different landscape characteristics. We evaluated topographical influences on dispersal directionality by comparing dispersal on a study area composed of long parallel ridges with one that had irregular topography. Further, because of numerous major roadways in both areas and a large river in one area, we investigated effects of these features on dispersal paths of deer and examined their potential role as barriers to dispersal movements. From a subset of deer fitted with Global Positioning System (GPS) radiocollars we obtained data on composite segments of actual dispersal paths and travel time of deer. Our objectives were to 1) analyze segmental arrangement and duration of dispersal of juvenile male white-tailed deer, 2) examine potential influence of landscape features on dispersal directions, and 3) evaluate effects of potential barriers, specifically major roads and rivers, on dispersal direction and distances of white-tailed

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deer. We hypothesized that linear landscape features, such as roads, rivers, and mountains, would restrict or redirect dispersal paths of white-tailed deer.

STUDY AREA

We studied dispersal movements of juvenile male white-tailed deer on 2 study areas in Pennsylvania, USA. The Western Study Area (WSA; 1,200 km²) was located in Armstrong County in the Appalachian Plateau region of western Pennsylvania. Mean daily temperatures ranged from -2.8°C in January to 22.8°C in July. Annually, there was a mean of 37.2 days with snow depth ≥ 2.5 cm and 4.6 days with snow depth ≥ 25 cm. Forested land (49% of the study area) was dominated by northern red oak (*Quercus rubra*) and white oak (*Quercus alba*) along with other species such as maple (*Acer* spp.), birch (*Betula* spp.), American beech (*Fagus grandifolia*), and hickory (*Carya* spp.). However, forests were fragmented by agricultural fields, which comprised most of the remainder of the landscape. Corn and soybeans were the most common crops, and much of the forested landscape existed as isolated woodlots. Elevations in the WSA ranged from 800 m to 1,500 m, but topography was irregular (i.e., the region lacked directionally oriented topography) and there were no large ridges in the area. In addition to roadways, the Allegheny River, which formed the western boundary of the capture area in the WSA, may have influenced dispersal in this area. Bisecting Armstrong County, this river, flowing north to south, had an average width of approximately 300 m and average discharge of approximately 475 m³/sec. Average discharge of all other streams in the study area was <16 m³/sec.

The Eastern Study Area (ESA; 620 km²) was located in Centre County, in the Appalachian Ridge and Valley region of central Pennsylvania, approximately 150 km east of the WSA. Mean daily temperatures ranged from -3.7°C in January to 21.8°C in July. Annually, there was a mean of 49.3 days with snow depth ≥ 2.5 cm and 4.0 days with snow depth ≥ 25 cm. Unlike the WSA, the ESA had regularly trending topography, with long, parallel ridges trending northeast–southwest across the region. Ridges were interspersed by long, narrow valleys, typically 2–4 km wide. Elevations ranged from 350 m to 650 m. Forests (57% of the study area) were less fragmented than in the WSA, because agriculture, including row-crops and dairy farming, was restricted to valleys. Dominant tree species were similar to those of the WSA, including oaks, red maple (*Acer rubrum*), and hickory. There were no major rivers in the ESA; average discharge of all streams was <10 m³/sec. Both study areas contained numerous large roadways (i.e., state routes, United States routes, and interstate highways) that may have influenced dispersal paths of white-tailed deer.

Deer density was approximately 11–13.5/km² in the WSA and 7–11/km² in the ESA (Long et al. 2008). Deer in both study areas were nonmigratory, and peak periods of natal dispersal were during May–June and October–November (Long 2005, Long et al. 2008).

METHODS

Capture and Monitoring

From December 2001 to April 2004, we captured and radiomarked 363 juvenile male white-tailed deer in the 2 study areas ($n_{\text{WSA}} = 239$, $n_{\text{ESA}} = 124$). We captured deer in late winter–early spring, such that at time of capture male fawns were approximately 7–10 months of age. Dispersal of white-tailed deer younger than 11 months is rare; thus, capture of fawns between late December and early April decreased the likelihood of capturing fawns that had already dispersed (Marchinton and Hirth 1984). Deer were captured using Clover traps, drop-nets, rocket-nets, and net gun from helicopter (Long et al. 2005).

We equipped most male fawns ($n = 340$) with very high frequency (VHF) radiotransmitters, either 245-g expandable neck collars or 19-g ear-tag transmitters (Advanced Telemetry Systems, Inc., Isanti, MN). We fitted the remaining 23 fawns with expandable automatic release GPS neck collars (Telonics, Inc., Mesa, AZ). We monitored deer via ground-based telemetry or, when we could not locate deer from the ground, aerial telemetry from fixed-wing aircraft. We estimated the location of deer 1–3 times weekly using Location of a Signal v. 2.04 (Ecological Software Solutions, Sacramento, CA) from intersections of ≥ 2 telemetry bearings. We monitored deer until they died or transmitters failed. We programmed GPS collars to record deer locations more frequently during peak dispersal periods (one location every 7 hr, May–Jun; one location every 2.5 hr, Sep–Dec). During periods when dispersal was less likely, scheduled locations were less frequent (one location every 23 hr, Jan–Apr and Jul–Aug). We programmed GPS collars to release automatically on 31 January, the year following capture. Capture, marking, and monitoring protocols were approved by the Pennsylvania State University Institutional Animal Care and Use Committee (Protocol no. 01R135).

We defined natal dispersal as permanent emigration from natal range to a distinct adult range, such that predispersal locations did not overlap postdispersal locations (Kenward et al. 2001, 2002; Long et al. 2005). We delineated natal and adult ranges using minimum convex polygons (MCP), which we estimated using the Animal Movement Extension (Hooge and Eichenlaub 1997) for ArcView 3.2. We determined dispersal fate (i.e., disperser or nondisperser) for 274 of the 363 fawns equipped with radiotransmitters; the remainder died or experienced premature transmitter failure (Long et al. 2008). Of those with confirmed dispersal fates, we estimated predispersal and postdispersal MCPs of 262 VHF-collared deer from an average (SD) of 30.3 (16.1) and 14.8 (13.5) locations, respectively. Similarly, we estimated pre- and postdispersal MCPs of 12 GPS-collared deer from an average of 578.1 (249.4) and 408.3 (288.3) locations, respectively.

Data Analysis

We used only data from juvenile males equipped with GPS collars to evaluate dispersal travel pathways, due to an

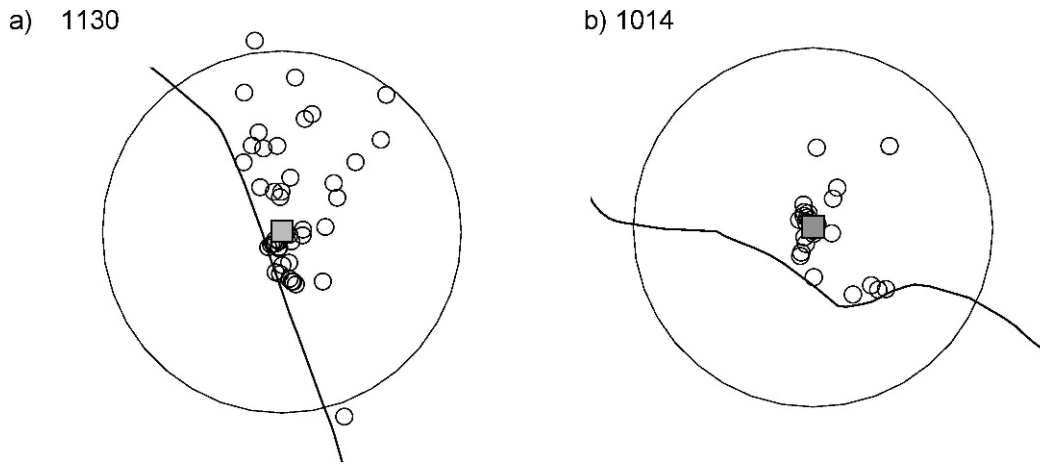


Figure 1. Two examples of postdispersal locations of male white-tailed deer in proximity to a major road in Pennsylvania, USA (2002–2005). We buffered median adult locations (gray squares) with a typical home range radius for the study area (1.2 km), and we plotted all postdispersal locations as empty circles. We labeled plots by deer identification number. We recorded no postdispersal locations for deer 1130 ($n = 44$) or deer 1014 ($n = 26$) on the far side of the road; however, the unused side represented 41% and 35% of expected use, respectively.

insufficient number of locations for deer equipped with VHF transmitters. We mapped dispersal paths using the last known location within natal range, locations during the transfer phase, and first known location within adult range. During the transfer phase, we considered only sequential movements >250 m (i.e., we retained only the first location of closely spaced sequential locations for path analyses). From these data, we estimated path straightness by dividing straight-line distance between first and last point of dispersal path by total path length (Alternate Animal Movement Routes Extension for ArcView 3.x, v2.1).

We calculated direction of dispersal as the azimuth between median natal and adult x and y coordinates (Kenward et al. 2002; Long et al. 2005, 2008). We used Rao's spacing test (Batschelet 1981, Russell and Levitin 1995) to test distribution of dispersal directions for deer in the WSA. We used Greenwood and Durand's (1955) V -test to test directionality of deer dispersal in the ESA. The V -test is recommended when an a priori direction is identified, which was the approximate alignment of the ridges, northeast–southwest ($\theta_0 = 65^\circ$ and 245°). We used the V -statistic to test whether observed dispersal directions deviated from random and clustered around the hypothesized directions. Because θ_0 was axial (i.e., 2 angles separated by 180°) rather than a single azimuth, we doubled all observed dispersal directions as recommended by Batschelet (1981). We calculated mean angles (θ) for axial data (Batschelet 1981) and estimated 95% confidence intervals from the 2.5 and 97.5 percentiles of 1 million Monte Carlo bootstrap samples.

To test the influence of major roads and rivers on dispersal movements, we first estimated dispersal paths for each radiomarked disperser as a straight line connecting median natal and adult locations. From these simplified straight-line dispersal paths, we summed the number of intersections between this line and major roads and rivers. We defined major roads as interstate highways, United States routes, and state routes. Although there are many small streams in

both study areas, the Allegheny River in the WSA was much larger than any other river in either area, and we treated it as the only river dispersal barrier.

We compared the number of road and river (hereafter, barrier) crossings of each deer's dispersal vector with barrier crossings of the same dispersal vector rotated in 30° increments about its median natal location. Thus, we generated 11 alternate dispersal vectors, of identical length to the actual estimated dispersal vector, for each disperser. For each deer, we compared the number of barrier crossings of the simulated vectors with the number of barrier crossings of the actual dispersal vector, using the Wilcoxon signed-ranks test for paired comparisons (SPSS 15.0; SPSS, Inc., an IBM Co., Chicago, IL).

To test whether barriers influenced placement of adult ranges on the landscape, we calculated the distance from median adult (i.e., postdispersal) location to nearest barrier for all dispersers with ≥ 10 postdispersal locations. For comparison, in each study area, we calculated distances from 1,000 random points to nearest barrier. We constrained random points to within the MCP formed by all postdispersal median locations in the study area. We compared the distribution of distance from nearest barrier for adult median locations with distances for random points using the Kolmogorov–Smirnov 2-sample Z -test (SPSS 15.0).

Further, we investigated whether deer that terminated dispersal in proximity of a barrier preferentially established their adult range on the near or far side of that barrier. To identify dispersers that likely had an interaction with a barrier near their dispersal terminus, we buffered adult median locations by a radius equal to the radius of typical postdispersal home ranges, identifying those deer whose buffer intersected ≥ 1 barrier (Fig. 1). For each study area, we estimated area of a typical home range by estimating postdispersal MCP home-range sizes of yearling males equipped with GPS collars (because of the large no. of locations for these deer). From these MCPs, we estimated median home-range area and, from this, calculated radius

Table 1. Summary statistics of dispersal paths of 9 juvenile male white-tailed deer equipped with Global Positioning System radiocollars in the Eastern Study Area (ESA) and Western Study Area (WSA) of Pennsylvania, USA, 2002–2005.

Study area	Begin tracking	Begin dispersal	End tracking	Dispersal distance (km) ^a	Dispersal direction (°) ^a	Dispersal time (days) ^b	Path segments ^c	Path length (km) ^d	Straightness ^e
ESA	6 Feb 2003	9 Nov 2003	1 Dec 2003	4.9	87	0.3	3	4.8	0.87
ESA	24 Feb 2004	7 Dec 2004	31 Jan 2005	6.9	220	3.2	11	17	0.4
ESA	25 Mar 2004	23 Oct 2004	31 Jan 2005	4.7	74	0.4	2	4	0.96
WSA	8 Mar 2008	10 May 2002	31 Jan 2003	10.2	215	16.4	6	17.6	0.58
WSA	19 Feb 2003	16 Sep 2003	31 Jan 2004	6.6	21	0.2	3	4.5	0.99
WSA	26 Mar 2003	5 Oct 2003	31 Jan 2004	4.5	227	0.7	4	4.3	0.95
WSA	28 Jan 2004	17 Oct 2004	31 Jan 2005	8.5	146	10.8	6 ^f	9.2	0.84
WSA	11 Feb 2004	20 Oct 2004	31 Jan 2005	5.8	290	0.1	2	3.1	0.93
WSA	11 Feb 2004	21 Oct 2004	29 Nov 2004	4.3	249	0.5	5	5	0.77

^a Estimated as straight-line distance and direction between median locations of natal and ad ranges.

^b Estimated as difference between time of last known location in natal range and first known location in ad range.

^c No. of path segments, excluding consecutive locations separated by <250 m, connecting last point in natal range and first point in ad range.

^d Sum of all segment lengths.

^e Ranges from 0 to 1, with 1 being perfectly straight. We calculated straightness by dividing straight line distance between first and last points along dispersal path by total path length.

^f Excludes movements within a 10-day temporary range established between natal and ad ranges.

length, assuming a circular home range (WSA: 1.2 km, $n = 7$, average no. of locations = 511.4, range = 223–987; ESA: 1.1 km, $n = 5$, average no. of locations = 286.2, range = 112–687). For the subset of deer that terminated dispersal within one home-range radius of a barrier, we categorized median locations as on either the near or far side of the nearest barrier, relative to dispersal origin, and tested preference for near-side versus far-side range establishment using the sign test (SPSS 15.0).

Finally, we investigated whether potential barriers influenced intra-range movement of dispersers after they had established their adult ranges. If barriers did not affect intra-range movements, we expected locations would be distributed on both sides of the barrier. To calculate expected use patterns, we buffered adult median locations with one typical adult home-range radius to generate a standardized, hypothetical, circular adult range (as described above, Fig. 1), and we calculated the proportion of this range on either side of the barrier using ArcView 3.2. Number of expected locations (\hat{f}_{ij}) for each deer, i , for each side of the nearest barrier, j , was

$$\hat{f}_{ij} = f_i \times p_{ij},$$

where f_i is the total number of locations for deer i , and p_{ij} is proportion of standardized range of deer i on side j of the nearest barrier. We tested deviations from expected distributions for use on either side of the barrier for each deer using chi-square goodness-of-fit tests. Further, we calculated an overall chi-square goodness-of-fit statistic within each study area and across both study areas, by summing individual chi-square values and degrees of freedom. Because many dispersers established home ranges far from barriers, this analysis was limited to the subset of deer that had ≥ 1 expected location on each side of a barrier.

RESULTS

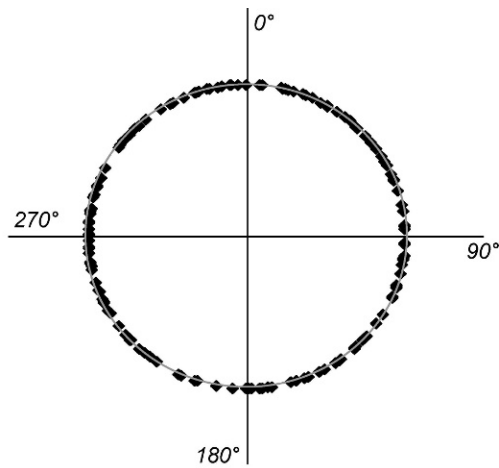
Of 274 juvenile white-tailed deer whose dispersal fates could be determined, 212 or 77% dispersed ($n_{WSA} = 151$,

$n_{ESA} = 61$). For these, average dispersal distance (SE) was 7.78 (0.52) km in the WSA and 8.83 (0.89) km in the ESA. Further, of these 274, 9 of 23 deer equipped with GPS radiocollars dispersed ($n_{WSA} = 6$, $n_{ESA} = 3$), yielding data useful for quantifying actual dispersal paths (Table 1). Based on data from the GPS radiocollared deer, dispersal occurred over a short time period (median = 12 hr, range = 2.5–394 hr), and dispersal paths were generally straight (average straightness = 0.81, SE = 0.07). Seven of the 9 deer maintained approximately straight travel paths (straightness = 0.77–0.99), and ultimate dispersal destinations were in similar direction to initial dispersal movements.

Dispersal directions in the WSA, where there is no regular directional trend in topography, were not different from random ($U_{Rao} = 122.7$, $n = 151$, $P > 0.9$), suggesting that dispersal in this study area is not directionally biased (Fig. 2a). In the ESA, however, dispersal was directed ($U_{GD} = 2.18$, $n = 61$, $P < 0.05$). Mean axial dispersal directions were 75° (95% CI = 51 – 108°) and 255° (95% CI = 231 – 287°), which did not differ from the directional trend of ridges in the study area ($\theta_0 = 65^\circ$ and 245° ; Fig. 2b).

In the WSA, the average number of barrier intersections for simulated dispersal paths ($\bar{x} = 0.79$, SE = 0.08) was 52% greater than the average number of intersections for actual dispersal paths ($\bar{x} = 0.52$, SE = 0.09). Wilcoxon's paired comparisons indicated actual dispersal paths intersected fewer barriers than simulated dispersal paths ($Z = -5.17$, $n = 151$, $P < 0.001$). Further, in the WSA, 5 dispersers crossed the Allegheny River area, indicating that large rivers are not complete barriers to dispersal movements of white-tailed deer. In the ESA, the average number of intersections of roads and simulated dispersal paths ($\bar{x} = 1.15$, SE = 0.15) was 105% greater than the average number of intersections for actual dispersal paths ($\bar{x} = 0.56$, SE = 0.16), with actual dispersal paths intersecting fewer roads than simulated pathways, based on paired comparisons ($Z = -4.46$, $n = 61$, $P < 0.001$). We found no evidence for deer establishing adult home ranges near to or far from dispersal

a) WSA



b) ESA

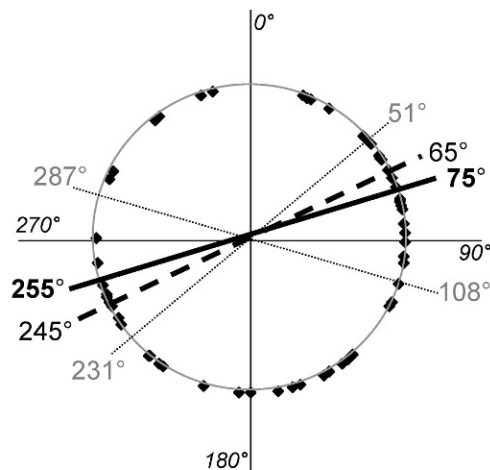


Figure 2. Dispersal directions for (a) 151 juvenile male white-tailed deer radiomarked in the Western Study Area (WSA) of Pennsylvania and (b) 61 juvenile male white-tailed deer radiomarked in the Eastern Study Area (ESA) of Pennsylvania, USA, from 2002 to 2005. Distribution of dispersal directions did not differ from uniformity in the WSA ($P > 0.90$), but dispersal was directed in the ESA ($P < 0.05$). Mean axial dispersal directions (solid line) corresponded closely with the directional trend of ridges and valleys in the ESA (dashed line), which was contained within 95% confidence limits of mean dispersal directions (dotted gray lines).

barriers because we failed to detect a difference between the distribution of randomly placed points and actual median locations of home ranges in both the WSA ($Z = 0.877$, $n = 86$, $P = 0.425$) and in the ESA ($Z = 0.156$, $n = 38$, $P = 0.156$).

In both study areas, deer that terminated dispersal within one home range radius of a potential barrier were more likely to establish their home range on the near side of those features (WSA: 42 of 51, $P < 0.001$; ESA: 16 of 21, $P = 0.03$). Further, the Allegheny River was the nearest barrier for 7 of the 51 deer included in the WSA sample, and all 7 of these deer established their adult range on the near side of that barrier ($P = 0.02$). However, even after excluding these deer from the WSA sample, we found that roads alone influenced postdispersal range establishment (35 of 44, $P < 0.001$), similar to findings in the ESA, where there was no major river to influence dispersal movements.

Finally, for deer whose postdispersal home range was established in proximity to a potential barrier, we compared usage on both sides of the barrier to investigate whether these features influenced movements within adult ranges. In the WSA, 26 deer established home ranges in which ≥ 1 location was expected on each side of a barrier. Of these, 17 (65%) showed significant clustering of locations on one side (for tests with significance, $\chi^2_1 \geq 3.90$, $P < 0.05$). Of the 17 deer that demonstrated significant side-bias, 12 were never observed on the far side of the barrier and one deer was located on the far side once. Further, of the 26 deer included in this analysis, only 5 were located in proximity to the river. Summed chi-square values for these 26 deer in the WSA indicated an overall tendency to bias locations on one side of barriers ($\chi^2_{26} = 346.98$, $P < 0.001$).

Likewise, in the ESA, 4 of 7 (57%) deer demonstrated similarly differential range-use relative to the nearest road (for tests with significance, $\chi^2_1 \geq 4.38$, $P < 0.05$). Two of these 4 deer were never observed on the far side the road, and 1 additional deer was observed only once on the far side of the road. Summed chi-square values for the 7 deer included in the ESA analysis indicated a pattern comparable to the WSA, wherein deer tended to cluster locations on one side of a road ($\chi^2_7 = 63.91$, $P < 0.001$), and summing across both study areas yielded similar results ($\chi^2_{33} = 410.89$, $P < 0.001$).

DISCUSSION

Dispersal Paths

Dispersing juvenile male white-tailed deer did not spend a long time exploring the local landscape to establish an adult home range; rather, dispersal movements were generally brief and unidirectional. Further, direction of first movement from the natal range usually was similar to the ultimate direction of dispersal. Dispersal and other long-distance movements have important implications for ecological processes such as gene flow and disease transmission (Nelson 1993, Smith et al. 1996, Rosatte 2002). Whereas gene flow depends on survival and successful breeding on the adult home range, disease transmission could potentially occur along the entire travel route of a disperser wherever conspecific interaction occurs. Thus, the short duration and direct movements of white-tailed deer during the transfer phase of dispersal suggest that potential for disease transmission along dispersal paths is small.

Additionally, because we found dispersal movements were generally linear, dispersal in the absence of actual transitional locations may be reasonably modeled as simple straight-line vectors for the purpose of many investigations, including analyses of directionality and barrier-crossing. However, caution should be used if modeling dispersal movements as straight lines for the purpose of evaluating habitat use along dispersal routes.

Both inbreeding avoidance and reduction of mate competition ultimately motivate emigration of juvenile male white-tailed deer (Long et al. 2008). Quick and straight dispersal movements would effectively remove a disperser

from closely related opposite-sex conspecifics, thereby minimizing potential for inbreeding. However, unidirectional dispersal paths suggest minimal habitat exploration during the transfer phase of dispersal, and it remains unclear whether dispersing deer preferentially establish adult ranges in areas with fewer same-sex competitors. Perhaps visual and olfactory signposts such as scrapes and rubs provide easily assessable indices of potential mate competition, but factors influencing immigration into existing populations remain poorly understood (Miller et al. 1987, Miller and Marchinton 1999).

Dispersal Directionality

Violation of the simple assumption of random dispersal direction has important implications for modeling processes such as gene flow, disease transmission, population growth, and invasion dynamics, and directional long-distance movements of white-tailed deer have been noted previously (Sparrow and Springer 1970, Dusek et al. 1989, Kernohan et al. 1994, Kilgo et al. 1996). Dusek et al. (1989) observed a bimodal frequency distribution of dispersal directions that paralleled the Lower Yellowstone River in eastern Montana, USA. In central South Dakota, USA, Kernohan et al. (1994), studying dispersal and migration, reported long-distance movements of deer were oriented along the James River, which is of similar size to the Allegheny River in Pennsylvania. Similarly, in eastern South Dakota, Sparrow and Springer (1970) noted that migratory movements were predominantly northward, following the Big Sioux River. Kilgo et al. (1996) also observed directional dispersal in northern Florida, USA, although there were no apparent landscape features that directed movement.

Similar to the Montana (Dusek et al. 1989) and South Dakota (Sparrow and Springer 1970, Kernohan et al. 1994) studies, we observed directional dispersal among deer captured in the ESA that was parallel to the direction of ridges in the area, suggesting that these prominent landscape features influenced dispersal paths of deer. However, it is difficult to ascertain whether these ridges directly or indirectly influenced dispersal direction, because roads, rivers, and other landscape features were spatially correlated with local topography.

Despite the presence of a major river in the WSA, deer did not disperse with directional bias in this area. Lack of directionality may be attributable to 2 related factors. First, in the Montana (Dusek et al. 1989) and South Dakota (Sparrow and Springer 1970, Kernohan et al. 1994) studies, deer were captured in proximity to the river (<3–4 km, and often within the floodplain), but we captured most (144 of 151) dispersing deer in the WSA >4 km (i.e., >1.5 typical range diam) from the Allegheny River. Second, unlike the large rivers in Montana and South Dakota, the Allegheny River in the WSA has a narrow floodplain. The landscape in this area is varied, such that steep slopes bordered the river, but beyond the immediate area of the river, there was no large-scale topographic pattern. Therefore, although the Allegheny River flows north to south through the study area, a corresponding pattern is lacking in the surrounding

landscape. Although the Allegheny River may block most dispersal movements of deer, it does not appear to guide them.

Dispersal Barriers

Although dispersal distances of white-tailed deer are inversely related to forest cover (Long et al. 2005, Diefenbach et al. 2008), decreased habitat connectivity via increased road density may further reduce dispersal distances. Here, roads and a major river affected dispersal paths by acting as semipermeable barriers to movement. Although some deer did cross major roads and the river, deer generally avoided crossing these landscape features and often terminated dispersal movements on the near side of these barriers. Frequent occurrence of death by vehicular collision during dispersal could introduce a confounding source of error in this analysis; however, of 212 dispersers, we observed only one case of road-kill during dispersal. Further, following dispersal and adult home range establishment, 57–65% of deer avoided crossing roads, similar to patterns seen in other cervids, such as caribou (*Rangifer tarandus*; Dyer et al. 2002) and moose (*Alces alces*; Laurian et al. 2008). Interestingly, although crossing of roads was avoided, we did not observe avoidance of roadway corridors because locations of deer often occurred in close proximity to roads (Fig. 1).

Roads and rivers previously have been shown to affect animal movement patterns, and typically these features impede dispersal and reduce gene flow (Mader 1984, Trombulak and Frissell 2000). In our study, road crossings were not uncommon because deer crossed an average of 0.5 major roads per dispersal event, but road crossings were less common than expected, based on crossing frequency of simulated dispersal paths of identical distance. With this level of successful road crossing it is unclear the extent to which gene flow was reduced. Blanchong et al. (2007) demonstrated that landscape features such as roads and rivers influence population genetic structure, and our research suggests a possible mechanism. Additional research could investigate effects of specific roadway characteristics (e.g., traffic volume, bordering habitat types) on dispersal movements and could directly address associations among dispersal, landscape barriers, and spatial genetic heterogeneity in deer populations.

MANAGEMENT IMPLICATIONS

Identification of dispersal barriers and landscape features that direct dispersal may facilitate delineation of appropriate management zones. For example, deer populations may be managed within units delineated by a combination of landscape features and nontopographic boundaries (e.g., county lines). Because roads, rivers, and mountains restrict and direct dispersal movements, these landscape features likely represent biologically meaningful boundaries for management zones. Further, because white-tailed deer serve as vectors or hosts for ecologically and economically important diseases, such as chronic wasting disease (Gross and Miller 2001, Williams et al. 2002) and Lyme disease

(Piesman 2002), managers attempting to control or contain disease spread would benefit by identifying potential topographic barriers to long-distance movement.

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LITERATURE CITED

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