Research Article

Proximate Influences on Female Dispersal in White-Tailed Deer

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ABSTRACT Ultimate causes of animal dispersal have been hypothesized to benefit the dispersing individual because dispersal reduces competition for local resources, potential for inbreeding, and competition for breeding partners. However, proximate cues influence important features of dispersal behavior, including when dispersal occurs, how long it lasts, and direction, straightness, and distance of the dispersal path. Therefore, proximate cues that affect dispersal influence ecological processes (e.g., population dynamics, disease transmission, gene flow). We captured and radio-marked 277 juvenile female white-tailed deer (*Odocoileus virginianus*), of which 27 dispersed, to evaluate dispersal behavior and to determine proximate cues that may influence dispersal behavior. Female dispersal largely occurred at 1 year of age and coincided with the fawning season. Dispersal paths varied but generally were non-linear and prolonged. Physical landscape features (i.e., roadways, rivers, residential areas) influenced dispersal path direction and where dispersal terminated. Additionally, forays outside of the natal range that did not result in dispersal occurred among 52% of global positioning system (GPS)-collared deer ($n = 25$) during the dispersal period. Our results suggest intra-specific social interactions and physical landscape features influence dispersal behavior in female deer. Female dispersal behavior, particularly the lack of directionality, the semi-permeable nature of physical barriers, and the frequency of forays outside of the natal range, should be considered in regard to population management and controlling the spread of disease. © 2016 The Wildlife Society.

KEY WORDS barriers, chronic wasting disease, disease spread, dispersal, foray, movement, *Odocoileus virginianus*, Pennsylvania, proximate causes, white-tailed deer.

Dispersal, defined as a permanent movement of an organism away from its place of origin (Murray 1967, Nathan 2001), is an important behavior in white-tailed deer (*Odocoileus virginianus*) ecology because it affects gene flow, population dynamics, colonization, and the spread of disease (Murray 1967, Slatkin 1987, Rosenberry et al. 1999, Conner and Miller 2004, Porter et al. 2004). Documenting an organism's dispersal behavior and identifying factors that influence that behavior are important to understand the basic ecology of a species and to provide critical information for the conservation and management of that species. Dispersal in male white-tailed deer occurs at a relatively high rate (46–75%; Long et al. 2005) and factors that influence male dispersal have been studied (Long et al. 2005, 2010; Diefenbach et al.

2008). However, female dispersal occurs at low rates (4–49%; Lutz et al. 2015), which has limited the ability to identify influences on female dispersal behavior.

Dispersal is of particular importance for deer management (Rosenberry et al. 1999). For example, identifying potential barriers to dispersal and defining the parameters that influence dispersal rates and distances are critical to understanding the potential for the spread of diseases (e.g., chronic wasting disease [CWD]) across the landscape (McCoy et al. 2005, Grear et al. 2006, Oyer et al. 2007). Knowledge of female dispersal also is important for localized management of deer population densities. Managers are increasingly looking for methods to control deer densities in areas closed to hunting (e.g., parks, areas of suburban development). Currently used and proposed strategies often target females through trap-and-transfer, lethal removal, or the use of contraceptives. However, for these management strategies to be effective, they must incorporate the effect of immigration from dispersing females on the target population (Campbell et al. 2004, Porter et al. 2004, Frost et al. 2009).

The reasons animals disperse can be separated into ultimate or proximate causes (Alcock 2005). Ultimate causes of dispersal refer to the evolutionary advantages of dispersal and why dispersal behavior persists at the population level. Ultimate causes of dispersal have been attributed to reduced competition for local resources (Murray 1967, Lutz et al. 2015), inbreeding avoidance (Wolff et al. 1988, Long et al. 2008), reduced competition for mates (Dobson 1982, Long et al. 2008), or a combination of these factors (Brandt 1992, Lidicker and Stenseth 1992). Proximate causes refer to direct influences on an individual that stimulate dispersal or otherwise affects the individual's dispersal behavior. Proximate influences on deer dispersal include intra-specific social cues (e.g., aggressive behavior, maternal abandonment; Miller and Ozoga 1997, Long et al. 2008), and landscape features (e.g., roads, topography, rivers; Long et al. 2010).

Dispersal behavior of vertebrates can be separated into 3 discrete phases: initiation, wherein an individual leaves its natal range; transfer, the process of the animal moving across the landscape in search of an adult range; and termination, where an animal settles upon an adult range distinct from the natal range (Ims and Yoccoz 1997, Andreassen et al. 2002). Proximate influences shape the individual's dispersal behavior during all 3 of these phases. Intra-specific social interactions and behavioral responses are cited as proximate causes that initiate dispersal (Brandt 1992). Whereas, dispersal behavior is thought to be influenced by social interactions among individuals and features of the physical landscape during the transfer phase (Brandt 1992, Wiens 2001). Termination of dispersal is believed to occur when proximate influences that prolong the transfer phase are no longer present (Nixon et al. 1991), and also may be influenced by physical landscape features such as barriers (Long et al. 2010). However, proximate influences on the 3 phases of dispersal remain poorly understood because of the logistical problems of collecting data on movement paths of dispersing animals (Bennets et al. 2001, Andreassen et al. 2002) and the difficulty of observing social and physical interactions experienced by the disperser.

Social cues, particularly aggression, by sympatric members of the same species play an important role in initiating dispersal in mammals (Brandt 1992). In white-tailed deer, intra-specific competition and aggression peak during parturition and again during the breeding season. During parturition, pregnant females seek isolation and display agonistic behavior toward other deer, including relatives (Ozoga et al. 1982, Schwede et al. 1993). The proximate cause of male deer dispersal initiated during parturition has been attributed to intersexual aggression that cues males to disperse so that inbreeding potential is ultimately reduced (Woodson et al. 1980, Holzenbein and Marchinton 1992, Long et al. 2008). During the rut, conversely, males compete with other males to maximize breeding opportunities and intrasexual aggression cues that reduce competition for mates have been cited as the proximate cause of male dispersal during the fall (Wahlstrom 1994, Rosenberry et al. 2001, Long et al. 2008). Competition for space when pregnant females seek to isolate themselves before and after parturition

has been proposed as the ultimate cause of female dispersal (Lutz et al. 2015). Therefore, we propose that female dispersal is proximately cued by aggression from females seeking isolation during parturition, and we predicted that female dispersal will occur during the fawning period.

The transfer phase of dispersal is prolonged by the continued presence of proximate cues that initiated dispersal and observed dispersal paths may be explained by individuals moving to the first unoccupied or uncontested home range encountered (Waser 1985). Long et al. (2010) reported dispersal paths of male white-tailed deer in Pennsylvania to be brief and straight. Therefore, we expected female dispersal paths to have similar characteristics.

The transfer phase of dispersal also can be influenced by landscape features (Wiens 2001). Deer movement can be directionally influenced by landscape features such as watersheds (Sparrow and Springer 1970, Kernohan et al. 1994, Nixon et al. 1994) and ridges (Long et al. 2010). However, other studies reported landscape features have no influence on deer movements (Verme 1973, Kilgo et al. 1996). We predicted that female dispersal direction would be axially aligned with parallel running ridges in our study area that had similar topographic features to those found in the Long et al. (2010) study.

Both anthropogenic and natural landscape features can act as barriers to dispersal (Mader 1984, Ayres and Clutton-Brock 1992, Matics 2003) and influence the termination of a dispersal path (Long et al. 2010). Barriers to dispersal have important implications for population dynamics (Lutscher et al. 2005) and disease transfer (Xu and Ridout 2001, Conner and Miller 2004) because they limit connectivity between population segments. Identifying barriers to connectivity is relevant for wildlife conservation because of increasing habitat fragmentation (Coulon et al. 2004, Lindenmayer et al. 2008) and the influences of climate change on species' habitat distributions (Doerr et al. 2011). We evaluated termination of dispersal paths and hypothesized that termination of dispersal would be influenced by landscape features (e.g., rivers, roads, dense residential, or other developed areas).

We studied dispersal behavior in female white-tailed deer in Pennsylvania to examine proximate influences affecting dispersal behavior. Our objectives were to describe traits of dispersal among female white-tailed deer and identify influences on female dispersal by testing hypothesized proximate influences on dispersal behavior.

STUDY AREA

We monitored dispersal behavior of female white-tailed deer in 4 study areas in Pennsylvania, USA (Table 1). Study areas consisted of Wildlife Management Units (WMUs) 2D, 2G, 3C, and 4B, as delineated by the Pennsylvania Game Commission (PGC; Fig. 1; Rosenberry and Lovallo 2003, Rosenberry et al. 2009). Study areas were large (Table 1); however, general landscape features, forest types (Fike 1999), and other habitat features remained relatively consistent within each study area. We reported deer density as a range of population estimates that were calculated during capture

Table 1. Study area characteristics and dispersal statistics for juvenile female white-tailed deer captured in Pennsylvania, USA, 2005–2011.

Study area	Study area size (km²)	Range in elevation (m)	Forest cover (%)	Predominant forest type(s)	Population density range (deer/km²)	No. females dispersed (GPS, VHF)[a]	No. females monitored
2D	6,440	235–660	60	Red oak-mixed hardwood, northern hardwood	17.4–21.1	2 (1,1)	24
2G	10,658	175–775	88	Red oak-mixed hardwood, northern hardwood	6.0–10.3	4 (1,3)	73
3C	5,678	190–820	75	Northern hardwoods	15.0–19.6	4 (2,2)	17
4B	4,120	105–695	65	Red oak-mixed hardwood	9.1–14.2	17 (4,13)	115

[a] Radio-collar type indicated parenthetically, with number females that dispersed that were tracked with a global positioning system (GPS) collar listed first and the number tracked with a very high frequency (VHF) collar listed second.

years in each study area. Population estimates were generated by integrated population models (White and Lubow 2002, Buderman 2012) and provided by the Pennsylvania Game Commission (Rosenberry et al. 2012). In all study areas, agricultural fields typically were used to grow corn, soybeans, alfalfa, and grass hay.

The WMU 2D study area was located in the Pittsburgh Low Plateau physiographic region of western Pennsylvania where topography consisted of irregular, gradually sloped hills and topographical features lacked directional orientation. Forests in the WMU 2D study area generally were contained in small woodlots fragmented by agricultural fields, roadways, and small residential areas. The WMU 2G study area was located in the Deep Valleys section of the Appalachian Plateaus physiographic region of north-central Pennsylvania. The topography was dominated by high, flat plateaus, and steep mountain slopes, but these features lacked directional orientation. Agricultural land use in the WMU 2G study area was rare and residential areas were scarce. The WMU 3C study area was located in the Glaciated Low Plateau section of the Appalachian Plateaus physiographic region of northeastern Pennsylvania. The topography consisted of rounded hills and valleys that lacked directionality, and land use was a patchwork of forested woodlots, agricultural fields, wetlands, and small human population centers. The WMU 4B study area was located in the Ridge and Valley region of south-central Pennsylvania and

consisted of long, parallel ridges and valleys oriented along a northeast-southwest axis. The ridges were forested and the valleys were mostly agricultural. Roads and small waterways also were largely oriented along a northeast-southwest axis because of the topography dominated by the ridges.

METHODS

Deer Capture and Monitoring

We captured 277 juvenile (~8 months old at capture) female white-tailed deer from 2005 through 2011. We captured deer following the conclusion of deer hunting season in mid-January through mid-April using single-gate Clover traps (Clover 1956), rocket nets (Beringer et al. 1996), and drop nets (Ramsey 1968). We physically restrained, radio-tagged, and released without sedation deer captured in Clover traps. We chemically sedated deer immediately following capture in rocket or drop nets with 0.5 mg/kg of body mass of xylazine hydrochloride, fitted them with a radio-transmitter, and then intramuscularly administered an antagonist of 2 mg/kg of body mass of tolazoline hydrochloride (Rosenberry et al. 1999). We also fitted all deer with ear tags and released them at the capture location. We handled all animals in accordance with protocols approved by the Pennsylvania State University Institutional Animal Care and Use Committee (IACUC No. 34910).

We equipped juvenile females with either a very-high-frequency (VHF) neck collar (ATS, Isanti, MN, USA) or a global positioning system (GPS) neck collar (Vectronic Aerospace GmgH, Berlin, Germany, 863 g; Telonics, Mesa, AZ, USA, 700 g; H.A.B.I.T. Research, Victoria, British Columbia, Canada, 750 g). We fitted all deer captured with 2 uniquely numbered plastic ear tags (Original Tags, Temple Tag, Temple, TX, USA), 1 in each ear, that included a toll-free phone number for our research office.

We located individuals fitted with VHF collars at least once per week using ground-based radio-telemetry. We searched for missing deer using fixed-wing aircraft, typically in late summer and again in late fall. We estimated locations from ground-based telemetry data using LOAS 2.04 (Ecological Software Solutions, Sacramento, CA, USA). All GPS collars recorded locations at least once per day, and 17 GPS collars recorded locations every 1.5 hours from 1 May to 15 July, corresponding with the female dispersal period.
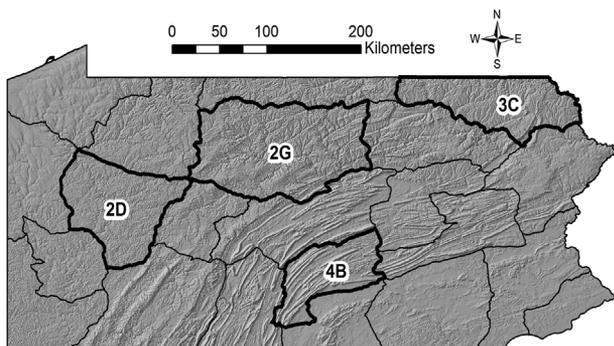

Figure 1. Map of study areas 2D, 2G, 3C, and 4B among the 22 Pennsylvania Game Commission wildlife management units, Pennsylvania, USA. Hillside shading illustrates the linear ridges of the 4B study area and the irregular topography in the 2D, 2G, and 3C study areas.

Analytical Methods

We defined dispersal as having occurred if an individual displayed a permanent, 1-way movement from a natal range to a distinct adult range (Kenward et al. 2001, 2002), such that pre-dispersal locations did not overlap post-dispersal locations (Long et al. 2005, Lutz et al. 2015). We estimated natal and adult home ranges using minimum convex polygons (MCP) when 30 or more locations were recorded. If <30 locations were recorded, we estimated the home range by calculating the mean female home range circumference within the same study area and buffered all locations recorded by this mean circumference to estimate the natal or adult range. Because dispersal in female deer younger than 11 months is not known to occur (Marchinton and Hirth 1984, Vreeland et al. 2004), we assumed that we captured juveniles on their natal range. We defined dispersal rate as the proportion of individuals that dispersed from natal to adult range. We calculated dispersal distance as the straight-line distance between the median x and y natal range coordinates and the median x and y adult coordinates (Kenward et al. 2002). We designated the date of dispersal as the first date a location was recorded outside the natal range, or the date when a search failed to locate the animal within its natal range and the deer was later located outside the natal range (Long et al. 2008). We designated a dispersal location as the first dispersal location when all subsequent locations did not occur within an MCP containing all previous locations. Similarly, the last location of a dispersal path was determined when it was the last dispersal location not contained within an MCP created by subsequent locations. We mapped dispersal path movements by beginning at the edge of the natal range nearest the first dispersal location and ending at the edge of the adult range nearest the last dispersal location (Karns et al. 2011). We performed all spatial data analysis using ArcGIS 9.2 (Environmental Systems Research Institute, Redlands, CA, USA).

We calculated the direction of dispersal as the azimuth measurement from true north between the median x and y natal range coordinates and the median x and y adult range coordinates. We used Rao's spacing test (Batschelet 1981) to test for a directional trend in dispersal direction. In the WMU 4B study area, we calculated the orientation of topographical features by estimating the azimuth orientation of each named ridge within the study area. We calculated the axial direction of dispersals and ridge orientation using modulus 360 and determined whether the mean varied from random using the Rayleigh Z test. We used Greenwood and Durand's V test to determine if there was a relationship between dispersal directions and mean axial orientation of ridges.

We used only deer fitted with GPS collars ($n = 25$) to evaluate dispersal paths, forays outside of the natal range, and interactions with barriers. We did not consider VHF-collared deer for these analyses because they were rarely located during a dispersal event and thus had an insufficient number of dispersal locations. We estimated dispersal path distance as the sum of distances between the nearest edge of the natal MCP to the first location of the dispersal event, subsequent points of the dispersal event, and the nearest edge of the adult MCP to the last point of the dispersal event. However, we considered only sequential movements >250 m (i.e., we retained only the first location of closely spaced sequential locations) to minimize the influence of high location frequencies (Long et al. 2010). We classified a movement as a foray if it was a movement >1.5 km from the edge of the natal MCP with a subsequent return to the natal MCP. We designated the foray date as the first date a foray location was recorded outside the natal range. We estimated the distance of a foray as the straight-line distance between the farthest foray location out of the natal range and the nearest edge of the natal range. We estimated foray path distance as the sum of distances between the nearest edge of the natal MCP to the first location of the foray, subsequent locations of the foray event, and the nearest edge of the natal MCP to the last location of the foray before the animal returned to the natal MCP. Again, we considered only sequential movements >250 m to minimize the influence of high location frequencies. We characterized path straightness as the straight-line distance between first and last points of the dispersal path divided by the total dispersal path length. Following Long et al. (2010), we considered potential barriers to dispersal to be highways (e.g., interstate highways, U.S. routes, state routes), dense residential or developed areas (as delineated on U.S. Geological Survey 7.5-minute Quadrangle topography maps and confirmed via aerial photographs; PA Department of Conservation and Natural Resources 2007), and large rivers (classified as fourth order or larger; Pennsylvania Natural Heritage Program 2010).

RESULTS

Of the 277 individuals captured, radio-marked, and released, we considered 229 (82.7%) for analysis (VHF, $n = 204$; GPS, $n = 25$). We censored the remaining 48 individuals because of death, shed transmitter, or permanent loss of signal prior to 1 August, by which time >95% of the dispersers had established adult ranges.

We observed dispersal of juvenile females in all 4 study areas, with an overall dispersal rate of 0.12 ± 0.02 (SE; $n = 229$). Average dispersal distance was 18.0 ± 7.0 km ($n = 27$) with a maximum dispersal distance of 52.9 km. The mean date of dispersal was 6 June ± 7.5 days ($n = 27$), with the earliest date of dispersal occurring 19 March and the latest occurring 13 November. However, 25 of the 27 females that dispersed did so from 2 May to 7 July with an average of 2 June ± 3.4 days. Two individuals (7.4%, $n = 27$) were killed during dispersal by vehicle and train collisions. We considered these individuals to have dispersed because the distance from their natal range to their mortality location were 15.3 km and 29.6 km and greater than mean distances of non-dispersal movements (forays) we observed outside of natal ranges (6.2 km). Additionally, we used data from these individuals to summarize dispersal path distance and straightness, even though this likely results in underestimating these parameters because the movements met

our definition of dispersal and the ecological function of dispersal.

Among the 3 study areas with irregular topography, the distribution of dispersal directions did not differ from uniformity ($U_{Rao} = 129$, $n = 10$, $P > 0.10$) nor was there a mean axial direction of dispersal ($Z = 1.859$, $n = 10$, $P > 0.10$). In the WMU 4B study area, the ridges were oriented along a 45–225° axis ($Z = 21.713$, $r = 0.897$, $n = 27$, $P < 0.05$); however, there was no relationship between deer dispersal direction and ridge orientation (Fig. 2; $V = 0.0271$, $P > 0.10$). Further, the distribution of dispersal directions in this study area did not differ from uniformity ($U_{Rao} = 139$, $n = 17$, $P > 0.10$) and we failed to detect an axial direction of dispersal ($Z = 1.14$, $n = 17$, $P > 0.10$). Distances of non-forested landscape type (mainly agricultural) between ridges in the WMU 4B study area ranged from 0 km to 10.8 km. Mean dispersal distance in the WMU 4B study area was 20.5 km (95% CI = 12.9–28.1), which did not differ from the 13.9 km mean dispersal distance for the other 3 study areas (95% CI = 7.0–20.8).

We obtained dispersal paths for 8 GPS-collared deer (6 of which recorded a location every 1.5 hr and 2 of which recorded a location every 24 hr). The duration of dispersal events ranged from 14 hours to 1,330 hours, with a mean of 355 hours ± 159 and median of 200 hours. The mean dispersal distance (straight-line distance from median natal range to median adult range) for these individuals was 15.3 ± 2.7 km (median = 16.4 km); however, the mean length of the dispersal paths was 51.8 ± 29.7 km (median = 22.5 km). Therefore, dispersal paths were generally non-linear (average straightness = 0.579 ± 0.097). Dispersal paths averaged 3.8 direction changes >45 ± 1.3° and 81% of those direction changes occurred when the animal encountered an apparent physical barrier on the landscape. However, most physical barriers were semi-permeable because 63% of the GPS-collared females that dispersed eventually crossed a barrier that had previously caused a direction change. Of the GPS-collared dispersers in the WMU 4B study area, 1 individual crossed ridges 3 times (twice using a water gap, once crossing directly over a ridge), 1 individual crossed directly over 2 ridges, and the other 2 did not transverse any ridges and generally aligned their dispersal direction with the adjacent ridges.

The termination of the dispersal path was influenced by a physical barrier in 5 of 7 GPS-collared dispersers. Four deer terminated dispersal on the near side of a barrier and established an adult home range within 1 home range radius of the barrier. One GPS-collared female stopped at the near side of a barrier, regressed 3.3 km along the previous dispersal path, and then established an adult home range. One GPS-collared female was killed during dispersal and was not considered in this analysis. Among radio-collared dispersers, 5 of 15 terminated the dispersal within 1 home range radius of a physical barrier. Four radio-collared dispersers were not considered for this analysis because they were either killed during dispersal or lacked adequate adult home range locations to estimate a home range. Of the 10 deer that terminated their dispersal at a barrier, 6 barriers were highways, 3 were residential or developed areas, and 1 was a large river.

Forays outside of the natal range (Fig. 3) that did not result in dispersal were recorded in 13 of the 25 GPS-collared females (Table 2). Four of 8 dispersers and 9 of 17 non-dispersers made forays, and 7 of those 13 individuals participated in multiple forays. The mean date of forays was 23 May ± 5.3 days and ranged from 20 March to 12 July ($n = 27$). The mean duration of the forays was 46.3 ± 8.3 hours and ranged from 11 hours
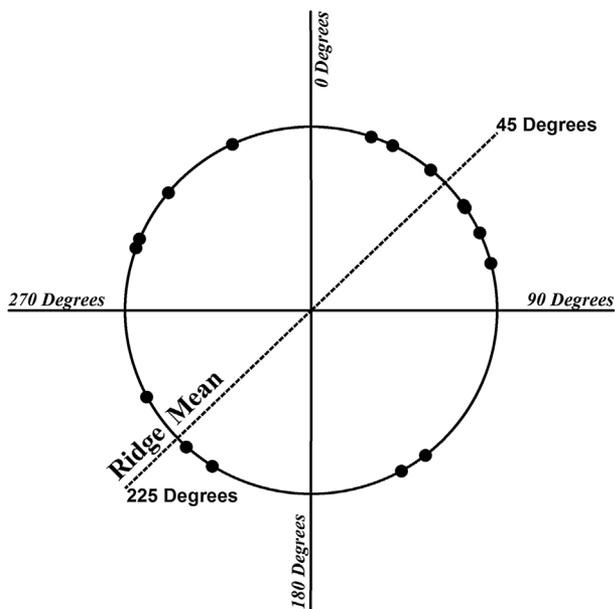

Figure 2. Dispersal direction for 17 juvenile white-tailed deer in the 4B study area, Pennsylvania, USA, 2005–2011. Distribution of dispersal directions (black dots) did not differ from uniformity ($P = 0.287$) nor was there a mean axial direction ($P > 0.10$). Directional orientation of the ridges in 4B were axially aligned ($P < 0.05$, dashed line); however, there is no relationship between dispersal direction and ridge orientation ($P > 0.10$).
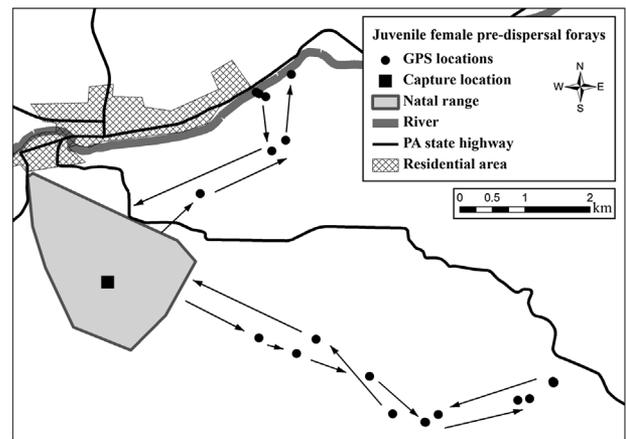

Figure 3. Example of pre-dispersal forays outside of the natal range by a juvenile female white-tailed deer equipped with a global positioning system (GPS)-transmitter in Pennsylvania, USA, 2011. Natal range is plotted as a minimum convex polygon and arrows indicate direction of movement. The foray to the north and east occurred 12 May 2011 and the foray to the south and east occurred 17 May 2011.

Table 2. Summary statistics for 25 juvenile female white-tailed deer fitted with global positioning system radio-collars set at 2 different recording schedules to evaluate forays outside of their natal range that did not result in dispersal, Pennsylvania, USA, 2005–2011.

Time between locations (hr)	n	Individuals displaying ≥1 foray	No. forays recorded	Foray begin date		Duration (hr)[a]		Straight-line distance (km)[b]		Dispersal path distance (km)[c]		Forays ended at a barrier
				$\bar{x}$	95% CI	$\bar{x}$	95% CI	$\bar{x}$	95% CI	$\bar{x}$	95% CI	
1.5	14	9	15	24 May	10 May–7 Jun	51	21–81	7.1	9.6–4.6	17.3	24.1–10.5	5
24	11	4	12	21 May	1 May–10 Jun	40	25–55	5.1	6.6–3.6	10.3	14.4–6.2	6
Pooled	25	13	27	23 May	12 May–3 Jun	46	29–63	6.2	7.7–4.7	14.2	18.3–10.1	11

[a] Estimated as difference between time of first and last location of foray outside of natal range.
[b] Estimated as straight-line distance between the farthest foray location out of the natal range and the nearest edge of the natal range.
[c] Estimated as the sum of distances between the nearest edge of the natal minimum convex polygon (MCP) to the first location of the foray, subsequent locations of the foray event, and the nearest edge of the natal MCP to the last location of the foray before the animal returned to the natal MCP. We considered only sequential movements >250 m (i.e., we retained only the first location of closely spaced sequential locations) to minimize the influence of high location frequencies.

to 228 hours ($n = 26$). The mean straight-line distance from the nearest edge of the natal home range to the farthest extent of the foray was 6.2 ± 0.7 km ($n = 27$), and the mean length of foray paths was 14.2 ± 14.2 km ($n = 27$). Forays also were influenced by barriers with 41% ($n = 27$) of forays ending at an obvious physical barrier prior to the animal returning to its natal home range. We also calculated summary statistics based on the frequency at which our GPS collars recorded locations during foray movements (Table 2); however, we did not find a difference between these groups.

DISCUSSION

In general, forays outside of the natal range were common even though female dispersal rates were low, timing of forays and dispersals largely coincided with the fawning season, and dispersal events were prolonged and non-linear. Also, highways, developed areas, and rivers were semi-permeable barriers that influenced dispersal behavior, but we failed to detect an influence of topography on directionality of dispersal. Also, we recorded anthropogenic causes of mortality during dispersal, which may have artificially reduced the survival rates of dispersing individuals and has conservation implications for wildlife (Trombulak and Frissell 2000).

As predicted, we found that female dispersal largely coincided with the fawning period. This supports our hypothesis that agonistic behavior displayed by socially dominant females toward other deer during parturition is a proximate cause of female dispersal. Of those individuals that dispersed outside of the fawning period: 1 dispersed on 19 March and the other on 13 November. Although dispersal in white-tailed deer has been widely documented to coincide with either the fawning season or the breeding season (Long et al. 2005, Lutz et al. 2015), we have found no record in the literature of deer dispersing in the late winter. The female that dispersed in March may have been influenced by its capture because the animal moved approximately 5.8 km from where it was trapped just 7 days after its capture. The

female that dispersed in November dispersed during the breeding season. This may have been proximately initiated by a dispersing male sibling because siblings have been documented to disperse together during the fawning period (Nelson and Mech 1992, Lutz et al. 2015), or by being pursued outside of its natal range by rutting males.

Counter to our prediction, we found female dispersal to be comparatively prolonged, long distanced, and non-linear (Fig. 4). Long et al. (2010) reported dispersal paths of male white-tailed deer in Pennsylvania to be brief and straight-lined, and proposed that these attributes efficiently reduced inbreeding potential. During the transfer phase, males may be proximately cued to continue dispersing as they interact with dominant males; however, they are ultimately motivated to continue to distance themselves from their natal range in a linear fashion to minimize inbreeding potential. Our results suggest that female dispersal is not ultimately motivated by inbreeding avoidance and that proximate social interactions with other agonistic, dominant females may prolong the transfer phase and alter the dispersal path in a non-linear manner. Furthermore, non-linear dispersal paths may facilitate habitat exploration, which may be disproportionately important for females searching for an adult range suitable for rearing offspring.

Also in contrast to our hypothesis, landscape features did not influence the directionality of female dispersal. This is contrary to what Long et al. (2010) reported in male dispersers in a similar landscape of Pennsylvania. We speculate that landscape features may have an important influence on dispersal direction during the initiation phase; however, intrasexual social cues from adult females during the transition phase may subsequently result in non-linear and randomly oriented female dispersal paths. Directional dispersal in deer also has been reported along river features in Montana (Dusek et al. 1989) and South Dakota (Sparrow and Springer 1970, Kernohan et al. 1994). However, directionality of movements may be attributed to animals favoring better habitat found along these river systems.
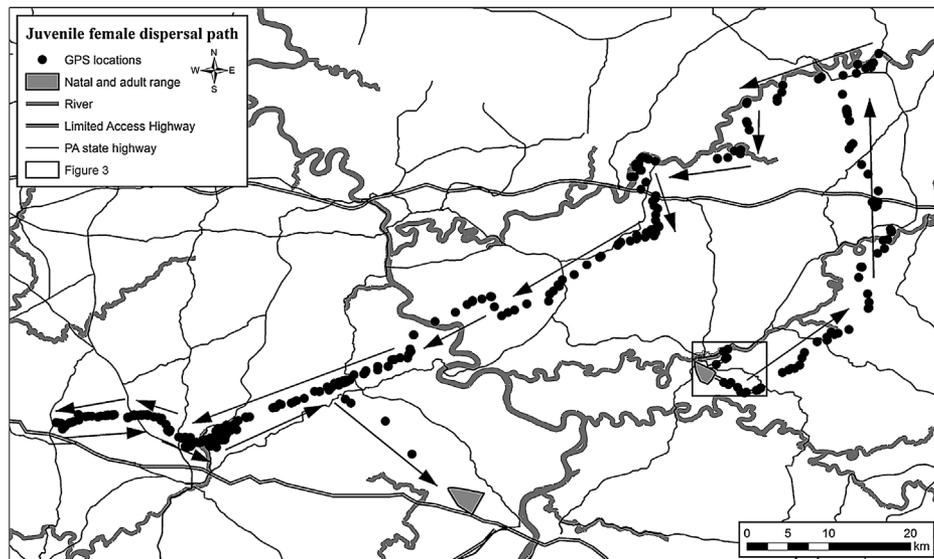
Figure 4. Example of a natal range, dispersal path, and adult range of a female white-tailed deer equipped with a global positioning system (GPS)-transmitter in Pennsylvania, USA, 2011. Figure 3 is inset, natal and adult ranges are plotted as minimum convex polygons, and arrows indicate direction of movement. Dispersal began on 25 May 2011 and concluded on 19 July 2011 (55 days, 10 hr), and the dispersal path was 258 km. State highways, limited-access highways (≥4 lanes), and rivers classified as fourth order or larger are shown because they acted as semi-permeable barriers, and often resulted in a dispersal direction change.

Our results were consistent with our hypothesis that barriers would influence the termination of the dispersal path. Similar to Long et al. (2010), we found that highways, large rivers, and developed areas were semi-permeable barriers during dispersal. However, many barriers that initially halted dispersal were subsequently crossed later in the dispersal event. This reinforces the concept that dispersal behavior is influenced by multiple, interacting cues and barriers may exhibit temporal variation in permeability (Sawyer et al. 2013).

We documented many forays outside of female natal ranges during the fawning period. Skuldt et al. (2008) also documented exploratory movements in 31% ($n = 32$) of yearling females and 43% ($n = 23$) of yearling males. This suggests that proximate cues that initiate dispersal are common during the fawning period but do not always result in dispersal. These forays may be dispersal attempts that were prevented by social or physical landscape interactions, or these temporary movements could have satisfied the catalyst cue to disperse, but the transition phase was not maintained by continued cues. Similar movements of deer outside of their normal range that have been observed have been attributed to breeding courtship, food sources, limited escape cover, and human disturbances (Kolodzinski et al. 2010, Karns et al. 2011). These extra-home range movements also may have implications on disease transmission that may not have been fully considered.

Barriers play a role in limiting permanent dispersal movements, and increased fragmentation in an anthropogenically modified landscape may reduce the distance and rates of dispersal (Shepard et al. 2008). Even in comparatively rural landscapes in Pennsylvania, barriers were associated with the termination of 46% of dispersal paths and 41% of forays. The termination of deer dispersal where there is not an apparent barrier remains poorly understood, and knowledge of proximate influences on dispersal is necessary to understand how barriers influence population connectivity (Zeller et al. 2012, Vasudev et al. 2015). Several other proximate factors (e.g., improved habitat resources, intra-specific interactions) have been identified to influence the termination of dispersal in animals, and an interaction of multiple factors may result in the settlement of the disperser (Clobert et al. 2012).

Although our results provide insight into the dispersal behavior of female white-tailed deer, the scope of our inferences is limited by small sample sizes as a consequence of low dispersal rates. Larger sample sizes and continued improvements in GPS-collar technology would improve the ability to identify the effect that landscape features, habitat characteristics, and intra-specific social interactions have on proximate dispersal cues.

MANAGEMENT IMPLICATIONS

The metrics (e.g., rate, distance, barriers) of female dispersal should be considered for the localized management of deer populations. For example, using landscape features that act as barriers to delineate biologically important management units, and accounting for female immigration is warranted for programs that aim to reduce local populations. Conversely, anthropogenic features, such as highways, that act as barriers to dispersal may influence ecological processes by reducing connectivity and increasing mortality rates. Additionally, the lack of directionality in female dispersal, the semi-permeable nature of physical barriers to dispersal, and the frequency of forays outside of the natal range should be considered in regard to management objectives aimed at controlling the spread of diseases, such as CWD.

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