Multiple proximate and ultimate causes of natal dispersal in white-tailed deer

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Proximate and ultimate causes of dispersal in vertebrates vary, and relative importance of these causes is poorly understood. Among populations, inter- and intrasexual social cues for dispersal are thought to reduce inbreeding and local mate competition, respectively, and specific emigration cue may affect dispersal distance, such that inbreeding avoidance dispersal tends to be farther than dispersal to reduce local competition. To investigate potential occurrence of multiple proximate and ultimate causes of dispersal within populations, we radio-marked 363 juvenile male white-tailed deer (*Odocoileus virginianus*) in 2 study areas in Pennsylvania. Natal dispersal probability and distance were monitored over a 3-year period when large-scale management changes reduced density of adult females and increased density of adult males. Most dispersal (95–97%) occurred during two 12-week periods: spring, when yearling males still closely associate with related females, and prior to fall breeding season, when yearling males closely associate with other breeding-age males. Following changes to sex and age structure that reduced potential for inbreeding and increased potential for mate competition, annual dispersal probability did not change; however, probability of spring dispersal decreased, whereas probability of fall dispersal increased. Spring dispersal distances were greater than fall dispersal distances, suggesting that adaptive inbreeding avoidance dispersal requires greater distance than mate competition dispersal where opposite-sex relatives are philopatric and populations are not patchily distributed. Both inbreeding avoidance and mate competition are important ultimate causes of dispersal of white-tailed deer, but ultimate motivations for dispersal are proximately cued by different social mechanisms and elicit different responses in dispersers. *Key words:* demography, dispersal probability, dispersal rate, proximate cause, sex-biased dispersal, sociobiology. *[Behav Ecol 19:1235–1242 (2008)]*

Natal dispersal, or permanent emigration from birth site to site of potential first reproduction (Howard 1960), may be caused by multiple processes (Dobson and Jones 1985; Gandon and Michalakis 2001), and the relative importance of these mechanisms has been widely debated (Pusey 1987; Johnson and Gaines 1990). Explanations for the ultimate causes of emigration typically attribute increased fitness of dispersers to 1) avoidance of inbreeding (Wolff et al. 1988; Pusey and Wolf 1996), 2) reduction of competition for mates (Dobson 1982; Moore and Ali 1984), or 3) reduction of competition for resources (Murray 1967). When competition for limited resources or mates occurs at a local level, dispersal can be further reinforced through gains in inclusive fitness by reducing competition with kin (Hamilton and May 1977). Of these ultimate causes of natal dispersal, emigration related to inbreeding avoidance and mate competition tends to be sex biased according to breeding system (Greenwood 1980), such that in polygynous mammals, juvenile males are more likely to emigrate than females (Perrin and Mazalov 2000). In addition to multiple causes of dispersal occurring across species, it has been hypothesized that multiple ultimate causes may influence dispersal within a single population (Brandt 1992; Lidicker and Stenseth 1992). Perrin and Goudet (2001) suggest that inbreeding avoidance and kin competition interact frequently to shape dispersal patterns; however, empirically detecting multiple causes of dispersal within populations is difficult because different ultimate causes often qualitatively influence emigration similarly.

Proximate causes of dispersal also vary (Lambin et al. 2001). For instance, dispersal in animals has been shown to relate to environmental and habitat conditions such as crowding (Denno and Peterson 1995; Nunes et al. 1997) and food availability (Arcese 1989). In mammals, social structure plays an important role in eliciting dispersal behavior (Brandt 1992), with different social cues relating to specific ultimate causes of dispersal. For example, emigration proximately motivated by male–male agonism ultimately reduces local competition for mates (Wahlstrom 1994; Wauters et al. 2004), whereas male dispersal cued by the presence of closely related females ultimately reduces probability of inbreeding (Pusey 1987; Wolff 1993). Consequently, demographic manipulation, herein defined as changes in sex and age structure of populations, can be used to test causes of emigration. Removal of opposite-sex parent (Brody and Armitage 1985; Holzenbein and Marchinton 1992; Wolff 1992) or same-sex conspecifics (Loew 1999) has been shown to reduce emigration probability, whereas increasing the density of same-sex conspecifics may increase dispersal probability (Bollinger et al. 1993).

Dispersal distances of vertebrates also differ according to ultimate cause of dispersal (Waser 1987; Sutherland et al. 2000). Relatively short movements (e.g., outside immediate home range or territory) may be sufficient for escaping local mate competition, but when opposite-sex relatives are philopatric, longer dispersal distances (e.g., outside social group) may be necessary to escape inbreeding (Ronce et al. 2001). For example, natal dispersal of birds is typically longer than breeding dispersal (i.e., dispersal after first breeding attempt; Paradis et al. 1998), and natal dispersal is more likely to relate to inbreeding avoidance than is breeding dispersal, which

typically relates to competition for mates or nest sites (Greenwood and Harvey 1982).

The cooccurrence of multiple ultimate and proximate causes of emigration within vertebrate populations remains relatively poorly understood. Field-based studies to investigate various causes of dispersal operating together have been conducted (e.g., Dobson 1979; Lambin 1994), but most experimental studies have investigated dispersal in small mammals or birds. Comparable, large-scale investigations evaluating effects of demographic changes on emigration of large mammals are especially rare (Sinclair 1992), and field studies investigating links between ultimate causes and distances of dispersal are lacking (Ronce et al. 2001).

To investigate the potential occurrence of multiple causes of dispersal within populations, we studied natal dispersal of yearling (12–24 months) male white-tailed deer (*Odocoileus virginianus* Boddaert) during a period of large-scale management changes that reduced the density of adult females (>12 months old) and increased the density of adult males (>24 months old). Male white-tailed deer reach reproductive maturity as yearlings (~18 months), whereas females may reproduce as fawns, though reproduction is condition dependent (Smith 1981), as has been shown for other deer (Gaillard et al. 1992). As in most mammals, dispersal in deer is typically male biased (Hjeljord 2001), and natal dispersal of male deer has been attributed to intersexual cues related to inbreeding avoidance (Woodson et al. 1980; Holzenbein and Marchinton 1992) or intrasexual cues related to local mate competition (Wahlstrom 1994; Rosenberry et al. 2001; Shaw et al. 2006). Because natal dispersal of yearling male white-tailed deer is seasonal (Nixon et al. 1994), with emigration occurring in spring, when yearlings associate most closely with related adult females (Marchinton and Hirth 1984) and during fall, when yearlings associate most closely with other males (Hirth 1977; Ozoga and Verme 1985), we hypothesized that intersexual cues primarily motivate spring dispersal, whereas intrasexual cues primarily motivate fall dispersal.

Hence, we predicted that changes in sex and age structure would influence seasonal dispersal probabilities differently. If inbreeding avoidance dispersal, cued by presence of related females, were the only ultimate cause of dispersal of juvenile males, then we predicted that only spring dispersal probabilities would change. Specifically, as harvest of females increased (and survival decreased), proximate cues for inbreeding avoidance dispersal would be lessened, and spring dispersal would decrease. Alternatively, if local mate competition dispersal, triggered by presence of male conspecifics, were the only ultimate cause of dispersal, then we predicted that only fall dispersal probabilities would change. Specifically, as harvest of males decreased (and survival increased), proximate cues for mate competition dispersal would be amplified, and fall dispersal, immediately prior to breeding season, would increase. If both inbreeding avoidance and mate competition were important ultimate causes of dispersal, then we expected both changes to occur; specifically, spring dispersal probability would decrease and fall dispersal probability would increase.

Likewise, we hypothesized that if ultimate causes of dispersal differed by season, then seasonal dispersal distances would differ as well. Because female white-tailed deer are typically less likely to disperse than males (Nelson and Mech 1992), localized genetic structuring of females is common (Mathews and Porter 1993; Purdue et al. 2000). Local structures of some populations of female white-tailed deer have been described as home ranges arranged like rose petals (Porter et al. 1991), with ranges of closely related females (e.g., mother/daughter pairs) overlapping greatly and ranges of less related individuals radiating outward, such that genetic distance increases with linear distance from center (Comer et al. 2005). Therefore,

where such localized genetic structure is present, dispersal to avoid inbreeding with relatives would require movements of several home range diameters from origin. Theoretical work has suggested that, in polygynous species, female choice of unrelated males motivates male-biased dispersal to avoid inbreeding (Lehmann and Perrin 2003), and empirical evidence for this pattern in mammals has recently been demonstrated (Höner et al. 2007). Although it is not known if female white-tailed deer actively discriminate against related males, such a mate-choice system would reinforce long-distance dispersal for juvenile males seeking to maximize reproductive opportunities and is consistent with observations of increased dispersal probability of non-orphaned male white-tailed deer (Holzenbein and Marchinton 1992).

Genetic structuring of male white-tailed deer is less understood, but dispersal of males is common (typically 50–80% disperse as yearlings, Long et al. 2005) and because of this, local populations of males are, presumably, less related than females (Purdue et al. 2000). Hence, dispersal to reduce kin competition would not necessarily be reinforced by long-distance movements from natal range. Fall dispersal to avoid local mate competition could be effective with relatively short-distance movements, by removal from the immediate proximate cause (e.g., overlapping home range of local adult males), and could be theoretically accomplished by movements as short as one home range diameter. Although adult male white-tailed deer home ranges tend to be larger than female home ranges, especially during the fall breeding season, absolute differences in gender-specific home range diameters tend to be small (e.g, <1.0 km; Tierson et al. 1985; Beier and McCullough 1990). Therefore, we predict that if intersexually cued spring dispersal were ultimately caused by inbreeding avoidance and intrasexually cued fall dispersal were ultimately caused by mate competition, then spring dispersal distances would be greater than fall dispersal distances.

MATERIALS AND METHODS

Study areas

From 2002 to 2004, dispersal parameters of deer were measured in 2 study areas in Pennsylvania, separated by approximately 150 km, including the western study area (WSA, 1200 km^2) in the Appalachian Plateau region of western Pennsylvania and the eastern study area (ESA, 620 km^2) in the Ridge and Valley region of central Pennsylvania. In both areas, dominant tree species included northern red oak (*Quercus rubra*) and white oak (*Quercus alba*) along with maple (*Acer* spp.), birch (*Betula* spp.), beech (*Fagus grandifolia*), and hickory (*Carya* spp.). The WSA was 49% forested, the ESA was 57% forested, and the remaining land in both areas was predominantly cropland, consisting of corn, soybeans, and grain. In the WSA, forests were extensively fragmented by agricultural fields, and much of the forested landscape existed as isolated woodlots, whereas in the ESA, agriculture was restricted to valleys, and ridges were composed of large tracts of forest. Although black bear and coyote predation of neonatal deer is common in Pennsylvania (Vreeland et al. 2004), we observed no predation of juvenile or adult deer (≥7 months) in either study area; however, extensive hunting of both sexes of deer occurred throughout both areas. In both areas, alternative-weapon hunting seasons (e.g., archery) began in early October, but >80% of annual hunting mortality occurred after the end of November, when firearm seasons commenced.

Changes in population sex and age structure

Pennsylvania has experienced historically intense hunting pressure on antlered deer, with approximately 80% of yearling

males annually harvested statewide and <1% of males surviving to 4.5 years (Diefenbach et al. 1997). Because of this hunting pressure, deer populations in Pennsylvania demonstrated skewed sex and age structure, such that relatively few adult bucks persisted in the population, and sex ratios were heavily skewed toward adult females, conditions that are common in many extensively hunted white-tailed deer populations (Miller and Marchinton 1995). To restore a demography less skewed toward females and yearling males, statewide management changes were instituted in late fall 2002 to decrease abundance of female deer and increase abundance of adult male deer. Harvest of female deer was increased by increasing the allocation of hunting permits for antlerless deer. Survival of yearling males was increased via statewide regulations that required deer to possess ≥3 or 4 antler point projections, depending on the region of the state, on a single antler to be legal for harvest. Less restrictive regulations prior to 2002 (i.e., a single antler ≥7.5 cm) protected relatively few yearling bucks from harvest. Although male white-tailed deer shed antlers annually, mass and number of points per antler tend to increase with age (Lukefahr and Jacobson 1998), especially as deer transition through the first few years of life. Consequently, the new regulations protected the majority of yearling bucks from harvest, but most adult bucks remained eligible for harvest.

Sex- and age-specific changes in density resulting from these new management practices were calculated using a modified sex–age–kill (SAK) model, which is an accounting model that uses sex- and age-specific harvest demographics to estimate survival, recruitment, and population density (Skalski et al. 2005). To eliminate the restrictive assumption common in SAK models of a stable age distribution, we used survival and harvest rate estimates from our radio-marked deer in the study areas to estimate the age-specific abundances of males. Estimated density of adult females, which we predicted would be an important predictor of spring dispersal rate, decreased in both study areas (WSA: 6.0 to 4.4/km^2, ESA: 5.5 to 3.4/km^2). Similarly, through decreased recruitment, density of yearling males decreased in both areas (WSA: 2.3 to 1.6/km^2, ESA: 1.6 to 0.90/km^2), but through increased survival, density of adult males increased in both areas (WSA: 0.6 to 1.3/km^2, ESA: 0.9 to 1.0/km^2). In this way, breeding ratios of adult females per adult male, which we hypothesized may influence mate competition and fall dispersal, decreased substantially during the period of management changes (WSA: 9.8:1 to 3.4:1, ESA: 6.2:1 to 3.3:1). During the same period, overall deer density was reduced in both areas (WSA: 13.5 to 11.0/km^2, ESA: 11.3 to 7.2/km^2).

Deer capture and monitoring

We captured, radio-marked, and monitored 363 juvenile male white-tailed deer in the 2 study areas ($n_{WSA} = 239$, $n_{ESA} = 124$). Deer were captured in winters from late December to early April 1 year before (2001–2002, $n = 108$) and 2 years after demographic manipulation (2002–2003, $n = 133$; 2003–2004, $n = 122$), using net gun from helicopter (Hawkins and Powers Aviation, Greybull, WY), box traps (Clover 1956), drop nets (Conner et al. 1987), and rocket nets. At the time of capture, fawns were approximately 7–10 months of age, and because dispersal of male fawns younger than 11 months is rare (Marchinton and Hirth 1984), capture of deer during late winter and early spring reduced the likelihood of capturing fawns that had already dispersed.

Male fawns were equipped with one of 3 types of radio transmitters, including 245-g expandable very high–frequency (VHF) neck collars (Advanced Telemetry Systems, Isanti, MN), 19-g VHF ear tag transmitters (Advanced Telemetry Systems), or 700-g expandable, automatic release global positioning system (GPS) neck collars (Telonics, Mesa, AZ). Additionally, fawns maintaining functional radio collars from an earlier study in the ESA (Vreeland et al. 2004) also were included in our study. In spring 2001, these fawns were caught as neonates (1–2 weeks of age) and were equipped with 97-g expandable VHF neck collars (Advanced Telemetry Systems; Diefenbach et al. 2003). Capture and marking protocols were approved by the Pennsylvania State University Institutional Animal Care and Use Committee (Protocol no. 01R135) and adhered to guidelines established by the Animal Behavior Society and the Association for the Study of Animal Behavior.

We monitored radio-marked deer using ground-based and aerial telemetry, locating VHF radio-marked deer 1–3 times per week. Locations were based on intersections of ≥2 telemetry bearings and were estimated using LOAS v. 2.04 (Ecological Software Solutions, Sacramento, CA). When deer could not be located from the ground, we used fixed-wing aircraft to locate deer. For deer equipped with GPS collars, we monitored survival once per week. GPS fixes were programmed to occur more frequently during peak dispersal periods (one fix every 7 h, May–June; one fix every 2.5 h, September–December) as compared with winter and summer (one fix every 23 h, January–April and July–August), when dispersal was rare. GPS collars on juvenile bucks were set to release automatically on 31 January of the year after capture, at which time location data were offloaded from the collar.

Dispersal rate

Natal dispersal of yearling male white-tailed deer was defined 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). Nonoverlapping locations were determined using a minimum convex polygon (MCP) to approximate natal ranges, and locations outside the MCP boundaries were considered extranatal movements. We identified this movement as a dispersal event if all subsequent locations remained outside the previously determined MCP boundary. Similarly, adult ranges of dispersers were defined via MCP, and any transitional locations between natal and adult ranges were not included as part of adult range if they were not contained within the MCP boundary formed by subsequent adult locations. Thus, first adult location of a disperser was defined as the first location outside the natal MCP and within the boundaries of an MCP delineated by the set of all subsequent locations. On rare occasions, deer that established separate adult ranges made brief return forays into their natal range, and to ensure that these deer were reproductively isolated from individuals within their natal range, they were considered dispersers only if these brief return movements occurred outside the fall breeding season. For 262 VHF-collared deer, whose dispersal fate could be determined, an average (±standard deviation) of 30.3 (16.1) natal locations and 14.8 (13.5) adult locations were estimated and used to construct MCPs. Similarly, an average of 578.1 (249.4) natal and 408.3 (288.3) adult locations were estimated for 12 GPS-collared deer with known dispersal fates.

To estimate and model dispersal rates (i.e., probability of dispersal) and timing of dispersal, we used the known-fates procedure in program MARK v. 4.2 (White and Burnham 1999). This procedure is based on the Kaplan–Meier survival model (Kaplan and Meier 1958; Pollock et al. 1989), because similar to mortality in survival studies, natal dispersal can occur only once (i.e., deer that disperse from their natal range are not at risk of future natal dispersal). When dispersal is an "event" in a Kaplan–Meier model, a philopatry rate is estimated, and the complement of this estimate is the dispersal rate.

Date of dispersal was defined as the first date that a deer was located outside its natal range without returning or,

alternatively, the first date we failed to locate a deer within its natal range and subsequently located it within a distinct, nonoverlapping adult range. For the known fates procedure, a biweekly monitoring interval was used, beginning in mid-April, after the end of capture, and continuing through the end of the calendar year, yielding 19 monitoring periods per year. This period was chosen because no yearling male deer were observed to have dispersed prior to mid-April or after the end of December. Deer that died before dispersing and deer with which we permanently lost contact prior to dispersal were censored from analyses.

Seven candidate models of dispersal probability were developed and tested based on 3 grouping variables: time (biweekly monitoring period), site (WSA and ESA), and year (2002, 2003, and 2004). Akaike's information criterion, corrected for small sample size (AIC_c), was used to select the most parsimonious model of dispersal (Burnham and Anderson 1998). From the best model, annual dispersal rates and standard errors as generated by MARK are reported.

To investigate within-year trends in dispersal, seasonal dispersal rates during the periods of peak dispersal were calculated, categorizing spring dispersal as the 6 biweekly monitoring periods from third week of April through the first week of July and fall dispersal as the 6 biweekly monitoring periods from the third week of September through the first week of December. We calculated seasonal dispersal rates independently of one another, such that individuals that dispersed in the spring were not included (i.e., they were not considered "at risk") in fall analyses. Standard error (SE) for seasonal dispersal rates were calculated from interval-specific variance estimates, using a Taylor series approximation (Seber 1982).

Dispersal distance

A fully crossed, fixed factor, 3-way analysis of variance was used to test for differences in mean dispersal distance among years, sites, and seasons, thereby allowing for the control of potentially confounding effects of year and study site. Dispersal distance was calculated as the straight-line distance between median x and y locations of natal and adult ranges (Kenward et al. 2002; Long et al. 2005). In rare cases (19 of 212 dispersers), only a single adult location was available, typically resulting from tag return data after transmitter failure. In these cases, a single-point estimate for adult range was used to calculate dispersal distance. Dispersal distances were normalized using ln transformation, and results are presented as back-transformed mean and SE. Normality of transformed dispersal distances was confirmed using the Kolmogorov–Smirnov normality test ($P > 0.15$), and equality of variances was confirmed using Levene's test ($P > 0.60$). All statistical tests were performed using MINITAB 13 (Minitab, State College, PA).

RESULTS

Dispersal rate

Of 363 males included in analysis, 212 dispersed as yearlings, 62 remained philopatric, and natal dispersal fates of 89 could not be determined due to death or lost contact prior to the end of the year. Although most hunting occurred after the conclusion of fall dispersal, 11 deer were harvested in early hunting seasons, before their dispersal fates could be determined. Deer were no longer considered at risk for natal dispersal after permanent emigration from their natal range occurred or after being censored during the period in which they died or when contact was initially lost (Pollock et al. 1989). For the most parsimonious model of dispersal rate (AIC_c weight = 92.3%), dispersal probability did not vary between study sites, but dispersal probabilities were not constant among years, such that season-specific dispersal probability in 2002 (i.e., before management changes) differed from seasonal dispersal in 2003 and 2004 (i.e., after management changes, Table 1). Based on this model (Figure 1), management changes did not alter annual dispersal rates (i.e., cumulative dispersal probability for the entire year) as annual dispersal probability prior to demographic changes was 0.68 (SE = 0.063) and annual dispersal after management changes was 0.70 (SE = 0.031). In all years, dispersal was seasonally synchronized, with most dispersal occurring during spring and fall (Figure 1). Of 204 dispersal events for which date was known, 82 occurred in spring, 117 occurred in fall, 4 occurred between these periods, and 1 occurred after the first week of December.

Although annual dispersal rates were similar throughout the study, model selection procedures indicated that dispersal rate functions after management changes differed from dispersal

Table 1

Performance of 7 candidate models estimating dispersal rates (D) of juvenile male white-tailed deer

Model	Model description	k^a	ΔAIC_c^b	w^c
D(time $\times$ 2002 vs. 2003/2004)	Dispersal varied within year and 2002 differed from 2003 to 2004.	38	0	0.923
D(time)	Dispersal varied within year but did not vary among sites or years.	19	5.04	0.074
D(time $\times$ year)	Dispersal varied within and among years but did not vary between sites.	57	11.81	0.003
D(time $\times$ site)	Dispersal varied within year and among sites but did not vary among years.	38	14.97	0.001
D(time $\times$ site $\times$ 2002 vs. 2003/2004)	Dispersal varied within year and among sites and 2002 differed from 2003 to 2004.	75	42.98	0.000
D(time $\times$ site $\times$ year)	Dispersal varied within and among years, and between sites.	113	70.5	0.000
D(null)	Dispersal probability was constant within and among years and between sites.	1	285.45	0.000

Models were tested based on 19 biweekly monitoring periods in each year (2002–2004) at 2 study sites. The first period was set to coincide with the earliest observed dispersal for any year (i.e., mid-April) and continued through the end of the calendar year.

[a] Number of model parameters.

[b] Difference between AIC_c and AIC_c of best-fit model.
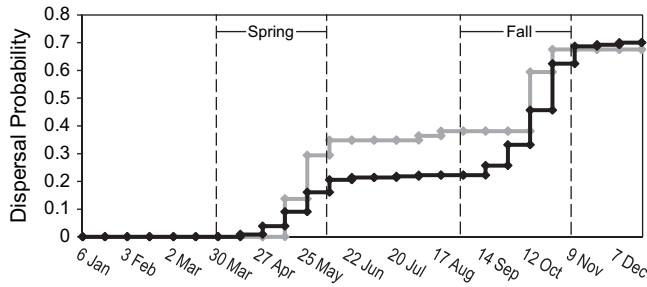
[c] Relative weight of AIC_c.

Figure 1
Kaplan–Meier dispersal probability for 363 radio-marked juvenile male white-tailed deer in Pennsylvania. Monitoring periods were defined as 2-week periods beginning the first full week of January for each year. The most parsimonious model of dispersal from beginning of dispersal in mid-April through the end of December indicated dispersal probability varied by time (i.e., monitoring period) and year (i.e., 2002 vs. 2003/2004) but not by study site (Table 1). The gray line represents dispersal functions prior to demographic changes (2002), and the black line represents dispersal functions following demographic changes (2003/2004).

patterns prior to changes, and examination of interval-specific dispersal probabilities indicated seasonal changes in dispersal probability. Winter and summer dispersal was uncommon both before and after changes; however, spring dispersal decreased and fall dispersal increased after management changes (Figure 1). Specifically, spring dispersal prior to management changes (0.35, SE = 0.05) was 67% greater than spring dispersal after management changes (0.21 ± 0.03), and fall dispersal after management changes (0.61 ± 0.04) was 27% greater than fall dispersal prior to changes (0.48 ± 0.09).

Dispersal distance

Mean spring dispersal distance (9.0 ± 0.6 km, mean ± SE) was 76% greater than fall dispersal distance (5.1 ± 0.3 km; $F_{1,198}$ = 20.92, $P < 0.001$; Figure 2). Study area and year, as well as all interaction terms, were not significant (Table 2). Maximum spring (40.2 km) and fall (40.6 km) dispersal distances were similar; however, 52% of spring dispersals, compared with 18% of fall dispersals, were greater than 9 km (Figure 2).
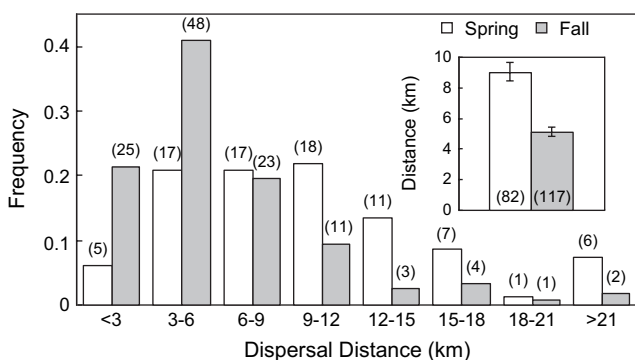

Figure 2
Histogram of dispersal distances by season for 199 radio-marked juvenile male white-tailed deer in Pennsylvania. Data for philopatric deer (i.e., deer whose adult locations overlapped natal locations) are not included. Inset shows mean dispersal distance (±SE) by season. Mean dispersal distance varied by season ($F_{1,198}$ = 20.92, $P < 0.001$) but did not vary by study site or year.

Table 2
Fully crossed, fixed-factor, 3-way analysis of variance table for the effects of study site, year (2002–2004), and season (fall vs. spring) on dispersal distances of white-tailed deer in Pennsylvania

Source	df	Type III Sum of Squares	Mean Square	F	P
Site	1	0.525	0.525	1.45	0.230
Year	2	0.457	0.229	0.63	0.533
Season	1	7.572	7.572	20.92	<0.001
Site × year	2	0.133	0.067	0.18	0.832
Site × season	1	0.023	0.023	0.06	0.803
Year × season	2	0.272	0.136	0.38	0.687
Site × year × season	2	0.476	0.238	0.66	0.520
Error	187	67.67	0.362		
Total	198	87.90			

DISCUSSION

Dispersal rate

Large-scale changes in management provided an opportunity to evaluate the effects of changes in sex and age structure on dispersal patterns of juvenile male white-tailed deer. Following management that reduced density of adult females and increased density of adult males, dispersal patterns of male white-tailed deer changed. The most parsimonious model of dispersal included terms that captured variation in seasonality (i.e., time) as well as variation before and after management changes (Table 1). Probability of dispersal did not vary between areas, and models including a term for study site consistently were not competitive compared with models excluding this term (Table 1). Despite landscape differences between the WSA and ESA and separation of approximately 150 km between sites, similar demographic changes were initiated at the same time on both study sites, and dispersal patterns responded similarly, suggesting that dispersal probability of white-tailed deer relates closely to population structure (Long et al. 2005).

Annual dispersal rates remained consistent throughout the study; however intraannual (i.e., seasonal) dispersal patterns changed. These results are consistent with hypotheses that seasonally distinct social cues are important proximate causes of dispersal in white-tailed deer. Specifically, as density of adult females decreased, spring dispersal became less common, and during the same period, fall dispersal became more common as density of adult males increased. Although density of adult males increased only slightly in the ESA (0.9 to 1.0/km²), breeding-age sex ratios became much less biased toward females in both study areas, a demographic change that likely increased intensity of mate competition among males (Clutton-Brock et al. 1982; Bonenfant et al. 2004). In both years, approximately 30% of juvenile males did not disperse, a philopatry rate consistent with other populations of white-tailed deer (Long et al. 2005). Although with our data we could not decisively identify factors that caused philopatry in individual males, possible mechanisms include orphaning, low levels of local mate competition, or even avoidance of conspecifics without removal from natal range.

Reduced harvest of yearlings during hunting seasons after the implementation of antler restrictions (harvest rate = 0.31 ± 0.04) combined with high survival of bucks from the end of hunting season to the following fall (0.92 ± 0.02; Wallingford et al. 2006) resulted in increased recruitment of yearling bucks into older age classes, as suggested by our SAK model estimates of adult male density. Although estimating population density of large mammals is difficult (Skalski et al. 2005), the direction and magnitude of trends we observed in

sex- and age-specific density estimates were consistent with management goals and we believe provided reasonable estimates of population changes. From 2001 to 2003, female harvest increased in the counties containing our study areas by approximately 44%, and as harvest of adult females increased in our study areas, SAK model estimates indicated that adult female density decreased.

Although we could not determine whether local mate competition dispersal related directly to reduction of kin competition, because we did not determine genetic relatedness of individuals within the population, kinship considerations could have reinforced fall dispersal as relative abundance of adult males increased. For example, as yearling male dispersal in spring decreased, average relatedness of yearling males in fall likely increased, thereby providing additional motivation for fall dispersal (i.e., reduction of competition among kin for mates). Alternatively, in animals with strong social structures, kin selection may favor philopatry if kin cooperation improves reproductive success (Pusey 1987; Perrin and Goudet 2001); however, as male white-tailed deer are not cooperative breeders, it is likely that increased competition for mates, whether among relatives or nonrelatives, would increase, rather than decrease, dispersal probability. Further, because philopatry of males in our study was low, most adult males in a given area likely emigrated into that area; therefore, we suspect most mate competition between age classes (i.e., between yearling and adult males) was between nonrelatives, and importance of kin selection in reducing local mate competition in these cases was low.

Previous studies investigating proximate mechanisms of dispersal in deer have identified individual important social cues, such as cues from related females (Woodson et al. 1980; Holzenbein and Marchinton 1992) or intrasexual aggression (Wahlstrom 1994). However, Rosenberry et al. (2001) recommended simultaneous testing of inter- and intrasexual cues because these causes of dispersal are not likely mutually exclusive (Dobson and Jones 1985; Shields 1987), and our data suggested that multiple proximate mechanisms motivated dispersal of juvenile male white-tailed deer within a population.

Further, in a previous meta-analysis study, we found that annual dispersal rates of juvenile male white-tailed deer ranged from 0.46 to 0.80, but we found no relationship between population density and annual dispersal rate (Long et al. 2005). However, these studies compared absolute density of white-tailed deer across many habitats and did not investigate interannual variation in population density or dispersal rate. Density-dependent dispersal has been reported for some mammal populations (Sutherland et al. 2002; Matthysen 2005), but there was no evidence that total population density influenced annual dispersal rate of white-tailed deer. Population density decreased 19–36% within sites during the study, but annual dispersal rate did not change appreciably after management changes, suggesting that sex-specific densities and relative densities (i.e., sex ratios) were more important for eliciting dispersal than total density (re: Wauters et al. 2004; Shaw et al. 2006). In this way, competition for local resources did not seem to be a likely ultimate cause of white-tailed deer dispersal based on observations that dispersal is commonly sex biased, dispersal occurred during times of abundant food, spring and fall dispersal rates changed in opposite directions but predictably with changes in sex and age structure, and that reductions in total population density did not affect annual dispersal rates.

Dispersal distance

Although intraspecific differences in dispersal distances among populations have been shown to relate to landscape char-

acteristics such as spatial arrangement of suitable patches (Wiggett and Boag 1989) degree of fragmentation (Matthysen et al. 1995), and coverage of preferred habitat (Long et al. 2005), variation in dispersal distances within populations may relate more strongly to underlying causes of dispersal. Consequently, different ultimate causes of dispersal may be associated with different proximate cues, and these social cues may effect different dispersal distances within a population. In this way, intrasexual aggression prior to the breeding season is thought to reduce competition for mates, thus yielding relatively short dispersal; however, intersexual cues from opposite-sex parent or close relatives motivate dispersal to avoid incestuous breeding, thus yielding potentially longer dispersal distances (Ronce et al. 2001). Although different causes of dispersal may elicit different dispersal distances, trade-offs exist between distance traveled and fitness gained, and dispersers should travel minimum distances necessary to secure high-quality breeding opportunities (Baker and Rao 2004).

Dispersal distances of white-tailed deer were greater in spring than fall, consistent with the prediction that inbreeding avoidance dispersal would be longer than dispersal to reduce local mate competition. The classic rule of competition dispersal states that individuals should disperse to the first vacant territory and then stop because longer distance dispersal incurs more risks (Murray 1967). This process may be accomplished by moving relatively few home range diameters from the natal source, especially when populations are not saturated or widely dispersed or when immigrants are not actively excluded. White-tailed deer are habitat generalists (Harlow 1984), and based on radio location data of marked individuals in our study, we found no evidence of white-tailed deer being restricted to widely spaced habitat patches. Further, although male–male aggression is an important cue for emigration prior to breeding season, the process of settlement (i.e., immigration) in deer remains poorly understood (Rosenberry et al. 1999), but white-tailed deer are not territorial (Graf 1956).

As a result of these conditions, mate competition dispersal could be accomplished by relatively short-distance movements. In our study areas, the average size of male home ranges during the breeding season was 3.1 km^2, and assuming approximately circular ranges, the diameter of fall home ranges averaged 2.0 km. Hence, fall dispersers traveled, on average, 2.6 home range diameters from their natal range, and 63% traveled less than 3 home range diameters before establishing an adult range (Figure 2).

In contrast, inbreeding avoidance dispersal may require longer dispersal distances to remove individuals from philopatric, opposite-sex relatives, and to be effective, dispersers may need to travel a greater number of home range diameters (Pusey 1987; Ronce et al. 2001). Although we did not radiomark adult females to measure home range diameter, spring home ranges of young males prior to dispersal, when they were still closely associated with adult females, averaged 2.1 km^2, yielding an average home range diameter of 1.6 km. Spring dispersers traveled significantly farther than fall dispersers, moving 5.6 range diameters before establishing adult ranges. Only 15% dispersed less than 3 home range diameters, whereas 57% dispersed greater than 5 home range diameters. Conversely, associated with potential costs of dispersal, extremely long-distance dispersals related either to mate competition or inbreeding avoidance should not be common in nonpatchy, stable habitats, and during both seasons 95% of natal dispersers traveled less than 15 home range diameters before establishing adult ranges.

Multiple causes of dispersal likely occur within populations of vertebrates, but field-based enquiries addressing this hypothesis are rare, especially for large mammals. Because

white-tailed deer are actively managed through regulated hunting, we were able to investigate influences of population-level effects on emigration and transition patterns during a time when intentional large-scale changes in sex and age structure were implemented. Although demographic changes in our study were effected via management, white-tailed deer populations throughout the majority of their range in the United States live in human-modified landscapes and are actively managed through hunting to achieve desired population size and structure. Therefore, we expect these underlying patterns are not unique to our study system and suggest that management can yield data useful for investigating ecological relationships, especially for species that exist largely in managed populations and landscapes.

Our study suggests that both inbreeding avoidance and mate competition ultimately underlie emigration of juvenile male white-tailed deer, and that, proximately, these ultimate causes of dispersal are elicited by different social cues during different seasons. Further, in addition to being differentially prompted, ultimate causes of dispersal are differentially enacted during transitional movements, such that mate competition dispersal is shorter than inbreeding avoidance dispersal. Additional studies of dispersal behavior in unhunted deer populations, which are typically less biased toward females and demonstrate older age structures (Miller and Marchinton 1995), could provide valuable points of comparison among populations with different demographics and population densities. For instance, in unexploited populations with greater adult male to female gender ratios, we would predict greater fall dispersal and less spring dispersal than in heavily hunted populations with female-biased sex structures.

Although this study investigated emigration cues and distance of transitional movements, the final phase of dispersal, settlement, remains poorly understood for most vertebrates. In this study, we did not evaluate small-scale demographic and genetic composition of deer in postdispersal, adult ranges. Future studies would benefit by assessing degree of genetic relatedness of deer in natal and adult (i.e., extranatal) ranges and by assessing sex and age structures of conspecifics within each settlement range. In this way, factors important for immigration, in addition to emigration, could be identified.

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