Population density influences dispersal in female white-tailed deer

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Dispersal behavior in white-tailed deer (*Odocoileus virginianus*) predominantly occurs in 1-year-old males; however, females of the same age also disperse. The timing of female dispersal during fawning season and low dispersal rates suggest that competition for mates and reduced inbreeding are not ultimate causes of female dispersal, as suggested for males. We proposed that female dispersal is the result of competition for space when pregnant females seek to isolate themselves before and after parturition. To test this hypothesis, we conducted a meta-analysis of female dispersal rates from 12 populations of white-tailed deer and predicted dispersal rate and distance were positively related to deer density. We found a positive relationship between dispersal rate and deer per forested km^2 and between dispersal distance and deer per forested km^2. These results are consistent with the hypothesis that female dispersal is density-dependent and caused by the exclusion of subordinate 1-year-olds as adult females seek isolation before and after parturition.

Key words: density-dependent dispersal, dispersal distance, dispersal rate, female dispersal, *Odocoileus virginianus*, parturition, white-tailed deer

Dispersal can be defined as permanent movement of an organism away from its place of origin (Nathan 2001). Dispersal is a common life-history trait across taxa and is ecologically important because it influences 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). For dispersal behavior to persist, the benefits of dispersal must outweigh the risks and costs associated with traversing the landscape and inhabiting an unfamiliar location (Dobson 1982). Such benefits may include reducing potential for inbreeding (Pusey 1987; Pusey and Wolf 1996), competition for local resources (Murray 1967), and competition for breeding partners (Dobson 1982; Moore and Ali 1984).

Vertebrate dispersal is most common among juveniles or young adults and often sex-biased in sexually dimorphic species (Pusey 1987; Pusey and Wolf 1996). In particular, dispersal behavior typically occurs among juvenile females in birds and juvenile males in mammals (Greenwood 1980). This pattern is consistent with hypothesized ultimate causes of dispersal because young age classes are more likely to have reduced access to local resources and mates, and inbreeding avoidance is maximized when individuals of only 1 sex exhibit prominent dispersal behavior (Long et al. 2008). In contrast, sex-biased dispersal does not occur among mammalian species with minimal sexual dimorphism and that exhibit resource-defense polygyny (similar to most birds), and inbreeding avoidance may be achieved via excursions by adult females during the breeding season (Gaillard et al. 2008).

Maximum fitness could occur where the sex that requires the greatest familiarity with its local environment remains philopatric (Greenwood 1980). In red deer (*Cervus elaphus*), costs of dispersing are likely lower among males than females because variation in male reproductive success is less closely related to differences in home range quality compared with females (Clutton-Brock et al. 1982). In white-tailed deer (*Odocoileus virginianus*), females provide parental care; therefore, female familiarity with local resources likely increases offspring fitness. Consequently, male white-tailed deer exhibiting female-defense polygyny would display dispersal behavior, and females would remain philopatric. Indeed, dispersal behavior is most prevalent among 1-year-old males (Marchinton and Hirth 1984) and has been documented

Table 1.—Dispersal statistics for yearling female white-tailed deer (*Odocoileus virginianus*) from 12 North American populations. Dispersal rate is the proportion of individuals that dispersed. WMU, Wildlife Management Units.

Region	Reference	Forest cover (%)	Study area size (km^2)	Mean dispersal distance (km)	Landscape population density (deer/km^2)	Population density (deer/forested km^2)	Dispersal rate	Number of individuals monitored
Southern Illinois	Hawkins and Klimstra 1970	56	73	7	38.4	69	0.13	79
East-central Illinois	Nixon et al. 1991, 1994, 2007	3	30	37	15.3	510	0.49	41
West-central Illinois	Nixon et al. 1991, 1994, 2007	20	59	41	25.0	125	0.22	32
Northern Illinois	Nixon et al. 1991, 1994, 2007	2	16	37	18.4	920	0.45	29
South-central Wisconsin	Oyer et al. 2007; Skuldt et al. 2008	57		35	11.2	20	0.03	32
Eastern Montana	Dusek et al. 1989	32	224	20	36.8	115	0.17	53
West Virginia	Langdon 2001; Campbell et al. 2004	97	34	15	16.0	16	0.04	28
New York	Rudolph et al. 2000; Porter et al. 2004	37	43		18.0	49	0.12	25
Pennsylvania WMU 2D	This study	60	6,440	17	19.4	32	0.08	24
Pennsylvania WMU 2G	This study	88	10,658	18	7.6	9	0.06	73
Pennsylvania WMU 3C	This study	75	5,678	8	17.3	23	0.24	17
Pennsylvania WMU 4B	This study	65	4,120	20	10.8	17	0.15	115

to occur in 46–75% of young male white-tailed deer (Long et al. 2005). Although females are more philopatric than males, dispersal occurs in 4–49% of female white-tailed deer (Table 1).

Understanding white-tailed deer dispersal in females not only provides insights into evolutionary strategy of behavior (Holzenbein and Marchinton 1992; Long et al. 2008) but also provides guidance for informed population and disease management (Rosenberry et al. 1999; McCoy et al. 2005; Diefenbach et al. 2008). In white-tailed deer, female dispersal has population and disease management implications. Defining parameters that influence dispersal rates and distances are critical to understanding the potential for the spread of diseases, such as chronic wasting disease, across the landscape (Grear et al. 2006; Cullingham et al. 2011). Knowledge of female deer dispersal also is relevant to localized management of deer population densities because managers increasingly look for methods to control deer densities in areas closed to hunting, such as parks and areas of suburban development. Current and proposed strategies often remove females from the target population or attempt to reduce reproduction. However, for these management strategies to be effective, one must understand the effect of female dispersal on the target population (Porter et al. 1991; Campbell et al. 2004).

Ultimate causes for dispersal behavior in female white-tailed deer remain poorly understood. Long et al. (2008) proposed inbreeding avoidance and reduced mate competition as ultimate causes of dispersal in male white-tailed deer. However, high rates of male dispersal (46–75%—Long et al. 2005) suggest that females do not need to disperse to avoid inbreeding. Additionally, white-tailed deer are polygynous. Thus, only

males benefit from behavior that reduces competition for mates because the number of offspring that a male can sire is limited by the number of mates (Perrin and Mazalov 2000). Conversely, females are limited to a finite number of offspring they can rear and only require 1 mate to produce multiple offspring. Dispersal to reduce competition for mates also would be predicted to occur during the breeding season (Long et al. 2008), but female dispersal predominantly occurs during the fawning season (Hawkins et al. 1971; Dusek et al. 1989; Porter et al. 2004).

Although many resources, such as food and cover, are increasing or stable during the fawning period for white-tailed deer, habitat and space for fawning are finite and may be important. Pregnant females become agonistic towards other deer, including relatives, around the time of parturition (Schwede et al. 1993; Jones et al. 1997). Ozoga et al. (1982) observed that all females in a captive herd isolated themselves and demonstrated territorial characteristics for several weeks at the time of parturition, and the authors concluded that crowding limited fawn rearing space, disrupted maternal behavior, and caused excessive mortality among fawns. Importantly, isolation of females and offspring for several weeks after parturition allows formation of proper mother–offspring bonds (Ozoga et al. 1982). Additionally, predation rates on fawns are highest during the 1st few weeks after birth (Carroll and Brown 1977; Ballard et al. 1999; Vreeland et al. 2004), and isolation provides an important defensive strategy against predation (Edmunds 1974; Marchinton and Hirth 1984).

We proposed that female dispersal is initiated by socially dominant females excluding subordinate individuals during parturition, the relocation phase is perpetuated by continued

exclusion by other socially dominant females, and dispersal is terminated when the disperser is not excluded from an area because of adequate habitat conditions or acceptance into a local social group. This mechanism of density-dependent exclusion at parturition would result in the disperser establishing an adult home range where it potentially could occupy a position of higher social standing and gain access to adequate habitat for its current or future fawning needs.

If the ultimate cause of female dispersal is to seek an area with reduced competition for space, then we expect dispersal behavior to be influenced by an individual's access to those resources. We proposed that physical space in suitable fawning habitat is a limited resource and as space becomes limited by the density of individuals, the rate and distance of dispersal are likely to increase. To evaluate this hypothesis, we tested predictions that dispersal rate and dispersal distance are positively correlated with deer per forested km^2. We combined data from 4 radiocollared populations of female white-tailed deer with data from 8 previously studied populations to conduct a meta-analysis of female dispersal rates, distances, and deer densities.

MATERIALS AND METHODS

Study areas.—We monitored dispersal behavior of female white-tailed deer in 4 study areas in Pennsylvania delineated as Wildlife Management Units (WMU) 2D, 2G, 3C, and 4B (Fig. 1) by the Pennsylvania Game Commission (PGC—Rosenberry and Lovallo 2003; Rosenberry et al. 2009). The WMU 2D study area was located in the Pittsburgh Low Plateau physiographic region of western Pennsylvania with topography of gradually sloped hills (Cuff et al. 1989). The area was approximately 6,440 km^2 and consisted primarily of privately owned property that was farmland, woodlots, and small residential areas. In all study areas, agricultural fields commonly were used to grow corn, soybeans, alfalfa, and grass hay. In WMU 2D, forests were generally contained in small, fragmented woodlots. Forest types were predominantly red oak (*Quercus rubra*)-mixed hardwood and northern hardwood (Fike 1999), and 60% of the landscape was forested.

The WMU 2G study area was located in the deep valleys section of the Appalachian Plateaus physiographic region of north-central Pennsylvania (Cuff et al. 1989). The topography is dominated by high, flat plateaus and steep mountain slopes. The 10,658-km^2 area consisted mostly of large tracts of publicly owned forest. Agricultural land use was rare, and 88% of the landscape was forested. Forest types were similar to the WMU 2D study area.

The WMU 3C study area was located in the Glaciated Low Plateau section of the Appalachian Plateaus physiographic region of northeastern Pennsylvania (Cuff et al. 1989). The topography consisted of rounded hills and valleys. The 5,678-km^2 study area was a patchwork of forested woodlots, agricultural fields, wetlands, and small human population centers. The landscape was 75% forested, with northern hardwoods being the most common forest type.

The WMU 4B study area was located in the ridge and valley region of south-central Pennsylvania and was 65% forested (Cuff et al. 1989). The 4,120-km^2 area consisted of long, parallel ridges and valleys along a northeast–southwest axis. The ridges were forested, predominantly red oak-mixed hardwood type, and the valleys were mostly agricultural land use.

Deer capture and data collection.—From 2005 through 2011, we captured and radiomarked 277 approximately 8-month-old female white-tailed deer from January through mid-April using rocket nets (Beringer et al. 1996), single-gate Clover traps (Clover 1956), and drop nets (modified from Ramsey 1968).
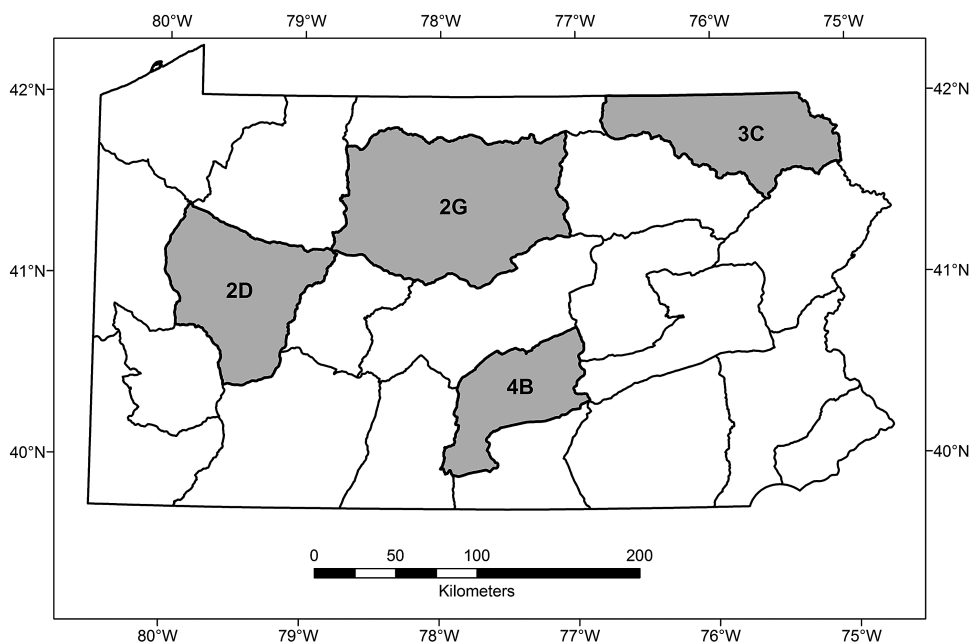

Fig. 1.—Map of Pennsylvania showing locations of Wildlife Management Units 2D, 2G, 3C, and 4B. From 2005 to 2011, we tracked 229 radiomarked 1-year-old female white-tailed deer (*Odocoileus virginianus*) in these study areas to record dispersal behavior.

We physically restrained, processed, and released without sedation deer captured in Clover traps. We chemically sedated deer captured in rocket or drop nets with 0.5 mg/kg of body mass of xylazine hydrochloride, fitted them with a radiotransmitter and then intramuscularly administered an antagonist of 2 mg/kg of body mass of tolazoline hydrochloride (Rosenberry et al. 1999). We fitted deer with either a very high-frequency (VHF) neck collar (ATS, Inc., Isanti, Minnesota) or a global positioning system (GPS) neck collar (Vectronic Aerospace GmgH, Berlin, Germany, 863 g; Telonics, Inc., Mesa, Arizona, 700 g; H.A.B.I.T. Research Ltd., Victoria, British Columbia, 750 g). We released all deer at the capture location, and we handled all animals in accordance with protocols approved by the Pennsylvania State University Institutional Animal Care and Use Committee (IACUC No. 34910) and followed guidelines of the American Society of Mammalogists (Sikes et al. 2011).

We defined dispersal to have 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 the natal minimum convex polygon (MCP) range did not overlap the adult MCP range (Long et al. 2005). Because dispersal in female white-tailed deer younger than 11 months is not known to occur (Marchinton and Hirth 1984; Vreeland 2002), we assumed all captured females < 1 year old had not dispersed. We estimated dispersal rate as the proportion of individuals that dispersed from a natal range to an adult range. Dispersal distance was estimated by calculating the Euclidean distance between median x and y locations of the natal and adult ranges (Kenward et al. 2002; Long et al. 2005).

We located individuals fitted with VHF collars at least once per week using ground-based radiotelemetry and located deer missing after ground-based searches using fixed-wing aircraft. We estimated locations from ground-based telemetry data using LOAS (Ecological Software Solutions 2002). All GPS collars recorded locations at least once per day, and 17 GPS collars recorded locations every 1.5 h from 1 May to 15 July, corresponding with the female dispersal period.

We analyzed all spatial data using ArcGIS (ESRI 2006) and calculated percent forest cover from PAMAP Land Cover for Pennsylvania data (Pennsylvania Spatial Data Access Center, Pennsylvania State University, University Park, Pennsylvania). We estimated deer density (per forested km^2) using population estimates provided by the PGC (Rosenberry et al. 2012) that were based on integrated population models (White and Lubow 2002; Buderman 2012).

Meta-analysis.—We searched peer-reviewed literature for studies that reported dispersal data for female white-tailed deer. We included studies if we could extract the following variables: dispersal rate (i.e., proportion of 1-year-old females in the sample that dispersed), deer population density, and percentage of forest cover (Table 1). All studies used in the meta-analysis considered dispersal to have occurred if the individual made a permanent movement away from its natal range without returning. We used preharvest population estimates for our analyses. If population estimates were reported as a range, we used the midpoint of the range as the point estimate for our

meta-analysis. If multiple population estimates were reported, we used the mean of those estimates. Most studies reported total population densities, but Nixon et al. (1994, 2007) provided female deer density that we extrapolated to total deer density by dividing by the proportion of adult females in the population given in Nixon et al. (1991).

We used logistic regression to estimate the relationship between dispersal rate (response variable) and deer per forested km^2 (independent variable), and we used Akaike's Information Criterion (Burnham and Anderson 2002) adjusted for small sample size (AIC$_c$) to evaluate whether this model was better than an intercept-only model. We used linear regression to estimate the relationship between mean dispersal distance and deer per forested km^2, and we evaluated this model using R^2 values and confidence intervals of parameter estimates. Sample size is intrinsic to the logistic regression analysis, and we used weighted least squares with the number of deer that dispersed as weights so that studies with a larger sample size had a proportionally greater influence on regression estimates. We conducted all analyses using R (R Development Core Team 2012) and considered results to be statistically significant at $P < 0.05$.

RESULTS

Of the 277 female deer captured and radiomarked in our Pennsylvania study, we used data from 229 (82.7%) for analysis (VHF, $n = 198$; GPS, $n = 30$). We censored the remaining 48 individuals because of death, cast transmitter, or permanent loss of signal prior to 1 August, by which time > 95% of dispersers had established adult home ranges. Among all 4 Pennsylvania study areas, dispersal rate ranged from 0.08 to 0.24 (Table 1; $\bar{X} = 0.133$, $SD = 0.081$). Of deer that dispersed ($n = 27$), mean dispersal distance was 18.0 km ($SE = 7.0$), and we observed a maximum dispersal distance of 52.9 km.

The meta-analysis included 6 studies of 8 populations of white-tailed deer along with our data from 4 populations in Pennsylvania (Table 1). Female white-tailed deer dispersal also was reported in 4 other studies (Tierson et al. 1985; Nelson and Mech 1992; Aycrigg and Porter 1997; Jones et al. 1997) that we did not include in the meta-analysis. Tierson et al. (1985) and Aycrigg and Porter (1997) reported rates that included adults, and data from only juveniles could not be distinguished. Nelson and Mech (1992) reported population estimates that varied widely (5–50 deer per km^2), and they defined dispersal as movement > 4 km; however, it was unclear if this resulted in a permanent, nonoverlapping movement from the natal range. We also did not include dispersal data from a study on translocated deer (Jones et al. 1997).

Using data from our meta-analysis, dispersal rate was positively related to deer per forested km^2 (Fig. 2) and better than an intercept-only model ($\Delta AIC_c = 36.6$ for intercept-only model). It was modeled as

$$\text{logit}\left(Y_{rate}\right) = -2.051\ (0.146) + 2.605 \times 10^{-3}$$
$$(0.041) \times \text{DENSITY},$$

where Y_{rate} is proportion of females that disperse, DENSITY is density of deer per forested km², and *SE* of coefficient estimates are shown in parentheses.

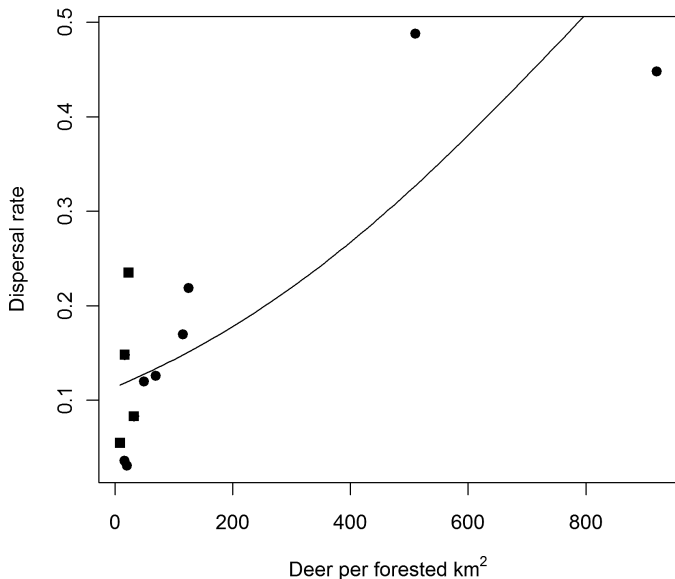Mean dispersal distance was positively related to deer per forested km² ($R_9^2 = 0.4926$, $P = 0.016$; Fig. 3). It was modeled as

$$Y_{distance} = 18.703 \; (3.710) \; + \; 2.533 \times 10^{-2}$$
$$(0.857) \; \times \; \text{DENSITY},$$

where $Y_{distance}$ is mean dispersal distance for a study area, DENSITY is density of deer per forested km², and *SE* of coefficient estimates are shown in parentheses.

Fig. 2.—Relationship of dispersal rate to density (deer per forested km²) for 1-year-old female white-tailed deer (*Odocoileus virginianus*) in North America. Data come from this study (squares) and published papers (circles).
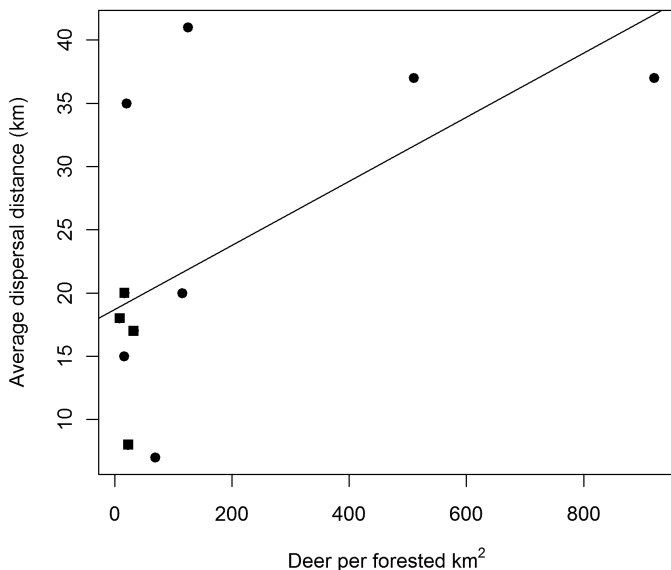

Fig. 3.—Relationship (weighted by sample size) of mean dispersal distance to density (deer per forested km²) for 1-year-old female white-tailed deer (*Odocoileus virginianus*) in North America. Data come from this study (squares) and published papers (circles).

DISCUSSION

Dispersal behavior is complex, and an individual's dispersal behavior likely is determined by multiple, interacting proximate factors that influence whether dispersal is ultimately beneficial. Although we demonstrated a density-dependent relationship in dispersal behavior, we lacked data to demonstrate any proximate factors that cause individuals to disperse, such as social standing in the local herd, whether the individual's mother survived to the dispersal period (Holzenbein and Marchinton 1992; Etter et al. 1995), and whether the individual was pregnant (Jones et al. 1997). Research to identify proximate factors that influence dispersal is necessary to further test hypotheses about dispersal behavior in white-tailed deer. Additionally, broadly measured parameters on the landscape may not reflect what an individual experiences; for example, population densities can vary locally and forest cover is not evenly distributed across the landscape. Population densities are also difficult to accurately estimate (Skalski et al. 2005), and methods varied across the studies that we used in the analyses. We speculate that aforementioned factors likely contributed to the unexplained variation in the regression models.

A meta-analysis can help to elucidate a pattern even though each study area contains different proximate factors that could influence dispersal behavior. For example, Nixon et al. (2007) attributed habitat scarcity and high juvenile survival to greater than expected dispersal rates, and Hawkins et al. (1971) concluded that dispersal appeared to be directly related to population levels. However, Nelson and Mech (1992) stated that female dispersal seemed voluntary and independent of deer density. Our analysis suggests dispersal behavior can be predicted based on deer density and provides insight into the ultimate cause of dispersal in female deer.

As predicted, we found a positive relationship between both dispersal rate and dispersal distance to deer per forested km². The analyses included a wide spectrum of deer densities per forested area (9–920; Table 1), including high densities reported in sparsely forested areas in the Midwestern United States. Removing the 2 highest densities as outliers from the analysis did not change the relationship between dispersal rate and deer per forested area, but it resulted in dispersal distance no longer being correlated to deer per forested area. Nonetheless, we do not believe these data points should be removed from consideration because we have no reason to suspect their accuracy.

Results of the meta-analysis are consistent with our hypothesis that as competition for fawning habitat increases (i.e., isolation from other females), female deer are more likely to disperse and more likely to disperse a greater distance. Forest cover is a valuable habitat resource for deer because it provides food, thermal cover, and protection from predators (Harlow 1984), and it is particularly important as females seek shelter and isolation before and after parturition. If our hypothesis is correct, we predict that an experimental increase (decrease) of deer densities should result in a corresponding increase (decrease) in dispersal rates.

We assert that female dispersal behavior persists because dominant females benefit by excluding other deer during

parturition and subordinate dispersers increase fitness by occupying a new adult home range in which they have access to habitat resources. We further suggest that dispersal may end in an area with less competition for space, which may allow dispersers to establish an adult home range where they have higher social standing compared with their natal area. Increasing social standing is beneficial because dominant females have greater survival than subordinate females (Nixon et al. 2010). Also, dominant female red deer and their offspring produced more offspring over their lifetime (Clutton-Brock et al. 1986).

Female white-tailed deer dispersal also is important for range expansion and colonization. If only males participate in long distance dispersal, then deer could not establish new populations in uninhabited areas, or it would occur more slowly. Females that colonize new habitats with lower competition for resources should accrue fitness benefits, as long as they find a mate. In British Columbia, strong genetic differentiation occurred at the local level, suggesting that a large portion of females remained philopatric, but weak differentiation occurred at the broad scale (Cullingham et al. 2011). This pattern could have resulted from a limited number of female dispersers preventing development of sex-biased differentiation following rapid range expansion (Cullingham et al. 2011).

Long et al. (2005) did not find a density-dependent relationship in male white-tailed deer dispersal, but their analysis did not examine male dispersal occurring during the fawning and breeding seasons separately. Nonetheless, Long et al. (2008) reported spring male dispersal was greater when adult female density was greater, and spring male dispersal decreased as female density decreased. Both male and female 1-year-olds likely experience similar cues to disperse during the fawning season; therefore, male dispersal during the fawning season also may be density-dependent. Siblings have been known to disperse together (Nelson and Mech 1992; Nixon et al. 2007), and genetic analysis we conducted on a dispersed male and female pair subsequently killed simultaneously by a vehicle confirmed they were siblings (C. L. Lutz, pers. obs.).

The ability to predict dispersal behavior characteristics of a population has important management implications (Long et al. 2005). Dispersal can be an important means of disease spread among populations (Hansson 1992), and dispersal has implications for the spread of chronic wasting disease (Gross and Miller 2001; Joly et al. 2006; Blanchong et al. 2008). Dispersal behavior also plays an important role in population dynamics (Rosenberry et al. 1999). Although female dispersal rates are comparatively low, females can influence disease spread and population dynamics, and modeling of disease spread could benefit by including female dispersal behavior.

In addition, our study can explain when localized management to reduce deer densities is likely to be successful. Porter et al. (1991) hypothesized that persistent, localized areas of low deer density could be accomplished by removing groups of female deer because females are philopatric and exhibit low dispersal rates. To test this hypothesis, McNulty et al. (1997) removed a group of female deer in a nonhunted, seasonally migratory population and failed to detect shifts in home range location of adjacent deer. Oyer and Porter (2004) reported reduced deer densities in the same area for 5 years following deer removal. However, in a test of this management technique in a high-density deer population, Miller et al. (2010) only reduced deer densities for ≤ 2 years. Our results, which indicate that dispersal rates of females increase with increasing population density, partly explain why localized management fails in deer populations of high density. Finally, our results will help modeling efforts to evaluate effective strategies for managing deer populations (e.g., Porter et al. 2004) by providing better informed estimates of female dispersal rates.

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