

FOREST COVER INFLUENCES DISPERSAL DISTANCE OF WHITE-TAILED DEER

ERIC S. LONG,* DUANE R. DIEFENBACH, CHRISTOPHER S. ROSENBERRY, BRET D. WALLINGFORD, AND MARRETT D. GRUND

Pennsylvania Cooperative Fish and Wildlife Research Unit, Pennsylvania State University, University Park, PA 16802, USA (ESL, BDW)

United States Geological Survey, Pennsylvania Cooperative Fish and Wildlife Research Unit, Pennsylvania State University, University Park, PA 16802 (DRD)

Pennsylvania Game Commission, Bureau of Wildlife Management, 2001 Elmerton Avenue, Harrisburg, PA 17110, USA (CSR, BDW, MDG)

Present address of MDG: Farmland Wildlife Populations & Research Group, Minnesota Department of Natural Resources, 35365, 800th Avenue, Madelia, MN 56062, USA

Animal dispersal patterns influence gene flow, disease spread, population dynamics, spread of invasive species, and establishment of rare or endangered species. Although differences in dispersal distances among taxa have been reported, few studies have described plasticity of dispersal distance among populations of a single species. In 2002–2003, we radiomarked 308 juvenile (7- to 10-month-old), male white-tailed deer (*Odocoileus virginianus*) in 2 study areas in Pennsylvania. By using a meta-analysis approach, we compared dispersal rates and distances from these populations together with published reports of 10 other nonmigratory populations of white-tailed deer. Population density did not influence dispersal rate or dispersal distance, nor did forest cover influence dispersal rate. However, average ($r^2 = 0.94$, $P < 0.001$, $d.f. = 9$) and maximum ($r^2 = 0.86$, $P = 0.001$, $d.f. = 7$) dispersal distances of juvenile male deer were greater in habitats with less forest cover. Hence, dispersal behavior of this habitat generalist varies, and use of landscape data to predict population-specific dispersal distances may aid efforts to model population spread, gene flow, or disease transmission.

Key words: dispersal distance, dispersal rate, emigration, forest cover, fragmentation, landscape, *Odocoileus virginianus*, transfer, white-tailed deer

Understanding animal dispersal patterns is important for the study of gene flow, disease spread, population dynamics, spread of invasive species, and establishment of rare or endangered species. However, dispersal remains one of the least understood aspects of animal ecology (Bowman 2003; Macdonald and Johnson 2001).

Andreassen et al. (2002) divide dispersal process of vertebrates into 3 distinct phases: emigration is initiation of dispersal, wherein an individual leaves its natal range; transfer is the process of the animal moving across the landscape in search of an adult range; and immigration is termination of dispersal, when an animal settles upon an adult range distinct from the natal range. Typically social cues and behavioral responses are cited as proximate causes of emigration (Brandt 1992), whereas proxi-

mate causes influencing immigration may be a combination of behavioral responses among individuals and interactions with the physical landscape (Brandt 1992; Wiens 2001). However, many aspects of the transfer phase of dispersal remain poorly understood (Andreassen et al. 2002), associated with logistical problems of collecting data on movement paths of dispersing animals (Bennetts et al. 2001).

An important component of the transfer phase is distance an individual moves from natal range to adult range, and factors influencing dispersal distance have been widely debated (Pusey 1987; South et al. 2002). Waser (1985) suggests that competition may drive dispersal distance distributions and observed distances could be explained by individuals moving to the 1st unoccupied or uncontested home range, a rule that South et al. (2002) mention has commonly been applied in dispersal models. Wolff (1993) suggests that dispersal distances of many mammals are not adequately explained by resource or mate competition, and inbreeding avoidance may drive dispersal distance distributions. Moore and Ali (1984) discount the role of inbreeding avoidance in dispersal patterns of mammals,

* Correspondent: esl140@psu.edu

whereas Dobson and Jones (1985) contend that inbreeding avoidance and competition may interact to produce observed patterns.

Some dispersal investigations have examined differences in dispersal distances among taxa (Bowman 2003; Bowman et al. 2002; Paradis et al. 1998), but plasticity of dispersal distances within vertebrate species has rarely been examined, and dispersal distances for a given species are often modeled as a fixed trait (Wiens 2001). Landscape structure may influence dispersal distances in vertebrates (South et al. 2002; Wiegand et al. 1999), and environmental variation may affect dispersal such that dispersal distances are longer in poorer environments (Hansson 1991; Trehwella et al. 1988) or in more fragmented landscapes (Matthysen et al. 1995; Wiens 2001; Wiggett and Boag 1989). Further, much of what is known about mammalian dispersal uses small mammals as a model (Stenseth and Lidicker 1992), but dispersal behavior of large mammals may not function similarly (Sinclair 1992).

Ability to predict population-specific dispersal parameters may have important management and conservation implications. For example, effectively accounting for variation in dispersal distance within a species may facilitate population-specific modeling of this parameter, which is important to studies of gene flow (Lidicker and Patton 1987; Nelson 1990), species range expansion (Shigesada and Kawasaki 2002), and transmission of disease (Hansson 1992). To assess how landscape structure, specifically percentage forest cover, and population density may be related to dispersal behavior of a large mammal, we analyzed data on dispersal distances of white-tailed deer (*Odocoileus virginianus*) by using a meta-analysis approach. We assessed influence of population density and percentage forest cover on dispersal rate, average dispersal distance, and maximum dispersal distance for 12 North American populations of white-tailed deer. Because white-tailed deer are habitat generalists, we evaluated dispersal among landscapes with a wide range of forest cover, from extensively agricultural to extensively forested habitats. Further, these study populations also represented a wide range of population densities. To our knowledge, this study represents the most complete effort to relate landscape to dispersal distance within a single vertebrate species across a broad geographic range, and this is the 1st effort to examine landscape-related plasticity of dispersal distances for a large mammal.

MATERIALS AND METHODS

Study areas.—Deer were captured and tracked in 2 study areas in Pennsylvania. One study area was located in the Allegheny Plateau region of western Pennsylvania, and deer were captured in Armstrong County east of the Allegheny River in an area of approximately 1,200 km². Land use is primarily agricultural, and common crops include corn, soybeans, and other grains. Appalachian oak forest (Cuff et al. 1989), dominated by red oak (*Quercus rubra*) and white oak (*Quercus alba*) along with other species such as maple (*Acer*), birch (*Betula*), beech (*Fagus grandifolia*), and hickory (*Carya*), covers 51% of the landscape. However, forests are extensively fragmented by agricultural fields, and much of the forested landscape exists as isolated woodlots.

The other study area was located in the Ridge and Valley region of Centre County (1,900 km²), approximately 150 km east of the study

area in the Allegheny Plateau. This region comprises more land that is forested (61% forest cover), and dominant tree species are similar to those of the Allegheny Plateau region. Land use also is primarily agricultural; however, crop growth is predominately restricted to valleys, whereas long, parallel ridges are forested and remain largely unfragmented. Common crops include corn, soybeans, alfalfa, and hay.

Deer capture and data collection.—During 2002 and 2003, we captured and radiomarked 286 juvenile (~8-month-old) male white-tailed deer, including 12 males that had been tagged as neonates (1–2 weeks of age—Vreeland et al. 2004). Juveniles were primarily captured by using single-gate Clover traps (laboratory-made, modified from Clover [1956]; $n = 110$), and drop nets (laboratory-made, modified from Ramsey [1968]; $n = 146$); additionally, some were captured by using helicopters (Hawkins and Powers Aviation, Inc., Greybull, Wyoming; $n = 9$), rocket nets (laboratory-made, $n = 7$), and dart guns (PneuDart, Inc., Williamsport, Pennsylvania; $n = 2$). Capture protocol was approved by the Pennsylvania State University Institutional Animal Care and Use Committee and followed guidelines of the American Society of Mammalogists (Animal Care and Use Committee 1998). Except for individuals tagged as neonates, which were captured between May and June (Vreeland et al. 2004), all juvenile bucks were captured between late December and early April. Because dispersal of male fawns younger than 11 months is rare (Marchinton and Hirth 1984), capturing deer during late winter and early spring reduced the likelihood of capturing fawns that had already dispersed.

Fawns caught at 1–2 weeks of age were equipped with 97-g expandable very-high-frequency (VHF) neck collars (ATS, Inc., Isanti, Minnesota; Diefenbach et al. 2003; Vreeland et al. 2004; $n = 12$). Male juveniles caught at ~8 months of age were equipped with 1 of 3 types of radiotransmitters, including 245-g expandable VHF neck collars (ATS; $n = 120$), 19-g VHF ear-tag transmitters (ATS; $n = 140$), or 700-g expandable, automatic-release global positioning system neck collars (Telonics, Inc., Mesa, Arizona, $n = 14$).

Dispersal was defined as permanent emigration from a natal range to a distinct adult range (i.e., ex-natal dispersal as defined by Kenward et al. [2001, 2002]), such that predispersal locations did not overlap postdispersal locations. We calculated dispersal distance as straight-line distance between median x and y natal and adult coordinates (Kenward et al. 2002), and we calculated dispersal rate (i.e., proportion of juvenile males that dispersed) by using a Kaplan–Meier survival model (Pollock et al. 1989) adapted for use with dispersal data (Bennetts et al. 2001; Rosenberry et al. 1999). For dispersers, timing of dispersal was used to define formation of adult range; however, for nondispersers, adult-range formation was defined to have begun on 1 November, at which point deer were approximately 1.5 years old, and subsequent locations of these nondispersers were considered to be adult locations that overlapped natal locations.

We radiotracked 102 juvenile bucks in the Ridge and Valley region and 184 juvenile bucks in the Allegheny Plateau region. Of these, 195 (68%) were located in both natal and adult ranges. The remaining 91 individuals (32%) died, shed their transmitter, or were censored because of lost contact without being located within their adult range. We located individuals equipped with VHF transmitters 1–3 times per week by using ground-based or aerial radiotelemetry. Each deer whose dispersal status could be determined (i.e., not censored before location within adult range) was located an average of 44 times, and 95% of deer were located ≥ 16 times ($n = 188$, range 5–83, $SD = 16.2$). Locations were estimated by using computer program LOAS 2.04 (Ecological Software Solutions, Sacramento, California). From January to April and July to August, global positioning system collars were programmed to record location once every 11 h. From May to

TABLE 1.—Dispersal statistics for juvenile male white-tailed deer from 12 nonmigratory North American populations. Dispersal rate is the proportion of individuals that dispersed.

Region	Citation	Forested (%)	Area (km ²)	Average distance (km)	Maximum distance (km)	Density (deer/km ²)	Dispersal rate
Central South Dakota	Kernohan et al. 1994	1	87		212.6		
Northern Illinois	Nixon et al. 1994	2	16	36		24	0.75
Eastern Illinois	Nixon et al. 1994	3	30	38	161	17	0.55
Western Illinois	Nixon et al. 1994	20	59	19		17	0.71
Eastern Montana	Dusek et al. 1989	32	224	18.5		37	0.46
Eastern Maryland	Rosenberry et al. 1999	50	13	10	56	50	0.7
Western Pennsylvania	This study	51	1,200	8	40.6	18	0.74
Southern Illinois	Hawkins and Klimstra 1970	55	73	8.5	35.8	31	0.8
Central Pennsylvania	This study	61	1,900	7	31.5	12	0.46
Northern Florida	Kilgo et al. 1996	65	636	6.4	22		
Western Virginia	Holzenbein and Marchinton 1992	70	12	3	7.1	40.3	0.52
Northwestern Georgia	Kammermeyer and Marchinton 1976			4.4		78	0.5

June and September to December, during peak dispersal seasons, locations were recorded once every 2.5 h. For deer equipped with global positioning system collars and whose dispersal status could be determined, an average of 1,027 locations ($n = 7$, range 103–1,723, $SD = 622.2$) was recorded.

Deer densities for our study areas (Table 1) were provided by the Pennsylvania Game Commission (in litt.) based on techniques described by Diefenbach et al. (1997). We determined percentage forest cover for our study areas (Table 1) by using land cover maps (Pennsylvania Spatial Data Access Center, Pennsylvania State University, University Park, Pennsylvania) in ArcView 3.2 (Environmental Systems Research Institute, Redlands, California).

Meta-analysis.—To evaluate potential landscape- and population-level differences in dispersal patterns, we reviewed the literature for studies reporting deer dispersal parameters over a range of habitats and performed a meta-analysis of our data together with published results from 8 additional studies of 10 populations of white-tailed deer (Table 1). In this species, dispersal is biased toward juvenile males (Hjeljord 2001; Nelson 1993) as is typical among mammals (Dobson 1982; Greenwood 1980); therefore, because of male bias and because dispersal differences between sexes is common (Pusey 1987), we restricted our analyses to juvenile males. Further, we excluded from analysis studies of migratory deer (i.e., populations of deer that make annual long-distance movements from winter range to summer range) because of limited data for these populations as well as observations that migratory deer may disperse differently than nonmigratory deer (Holzenbein and Marchinton 1992; Nelson 1998). When available, average dispersal distance (i.e., mean distance of dispersers not including 0 values), rate, deer density statistics, and percentage forest cover were taken directly from the literature. If average dispersal distance was not reported, we calculated this parameter from histograms or dispersal distributions.

We tested the ability of deer density and percentage forest cover to predict average and maximum dispersal distances and dispersal rate of a population. To present data in a linear, rather than curvilinear, format, maximum dispersal distance and deer density were transformed by using natural log transformation. Relationships between dependent variables (i.e., deer density and percentage forest cover) and independent variables (i.e., dispersal rate, average dispersal distance, and maximum dispersal distance) were tested by using linear regression. To test for potentially confounding relationships and lack of independence, correlations between both independent variables and among the 3 dependent variables were analyzed by using Pearson

correlation. To test for potentially confounding effects related to study area size, relationships between this variable and deer density and percentage forest cover were tested by using linear regression. All analyses were performed with SPSS 10.05 (SPSS, Inc., Chicago, Illinois). Results are presented as mean \pm SE.

RESULTS

In the Allegheny Plateau study area, 101 juvenile bucks dispersed. Average dispersal distance was 8.0 ± 0.61 km, maximum dispersal distance was 40.6 km, and dispersal rate was 0.74 ± 0.10 . In the Ridge and Valley study area, 36 juvenile bucks dispersed. Average dispersal distance was 7.0 ± 1.0 km, maximum dispersal distance was 31.5 km, and dispersal rate was 0.46 ± 0.10 .

When all studies were compared, dispersal rate was not related to deer density ($r^2 = 0.016$, $P = 0.731$, $d.f. = 9$) or percentage forest cover ($r^2 = 0.025$, $P = 0.687$, $d.f. = 9$; Fig. 1). Likewise, neither average dispersal distance ($r^2 = 0.143$, $P = 0.282$, $d.f. = 9$) nor maximum dispersal distance ($r^2 = 0.123$, $P = 0.495$, $d.f. = 5$) was related to deer density (Fig. 1). However, average dispersal distance of juvenile bucks within a population was related to proportion of forest cover ($r^2 = 0.94$, $P < 0.001$, $d.f. = 9$; Fig. 1), and was modeled as

$$\bar{d} = 35.07 (\pm 2.05) - 48.14 (\pm 4.34)x, \quad (1)$$

where \bar{d} is average dispersal distance in kilometers, x is proportion forest cover, and values in parentheses are standard errors of coefficient estimates. Similarly, maximum dispersal distance was related to proportion forest cover ($r^2 = 0.86$, $P = 0.001$, $d.f. = 7$; Fig. 1) and was modeled as

$$\ln(d_{\max}) = 5.43 (\pm 0.32) - 3.70 (\pm 0.62)x, \quad (2)$$

where d_{\max} is maximum dispersal distance in kilometers.

Because study areas included in the meta-analysis were of unequal size, we checked for potential confounding spatial scale effects in the meta-analysis by testing relationships between study area size (ln-transformed) and percentage forest cover as well as study area size and deer density; however, neither relationship was significant ($r^2 = 0.124$, $P = 0.288$, $d.f. = 10$; $r^2 = 0.366$, $P = 0.084$, $d.f. = 10$, respectively).

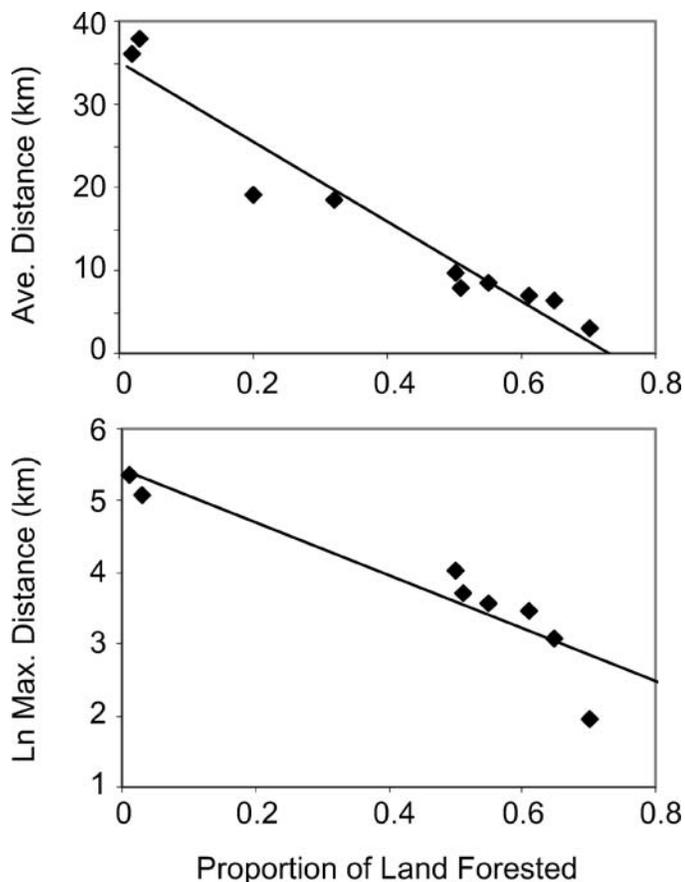


FIG. 1.—Regression of forest cover (i.e., proportion of land forested) to average and maximum dispersal distance for juvenile male white-tailed deer in North America. Data are for 12 populations in Table 1. For both plots, $P < 0.05$.

Further, the 2 independent variables used in the meta-analysis, percentage forest cover and deer density, were not correlated ($r = 0.266$, $P = 0.489$, $df. = 8$). Similarly, neither dispersal rate and average distance ($r = 0.218$, $P = 0.496$, $df. = 11$), nor dispersal rate and maximum distance ($r = 0.259$, $P = 0.536$, $df. = 7$) were correlated; however, average dispersal distance and maximum dispersal distance were related ($r = 0.826$, $P = 0.006$, $df. = 8$).

DISCUSSION

Meta-analysis of dispersal data indicates that dispersal rate of juvenile male white-tailed deer is not correlated with population density or forest cover, which suggests that white-tailed deer, as habitat generalists, disperse with similar likelihood in forested and nonforested habitats and that dispersal is not more likely in populations with greater density. Proposed proximate causes of dispersal for juvenile male deer are generally considered to be sociobiological, such that maternal aggression (Holzeinbein and Marchinton 1992) or intrasexual competition among males (Hjeljord 2001; Kammermeyer and Marchinton 1976; Rosenberry et al. 2001; Wahlström 1994) may increase likelihood of dispersal. Data presented here do not show a relationship be-

tween population density and dispersal rate, and dispersal rate may relate more closely to population structure (e.g., sex ratio and age structure) than overall population density or forest cover (Wauters et al. 2004; M. Conner, pers. comm.). More research is needed to examine population-level influences on dispersal rate, and this may be best approached by experiments in which population density, age structure, and sex structure are manipulated.

Similar to dispersal rate, dispersal distance is not related to population density. Unlike patterns shown for some medium-sized mammals, such as red fox (*Vulpes vulpes*—Trehwella et al. 1988) and European rabbits (*Oryctolagus cuniculus*—Richardson et al. 2002), dispersal distances of white-tailed deer are not shorter in populations with greater density. However, average dispersal distances are correlated with percentage forest cover, which explains 94% of variation in average dispersal distance. Although white-tailed deer are considered habitat generalists, forest cover is an important component of deer habitat, because forest stands provide thermal cover, escape shelter, and food resources (Harlow 1984). In less-forested landscapes, then, deer may need to travel farther to find suitable forested habitat patches. Although more intricate landscape metrics of fragmentation have been developed (e.g., patch size, connectivity, and lacunarity), these data were not available for inclusion in the meta-analysis. Percentage forest cover, a much cruder but widely reported metric, explains most interpopulation variation in average and maximum dispersal distances. Interestingly, forest cover also influences other behavioral responses of this species, because white-tailed deer in less-forested landscapes have been shown to form larger social groups than those in more-forested habitats (Hirth 1977).

By using the Kenward et al. (2001, 2002) concept of ex-natal dispersal, which is movement of an individual from its natal range to the adult range in which it 1st settles, we defined dispersal as nonoverlapping natal and adult locations. However, detecting dispersal, using nearly any functional definition of the term, becomes difficult with short dispersal distances or few relocations of marked animals, and tag-return studies are especially susceptible to these difficulties. Use of radio-transmitters improves ability to detect dispersal, but detecting short dispersals and distinguishing these movements from within-home-range movements can still be problematic. As in other dispersal studies (e.g., Nixon et al. 1994; Rosenberry 1997), we had insufficient number of locations for many of our radiomarked animals to construct valid natal and adult kernel home ranges, based on the recommendation of Seaman et al. (1999) of >50 locations per animal per range. As number of locations per animal decreases, probability of detecting overlap between natal and adult ranges also decreases, which may consequently overestimate dispersal. However, of our radiomarked deer that dispersed, 95% dispersed ≥ 2.1 km, which greatly exceeds typical home-range diameters of juvenile male white-tailed deer in the northeastern United States (Holzeinbein and Marchinton 1992; C. S. Rosenberry, pers. comm.); consequently, these movements most likely were dispersal events.

Similarly, maximum dispersal distance is a difficult parameter to measure and is typically underestimated because of

decreased probability of detection with increased distance from source. We found average and maximum dispersal distance, which were correlated, to be shorter in more forested habitats. Use of radiotransmitters can reduce bias associated with underestimating dispersal distances (Kenward et al. 2002), and most studies included in this analysis used radiotransmitters and aircraft to locate long-distance dispersers; therefore, detection bias associated with habitat type may be present but its influence is likely small. To reduce the disproportionate influence of long-distance values on average distance, it would have been advantageous to use median dispersal distance, but unfortunately, this parameter was not reported for most studies.

Spatial scale is another factor that may influence interpretation of results. Study areas examined in the meta-analysis ranged in size from 12 to 1,900 km² (Table 1), but area was not correlated with forest cover or deer density, the 2 independent variables included in analyses, suggesting that spatial scale of study areas was not a confounding factor. Additionally, density and forest cover statistics included in the meta-analysis were taken directly from the literature and were reported for each study area; however, many dispersing deer left the study area, and these metrics were typically not reported for establishment areas. In most cases, forest cover of surrounding areas was likely similar to cover within the study areas; however, because of differences in some localized deer management strategies, deer density was likely to have varied more across spatial scales. For instance, Holzenbein and Marchinton (1992) report that deer density on their study area was 40.3 deer/km², but densities adjacent to the study area were much lower (11.7 deer/km²).

Studies examining interpopulation differences in dispersal distances are rare (Wiens 2001), but greater dispersal distances have been linked to increased fragmentation for birds (Matthysen et al. 1995) and small mammals (Wiggett and Boag 1989). Within fragmented landscapes, dispersal success (i.e., ability to become established in a suitable habitat patch) increases as a function of dispersal distance (With and King 1999), and ability of deer and other animals to disperse farther in more fragmented landscapes or environments with fewer patches of suitable habitat may increase population sustainability and growth. In a spatially explicit metapopulation model of white-tailed deer dynamics, Walters (2001) defined available habitat as forest patches and found that increasing potential maximum dispersal distance for deer strongly influences source-sink dynamics, even though the range of maximum dispersal distances modeled in his analyses were shorter than those reported here.

Ability to predict average and maximum dispersal distances within a population has important management implications. For instance, dispersal has been suggested as a primary means of spreading disease among populations (Hansson 1992). Further, dispersal has been identified as an important parameter to model spread of chronic wasting disease (Gross and Miller 2001), a lethal disease infecting some white-tailed deer populations in the United States and Canada (Williams et al. 2002), and dispersal distance parameters are an important component of many models of spread of mammalian diseases (Barlow 1993; Byrom 2002; Leung and Grenfell 2003). When

population-specific dispersal data are not available, models must incorporate data from other populations, and in this way, population- or landscape-specific differences often are ignored. Because of the strong relationship between percentage forest cover and average dispersal distance in juvenile male white-tailed deer, it may be possible to model population-specific dispersal distance distributions without 1st conducting costly, labor-intensive, and time-consuming tag-return or radiotelemetry studies.

ACKNOWLEDGMENTS

We thank many wildlife technicians who worked long hours to assist with deer capture and radiotracking and numerous landowners who graciously allowed access to their land. This work was supported by the Pennsylvania Game Commission; United States Geological Survey, Pennsylvania Cooperative Fish and Wildlife Research Unit; Pennsylvania State University; Pennsylvania Audubon Society; the Susquehanna, Southeast, and Northcentral Pennsylvania Branches of the Quality Deer Management Association; Pennsylvania Deer Association; and the Pennsylvania Department of Conservation and Natural Resources.

LITERATURE CITED

- ANDREASSEN, H. P., N. C. STENSETH, AND R. A. IMS. 2002. Dispersal behavior and population dynamics of vertebrates. Pp. 237–256 in *Dispersal ecology* (J. M. Bullock, R. E. Kenward, and R. S. Hails, eds.). Blackwell Publishing, Malden, Massachusetts.
- ANIMAL CARE AND USE COMMITTEE. 1998. Guidelines for the capture, handling, and care of mammals as approved by the American Society of Mammalogists. *Journal of Mammalogy* 79:1416–1431.
- BARLOW, N. D. 1993. A model for the spread of bovine Tb in New Zealand possum populations. *Journal of Applied Ecology* 30: 156–164.
- BENNETTS, R. E., J. D. NICHOLS, J. D. LEBRETON, R. PRADEL, J. E. HINES, AND W. M. KITCHENS. 2001. Methods for estimating dispersal probabilities and related parameters using marked animals. Pp. 3–17 in *Dispersal* (J. Clobert, E. Danchin, A. A. Dhondt, and J. D. Nichols, eds.). Oxford University Press, Oxford, United Kingdom.
- BOWMAN, J. 2003. Is dispersal distance of birds proportional to territory size? *Canadian Journal of Zoology* 81:195–202.
- BOWMAN, J., J. A. G. JAEGER, AND L. FAHRIG. 2002. Dispersal distance of mammals is proportional to home range size. *Ecology* 83: 2049–2055.
- BRANDT, C. A. 1992. Social factors in immigration and emigration. Pp. 96–141 in *Animal dispersal: small mammals as a model* (N. C. Stenseth and W. Z. Lidicker, Jr., eds.). Chapman & Hall, London, United Kingdom.
- BYROM, A. E. 2002. Dispersal and survival of juvenile ferrets *Mustela furo* in New Zealand. *Journal of Applied Ecology* 39:67–78.
- CLOVER, M. R. 1956. Single-gate deer trap. *California Fish and Game* 42:199–201.
- CUFF, D. J., W. J. YOUNG, E. K. MULLER, W. ZELINSKY, AND R. F. ABLER (EDS.). 1989. *The atlas of Pennsylvania*. Temple University Press, Philadelphia, Pennsylvania.
- DIEFENBACH, D. R., C. O. KOCHANNY, J. K. VREELAND, AND B. D. WALLINGFORD. 2003. Evaluation of an expandable, breakaway radio-collar for white-tailed deer fawns. *Wildlife Society Bulletin* 31: 756–761.

- DIEFENBACH, D. R., W. L. PALMER, AND W. K. SHOPE. 1997. Attitudes of Pennsylvania sportsmen towards managing white-tailed deer to protect the ecological integrity of forests. *Wildlife Society Bulletin* 25:244–251.
- DOBSON, F. S. 1982. Competition for mates and predominant juvenile male dispersal in mammals. *Animal Behaviour* 30:1183–1192.
- DOBSON, F. S., AND W. T. JONES. 1985. Multiple causes of dispersal. *American Naturalist* 126:855–858.
- DUSEK, G. L., R. J. MACKIE, J. D. HERRIGES, AND B. B. COMPTON. 1989. Population ecology of white-tailed deer along the lower Yellowstone River. *Wildlife Monographs* 104:1–68.
- GREENWOOD, P. J. 1980. Mating systems, philopatry and dispersal in birds and mammals. *Animal Behaviour* 28:1140–1162.
- GROSS, J. E., AND M. W. MILLER. 2001. Chronic wasting disease in mule deer: disease dynamics and control. *Journal of Wildlife Management* 65:205–215.
- HANSSON, L. 1991. Dispersal and connectivity in metapopulations. Pp. 89–103 in *Metapopulation dynamics: empirical and theoretical investigations* (M. Gilpin and I. Hanski, eds.). Academic Press, London, United Kingdom.
- HANSSON, L. 1992. Small mammal dispersal in pest management and conservation. Pp. 181–193 in *Animal dispersal: small mammals as a model* (N. C. Stenseth and W. Z. Lidicker, Jr., eds.). Chapman & Hall, London, United Kingdom.
- HARLOW, R. F. 1984. Habitat evaluation. Pp. 601–628 in *White-tailed deer ecology and management* (L. K. Halls, ed.). Stackpole Books, Harrisburg, Pennsylvania.
- HAWKINS, R. E., AND W. D. KLIMSTRA. 1970. A preliminary study of the social organization of white-tailed deer. *Journal of Wildlife Management* 34:407–419.
- HIRTH, D. H. 1977. Social behavior of white-tailed deer in relation to habitat. *Wildlife Monographs* 53:1–55.
- HJELJORD, O. 2001. Dispersal and migration in northern forest deer—are there unifying concepts? *Alces* 37:353–370.
- HOLZENBEIN, S., AND R. L. MARCHINTON. 1992. Spatial integration of maturing male white-tailed deer into the adult population. *Journal of Mammalogy* 73:326–334.
- KAMMERMEYER, K. E., AND R. L. MARCHINTON. 1976. Notes on dispersal of male white-tailed deer. *Journal of Mammalogy* 57:776–778.
- KENWARD, R. E., S. P. RUSHTON, C. M. PERRINS, D. W. MACDONALD, AND A. B. SOUTH. 2002. From marking to modelling: dispersal study techniques for land vertebrates. Pp. 50–71 in *Dispersal ecology* (J. M. Bullock, R. E. Kenward, and R. S. Hails, eds.). Blackwell Publishing, Malden, Massachusetts.
- KENWARD, R. E., S. S. WALLS, AND K. H. HODDER. 2001. Life path analysis: scaling indicates priming effects of social and habitat factors on dispersal distances. *Journal of Animal Ecology* 70:1–13.
- KERNOHAN, B. J., J. A. JENKS, AND D. E. NAUGLE. 1994. Movement patterns of white-tailed deer at Sand Lake National Wildlife Refuge, South Dakota. *Prairie Naturalist* 26:293–300.
- KILGO, J. C., R. R. LABISKY, AND D. E. FRITZEN. 1996. Direction long-distance movements by white-tailed deer *Odocoileus virginianus* in Florida. *Wildlife Biology* 2:289–292.
- LEUNG, B., AND B. T. GRENFELL. 2003. A spatial stochastic model simulating a scabies epidemic and coyote population dynamics. *Ecological Modelling* 166:41–52.
- LIDICKER, W. Z., JR., AND J. L. PATTON. 1987. Patterns of dispersal and genetic structure in populations of small rodents. Pp. 144–161 in *Mammalian dispersal patterns: the effects of social structure on population genetics* (B. D. Chepko-Sade and Z. T. Halpin, eds.). University of Chicago Press, Chicago, Illinois.
- MACDONALD, D. W., AND D. D. P. JOHNSON. 2001. Dispersal in theory and practice: consequences for conservation biology. Pp. 358–372 in *Dispersal* (J. Clobert, E. Danchin, A. A. Dhondt, and J. D. Nichols, eds.). Oxford University Press, Oxford, United Kingdom.
- MARCHINTON, R. L., AND D. H. HIRTH. 1984. Behaviour. Pp. 129–168 in *White-tailed deer ecology and management* (L. K. Halls, ed.). Stackpole Books, Harrisburg, Pennsylvania.
- MATTHYSEN, E., F. ADRIAENSEN, AND A. A. DHONDT. 1995. Dispersal distances of nuthatches, *Sitta europaea*, in a highly fragmented forest habitat. *Oikos* 72:375–381.
- MOORE, J., AND R. ALL. 1984. Are dispersal and inbreeding avoidance related? *Animal Behaviour* 32:94–112.
- NELSON, M. E. 1990. Gene flow, effective population size, and genetic population structure in white-tailed deer in northeastern Minnesota. Ph.D. dissertation, University of Minnesota, St. Paul.
- NELSON, M. E. 1993. Natal dispersal and gene flow in white-tailed deer in northeastern Minnesota. *Journal of Mammalogy* 74:316–322.
- NELSON, M. E. 1998. Development of migratory behavior in northern white-tailed deer. *Canadian Journal of Zoology* 76:426–432.
- NIXON, C. M., et al. 1994. Behavior, dispersal, and survival of male white-tailed deer in Illinois. *Illinois Natural History Survey Biological Notes* 139:1–29.
- PARADIS, E., S. R. BAILLIE, W. J. SUTHERLAND, AND R. D. GREGORY. 1998. Patterns of natal and breeding dispersal in birds. *Journal of Animal Ecology* 67:518–536.
- POLLOCK, K. H., S. R. WINTERSTEIN, C. M. BUNCK, AND P. D. CURTIS. 1989. Survival analysis in telemetry studies—the staggered entry design. *Journal of Wildlife Management* 53:7–15.
- PUSEY, A. E. 1987. Sex-biased dispersal and inbreeding avoidance in birds and mammals. *Trends in Ecology and Evolution* 2:295–299.
- RAMSEY, C. W. 1968. A drop net deer trap. *Journal of Wildlife Management* 32:187–190.
- RICHARDSON, B. J., R. A. HAYES, S. H. WHEELER, AND M. R. YARDIN. 2002. Social structures, genetic structures and dispersal strategies in Australian rabbit (*Oryctolagus cuniculus*) populations. *Behavioral Ecology and Sociobiology* 51:113–121.
- ROSENBERRY, C. S. 1997. Dispersal ecology and behavior of yearling male white-tailed deer. Ph.D. dissertation, North Carolina State University, Raleigh.
- ROSENBERRY, C. S., M. C. CONNER, AND R. A. LANCIA. 2001. Behavior and dispersal of white-tailed deer during the breeding season. *Canadian Journal of Zoology* 79:171–174.
- ROSENBERRY, C. S., R. A. LANCIA, AND M. C. CONNER. 1999. Population effects of white-tailed deer dispersal. *Wildlife Society Bulletin* 27:858–864.
- SEAMAN, D. E., J. J. MILLSPAUGH, B. J. KERNOHAN, G. C. BRUNDIGE, K. J. RAEDEKE, AND R. A. GITZEN. 1999. Effects of sample size on kernel home range estimates. *Journal of Wildlife Management* 63:739–747.
- SHIGESADA, N., AND K. KAWASAKI. 2002. Invasion and the range expansion of species: effects of long-distance dispersal. Pp. 350–373 in *Dispersal ecology* (J. M. Bullock, R. E. Kenward, and R. S. Hails, eds.). Blackwell Publishing, Malden, Massachusetts.
- SINCLAIR, A. R. E. 1992. Do large mammals disperse like small mammals? Pp. 229–239 in *Animal dispersal: small mammals as a model* (N. C. Stenseth and W. Z. Lidicker, Jr., eds.). Chapman & Hall, London, United Kingdom.
- SOUTH, A., S. P. RUSHTON, R. E. KENWARD, AND D. W. MACDONALD. 2002. Modelling vertebrate dispersal and demography in real landscapes: how does uncertainty regarding dispersal behaviour influence predictions of spatial population dynamics? Pp. 327–349

- in *Dispersal ecology* (J. M. Bullock, R. E. Kenward, and R. S. Hails, eds.). Blackwell Publishing, Malden, Massachusetts.
- STENSETH, N. C., AND W. Z. LIDICKER, JR. (EDS.). 1992. *Animal dispersal: small mammals as a model*. Chapman & Hall, London, United Kingdom.
- TREWHELLA, W. J., S. HARRIS, AND F. E. MCALLISTER. 1988. Dispersal distance, home-range size and population density in the red fox (*Vulpes vulpes*): a quantitative analysis. *Journal of Applied Ecology* 25:423–434.
- VREELAND, J. K., D. R. DIEFENBACH, AND B. D. WALLINGFORD. 2004. Survival rates, mortality causes, and habitats of Pennsylvania white-tailed deer fawns. *Wildlife Society Bulletin* 32:542–553.
- WAHLSTRÖM, L. K. 1994. The significance of male–male aggression for yearling dispersal in roe deer (*Capreolus capreolus*). *Behavioral Ecology and Sociobiology* 35:409–412.
- WALTERS, S. 2001. Landscape pattern and productivity effects on source–sink dynamics of deer populations. *Ecological Modelling* 143:17–32.
- WASER, P. M. 1985. Does competition drive dispersal? *Ecology* 66:1170–1175.
- WAUTERS, L. A., E. MATTHYSEN, F. ADRIAENSEN, AND G. TOSI. 2004. Within-sex density dependence and population dynamics of red squirrels *Sciurus vulgaris*. *Journal of Animal Ecology* 73:11–25.
- WIEGAND, T., K. A. MOLONEY, J. NAVES, AND F. KNAUER. 1999. Finding the missing link between landscape structure and population dynamics: a spatially explicit perspective. *American Naturalist* 154: 605–627.
- WIENS, J. A. 2001. The landscape context of dispersal. Pp. 96–109 in *Dispersal* (J. Clobert, E. Danchin, A. A. Dhondt, and J. D. Nichols, eds.). Oxford University Press, Oxford, United Kingdom.
- WIGGETT, D. R., AND D. A. BOAG. 1989. Intercolony natal dispersal in the Columbian ground squirrel. *Canadian Journal of Zoology* 67: 42–50.
- WILLIAMS, E. S., M. W. MILLER, T. J. KREEGER, R. H. KAHN, AND E. T. THORNE. 2002. Chronic wasting disease of deer and elk: a review with recommendations for management. *Journal of Wildlife Management* 66:551–563.
- WITH, K. A., AND A. W. KING. 1999. Dispersal success on fractal landscapes: a consequence of lacunarity thresholds. *Landscape Ecology* 14:73–82.
- WOLFF, J. O. 1993. What is the role of adults in mammalian juvenile dispersal. *Oikos* 68:173–176.

Submitted 4 August 2004. Accepted 30 September 2004.

Associate Editor was Floyd W. Weckerly.