Management and Conservation Article

Modeling Distribution of Dispersal Distances in Male White-Tailed Deer

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ABSTRACT Dispersal distances and their distribution pattern are important to understanding such phenomena as disease spread and gene flow, but oftentimes dispersal characteristics are modeled as a fixed trait for a given species. We found that dispersal distributions differ for spring and autumn dispersals of yearling male white-tailed deer (*Odocoileus virginianus*) but that combined data can be adequately modeled based on a log-normal distribution. We modeled distribution of dispersal distances from 3 distinct populations in Pennsylvania and Maryland, USA, based on the relationship between percent forest cover and mean dispersal distance and the relationship between mean and variance of dispersal distances. Our results suggest distributions of distances for dispersing yearling male white-tailed deer can be modeled by simply measuring a readily obtained landscape metric, percent forest cover, which could be used to create generalized spatially explicit disease or gene flow models. (JOURNAL OF WILDLIFE MANAGEMENT 72(6):1296–1303; 2008)

Population dynamics and species evolution are influenced greatly by dispersal mechanisms and movements, yet dispersal is one of the least understood life-history traits (Clobert et al. 2001, Williamson 2002). In applied ecology, the study of dispersal is fundamental to understanding such problems as the spread of diseases, invasions of exotic species, and escape of genetically modified organisms (Bullock et al. 2002*a*). Dispersal has been suggested as a primary means of spreading disease among populations, and dispersal distance is an important parameter in many mammalian disease spread models (Hansson 1992). However, dispersal patterns of mammals are often modeled as population- and landscape-specific and, thus, lack generality (Barlow 1993, Byrom 2002, Leung and Grenfell 2003).

The basic quantitative aspect of dispersal is the distribution of dispersal movements, yet the shape of this distribution depends upon causal mechanisms, which is the least understood aspect of dispersal (Williamson 2002). Williamson (2002) noted that from an empirical standpoint it is most important to understand the shape of the dispersal curve near the origin and at the tails, with the former being less studied than the latter.

In white-tailed deer (*Odocoileus virginianus*), yearling males are the primary sex and age class that disperses (Nelson 1993, Purdue et al. 2000), although female dispersal is known to occur (Nelson and Mech 1992). Dispersal of yearling males occurs during 2 distinct periods: the birthing period (Jun) and the rut (Oct–Nov). The mechanisms of dispersal are unknown but suspected to be caused by mother–fawn interactions in the spring (Holzenbein and Marchinton 1992) and male–male interactions in the autumn (Ozoga and Verme 1985, Rosenberry et al. 2001).

Juvenile dispersal is likely an important mechanism for disease transmission among individuals and populations of mammals (Barlow 1993, Gross and Miller 2001, Byrom 2002), especially in species such as white-tailed deer, where long-distance movements of adults are rare, although some northern populations do exhibit seasonal migratory movements in response to harsh winter weather (Nelson 1998). White-tailed deer are known to be reservoirs for a number of ecologically and economically important diseases, such as bovine tuberculosis, Lyme disease, and chronic wasting disease (CWD), a transmissible spongiform encephalopathy (Miller et al. 2000, Gross and Miller 2001, O'Brien et al. 2002, Piesman 2002). Further, dispersal likely plays an important role in inter-population transmission of these diseases (Gross and Miller 2001).

To date, CWD models have not included any explicit spatial modeling of disease transmission, although dispersal has been implicated as an important means of inter-population disease transmission, and buffer zones to accommodate dispersal have been proposed to reduce the spread of CWD from infected to uninfected populations (Gross and Miller 2001). Consequently, because spread of CWD in some populations is thought to relate to dispersal, modeling CWD dynamics in white-tailed deer may depend on an understanding of dispersal mechanisms and characteristics.

Long et al. (2005) conducted a meta-analysis of yearling male white-tailed deer dispersal to investigate if percent forest cover and population density were related to dispersal rates and distances in nonmigratory populations. Long et al. (2005) found a strong relationship between percent forest

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cover and average dispersal distance in juvenile male white-tailed deer but no predictive relationships for dispersal rates (i.e., proportion of the population that disperses). If a probability density function (pdf) could be identified to describe the distribution of dispersal distances, then a model of dispersal applicable to a variety of landscapes potentially could be developed. Moreover, the meta-analysis of Long et al. (2005) could be used to estimate the parameters of the pdf based on a readily measured landscape characteristic (i.e., % forest cover) without the time and expense involved in determining a population-specific dispersal distribution.

Our objective first was to identify a pdf that best described the distribution of dispersal distances for yearling male white-tailed deer from 3 populations in the eastern United States. If successful, our second objective was to develop a generalized model to predict the distribution of dispersal distances from the relationship between dispersal distance and percent forest cover presented by Long et al. (2005) and the relationship between mean and variance of dispersal distances.

METHODS

Collecting Dispersal Data
We used dispersal distances of yearling male white-tailed deer from 2 study areas in Pennsylvania, USA, during 2002 and 2003 (Long et al. 2005) and one study area in Kent County, Maryland, USA, during 1994–1996 (Rosenberry et al. 1999). Deer were captured either as fawns at 1–2 weeks of age or 4–10 months of age and monitored until after the dispersal period (18 months of age; Rosenberry et al. 1999, Vreeland et al. 2004, Long 2005). All deer were fitted with radiotransmitters and monitored via 1–3 telemetry locations/week.

We defined dispersal on the Pennsylvania study areas as permanent emigration from a natal to adult home range, in which postdispersal locations did not overlap predispersal locations (Long et al. 2005). On the Maryland study area we defined dispersal as the permanent movement of ≥ 1 natal range diameter away from the center of the natal range (Rosenberry et al. 1999). We calculated dispersal distance as the straight-line distance between the median x and y locations of natal and adult home ranges.

Modeling Dispersal Distributions
Monotonically decreasing distributions have been used to model plant and animal dispersal distributions (e.g., Leung and Grenfell 2003), in which many individuals fail to disperse and disperse short distances and fewer individuals disperse at increasing distances. However, for male white-tailed deer substantial variability has been observed in the proportion of individuals that fail to disperse (0.20–0.54) and no predictive variables have been identified that correlate with this proportion (Long et al. 2005). Therefore, we modeled only the distribution of deer that dispersed according to our definitions as described previously.

Dispersal in white-tailed deer is hypothesized to be caused by multiple ultimate and proximate influences related to inbreeding and mate acquisition; hence, expected dispersal

distributions might be difficult to predict (Waser 1985). Long et al. (in press) found that yearling male white-tailed deer dispersed greater distances in spring than autumn. Spring dispersal is thought to be motivated by inter-sexual cues from the opposite-sex parent or close relatives to avoid incestuous breeding (Holzenbein and Marchinton 1992), whereas autumn dispersal is thought to be motivated to seek reduced mate competition (Ozoga and Verme 1985, Rosenberry et al. 2001). The classic rule of competition dispersal suggests that dispersers should stop at the first vacant territory and travel minimum distances to obtain quality breeding opportunities (Murray 1967, Baker and Rao 2004). Thus, dispersal to avoid inbreeding is expected to yield potentially longer dispersal distances (Ronce et al. 2001).

These dispersal distances should exhibit a skewed distribution because mean values should be small and variances large, and values cannot be negative. The log-normal distribution has been found to represent such biological data across a range of disciplines (Limpert et al. 2001). In addition, we investigated the gamma and Weibull distributions because these are flexible distributions that have properties similar to the log-normal (i.e., nonnegative values and skewed). The negative exponential distribution is a special case of either the gamma or Weibull distributions but we included this distribution in our evaluation because of its widespread use in the study of dispersal patterns.

Spring dispersal distances have been reported to be greater than autumn dispersal distances (Long et al., in press) so we investigated whether dispersal distributions should be modeled as a mixture of 2 distributions. We obtained maximum-likelihood estimates (MLE) of the parameters for each of the log-normal, gamma, Weibull, and negative exponential distributions for each deer population and season. We used Akaike's Information Criterion adjusted for small sample size (AIC) and AIC relative weights (w_{AIC}) to identify the pdf that best modeled the distribution of the data. We used a Cramér-von Mises goodness-of-fit (GOF) test (PROC CAPABILITY; SAS Institute, Cary, NC) to test whether each distribution fit the data ($\alpha = 0.10$). Also, we estimated parameters for each pdf (log-normal, gamma, Weibull, and negative exponential) for each population, pooling spring and autumn dispersal data. We used a Cramér-von Mises GOF test to test model fit ($\alpha = 0.10$) and AIC to compare the single pdf (pooling spring and autumn data) to a mixture pdf that combined distributions specific to each season.

Predicting Dispersal Distributions
We used the relationship between mean dispersal distance and proportion of forest cover presented in Long et al. (2005) to estimate the mean dispersal distance for each study area. Long et al. (2005) reported that mean dispersal distance, $\bar{x}$, was linearly related to proportion of the landscape in forest (p_f; $R^2 = 0.94$, $n = 10$)

$$\bar{x} = 35.07 - 48.14p_f \qquad (1)$$

In addition, we used data compiled by Long et al. (2005) to estimate the relationship between the mean and variance of

Table 1. Difference in Akaike's Information Criterion (ΔAIC) relative to the distribution with the lowest AIC value and AIC relative weights (w_{AIC}) among 4 distributions fit to dispersal distances for yearling male white-tailed deer from 3 populations in Pennsylvania (2002–2003) and Maryland (1994–1996), USA.

| | Centre County, PA | | | | Armstrong County, PA | | | | Kent County, MD | | | |
| | Spring | | Autumn | | Spring | | Autumn | | Spring | | Autumn | |
Distribution	ΔAIC	w_{AIC}	ΔAIC	w_{AIC}	ΔAIC	w_{AIC}	ΔAIC	w_{AIC}	ΔAIC	w_{AIC}	ΔAIC	w_{AIC}
Log-normal	0.00	0.64	0.00	0.77	2.07	0.18	0.00	1.00	0.00	0.36	0.00	0.96
Gamma	2.21	0.21	2.79	0.19	0.00	0.51	16.27	0.00	0.37	0.30	7.80	0.02
Weibull	3.46	0.11	5.98	0.04	1.01	0.31	22.80	0.00	0.91	0.23	9.77	0.01
Negative exponential	5.43	0.04	14.01	0.00	32.87	0.00	24.69	0.00	2.11	0.12	8.10	0.02

dispersal distances. We modeled this relationship as a linear-log function:

$$\log_e(s^2) = a + b\bar{x}, \qquad (2)$$

where $\bar{x}$ is mean dispersal distance, $a = 3.51$ (SE = 0.597), and $b = 0.077$(SE = 0.025). This model explained a substantial amount of variation in the relationship between the mean and variance ($F_{1,4} = 9.17$, $P = 0.039$, $R^2 = 0.69$).

We used the proportion of the study area that was forested and equation 1 to predict mean ($\tilde{x}$) dispersal distance, and we used equation 2 (replacing $\bar{x}$ with $\tilde{x}$) to predict the variance ($\tilde{s}^2$) of dispersal distance for 6 populations of deer: 2 from Pennsylvania (Long et al. 2005), 1 from Maryland (Rosenberry et al. 1999), and 3 from Illinois, USA (northern, east-central, and west-central; Nixon et al. 1994). For all datasets, we removed counts of deer that failed to disperse such that we predicted the distribution of distances for dispersing deer. We used the predicted mean and variance ($\tilde{x}$, $\tilde{s}^2$; eqs 1 and 2) for each population and the first and second moments for the log-normal pdf to obtain the parameter inputs for the pdf. We used the log-normal pdf, not considering a mixture distribution for spring and autumn dispersals, because it fit the Maryland and Pennsylvania data (see Results).

For the log-normal distribution the pdf is

$$f(x) = \frac{1}{x\sqrt{2\pi}\sigma} e^{-(\log_e x - \mu)^2/2\sigma^2} - \infty < \mu < \infty, \sigma > 0, x > 0.$$

We obtained the parameter μ from the first moment using the predicted mean and variance, $\tilde{x}$, $\tilde{s}^2$, and the equation

$$\mu = \log_e\left[\frac{\tilde{x}^2}{\sqrt{\tilde{s}^2 + \tilde{x}^2}}\right]. \qquad (3)$$

We obtained the parameter σ from the second moment using the predicted mean and variance, $\tilde{x}$, $\tilde{s}^2$, and the equation

$$\sigma = \sqrt{\log_e\left[\frac{\tilde{s}^2}{\tilde{x}^2} + 1\right]}. \qquad (4)$$

We tested how well the log-normal distribution, based on pdf parameters estimated from the predicted mean and variance, matched the empirical distributions using a chi-square GOF test for 1-km intervals for the Pennsylvania and Maryland data and for 10-km intervals as published by Nixon et al. (1994) for the Illinois data. The u groups (bins of 1-km or 10-km intervals) contained sample sizes n_1, n_2, ..., n_u, and the values c_0, c_1, ..., c_u defined the cut-points between groups ($c_0 = 0$ and the interval defining n_u has no upper bound). The area under the estimated pdf $f(x)$ with q parameters ($q = 2$ for the log-normal pdf) between cut-points c_{i-1} and c_i is

$$\pi_i = \int_{c_{i-1}}^{c_i} f(x)dx.$$

We estimated π_i by integrating the pdf based on the MLEs. Then the chi-square statistic

$$\chi^2 = \sum_{i=1}^{u} \frac{(n_i - n\hat{\pi}_i)^2}{n\hat{\pi}_i}$$

had $u - q - 1$ degrees of freedom if the estimated distribution were the true distribution for the empirical data.

RESULTS

The log-normal distribution was the best model (ΔAIC = 0.0) and had the strongest support for autumn dispersals ($w_{AIC} = 0.77–1.00$; Table 1). However, for spring dispersals the log-normal distribution had less support ($w_{AIC} = 0.18–0.64$) and a gamma distribution was best for Armstrong County data. The log-normal distribution fit the data ($P > 0.472$) for all populations and seasons except in autumn for Armstrong County ($P = 0.094$; Table 2). The gamma, Weibull, and negative exponential distributions were less consistent in model fit (Table 2).

When we combined data from spring and autumn dispersal distances, the log-normal distribution was the best model (ΔAIC = 0.0; Table 3, Fig. 1) and no other models were competitive (gamma, Weibull, and negative exponential; $w_{AIC} < 0.01–0.06$). The log-normal distribution fit the data for all 3 populations (Cramér-von-Mises tests, $P > 0.467$). Separate estimation of log-normal distributions for each season were better models than pooling data from spring and autumn dispersals for Centre and Armstrong counties but not for Kent County (Table 4). However, because the means of the log-normal distribution were similar for spring and autumn distributions, the mixture

Table 2. Cramér-von-Mises goodness-of-fit statistics (W^2; null hypothesis is that the model fits the data, $\alpha = 0.10$) using gamma, negative exponential, log-normal, and Weibull distributions of dispersal distances (km) of yearling male white-tailed deer from 3 populations in Pennsylvania (2002–2003) and Maryland (1994–1996), USA.

| | Armstrong County, PA | | | | Centre County, PA | | | | Kent County, MD | | | |
| | Spring | | Autumn | | Spring | | Autumn | | Spring[a] | | Autumn | |
Distribution	W^2	P	W^2	P	W^2	P	W^2	P	W^2	P	W^2	P
Log-normal	0.07	0.324	0.11	0.094	0.02	>0.500	0.05	0.472	0.03	>0.500	0.05	>0.500
Gamma	0.05	>0.500	0.31	<0.001	0.06	>0.250	0.09	0.159			0.11	0.098
Weibull	0.05	>0.250	0.39	<0.010	0.07	0.240	0.14	0.023	0.05	>0.250	1.01	<0.010
Negative exponential	1.07	<0.001	0.61	<0.001	0.14	0.180	0.45	0.002	0.17	0.103	0.16	0.120

[a] We could not compute the Cramér-von-Mises test for Kent County, MD spring dispersal data.

distribution for all 3 populations remained unimodal (Fig. 2), which is why the log-normal distribution was the best model when we pooled data (Table 3, Fig. 1).

We used predicted means and variances from equations 1 and 2 to predict parameter estimates (eqs 3 and 4) for the log-normal distribution (Table 3). Although the predicted log-normal distribution was a reasonable approximation of the empirical distribution for most populations (Figs. 3, 4), GOF tests indicated the predicted distribution fit the observed distribution only for northern Illinois ($P = 0.17$, Table 5). The predicted distributions that did the poorest job of matching the empirical distribution were ones in which the difference between the predicted and empirical mean dispersal distance were greatest (Centre County and west-central IL; Figs. 3, 4).

DISCUSSION

We found that a log-normal distribution was most consistently selected as the best model that fit the dispersal distances observed in 3 nonmigratory white-tailed deer populations from Maryland and Pennsylvania, USA. Many models of dispersal for both plants and animals have used distributions in which the probability of dispersing decreases monotonically with increasing distance (e.g., Leung and Grenfell 2003), probably because of limited information about dispersal rates and dispersal distances. However, much less research has studied the fit of dispersal distributions near the origin compared to the tail of the distribution and whether a monotonic decline or some uni- or multimodal distribution is more common is not well known, even though this may be important ecologically (Bullock et al. 2002b, Williamson 2002). We found that the parameters of

dispersal distributions differed for spring and autumn dispersal and that mixture models fit the data better (Table 4). However, because even the mixture distributions were unimodal (Fig. 2) a log-normal distribution provided excellent fit when spring and autumn dispersal distances were modeled using a single log-normal pdf (Table 3, Fig. 1). We believe dispersing white-tailed deer are most likely to exhibit a skewed unimodal distribution for dispersal distances, as in Figures 1–4, because of the proposed causal mechanisms for dispersal.

Current hypotheses propose social mechanisms by which male yearlings are induced to disperse. In white-tailed deer, male dispersal is likely caused by a combination of mother–offspring and male–male interactions (Long et al., in press). Holzenbein and Marchinton (1992) suggested that interactions between the dam (or other closely related females) and male offspring is a possible proximate cause of dispersal, which could explain why orphaned males had lower dispersal rates than nonorphaned males. Ozoga and Verme (1985) proposed that autumn dispersal is the result of an internal drive to associate with other males, and Rosenberry et al. (2001) suggested that male–male agonistic interactions might induce autumn dispersal.

Some minimum distance of dispersal may be necessary to achieve adequate spacing because social mechanisms are thought to elicit dispersal in white-tailed deer. However, subsequent movement is likely mediated by landscape characteristics and Long et al. (2005) found that average dispersal distance increased with decreasing forest cover, probably because white-tailed deer select home ranges that contain forested habitat as hiding cover (Nixon et al. 1991). We used the model developed by Long et al. (2005) to

Table 3. Difference in Akaike's Information Criterion (ΔAIC) relative to the distribution with the lowest AIC value, and AIC relative weights (w_{AIC}), among 4 distributions fit to dispersal distances for yearling male white-tailed deer from 3 populations in Pennsylvania (2002–2003) and Maryland (1994–1996), USA.
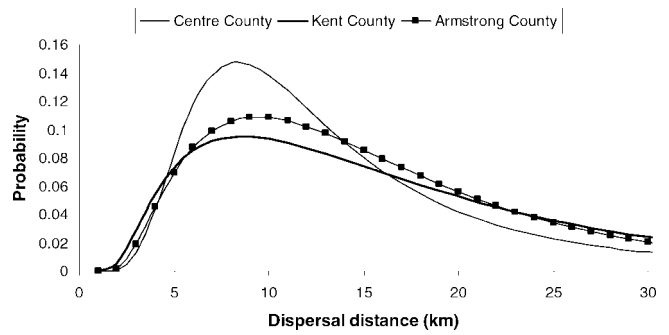
| | Armstrong County, PA | | Centre County, PA | | Kent County, MD | |
Distribution	ΔAIC	w_{AIC}	ΔAIC	w_{AIC}	ΔAIC	w_{AIC}
Log-normal	0.0	0.99	0.0	0.92	0.0	0.96
Gamma	9.6	0.01	5.3	0.06	7.1	0.03
Weibull	19.0	<0.01	8.4	0.01	10.3	<0.01
Negative exponential	40.3	<0.01	11.7	<0.01	11.2	<0.01
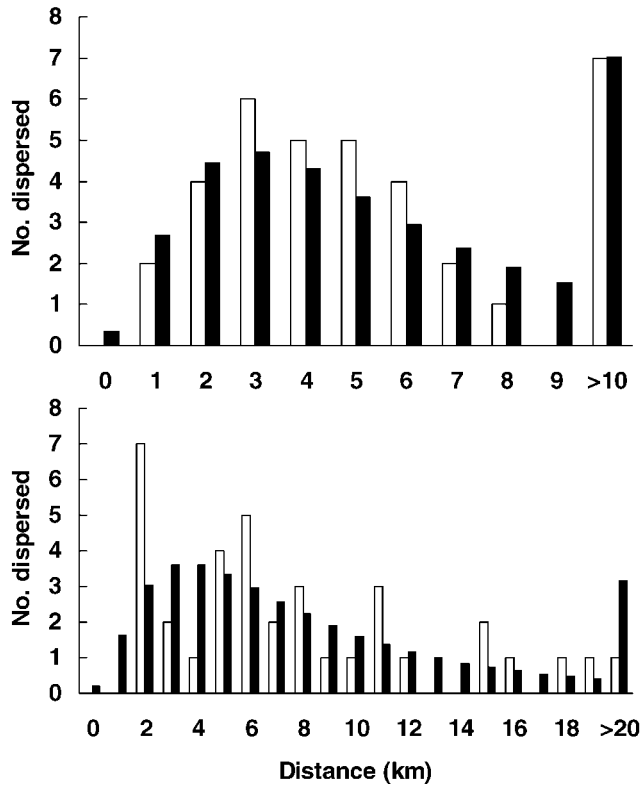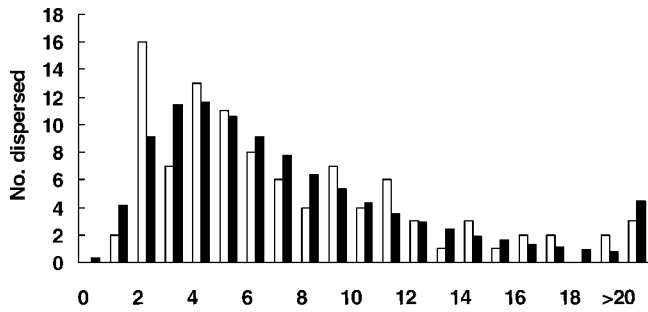
Figure 1. Observed dispersal distances (open bars) of yearling male white-tailed deer and predicted distances (solid bars) based on maximum-likelihood parameter estimates of a log-normal distribution for populations in Armstrong County (top) and Centre County (middle), Pennsylvania, USA, 2002–2003, and Kent County, Maryland (bottom), USA, 1994–1996. Distance in each category is the minimum distance of each group (e.g., >0 = >0 to <1 km).

Figure 2. Mixture of 2 log-normal distributions for spring and autumn dispersal distances of yearling male white-tailed deer in Armstrong and Centre counties, Pennsylvania, USA, 2002–2003, and Kent County, Maryland, USA, 1994–1996.
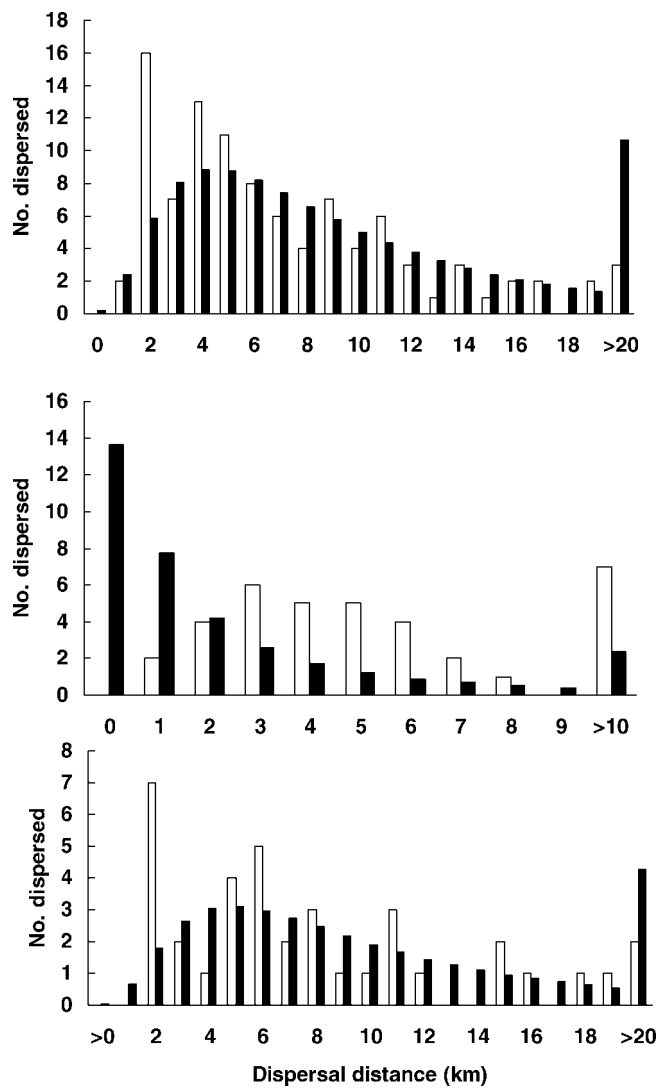
Figure 3. Observed dispersal distances (open bars) of yearling male white-tailed deer and predicted log-normal distribution (solid bars), in which the distance in each category is the minimum distance of each group (e.g., >0 = >0 to <1 km). Distributions based on predicted mean and variance of dispersal distances in Armstrong County (top) and Centre County (middle), Pennsylvania, USA, 2002–2003, and Kent County, Maryland (bottom), USA, 1994–1996.

Table 4. Difference in Akaike's Information Criterion (ΔAIC) relative to the distribution with the lowest AIC value, and AIC relative weights (w_{AIC}), between a mixture of log-normal models for spring and autumn dispersal (seasonal model) and a single log-normal model of pooled data (pooled model) to dispersal distances for yearling male white-tailed deer from 3 populations in Pennsylvania (2002–2003) and Maryland (1994–1996), USA.
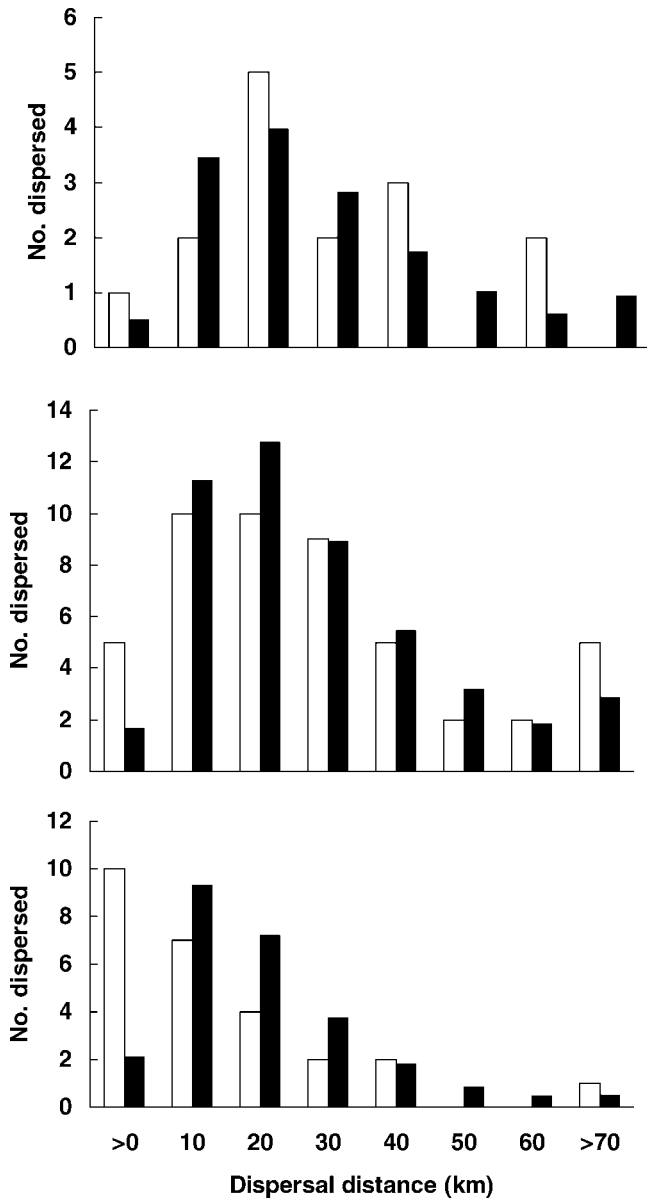
Model	Armstrong County, PA		Centre County, PA		Kent County, MD	
	ΔAIC	w_{AIC}	ΔAIC	w_{AIC}	ΔAIC	w_{AIC}
Pooled	18.06	0.00	3.91	0.12	0.00	0.76
Seasonal	0.00	1.00	0.00	0.88	2.31	0.24

Figure 4. Observed dispersal distances (open bars) of yearling male white-tailed deer and predicted log-normal distribution (solid bars), in which the distance in each category is the minimum distance of each group (e.g., >0 = >0 to <10 km). Distributions based on predicted mean and variance of dispersal distances in northern Illinois (top), east-central Illinois (middle), and west-central Illinois (bottom), USA, 1980–1992.

predict mean dispersal distance from forest cover, and the relationship between mean and variance for dispersal, to predict the distribution of dispersal distances. The difficulty with this approach to model dispersal distributions is that error in estimating the mean and variance of dispersal distances reduces the accuracy of the resulting distribution. Consequently, even though Long et al. (2005) reported a strong relationship between forest cover and mean dispersal distance, we reported a strong relationship between the mean and variance, and the log-normal distribution best described empirical distributions of dispersal distances from Maryland and Pennsylvania, and predicted distributions did not always match empirical distributions from a statistical standpoint (Table 5). We found that error in predicting mean dispersal distance (eq 1), rather than error in the mean–variance relationship (eq 2), had the greatest influence on the ability to predict the distribution pattern of dispersal. For example, the poor fit of predicted distributions for Centre County, Pennsylvania, and west-central Illinois had the greatest residual error in predicted mean dispersal distance of all populations (eq 1; Table 5).

Despite the potential errors in our approach to modeling distribution patterns of dispersal distances, there are important advantages to a probabilistic modeling approach. First, we provide a generalized approach to model dispersal distribution patterns that accounts for differences among deer populations, which should permit development of disease or gene flow models with greater generality. Second, and perhaps more importantly, understanding the distribution pattern of dispersal can be more informative than simply understanding relationships to means or maximum dispersal distances, especially the latter (cf. Long et al. 2005). We have shown that white-tailed deer exhibit a skewed distribution best modeled as log-normal. Consequently, wildlife managers or modelers can obtain better estimates of the probability of observing long dispersal events. If biologists are trying to identify an area to try to contain disease spread, understanding the distribution of dispersal events will help them assess the trade-off between reducing the risk of disease spread versus the cost of delineating larger containment areas. We believe more research to improve our understanding of how landscape factors, such as rivers (Dusek et al. 1989), topography and roads (Long 2005), and spatial distribution of forest cover

Table 5. Mean and variance estimates of dispersal distances based on empirical data ($\bar{x}$, s^2) and predicted from percent forest cover ($\tilde{x}$, $\tilde{s}^2$), and results of goodness-of-fit tests of actual versus predicted log-normal distributions of dispersal distances of yearling male white-tailed deer from 6 populations in Maryland (1994–1996), Pennsylvania (2002–2003), and Illinois (1980–1992), USA.

| Population | Binning interval (km) | n | Mean | | Variance | | χ^2 | df | P |
			$\bar{x}$	$\tilde{x}$	s^2	$\tilde{s}^2$			
Armstrong County, PA	1	101	8.0	10.5	37.6	75.28	32.97	18	0.017
Centre County, PA	1	36	7.0	3.3	37.4	43.19	63.99	8	<0.001
Kent County, MD	1	37	9.6	11.0	96.8	78.12	27.50	18	0.070
Northern IL	10	15	36	34.1	229.3	462.26	7.76	5	0.170
East-central IL	10	48	38	33.6	890.6	445.46	9.54	5	0.089
West-central IL	10	26	19	25.4	433.2	237.33	33.73	5	<0.001

influences dispersal (Long et al. 2005) will help biologists better describe distribution patterns in deer dispersal.

Unfortunately, no means currently exists to predict the proportion of yearling males that disperse. Gross and Miller (2001) modeled CWD disease dynamics with dispersal rates of mule deer (*Odocoileus hemionus*) related to population density and Walters (2001) modeled white-tailed deer dispersal rate as a function of population size relative to carrying capacity. Evidence for density-dependent dispersal in cervids, however, is ambiguous. For instance, Clutton-Brock et al. (1982) found that juvenile male dispersal within an island population of red deer (*Cervus elaphus*) decreased as population density increased, but later Clutton-Brock et al. (2002) found the reverse effect within the same population (i.e., M dispersal increased as population density was reduced through culling). Long et al. (2005) found no evidence to suggest dispersal rate of white-tailed deer is related to population density, which is concordant with results for several other mammalian species (Allen and Sargeant 1993, Loison et al. 1999, Byrom 2002).

If predictors of dispersal rate and timing could be identified, more complete models of dispersal may be considered. Dispersal rates range from 46% to 80% in nonmigratory white-tailed deer populations but cannot be predicted (Long et al. 2005). For example, including nondispersing deer in the distribution of dispersal distances may be best described by zero-inflated models instead of the negative exponential distribution. Furthermore, there is evidence autumn dispersal distances are shorter and that age–sex structure of the population influences the timing of dispersal (Long et al., in press). In Pennsylvania, over 3 years (2002–2004) spring dispersal of yearling males decreased and autumn dispersal increased with an increase in abundance of adult males and decrease in abundance of adult females (Long et al., in press). Thus, mixture models potentially could be useful; however, because spring and autumn distributions are similar we believe unimodal distributions are likely to be adequate when modeling the distribution patterns of white-tailed deer dispersal.

MANAGEMENT IMPLICATIONS

Data presented by Long et al. (2005) and this paper will facilitate the development of spatially explicit models of disease spread or gene flow. Moreover, because percent forest cover, a readily obtained landscape metric, is a predictor of dispersal parameters, population-specific dispersal characteristics can be estimated for white-tailed deer. Using predicted dispersal parameters from a log-normal pdf we found that reasonable distributions of dispersal can be constructed without conducting costly, labor-intensive, and time-consuming tag return or radiotelemetry studies (Kenward et al. 2002).

ACKNOWLEDGMENTS

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Associate Editor: Euler.