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Directional long-distance movements by white-tailed deer *Odocoileus virginianus* in Florida

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Knowledge of directional tendencies among long-distance movements by animals can be important in planning conservation and management strategies for wildlife at the landscape scale. The direction of 23 long-distance movements (≥ 2 km) among a non-migratory population of white-tailed deer *Odocoileus virginianus* on the Osceola National Forest, Florida, during 1989-1991 was examined. Direction of dispersal by 10 yearlings (7 males, 3 females) was non-uniform in distribution and averaged 95° . Direction of 13 excursions by 12 adults (2 males, 10 females) also was non-uniform but was bimodally (east-west) distributed; mean directions of the two distributions were 83° and 261° . Thus, both excursions and dispersals of radio-instrumented deer were on an east-west axis. No prominent landscape features that would direct deer movement were apparent. However, the fact that deer movements followed a consistent directional trend, even in a relatively homogeneous landscape, may have important implications for management of gene flow among small populations.

Key words: dispersal, Florida, *Odocoileus virginianus*, pine flatwoods, white-tailed deer

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White-tailed deer *Odocoileus virginianus* often undertake long-distance movements. Yearling males commonly disperse from natal ranges (Downing et al. 1969, Hawkins et al. 1971, Kammermeyer & Marchinton 1976, Nelson & Mech 1984, Hölzenbein & Marchinton 1992). Dispersal distance averaged 4.4 km in Georgia (Kammermeyer & Marchinton 1976), but greater distances have been reported for populations in northern and western North America (Nelson 1993). Additionally, individuals of many of the latter populations may migrate more than 50 km between summer and winter ranges (Marchinton & Hirth 1984, Nelson & Mech 1987). Distance, timing,

and rates of dispersal and migration have been well-documented (Marchinton & Hirth 1984, Nixon et al. 1991, Hölzenbein & Marchinton 1992, Nelson & Mech 1992). Direction of dispersal by deer may be as important in some situations as distance and timing of dispersal, but this aspect of deer movement ecology has received little attention. During a population ecology study of deer on the Osceola National Forest, Florida, we observed several long-distance movements, both dispersal and excursive, by radio-instrumented deer. Here, we report the non-random directional tendencies of these movements.

Methods

The study was conducted in the 63,631-ha Osceola National Forest, located in Baker and Columbia counties of northern Florida. The vegetation consists of an extensive matrix of longleaf pine *Pinus palustris* and slash pine *P. elliotii* flatwoods, and interspersed swamps. Pine flatwoods, which occupy 65% of the area, are moderately stocked (approximately 25 m² basal area/ha); canopy height, except in regenerating stands, ranges from 20 to 25 m. The understory consists of an almost continuous stand of saw palmetto *Serenoa repens* and common gallberry *Ilex glabra*. The physical structure of the flatwoods generally is uniform across the study area (Avers & Bracy 1979). The remainder of the area is comprised primarily of swamps, which are of two types: cypress *Taxodium* spp./black gum *Nyssa sylvatica* var. *sylvatica* and *N. s. var. biflora* and mixed bay (sweet bay *Magnolia virginiana*, red bay *Persea palustris*, and red maple *Acer rubrum*). The cypress/black gum association occurs in small (<5 ha) circular to elliptic ponds (cypress domes) scattered throughout the pine flatwoods and in larger swamps, whereas the mixed bay association occurs in irregularly-shaped swamps on more loamy soils (Avers & Bracy 1979). The physiographic homogeneity of the landscape is broken only by a large (>3 km diameter) circular lake in the center of the study area. Interstate Highway 10 bisects the study area running east-west.

Deer were captured in corral traps (Stafford et al. 1966) and rocket nets (Hawkins et al. 1968) and fitted with radio-collars during January-March 1989 and 1990 and during June 1990. Capture sites (N = 10) were spread over a distance of approximately 18 km within the study area. Each radio-instrumented deer was located by ground-triangulation eight times per month (two times per week, minimum 12 hours between successive locations), with two locations in each of four major diel periods: morning (sunrise $\pm$ 2 hours), day, evening (sunset $\pm$ 2 hours), and night (Labisky et al. 1991, Kilgo 1992). This monitoring schedule was designed to minimize bias that may be associated with unstratified temporal monitoring, e.g. autocorrelation. Triangulation was conducted from three locations by one observer using a hand-held, directional 'H' antenna. When individual deer undertook long-distance movements, their general location was determined from fixed-wing aircraft. The area was subsequently visited on the ground and triangulation procedures were resumed.

Natal ranges were determined from postcapture movements of 8-month old fawns. Dam/fawn associations still are strong at this age so fawns were assumed to be captured on natal ranges (Nelson 1993). Movements of eight known family units confirmed this assumption. Because no sibling groups in which both members dispersed were monitored, all deer included in the sample of dispersals had geographically separate natal ranges. Two dam/

daughter pairs were included in the sample of excursional movements, but movements by the members of each pair were solitary and in opposite directions (69° vs 250°; 93° vs 255°). Thus, all dispersal and excursional movements were considered independent. Dispersal and excursional movements were defined to be movements $\geq$ 2 km from the natal or home range. Distance and direction of movements were measured between arithmetic centers of natal or home ranges and postdispersal range or destination point. Mean direction of movement was calculated by the center of gravity method (Batschelet 1981). The null hypothesis of uniformity of directional movement between 0° and 360° was tested with Rao's spacing test (Batschelet 1981), which has power to detect multimodal distributions. The alternative hypothesis for this test is that the data are non-uniform in distribution, i.e. that a directional bias exists. The amount of directionality of dispersal $E(X)$ and $E(Y)$ was estimated using the sample means $\bar{X}$ and $\bar{Y}$ of the movement vectors (X, Y) of all dispersals. The variances $Var(X)$ and $Var(Y)$ of the movement vector, which are the relevant quantities that determine opportunities for local adaptations (Slatkin 1973), were calculated as $s_x = 1/(n-1)\sum(X-\bar{X})^2$ and $s_y = 1/(n-1)\sum(Y-\bar{Y})^2$.

Results

Fourteen fawns (7 females, 7 males), captured at approximately eight months of age, were monitored to determine dispersal. All females were monitored through the age of 2.0 years and six were monitored through the age of $\geq$ 2.5 years; average age at termination of monitoring was 2.6 years. Two of seven (29%) females dispersed as yearlings, one in June and one in February. All males were monitored through the age of $\geq$ 1.5 years; average age at termination of tracking (due to death or transmitter failure) was 1.7 years. Six of seven (86%) males dispersed at 1.5 years, usually during fall (one fawn dispersed at 1.5 years of age in May). One additional female and male made dispersal-like movements at 1.5 years but eventually returned to their natal ranges. Mean direction of dispersal by the 10 yearlings was 95° (Fig. 1). Direction of dispersal was non-uniform in distribution ($U = 249$, $U_{crit} = 189.7$, $P < 0.01$; see Fig. 1). Dispersal distance averaged 6.4 ± 4.1 km (SD). The mean of the movement vector was $\bar{X} = 5.9$ km, $\bar{Y} = -0.4$ km, and the estimated variance of the components of the movement vector was $s_x = 16.9$ km and $s_y = 7.4$ km. Correlation between $\bar{X}$ and $\bar{Y}$ was 0.29.

Thirteen long-distance movements by 12 deer (11 by females, 2 by males) were observed among 36 deer radio-monitored as adults. Movements took place during spring and fall. Direction of long-distance movements was non-

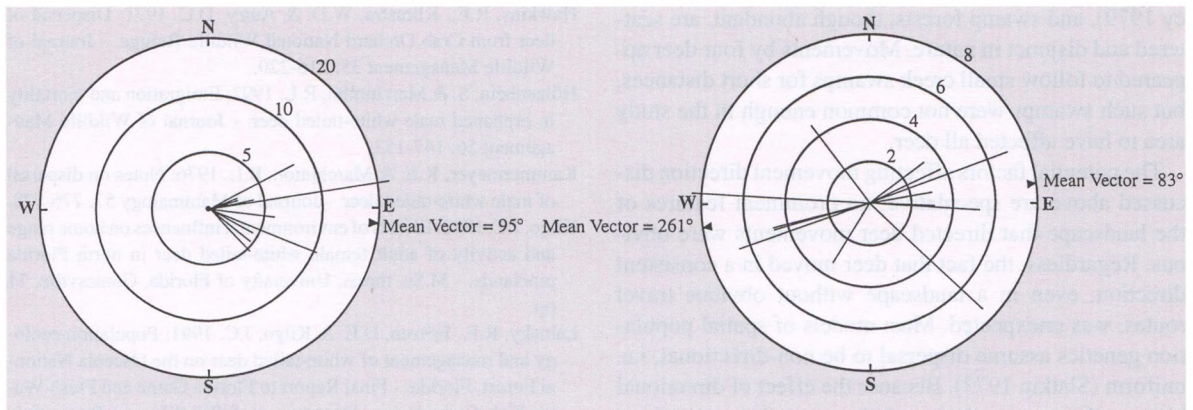


Figure 1. Direction and distance (km) of dispersals by 10 yearling white-tailed deer (3 females, 7 males) during June 1989–September 1991 (left), and of 13 excursions by 12 adult white-tailed deer (10 females, 2 males) during June 1989–1991 (right), on the Osceola National Forest, Florida. Because movements by adults were bimodally distributed, mean directions are given for each of the two distributions.

uniform ($U = 186.2$, $U_{crit} = 185.8$, $P < 0.01$) and bimodal in distribution; mean directions of the two distributions, also calculated by the center of gravity method (Batschelet 1981), were 83° and 261° (see Fig. 1). Distance of these movements averaged 5.1 ± 1.8 km.

Discussion

Long-distance movements by radio-instrumented deer at Osceola were on an east-west axis; dispersals were strictly east-southeast whereas excursions were either east or west. It is difficult to ascertain what factors influenced these observed directional tendencies. Movements by adults may represent return trips to natal ranges, but this possibility fails to explain the ultimate cause of directional dispersal among yearlings. Michael (1965) reported that most re-sightings of marked fawns in Texas were made either south or east of their capture site, but also was unable to explain the observation. Influences on animal movements such as food quality, water, and refugia, while possibly affecting movements by a few individuals at Osceola (Kilgo 1992), likewise do not offer satisfactory explanations: food and water were essentially uniform in distribution across the study area and the only true refugia (closed to hunting) was the city of Lake City, Florida (west of Osceola), into which only one animal ventured.

Another possible explanation involves the interactive effects of habitat quality and population density in the destination range relative to the home range of yearlings. Dispersing deer have been reported to avoid areas of poor habitat quality and to settle in areas devoid of other deer (Nixon et al. 1991), a pattern consistent with Murray's (1967) rule of dispersal: move to the first uncontested site and no further. In these cases, exploratory movements in

random directions were observed prior to dispersal (Nixon et al. 1991). Though we may have overlooked a few such exploratory movements because we did not locate deer daily, each of the 10 yearlings were located ≥ 50 times prior to dispersal, and none of these >500 locations were outside of established home ranges. Thus, deer presumably had little knowledge of the larger landscape prior to their dispersal. Deer tracked en route moved rapidly in a straight-line direction, a behavior apparently typical of dispersing deer (Marchinton & Hirth 1984). Additionally, track count indices of population density indicated that density was lower in the western one-third of the study area, which was open to hunting with dogs, than in the remainder. Natal ranges of all monitored yearlings were east of this low-density area (i.e. dog hunt area), so dispersal was away from it rather than into it. Disturbance by dogs from this area may have affected movements by some deer but we believe these effects were minimal; natal ranges of eight monitored deer were >5 km from the edge of the dog hunt area and all were >1 km.

Animal movement patterns often follow prominent physical features of the landscape such as mountain ranges or riparian systems. Sparrowe & Springer (1970) reported that deer in South Dakota migrated along a major river and its tributaries. Remnants of two Pleistocene terraces, the Coharie and Sunderland, form a broad east-west ridge across the southern portion of Osceola (Avers & Bracy 1979). The ridge acts as a surface water divide, on the north slope of which (which constituted most of the study area), surface flow is either northwestward or eastward (Avers & Bracy 1979). Despite the directional trends of the ridge and surface water flow, examination of vegetation and topographic maps revealed no gross patterns that might have directed deer movements; the general topography of the 'ridge' is flat, falling only 18 m over the 40 km to the Georgia-Florida line (Avers & Bra-

cy 1979), and swamp forests, though abundant, are scattered and disjunct in nature. Movements by four deer appeared to follow small creek swamps for short distances, but such swamps were not common enough in the study area to have affected all deer.

The potential factors affecting movement direction discussed above are speculative; no prominent features of the landscape that directed deer movements were obvious. Regardless, the fact that deer moved in a consistent direction, even in a landscape without obvious travel routes, was unexpected. Most models of spatial population genetics assume dispersal to be non-directional, i.e. uniform (Slatkin 1973). Because the effect of directional bias may be to move the population away from a local optimum trait value, such a bias appears non-adaptive. Further, these results may have important implications for management of gene flow among small populations of endangered species (e.g. Florida Key deer *O. v. clavium*, Columbian white-tailed deer *O. v. leucurus*). Management plans that include corridor acquisition should consider animal movement; a north-south corridor may be of little use to a population that moves on an east-west axis.

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