

Behavior and dispersal of white-tailed deer during the breeding season

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Abstract: Sexual competition and aggression by adult females have been hypothesized to prompt dispersal by male white-tailed deer (*Odocoileus virginianus*). We observed behavioral interactions of 21 yearling males (14 dispersers and 7 nondispersers) at Chesapeake Farms during the early part of the breeding season prior to actual breeding. Interactions with adult males and females constituted a small portion of all interactions and yearling males were similarly subordinate to adults. Dispersers participated in breeding-season behaviors with yearling males more often than nondispersers did ($P = 0.005$), and tended to be more subordinate than nondispersers ($P = 0.095$). Behavioral differences related to sexual competition with other yearlings appeared to be correlated with dispersal by yearling males at Chesapeake Farms. We recommend that both sexual competition and aggression by adult females be considered in future attempts to understand the dispersal behavior of white-tailed deer.

Résumé : On attribue parfois le déclenchement de la dispersion des Cerfs de Virginie (*Odocoileus virginianus*) mâles à la compétition sexuelle et aux agressions des femelles adultes. Nous avons observé les interactions comportementales chez 21 mâles de l'année (14 qui ont quitté leur site natal et 7 sédentaires) à Chesapeake Farms au début de la saison de la reproduction, avant l'accouplement lui-même. Les interactions entre mâles adultes et femelles adultes constituent une faible proportion de toutes les interactions et les mâles de l'année des deux groupes sont également subordonnés aux adultes. Les individus qui quittent leur lieu de naissance ont des comportements avec les mâles de l'année plus souvent que les individus qui restent au site ($P = 0,005$) et ont plus tendance à être subordonnés que les individus qui restent au site ($P = 0,095$). Les différences de comportement reliées à la compétition sexuelle avec les autres individus de l'année semblent en corrélation avec la dispersion des mâles de l'année à Chesapeake Farms. Nous recommandons de tenir compte à la fois de la compétition sexuelle et des agressions par les femelles pour mieux comprendre le comportement de dispersion chez le Cerf de Virginie.

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Introduction

Social pressures have been hypothesized to prompt natal dispersal of yearling male white-tailed deer (*Odocoileus virginianus*) during the breeding season (i.e., August to November). For example, sexual competition with other males (Kammermeyer and Marchinton 1976) and aggression from a yearling male's mother (Holzenbein and Marchinton 1992a) or related adult females (Ozoga and Verme 1985) have been implicated as potential proximate mechanisms of dispersal. Most studies of dispersal have been limited to movement data, with inferences concerning proximate mechanisms. Although some reports have presented behavioral data (Ozoga

and Verme 1985; Holzenbein 1990), none have simultaneously evaluated the roles of sexual competition and aggression by adult females as mechanisms of dispersal, nor compared the behavioral patterns of dispersers and nondispersers.

Coincidence of behavioral patterns and dispersal movements support both hypothesized mechanisms. During the breeding season, the frequency of agonistic (e.g., hard look – ear drop, sidle) and breeding-season behaviors (e.g., antler threat, sparring) among males increases (Hirth 1977; Schwede et al. 1990) and dispersal occurs (Hawkins et al. 1971; Holzenbein and Marchinton 1992b; Rosenberry et al. 1999). Likewise, aggression by adult females towards yearling males can increase during the breeding season (Ozoga and Verme 1985; Holzenbein 1990).

General behavior and movement data cannot provide details necessary to evaluate the role of proximate mechanisms. Although proximate mechanisms have been inferred, no quantitative behavioral comparisons of dispersers with nondispersers have been reported. Our objectives were to quantify behavioral interactions of dispersers and nondispersers and determine whether behavioral differences existed between these 2 groups.

Methods

We conducted our study at Chesapeake Farms, a 1330-ha agricultural and wildlife management research and demonstration area

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operated by DuPont Agricultural Enterprise, located on Maryland's Eastern Shore. The area was 50% forested, 20% active crop fields of mostly corn, soybeans, and winter wheat, and 30% fallow fields, wildlife cover areas, and man-made waterfowl impoundments.

Chesapeake Farms supports a free-ranging white-tailed deer population of approximately 50/km² prior to the hunting season in late November. Deer harvests during the 3 years of our study averaged 187 annually (range 168–212), with adult females and fawns constituting >80% of total harvest. Beginning in 1994, harvest restrictions protected most yearling males. Based on road counts conducted after fall dispersal and prior to the firearms hunting season, antlered animals constituted <10% of the population, the ratio of yearling males to adult males being 2:1. Based upon radiotelemetry data, fall dispersal began in mid-September and concluded in early November. The median dispersal distance for yearling males at Chesapeake Farms was 6 km.

We captured male fawns 4–10 months of age in drop nets and marked them with colored streamers and numbered ear tags. Most animals received solar-powered ear-tag transmitters (Advanced Telemetry Systems, Asanti, MN 55040, U.S.A.). Because dispersal of male fawns prior to 11 months of age is rare (Marchinton and Hirth 1984), capturing males 4–10 months of age increased the probability that animals were not immigrants from surrounding areas. The Institutional Animal Care and Use Committee at North Carolina State University approved animal capture and handling procedures (No. 93-195).

We studied the social behavior of individually marked yearling male white-tailed deer by means of focal-animal sampling (Altmann 1974) throughout the early part of the breeding season in 1995 and 1996. We observed yearling males from the beginning of the breeding season, as defined by initiation of sparring activity (Hirth 1977), to the end of fall dispersal in early November. Based on behavioral observations and fawn captures ($n = 125$), the peak of conception occurred in mid-November after fall dispersal.

The social behavior of yearling males was observed primarily during mornings and evenings, although we recorded observations at other times. We used a 15–60× spotting scope or 10 × 50 binoculars to observe deer from tree stands along edges between woods and fields and from vehicles on study-area roads. Sessions of observing undisturbed marked deer were timed and data were dictated into a tape recorder. We observed marked animals as long as they remained visible, but if other marked animals were visible, observation sessions ended after 10 min.

We defined behaviors as described in Thomas et al. (1965) and Hirth (1977) and analyzed male-only breeding-season behaviors (e.g., present threat, sparring) separately from agonistic behaviors common to the two sexes (e.g., hard look – ear drop, strike) (Koutnik 1981). Age and sex of interactants were recorded. We determined sex from the presence or absence of antlers, fawns excluded, and categorized age as fawn (<12 months), yearling (12–24 months of age), or adult (>24 months of age) on the basis of age-related morphological characteristics such as body size, antler size, and facial conformation. We determined dominance by noting the initiator and winner of agonistic and breeding season behaviors (Forand et al. 1985). We calculated the interaction rate as the number of interactions per hour.

We used nearest neighbors to measure associations of marked yearling males. We recorded sex, age, and distance of the 2 nearest neighbors at 2-min intervals during the first 10 min of an observation bout. We included animals within 10 m of the focal animal in the analysis. If there were no deer or only 1 deer within 10 m of the focal animal, “none” was recorded in place of each potential, but nonexistent, nearest neighbor. For analysis, the “none” category was used as other age–sex classes.

We divided marked yearling males post hoc into 2 groups, dispersers and nondispersers. We classified yearling males as dispersers if they moved at least 1 natal-range diameter (≈ 2.0 km)

from their natal range and nondispersers if they stayed within 1 natal-range diameter of their natal range. Natal ranges represented use areas prior to 11 months of age for each animal, based on telemetry or observed locations (Rosenberry 1997).

We compared individual observation times and interaction rates (number of interactions per hour) with two-sample t tests. Because samples sizes differed, we used Welch's approximate t test for comparisons when sample variances differed greatly (Zar 1999). We used χ^2 tests to evaluate association and behavioral differences between the 2 groups during the breeding season. Where sample sizes were not appropriate for χ^2 analyses (i.e., expected values <5), proportions are presented. Estimates are presented as the mean \pm standard error.

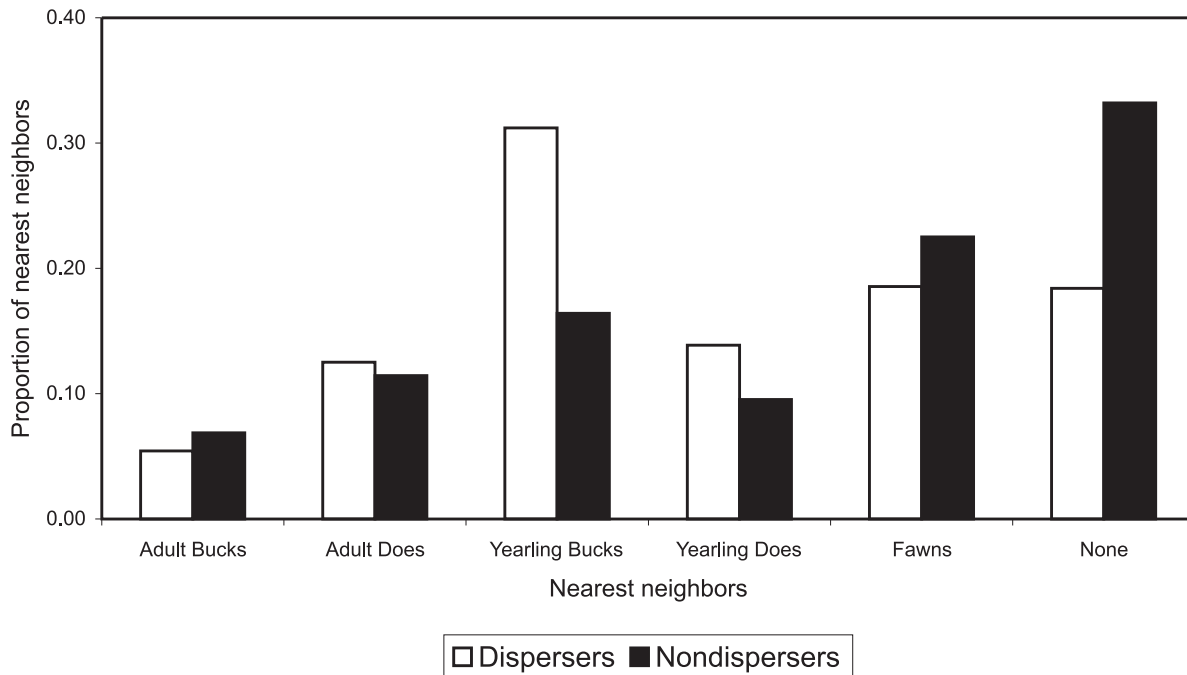
Results

We collected behavior data during the breeding season on 21 yearling males of known dispersal status (14 dispersers and 7 nondispersers). We used radiotelemetry to determine the dispersal status of 16 yearling males. We used observations or kill reports to determine the dispersal status of 3 ear-tagged yearling males and we assumed that 2 uniquely marked piebald yearling males had dispersed because these conspicuous males were not seen after fall dispersal. Mortality of these 2 males at Chesapeake Farms is unlikely, based upon high survival rates of transmitter-equipped yearling males at Chesapeake Farms during fall dispersal (2 mortalities out of 57 yearling males at risk over 3 years). Therefore, the fact that they were not observed after the fall dispersal period probably indicates that they had dispersed. Marked yearling males dispersed between 22 September and 26 October. Exact dispersal dates of 5 yearling males without radio transmitters are not known. We observed dispersers for 23.75 h and nondispersers for 8.73 h. Individual observation times for dispersers (1.69 ± 0.28 h, $n = 14$) and nondispersers (1.24 ± 0.39 h, $n = 7$) did not differ significantly ($t_{19} = 0.92$, $P = 0.368$).

Overall associations of dispersers and nondispersers differed significantly ($\chi^2_5 = 38.6$, $P < 0.001$), particularly in the yearling male and “none” categories (Fig. 1). Most agonistic behaviors (81%) of marked animals during the breeding season involved other yearling males. Agonistic interactions with adult males represented $\approx 10\%$ of agonistic interactions for each group of yearling males, and yearling males were always subordinate to adult males. We did not detect a difference (Welch's test, $t_6 = 1.65$, $P > 0.10$) between nondispersers (1.36 ± 0.69 interactions/h, $n = 7$) and dispersers (0.18 ± 0.15 interactions/h, $n = 14$) in agonistic interactions with adult females, and each group was similarly subordinate to adult females (nondispersers were subordinate in 8 of 9 interactions; dispersers were subordinate in 4 of 5 interactions). Dispersers (2.33 ± 0.49 interactions/h, $n = 14$) and nondispersers (3.11 ± 1.25 interactions/h, $n = 7$) did not differ significantly in agonistic interactions with yearling males (Welch's test, $t_7 = 0.58$, $P > 0.50$) or in dominance ($\chi^2_1 = 1.828$, $P = 0.176$).

Dispersers (3.21 ± 0.40 interactions/h, $n = 14$) participated in breeding-season behaviors with other yearling males 3 times more often ($t_{19} = 3.22$, $P = 0.005$) than nondispersers (0.99 ± 0.55 interactions/h, $n = 7$), and in interactions where dominance could be determined, dispersers tended to be more subordinate than nondispersers ($\chi^2_1 = 2.786$, $P = 0.095$). Only dispersers participated in breeding-season behaviors with

Fig. 1. Nearest neighbors within 10 m of marked yearling male white-tailed deer (*Odocoileus virginianus*) at Chesapeake Farms, Maryland, in 1995 and 1996.



adult males and these constituted a small proportion (8.5%) of all breeding-season behaviors exhibited by dispersers.

Discussion

Dispersers and nondispersers differed in breeding-season behaviors with other yearling males. Breeding-season behaviors related to male fighting (such as antler threat and sparring in white-tailed deer) characterize sexual competition (Wilson 1975). Under the sexual-competition hypothesis, subordinate individuals of the sex experiencing the most intense competition are expected to disperse (Dobson 1982). In white-tailed deer, sexual competition occurs between males as sparring interactions increase during the breeding season (Hirth 1977; Schwede et al. 1990), and functions in the establishment and maintenance of dominance hierarchies (Hirth 1977; Townsend and Bailey 1981; Schwede et al. 1990). In our study, dispersers experienced more intense sexual competition (based upon interaction rates) and appeared more subordinate than nondispersers (based upon interaction outcomes). Thus, we suggest sexual competition, as exemplified by differences in breeding-season behaviors between nondispersers and dispersers, as a potential behavior-related explanation for dispersal patterns at Chesapeake Farms.

Interactions with adult animals did not appear to influence the dispersal of yearling males. We observed no behavioral differences which would suggest that aggression by adult females prompted dispersal. According to the inbreeding-avoidance hypothesis, dispersal is expected to be related to increased levels of aggression between related adult females and yearling males (Ozoga and Verme 1985; Holzenbein and Marchinton 1992a). Although there were opportunities for yearling males to interact with females in large feeding groups (>10 deer), they rarely did so. We did not observe many interactions of adult females with yearling males; most that oc-

curred involved nondispersers, and dispersers and nondispersers were equally subordinate to adult females. We did not attempt to distinguish between related and unrelated adult females because our observations were made during a time when yearling males are less likely to be closely associating with their mothers (Hawkins and Klimstra 1970; Ozoga and Verme 1985), and without sufficient numbers of marked adult females we could not determine relatedness of adult females and yearling males. Therefore, our analysis included all adult females, but would have included interactions between yearling males and related adult females. Based upon observed behavioral patterns, we find no indication that interactions with adult females explained the dispersal of marked yearling males at Chesapeake Farms.

It is often implied that older males are the source of sexual competition in white-tailed deer (Kammermeyer and Marchinton 1976; Ozoga and Verme 1985; Nixon et al. 1994). Breeding-season behaviors between adult and yearling males occurred among dispersers; however, adult males contributed a small portion of breeding-season behaviors. We suggest that this lack of interactions with adult males results from the young-male age structure at Chesapeake Farms, which is a result of past harvesting pressure; hence, the opportunity for yearlings to interact with older males was limited. Although sexual competition with adult males might prompt dispersal of yearling males, direct interactions with adult males were few relative to interactions with yearling males. Thus, adult males appeared to have a limited influence on dispersal patterns at Chesapeake Farms.

Our results differ from those obtained by Holzenbein and Marchinton (1992a), who concluded that interactions with a yearling male's dam prompt dispersal. Observed social behavior and probabilities of dispersal of orphaned and non-orphaned yearling males supported the maternal-aggression hypothesis (Holzenbein and Marchinton 1992a). Orphaned

yearling males dispersed less often (1 of 13 dispersed) than nonorphaned yearling males (7 of 8 dispersed) (Holzenbein and Marchinton 1992b). In addition, there was a seasonal pattern of peaks in aggression between adult females and their male offspring during the rut (Holzenbein 1990).

Other studies have reported no effect of orphaning on dispersal (Woodson et al. 1980; Nixon et al. 1991). According to Woodson et al. (1980), the presence of male siblings and use of an enclosure could have effected dispersal behavior, and according to Nixon et al. (1991), limited forest cover probably influenced dispersal behavior. In addition, aggression from related adult females, not necessarily mothers, has been implicated in dispersal movements of yearling males (Ozoga and Verme 1985; Nixon et al. 1991).

Numerous mechanisms have been hypothesized to influence dispersal of yearling male white-tailed deer. Because social changes coincide with discrete periods of dispersal, social pressures have received most of the attention. To our knowledge, 2 studies (Holzenbein 1990; our study) yielding different results have reported direct observations of social behavior of yearling males in free-ranging populations before fall dispersal. Just as social behavior varies among deer populations (Hirth 1977), so too would the influence of mechanisms based on social behavior be expected to vary. In addition, data supporting one mechanism do not necessarily exclude another as an alternative mechanism of dispersal (Dobson and Jones 1985; Shields 1987). As a result, we recommend simultaneous testing of hypotheses of sexual competition and aggression by adult females in future attempts to understand the influence of social pressures on dispersal of yearling male white-tailed deer. In addition, testing hypotheses across demographically different populations would permit evaluation of the potentially variable influence of social pressures on dispersal.

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