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2. Demes within a Northeastern Minnesota Deer Population

Michael E. Nelson and L. David Mech

Vertebrate populations in general are genetically subdivided (Smith, Garten, and Ramsey 1975), but large mobile vertebrates with greater dispersal capacity might be expected to have less heterogeneous populations than smaller vertebrates (Wright 1978). However, physical and biochemical evidence suggests that white-tailed deer (*Odocoileus virginianus*) populations are genetically subdivided into demes across short distances (Rees 1969; Harris, Huisman, and Hayes 1973; Manlove et al. 1976; Ramsey et al. 1979; Chesser et al. 1982). Cothran et al. (1983) hypothesized that deer demes result from the matriarchal society of white-tailed deer, which facilitates father-daughter incest.

The relationship between genetics and deer social organization, however, has just begun to be defined, and many questions remain unanswered. Ramsey et al. (1979) suggested that genetic analyses of multiple, geographically dispersed samples could be used for detection of genetic subdivision. Nevertheless, temporal and spatial characteristics of deer demes have not been described and the effects of movement traditions, home range tenacity, juvenile dispersal, and breeding movements on deme structure and discreteness have not been examined. This chapter analyzes deer movements and social behavior as a basis for identifying deer demes in part of northeastern Minnesota.

STUDY AREA

The study was conducted in the east-central Superior National Forest of northeastern Minnesota, 48° N, 92° W, from 1974 through 1984. This area is roughly 50 km square (2,500 km^2) and is near the northeastern limit of white-tailed deer distribution. The climate is cool temperate, with snow cover averaging over 1 m during 5 months of winter starting in mid-November. The region is relatively flat, with mixed coniferous-deciduous

forests (Nelson and Mech 1981). The deer population in this area declined from 1968 through 1977 by 80% to 90% as a result of severe winters, a high wolf (*Canis lupus*) population, and maturing habitat (Mech and Karns 1977). Deer densities varied from 0.2 to 0.4 deer/km² during this study (Floyd, Mech, and Nelson 1979; Nelson and Mech, 1986). Several areas that became devoid of wintering deer after 1974 (Mech and Karns 1977) remained so through 1984.

Most deer in the study area concentrate during winter in four areas we refer to as *deeryards* (fig. 2.1). The Garden Lake deeryard is the largest, encompassing 33 km² and holding no more than 800 deer. The Isabella yard is the second largest, covering 27 km² with 400 deer present in March

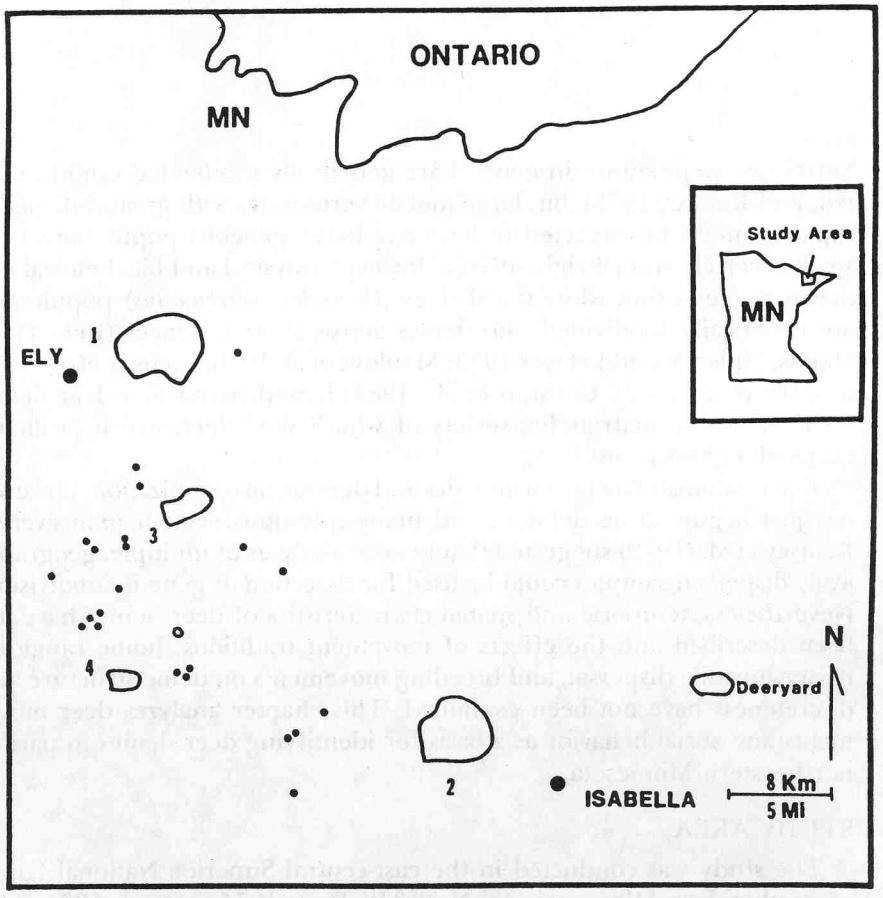

FIGURE 2.1. Study area and locations of the winter deeryards studied: 1 = Garden Lake yard; 2 = Isabella yard; 3 = Kawishiwi Campground yard; and 4 = Snort Lake yard. Dots represent individual deer wintering outside the yards, and the blank region northeast of the yards indicates that no deer used that region during winter. Ely and Isabella are towns.

1984 (Nelson and Mech, 1986). The Kawishiwi Campground and Snort Lake yards are smaller, measuring 7 km² and 6 km² respectively and probably have no more than 40 to 50 deer each. Study area regions outside the major deeryards are devoid of wintering deer, except for the west and southwestern portions of the area where a few singles and small groups of deer are observed outside of yards (fig. 2.1).

In spring, most deer migrate a mean of 17 km (range = 4–40 km) to individual summer ranges that average 319 ha for adult males and 83 ha for adult females (Hoskinson and Mech 1976; Nelson and Mech 1981). An average migration takes 1.8 days for deer traveling 20 km or less and 7 days for deer traveling farther (Nelson and Mech 1981). Migrations are typically very directional and site-specific with no extensive wandering.

Fawns are born on summer ranges in June and accompany their mothers during their first year (Hoskinson and Mech 1976; Nelson and Mech 1981, 1984). Seventy percent of the 1- and 2-year-old males disperse an average of 7 km (range = 4.0–9.6 km) from their birth ranges to new ranges, but females continue to occupy summer ranges adjacent to, or overlapping, their mothers' ranges (Nelson and Mech 1984). During the breeding season in October and November, some adult males travel up to 8 km in search of receptive does near their summer ranges (Nelson and Mech 1981). With the onset of winter weather in November, deer return to their winter ranges (Hoskinson and Mech 1976; Nelson and Mech 1981). Migrations and home ranges are traditional, apparently perpetuated by cohesive family units that influence offspring movements. Thus, deer movements can be classified as spring and fall migration (rapid, site-oriented movement), summer range, winter range, rutting (males only), and dispersal (1- and 2-year-old males).

Wolf predation and bucks-only hunting are the major sources of mortality for deer (Hoskinson and Mech 1976; Nelson and Mech 1981). On an annual basis, wolf predation accounts for 81% and 31% of the mortality for adult females and males respectively (Nelson and Mech, 1986). Bucks-only hunting accounts for an additional 53% of the mortality for males. Adult annual survival is 47% for males and 79% for females.

METHODS

Deer were captured on winter ranges from November 1974 through April 1984, primarily by rocket-net and clover traps. Most were immobilized (Seal, Erickson, and Mayo 1970), sexed, aged via incisor sectioning (Gilbert 1966), blood sampled (Seal, Nelson, and Hoskinson 1978), and radio tracked from the ground and air (Hoskinson and Mech 1976; Nelson and Mech 1981, 1984). Deer up to 1 year old will be called fawns, those 1 to 2 years old, yearlings, and those older than 2 years, adults.

The Garden Lake, Isabella, and Kawishiwi Campground deeryards had similar trapping effort and success throughout the study (table 2.1). Snort Lake deer, however, have only been followed since 1982.

TABLE 2.1 Sex, Age, and Capture Location of Radioed Deer in Northeastern Minnesota, 1974–1984

	Sex		
DEERYARDS	Male	Female	TOTAL
Garden Lake			
Adult	12	27	39
Yearling	6	4	10
Kawishiwi Camp			
Adult	2	15	17
Yearling	8	6	14
Isabella			
Adult	10	16	26
Yearling	8	10	18
Snort Lake			
Adult	1	8	9
Yearling	2	4	6
Total			
Adult	25	66	91
Yearling	24	24	48
All Deer	49	90	139

Radioed deer were located one to three times a week throughout the year with essentially 100% success. Home ranges were identified by the minimum-area method, that is, the area described by connecting only the outermost locations that make a convex polygon (Mohr 1947). Summer range polygons of adult does vary in size from 67 ha to 114 ha (Nelson and Mech 1981).

Radioed deer were rarely observed during summer, but were seen frequently during late fall and winter radio tracking. Fawn-doe relatedness was inferred from social cohesiveness, combined capture, and subsequent movement together (Hawkins and Klimstra 1970; Nelson and Mech 1981, 1984). Because female summer ranges are traditional (Nelson and Mech 1981), birth locations for our fawns had to have been the summer ranges of their does, and subsequent yearling movement away from them was considered dispersal.

Some fawns were captured alone, in which case their mothers' identities and home ranges were unknown. However, the mothers' home ranges were determined based on the movements of their fawns since fawns are highly associated with their does up to 12 months of age (Hawkins and Klimstra 1970; Nelson and Mech 1981, 1984). Several of these radioed fawns were observed with unmarked adult deer which presumably were their mothers or other close kin. Accordingly, when fawns of unknown maternity migrated to summer ranges, their migration patterns and home ranges were considered to mirror those of their does. Subsequent yearling movements and home range use away from those locations were then considered dispersal.

Some fawns did not migrate and were considered to be the offspring of nonmigratory does.

Calculations of average migration distances excluded data from radioed fawns of radioed does since fawns traveled with their does. The area of summer range distribution for deer from each yard was measured from the polygon formed by connecting the outermost summer ranges of individual deer.

RESULTS

The locations of 161 deer summer ranges were determined from 139 individual deer, including 25 adult males, 66 adult females, 24 yearling males, and 24 yearling females (table 2.1). These included 22 doe ranges determined from the movements of 12-month-old fawns of unknown maternity. Fourteen of the fawns were from Isabella, 4 from Snort Lake, 3 from Kawishiwi Campground, and 1 from Garden Lake. Twelve family groups were studied, including 12 adult females, 12 yearling males, and 7 yearling females. Home range formation and dispersal for 11 of the groups were examined by Nelson and Mech (1984).

A total of 8,800 locations of deer were obtained during 1,760 hours of aerial radio tracking, supplemented by an additional 870 locations from ground tracking. Deer were tracked an average of 1.2 years each for a total of 172 deer-years of tracking. Eight adult does were followed for periods of 4.3 to 8.0 years.

Temporal and Spatial Distribution of Deer

Spring migration typically occurred in early April but varied from early March to late April (Nelson and Mech 1981). Seventeen percent ($N = 23$) of the deer failed to migrate and remained on their winter ranges throughout the year. Seventeen of those deer were from Kawishiwi Campground and Snort Lake yards.

Migrations from Garden Lake, Kawishiwi Campground, and Snort Lake yards displayed a strong northeast to east directionality (fig. 2.2, table 2.2). Migration directions from the Isabella yard were more variable, with a general north element to them while predominating to the northwest. The summer ranges of Garden Lake and Isabella deer were distributed over similar-sized areas, larger than those of the other two yards (table 2.2). Garden Lake migrations occurred within a much smaller area than those from Isabella, but they averaged twice the distance of Isabella migrations. The Kawishiwi Campground deer had the narrowest migration pattern and the smallest summer range distribution. Snort Lake deer had the shortest migrations yet with more variable directionality.

At least 95% ($N = 132$) of the deer used summer ranges clearly within the same regions as did other members of their winter yards (fig. 2.3). Only 5% percent of the deer had summer ranges that could be considered "in-

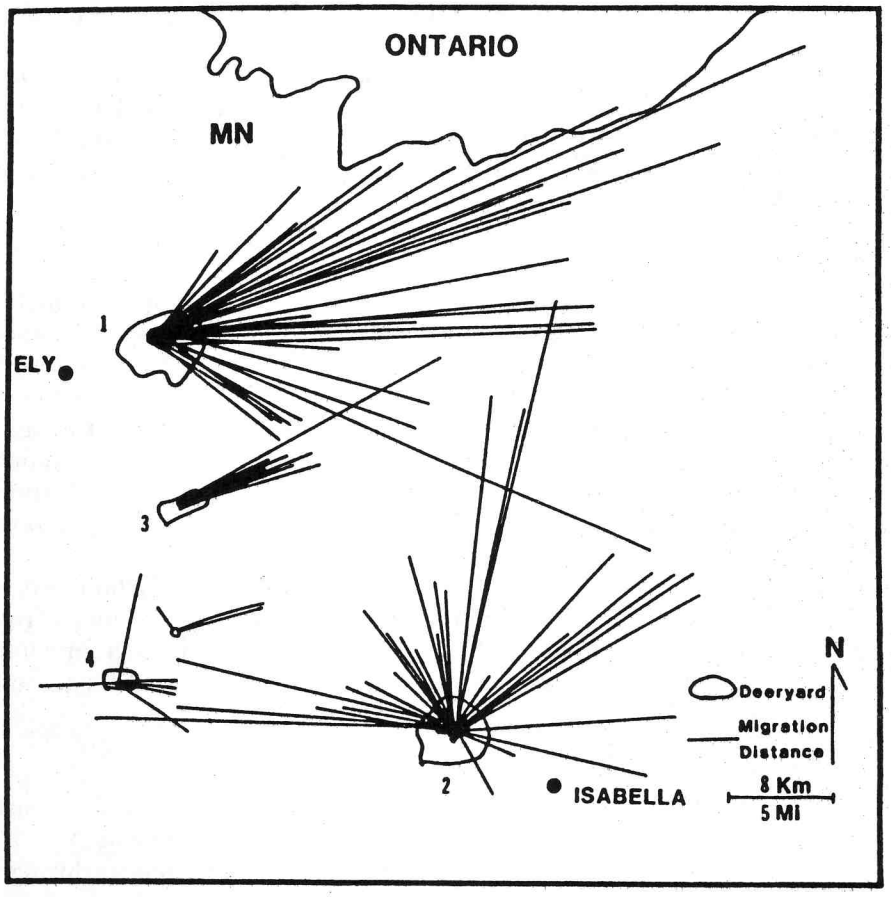

FIGURE 2.2. Distance and direction of spring migration from each of the winter yards. Each line represents data from individual deer.

TABLE 2.2 Migration Distance, Bearing, and Deme Size of White-tailed Deer from Four Deeryards in Northeastern Minnesota, 1974–1984

YARD	NO. MIGRATING DEER[a]	MIGRATION DISTANCE (km) $\bar{x}$ (SE)	MIGRATION BEARING $\bar{x}$ (SE)	DEME SIZE (km^2)
Garden Lake	42	25.0 (1.8)	77 (4)	753–1,157[b]
Isabella	41	12.0 (1.2)	352 (10)	805
Kawishiwi Camp	14	10.0 (1.1)	68 (1)	21–140[c]
Snort Lake	11	6.0 (0.5)	53 (20)	125

a. Excludes radioed fawns of radioed does.

b. The exclusion of one outlying buck range reduced the area to 753 km^2.

c. The exclusion of dispersing yearling ranges reduced the area to 21 km^2.

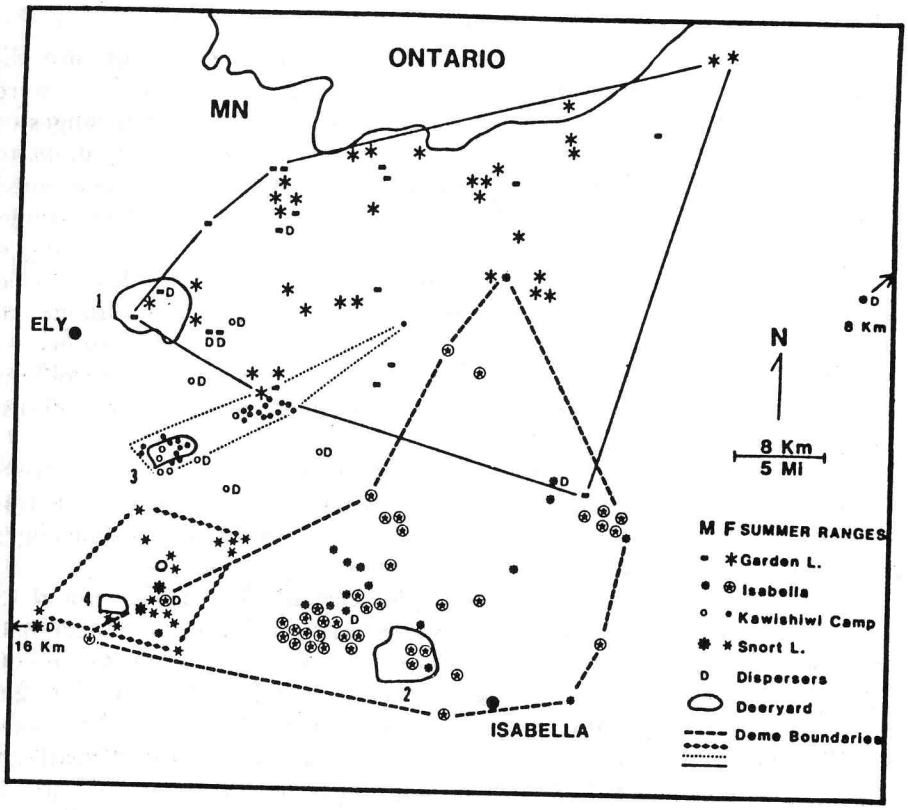

FIGURE 2.3. Summer ranges of deer from each of the winter yards. Symbols represent summer ranges of individual deer; lines are arbitrary borders indicating the authors' concept of the deme boundaries.

side" areas used by deer from other yards, depending on how borders of each yard's summer area are defined. One Garden Lake buck spent the summer 16 km within an area generally inhabited by Isabella deer. One Isabella buck summered 4.8 km inside the area used by Garden Lake deer, and another Isabella buck and two does summered 3.2 km to 8.0 km inside the Snort Lake deer summering area. A Kawishiwi Campground buck and doe summered 8.0 km and 12.8 km inside the Garden Lake deer group. The Kawishiwi buck and one of the Isabella does both had dispersed to the neighboring areas as yearlings.

Forty-two adult deer were radio tracked through two or more annual cycles, during which each continued to use the same summer and winter home ranges. Of that group, 10 adult does continued to use the same ranges during 3.1 to 8.0 years of radio tracking.

Dispersal and Home Range Formation

The movements of 22 yearling males were examined for distance, direction, and timing of dispersal. The birth ranges for 12 of them were known based on associations with radioed mothers. The birth ranges of the remaining 10 deer were assumed; 4 based on typical migrations to specific locations and 6 from the absence of migration, with continued summer use of winter ranges. By 1.5 years old, 13 (59%) of the yearlings had dispersed an average distance of 12.0 km (SE = 2.7) to new ranges. Seven dispersed during June through September and 6 in October and November. Two of the dispersals were two to nine times the distance of the others and, when excluded, lowered the mean dispersal distance to 8.2 km (SE = 0.9). Ten of the yearlings were followed to 2.5 years old, by which time 7 (70%) had dispersed to new ranges. Of those 7 deer, 6 dispersed from known birth ranges.

Of the 13 dispersing yearling males, 8 settled in areas used by deer from their same winter range. In fact, 5 deer dispersed to or toward their traditional winter ranges. The remaining 5 deer moved to the extreme edges of their own subpopulations or into other subpopulations.

Female dispersal was examined for 20 yearlings, 7 with known and 13 with assumed birth ranges. Of those with assumed ranges, 8 deer had migrated to specific summer sites while 5 were nonmigratory. Of the 20 yearlings, all were followed to 1.5 years old; 14 to 2.0 years old; 11 to 2.5 years old; 6 through 3.0 years old; and one through 5 years old, for a total of 28 deer-years of tracking. During that time, only one of the 20 yearlings (5%) dispersed. When 1 year old, a migratory yearling moved 22 km to a new home range after a 1-month stay on an assumed birth range. She was followed until 2.9 years old, during which time she became nonmigratory and remained on her new range throughout the year. The remaining 19 females (95%) continued to utilize the summer and winter ranges they first used as fawns.

Breeding Movements by Adult Males

October–November locations (N = 133) of 15 bucks aged 3.5 to 6.5 years old were examined to measure movements during the breeding season. The mean straight-line distances from their locations to the center of their ranges averaged 3.4 km (SE = 0.6). Three bucks shifted their movements to areas 8 km to 22 km away from their summer ranges but remained within their own subpopulation. The only buck followed through two breeding seasons shifted to the same area each year. The 12 bucks not shifting their ranges were located an average of 2.6 km (SE = 0.3) from their home range centers.

DISCUSSION

Our results suggest that the deer from each of the winter yards represent subpopulations that constitute genetic demes. Adult deer from each yard occupy summer ranges in largely exclusive areas that have little overlap with those of neighboring yards. This separation can last for years since adult movement patterns are traditional. Moreover, most yearling females establish home ranges on or near their birth ranges and continue the migration pattern of their mothers. This site tenacity could lead to inbreeding between daughters and their fathers since dominant bucks probably maintain breeding tenure on their ranges for more than one year. Female philopatry could also lead to inbreeding with brothers and other close kin that never disperse.

Outbreeding by adult bucks appears limited to deer on the edges of demes since average rutting movements are short relative to deme area. As such, most bucks must breed does within 3 km of their home ranges and, most likely, does using the same winter yards as themselves. In addition, some late breeding occurs in December when most deer are in their yards. Finally, while it appears that yearling male dispersal tends to promote outbreeding by removing males from their birth ranges, average dispersal distances would be insufficient to disperse many deer beyond the boundaries of our two larger demes. Eight of our 13 dispersering males established new ranges within their own demes. In fact, 4 of the 5 dispersers that moved to the edges of their demes or beyond were from small demes adjacent to larger ones, and therefore were more likely to enter an adjacent deme by chance alone.

Our deer spacing is surprisingly similar to that in New York, where ear-tagged deer from winter yards were distributed into contiguous and generally exclusive regions during summer (Gotie 1976) (fig. 2.4). Data from an additional 30 New York yards, not shown here, indicate a similar pattern, although some cases of summer range overlap are known to exist between deer from different winter ranges there (N. Dickinson, pers. comm.). Migration patterns and seasonal ranges of radio-tagged deer in northern New York are traditional, with female yearlings establishing ranges on or adjacent to their mothers' ranges (Tierson et al., 1985). One- and 2-year-old males also establish new ranges up to 28 km from their birth ranges. Thus, using our reasoning for deme recognition, we conclude that these New York deer are also genetically subdivided based on deeryard location. Similar patterns of deer distribution seem to exist in Michigan (Verme 1974) and Wisconsin; in the latter state, deer yarding 6 km and 18 km apart have little or no home range overlap on summer ranges (O'Brien 1976).

Pronghorn (*Antiolocapra americana*) herds in southeastern Idaho also winter and summer in adjacent areas with little or no exchange between herds (Hoskinson and Tester 1980). Their summer ranges are separated by

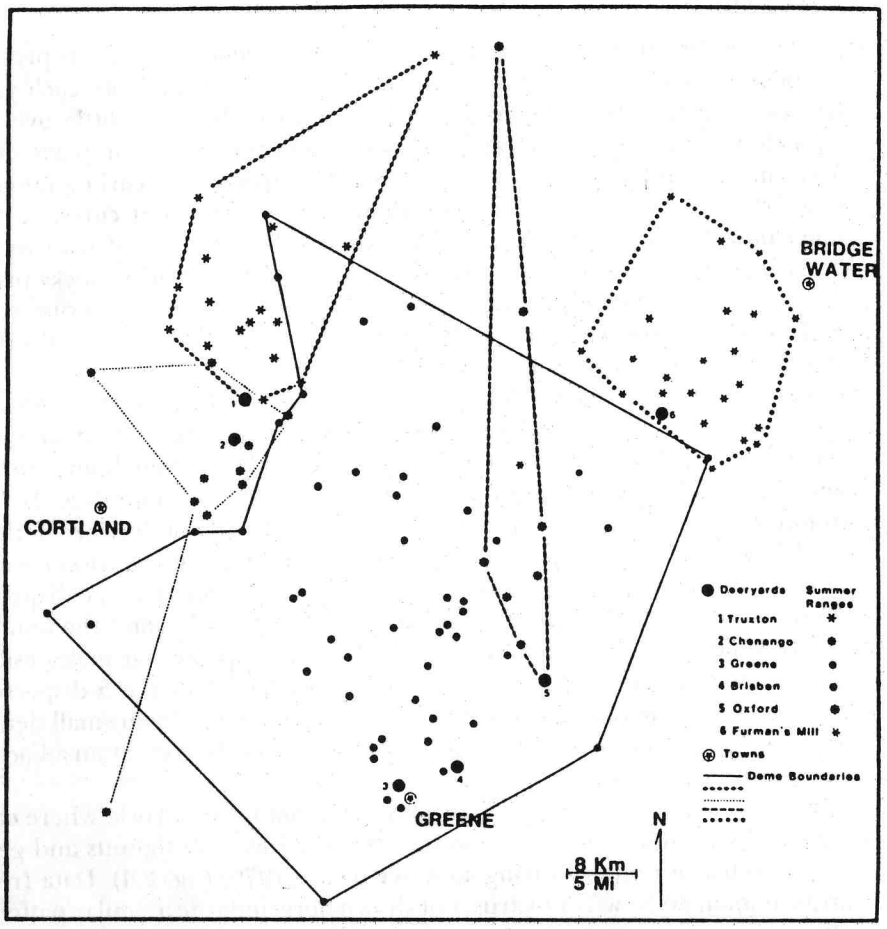

FIGURE 2.4. Apparent demes formed by deer in east-central New York. Symbols represent nonwinter locations of individual deer ear tagged in each winter yard. Data are from G. Mattfeld and R. W. Sage (pers. comm.); lines indicate Nelson and Mech's concept of the deme boundaries.

mountain ranges, but winter ranges are at the same elevation. Pronghorn herds use traditional ranges, and yearling females join their natal herds and drop fawns in the areas they were born (Pyrah 1970). Females breed almost exclusively with dominant males that establish traditional territories, which they defend from April to October (Kitchen 1974). Given this system of movement and breeding, it seems likely that pronghorns are also genetically subdivided.

Our hypothesis that deer populations consist of a conglomerate of demes is further supported by biochemical data from other populations and other species. Gene frequency differences have been found between adjacent

upland and lowland deer in South Carolina (Manlove et al. 1976; Ramsey et al. 1979; Chesser et al. 1982) and between moose occupying areas within 2 km to 50 km of each other (Chesser, Reutherwall, and Ryman 1982). Genotypic differences have also been documented in subgroups of other large mammals (red deer, *Cervus elaphus*, McDougall and Lowe 1968; Bergman 1976; Gyllensten et al. 1980; reindeer, *Rangifer tarandus*, Bræend 1964; and elephant, *Loxodonta africana*, Osterhoff et al. 1974).

Our results are also consistent with the model of Smith (1979) and Shields (1982), which considers dispersal as it occurs in most vertebrates to have evolved from selection for nonincestuous inbreeding. Adult home-range tenacity, female philopatry, relatively short male dispersal, short breeding movements, and little range overlap between deer from different yards suggest that deer populations composed of inbred groups are the rule.

Our study also raises several questions about the origin of demes, their sizes and configurations, and the mechanics of their separation. For instance, do demes originate from the infrequent female dispersal that eventually leads to a new migration pattern, or do they develop from gradual proliferation from an existing deme with a disruption in the traditional pattern? Conceivably a female fawn orphaned on its summer range could fail to make its mother's migration and thus become the progenitor of a new deme. Are the larger demes older than the smaller ones, thus reflecting the time each has had to develop? Our larger demes had approximately 8 to 16 times the number of deer occupying 6 to 9 times the area of our two smaller demes. Deer in our largest deme migrated 3 to 4 times as far as deer from the smaller demes. The two largest demes have histories of 40 years or more, but their origins and the origins of the smaller demes are unknown. Is deme size also related to the proportion of migrating versus nonmigrating deer comprising the deme? Our smallest two demes had 5 times the proportion of nonmigrants of the two larger demes. Is this difference somehow reflected in the relative survival of demes and their ultimate success? Are these small demes more inbred than the larger demes because of less migratory behavior or are females more apt to outbreed because they are closer to bucks from larger adjacent demes?

These latter questions lead to the subject of deme separation, since deme boundaries seem fairly well defined (fig. 2.2). Is there an active mechanism by which deer from one deme can recognize deer from another deme or recognize when they are in another deme? Or is the mechanism more passive in which boundaries simply reflect deme age and movement tradition? Conceivably, scent marking and aggression could be two mechanisms for active separation. Black-tailed deer (*O. hemionus columbianus*) frequently scent mark objects and tend to claim and defend localities (Muller-Schwarze 1971). Individual blacktails in coastal Oregon exclude others from their home ranges and form groups that exclude other groups from their preferred areas (Miller 1974). Female mule deer (*O. h. hemionus*) also occupy

traditional ranges and form closed social groups that are aggressive toward outsiders (Bouckhout 1972). White-tailed deer do form "scrapes" and scent mark during, but only during, the rut (Moore and Marchinton 1974; Hirth 1977). However, 7 of our 13 yearlings dispersed in summer, so they would not have encountered "scrapes" until fall, yet most settled down in their own demes before then. Thus the role of scent marking in deme separation remains unclear.

Aggression remains a possible mechanism for deme separation. Hirth (1977) observed adult bucks chasing 2-year-old bucks and driving them away. He also observed a group of three bucks excluding 2-year-olds from their group. Unfortunately, dense forest cover in our study area inhibited our ability to observe deer as they interacted with other deer.

Whatever the case with bucks, there appears to be no active mechanism by which females could know about deme boundaries since most never explore or disperse beyond their birth ranges. In addition, there are several cases, in both our study and those from New York and Wisconsin, of deme overlap and interdeme dispersal, which suggests that deme boundaries are not totally exclusive or actively guarded. Thus evidence suggests that site familiarity and tradition are major factors in determining where deer establish home ranges (Nelson 1979; Nelson and Mech 1981, 1984), and that deme size, configuration, and separation are passive results of movement tradition, differential deme survival, and deme age.

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