DEER DISTRIBUTION IN RELATION TO WOLF PACK TERRITORY EDGES

Densities of white-tailed deer (*Odocoileus virginianus*) are higher in areas of overlap between territories of wolf (*Canis lupus*) packs than in territory centers (Mech 1977*a,b*). Wolves apparently avoid hunting in areas of territory overlap or "buffer zones" until they cannot catch prey elsewhere. Therefore survivability of deer should be greater in the buffer zones due to less wolf predation.

Indications that deer are more abundant in buffer zones than in wolf pack territories were obtained in northeastern Minnesota. Deer that were radio-collared in winter yards following a drastic decline in deer numbers (Mech and Karns 1977) dispersed to summer ranges situated almost exclusively in buffer zones (Hoskinson and Mech 1976; Nelson and Mech, unpubl. data).

Buffer zones between territories of wolf packs remain in about the same locations from year to year except when prey becomes scarce (Mech 1977*b*). This stability of territorial boundaries appears to reduce strife between packs, but probably also helps maintain reservoirs of deer that may disperse into cores of territories (Mech 1977*b*). Such reservoirs might be particularly important when deer populations decline. At that time, wolf numbers also drop (Mech 1977*c*), so deer from the buffer zones could then increase and repopulate territory cores (Mech 1977*b*). Buffer zones between hostile tribes of Indians in Minnesota similarly may have served as reservoirs for deer during the 1800's (Hickerson 1965).

To obtain additional information on deer density in relation to wolf pack territories, we counted deer tracks in edges and centers of wolf pack territories during and following a deer decline.

STUDY AREA

This investigation was conducted in the central part of Superior National Forest (SNF) in northeastern Minnesota (48°N, 92°W) (Fig. 1). The area is in the transition zone between boreal and deciduous forest (Maycock and Curtis 1960). Some of the forest is virgin and the remainder has been cut over at various times since 1920. Ohmann and Ream (1971) and Peek et al. (1976) described vegetation and land-use history for this area. Annual temperatures range between -50 and +36 C, and snow depths sometimes reach 119 cm (Mech and Frenzel 1971). Deer have long been subject to intensive predation by wolves in this region (Stenlund 1955, Mech and Frenzel 1971, Van Ballenberghe et al. 1975), and some of the deer inhabit areas accessible to human hunters. The deer of the study area may migrate up to 40 km between summer and winter ranges (Hoskinson and Mech 1976; Nelson and Mech, unpubl. data).

The quality of deer habitat and the deer population density vary greatly in the study area; densities in 1936 ranged from 4 to 20 per km^2 (Civilian Conservation Corps deer drive records in Minnesota Dep. Natural Resources files, cited by Mech and Karns 1977). By 1955, a rough estimate of the average deer density of the entire SNF was about $4/km^2$ (Stenlund 1955). Little is known about deer numbers there between 1955 and 1968. However, in 1968-69 the deer herd began declining drastically as a result of a series of severe winters, maturing vegetation, and wolf predation (Mech and Karns 1977). Deer continued to decline until 1974 and then apparently stabilized. The decline became apparent first

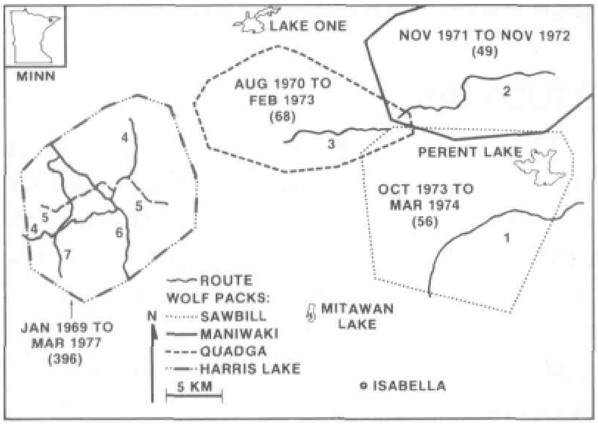

Fig. 1. The study area. Numbers refer to tracking routes for which data are plotted in Figs. 2 and 3. Routes 1-3 were surveyed during 1967 through 1969, and routes 4-7 in winter 1976-77. Dates refer to periods during which wolf pack territory data were obtained, and numbers in parentheses refer to number of radio-locations.

in virgin forest, including the northeast end of the current study area, and progressed westward until by 1974 a 3,000-km^2 area was devoid of overwintering deer (Mech and Karns 1977). Even in summer 1977, only 4 fresh trails of deer were found on 34 kin of gravel roads in that area. Just south and west of the void, deer persisted through winter 1977-78 but at about 0.40/km^2 (Floyd et al. 1979).

METHODS

Locations of fresh deer trails along roads were mapped in summers of 1967 through 1969 and in winter 1976-77. During 1967-69, fresh deer trails were recorded along 3 gravel roads totaling 40.6 km and extending from the edges to the centers of 3 wolf pack territories (Fig. 1). The routes were driven 5-24 times at intervals of a week or more from June through November in early morning when tracks made the previous night were most obvious. Only fresh tracks, i.e., those estimated to have been made within about the last 24 hours, were counted.

Habitat data within. 30 m of the tracks were recorded. These data included physiography, dominant overstory and understory species, stand density and height, and tree-shrub composition. To determine the availability of various habitat types along the 3 tracking routes, we also recorded habitat data for 130 stands classified in 60-m^2 semicircular plots adjacent to the road at 0.3-km intervals.

In winter 1976-77, we observed the distribution of deer trails within 1 wolf pack territory (Harris Lake Pack) by walking, skiing, and driving 4 routes totaling 109 km of roads and frozen streams passing through both edge and center of the territory (Fig. 1). This survey was conducted in snow depths up to 0.5 m, and only trails made during the previous 2 days were recorded.

Locations of wolf pack territories were determined by aerial radio-telemetry (Mech and Frenzel 1971, Mech 1974).

RESULTS

The mean number of deer trail crossings per km of route was 0.49 in 1967, 0.77 in 1968, and 0.38 in 1969. In winter 1976-77, when 4 routes were run through the Harris Lake Pack territory, a mean of 2.1 deer crossings per km was recorded.

Radio-tracking data from the 4 wolf pack territories through which the deer-tracking routes passed were available for various periods between 1970 and 1977 (Fig. 1). The territories described were based on 49 to 396 locations each. Although territory data were not available from the same years in which the deer trail data were collected, most pack territories in the study area were stable over periods of several years (Mech 1977a and unpubl. data).

The results can be divided into those obtained before the severe deer decline of winter 1968-69 and those after the decline began. Before the decline, deer in-

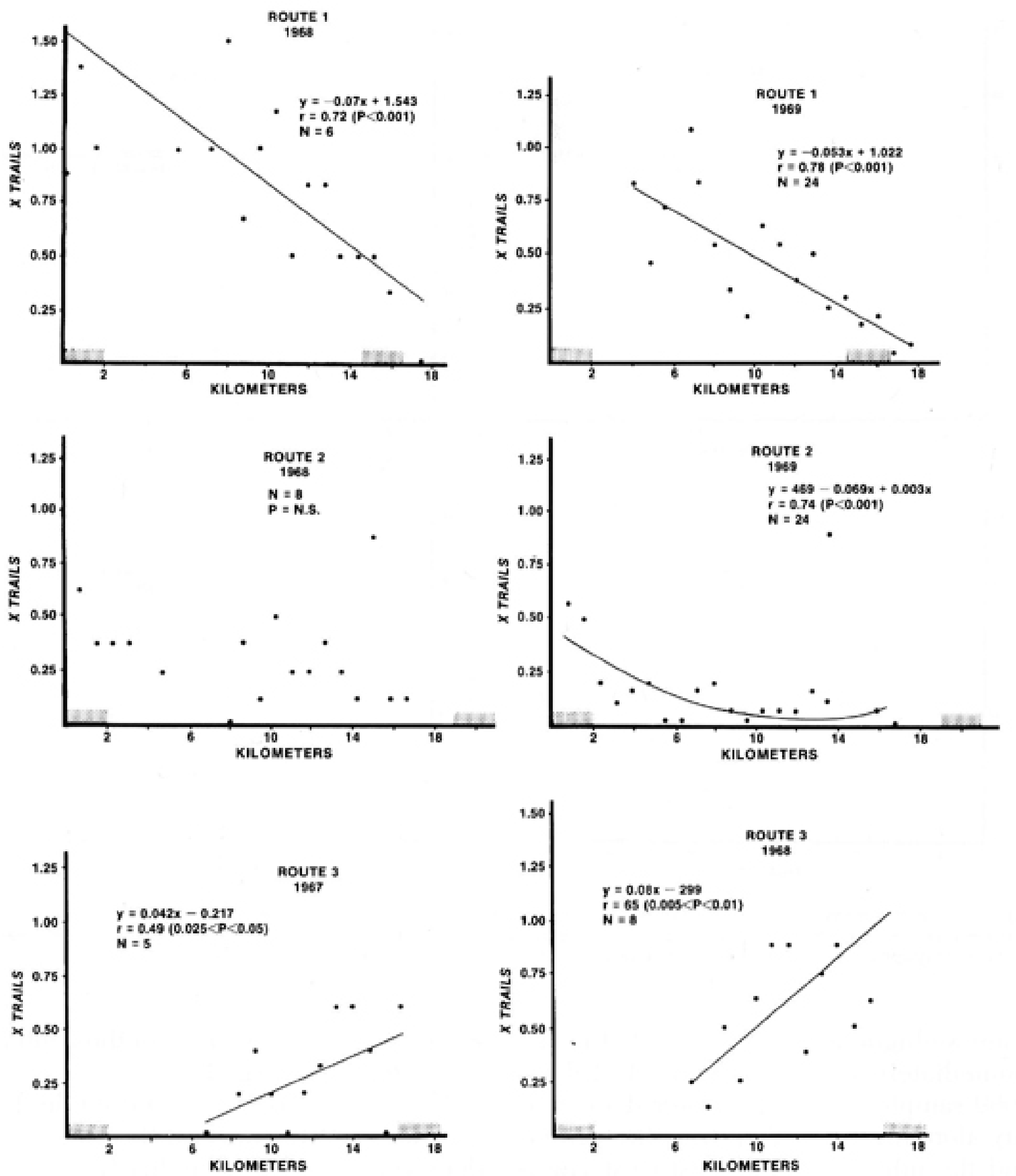

Fig. 2. Relation between number of fresh deer trails/km crossing the tracking routes and the distance along the routes. Left sides of graphs coincide with west ends of tracking routes. Shaded portions of graphs represent locations of estimated buffer zones between wolf packs. See Fig. 1. "N" is the number of times routes were examined.

habited the centers of wolf pack territories as well as the edges, as already reported (Mech 1977*a*, Mech and Karns 1977) (Fig. 2). However, even in 1967 and 1968, deer appeared scarce in the Quadga Lake Pack territory center (Route 3, Fig. 2).

Of 4 territory-years of predecline (1967 and 1968) data, 2 show more deer toward the territory edge than in the center, and

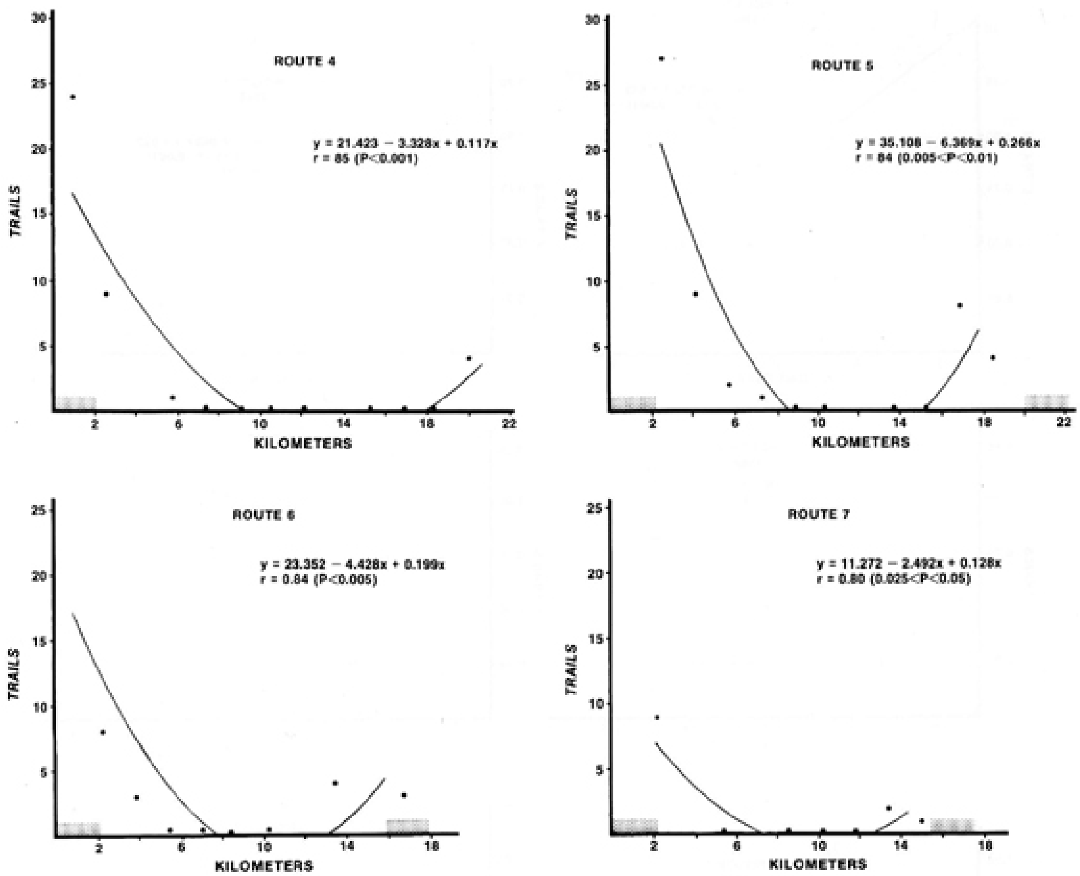

Fig. 3. Relation between number of fresh deer trails/km crossing the tracking routes and distance along the routes, all in the Harris Lake Pack territory (Fig. 1). Left side of graphs coincide with west or north ends of tracking routes. Shaded portions of graphs represent locations of estimated buffer zones. Each route was examined once.

2 are ambiguous in this respect (Fig. 2). Immediately after the decline, 1 of the 2 1969 samples shows a greater deer density along the edge than near the center, and the other shows an east-west gradient in density, with the peak occurring toward the western edge (Fig. 2).

Only routes 2 and 3 ran through the center of 1 wolf pack territory, through the buffer zone between that pack and its neighbor, and then into the center of the adjacent pack territory (Fig. 1). The data from both those routes show that deer density was greater in the buffer zone between the 2 packs than in the center of either territory (Fig. 2).

The winter 1976-77 data from the Harris Lake Pack territory, at the edge of the deer void, also show a clear preponderance of deer around the periphery of the territory compared with the center (Fig. 3). These data indicate that deer density in pack territories generally was greater at the edges than in the centers and that this trend increased with time.

Chi-square analysis of habitat for the 1967-69 data showed no difference ($P > 0.05$) between the centers of the pack territories and the edges for: dominant tree species, shrub density, overstory density, overstory height, or browse species. No habitat analysis was conducted for the Harris Lake Pack territory.

DISCUSSION AND CONCLUSIONS

The data generally support the hypotheses that deer densities tend to he greater along wolf pack territory buffer zones than in territory centers (Hoskinson and Mech 1976; Mech 1977*a,b*; Nelson and Mech, unpubl. data). Whether this is true only during a deer decline or whether it also applies to increasing or stable populations is unclear.

The east-west gradient in deer densities within wolf pack territories might be explained in terms of a gradient in wolf predation. The depletion of deer after winter 1968-69 progressed from east to west over a 6-year period in the 3,000-km^2 region that included the northeast end of our study area (Mech and Karns 1977). During the last 3 years of this progression there was an unusual migrating, shifting, and trespassing of wolf packs from east to west, especially during winter (Mech, unpubl. data). Such shifting no doubt increased predation on deer along the west edge of the zone of depletion and exacerbated the decline (Mech and Karns 1977).

Therefore, the east-west gradient in deer density seen in our data from 1968 to 1969 might have resulted from the beginnings of the above trend even before the severe winter of 1968-69 precipitated the major decline. It seems significant that the depletion of deer began in virgin forest, the poorest deer habitat of the region, just northeast of the current study area (Mech and Karns 1977).

Because habitat did not appear to differ between wolf pack territory edges and centers, the differences in deer density found in our study must be attributable to some other factor. This lends support to the hypothesis that the cause is reduced wolf predation in the pack territory buffer zones (Hoskinson and Mech 1976; Mech 1977*a,b*).

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