BUFFER ZONES OF TERRITORIES OF GRAY WOLVES AS REGIONS OF INTRASPECIFIC STRIFE

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The locations of 22 territorial gray wolves (*Canis lupus*) killed by conspecifics in northeastern Minnesota were analyzed in a study involving radio-telemetry from 1968 through 1992. Twenty-three percent of the wolves were killed precisely on the borders of their estimated territories; 41%, within 1.0 km (16% of the radius of their mean-estimated territory) inside or outside the estimated edge; 91%, within 3.2 km inside or outside (50% of the radius of their mean-estimated territory) of the estimated edge. This appears to be the first report of intraspecific mortality of mammals along territorial boundaries.

Key words: *Canis lupus*, wolf, territoriality, intraspecific strife, mortality, competition, buffer zone, predator-prey relations, deer, *Odocoileus virginianus*

Gray wolves (*Canis lupus*) are territorial. Mech (1970) summarized circumstantial evidence of territoriality among wolf packs and later described exclusive territories used by wolves in Minnesota (Mech, 1973). Territoriality of wolf packs has since been documented in several other areas (Ballard et al., 1987; Fritts and Mech, 1981; Fuller, 1989; Mech et al., 1991; Peterson et al., 1984; Ream et al., 1991). Most of the available information about territories of wolf packs involves their sizes in different areas.

However, there also is some evidence that boundaries of territories of neighboring wolf packs may overlap or be contested (Fritts and Mech, 1981; Hoskinson and Mech, 1976; Mech, 1977*a*, 1977*b*; Nelson and Mech, 1981; Peters and Mech, 1975; Rogers et al., 1980). The contested area has been referred to as a buffer zone, and the buffer zone has been estimated as a strip ca. 2 km wide (Hoskinson and Mech, 1976; Mech, 1977*a*, 1977*b*; Peters and Mech, 1975).

The existence of buffer zones between territories of neighboring wolf packs was deduced from the higher density of white-tailed deer (*Odocoileus virginianus*) that survived along the edges of territories of wolf packs during a decline in number of deer (Hoskinson and Mech, 1976). The theory was that a higher density of deer resulted from wolves spending less time along territorial edges because of the increased chance of meeting neighboring wolves at the edges and risking a fatal encounter. Considerable evidence of higher density or survival of deer along edges of territories of wolf packs was demonstrated (see previously mentioned references), but no documentation has been available that wolves spend less time along edges or that they risk fatal injuries from neighbors there. Furthermore, the width of the buffer zone was a gross, preliminary estimate with no quantitative support. The present study analyzes the locations of gray wolves killed by other gray wolves relative to their territorial boundaries and derives further information about buffer zones between neighboring wolfpacks.

METHODS

Gray wolves in the central Superior National Forest of northeastern Minnesota (48°N, 92°W) were live-trapped, anesthetized, ear-tagged, and

TABLE 1.—*Background information about gray wolves killed by other gray wolves in northeastern Minnesota.*

Wolf number	Dates of study	Number of locations	Size of territory (km²)	Radius of territory[b] (km)	Location of killed wolves: Km from territory edge	Location of killed wolves: Percent of radius from edge of territory
1	2 April–2 December 1990	33	205	8.0	−0.8	−10
35	27 August 1987–2 August 1988	60	115	6.0	0.0	0
93	1 April 1991–12 March 1992	53	110	5.9	−2.1	−35
119	1 April–3 December 1992	34	79	5.0	0.0	0
129	2 April 1990–14 March 1991	45	335	10.4	−0.8	−8
185	2 April–29 October 1990	(25)[d]	64	4.5	+6.4	+143
215	2 December 1990–2 December 1991	57	105	5.8	−1.4	−25
247	28 August 1991–8 February 1992	23	26	2.9	−1.9	−67
277	19 June 1990–10 February 1991	43	74	4.8	0.0	0
297	28 August–6 October 1991	7	44	3.7	−0.5	−13
299	28 August–6 October 1991	6	44	3.7	1.6	+44
1843	6 April 1988–24 March 1989	16	38	3.5	0.0	0
2491	2 April–15 December 1974	65	207	8.2	+2.4	+29
5059	10 July 1973–16 March 1974	90	420	11.5	+1.3	+11
5135	19 August–17 December 1974	40	253	9.0	−2.9	−32
5176	7 November 1984–3 November 1985	44	79	5.0	−1.0	−19
5180	27 January 1975–27 January 1976	40[a]	225	8.5	−3.5	−41
5926	3 July 1980–11 March 1981	81[a]	133	6.6	0.0	0
6037	16 July 1980–20 February 1981	66[a]	133	6.6	−1.6	−24
6041	8 January–31 December 1988	36	69	4.6	−1.3	−28
6689	8 October 1987–19 October 1988	60[a]	136	6.6	+3.2	+49
6797	1 October 1986–31 October 1987	66	333	10.2	+4.5	+44

[a] Excludes excursions.

[b] To provide a basis for scaling the size of the territory, a radius was calculated for each territory, as though territories were circular, and distances of locations where a wolf was killed by other wolves were given as percentages of the radii.

[c] Positive values represent distances outside the edge of the minimum-convex polygon (Mohr, 1947), where a wolf was killed by other wolves; negative values represent distances inside the edge of the minimum-convex polygon (Mohr, 1947) where a wolf was killed by other wolves.

[d] 1 year earlier.

fitted with radio-transmitters, and they and their packmates were aerially radiotracked and observed at least weekly from 1968 through 1992 (Gese and Mech, 1991; Mech, 1973, 1977*c*, 1986, 1987). During that period, the density of wolves varied between 15 and 42/1,000 km² (Mech, 1986) and territory size, between 90 and 310 km² (Mech, 1974). The primary prey of wolves in the area was white-tailed deer.

When radio signals indicated that a wolf had died, the location was investigated, and remains examined. Signs of wolves and a struggle in the snow around the remains or wounds on the carcass from bites were interpreted as evidence of killing by conspecifics. The location where each wolf was killed was plotted in relation to the minimum-convex polygon (Mohr, 1947) around the composite of the most points where the animal had been found during its previous 6 weeks to 12 months, depending on how long the animal had been studied. Obvious excursions out of the territory were excluded from the minimum-convex polygon in a few cases. In one instance, the area of an indentation by a neighboring pack into the minimum-convex polygon of the territory of a subject pack was subtracted from the area of the minimum-convex polygon of the subject pack. The distance a wolf was killed inside or outside the minimum-convex polygon was the perpendicular distance to the closest edge of the minimum-convex polygon. To relate the measurements to the scale of the territories, radii were calculated for the areas of the territories, assuming circular shapes, and the distances wolves were

killed inside or outside the territories also were presented as a percentage of the radius of the territory.

Results and Discussion

Of 443 gray wolves radiotracked, 30 were found that apparently had been killed by other wolves. Of these, 14 were males and 8 were females (chi-square test; no significant difference) in pairs or packs with known territories (Table 1). No definitive information was available about what wolves had killed the animals, but circumstantial evidence in a few cases indicated that neighboring packs were involved. Thirteen of the 22 wolves killed were alpha animals, three probably were alphas, one had been an alpha the year before, but its current status was unknown, and five were subordinate members of packs.

The subject wolves had estimated territories with minimum-convex polygons of 26–420 km² and radii of 2.9–11.5 km, with a mean radius of 6.4 km. There was a weak but significant relationship between the number of locations at which each wolf had been found and the size of their territory (simple linear regression: $r^2 = 0.36$, $P < 0.01$), but when five wolves with <33 locations were eliminated, the relationship was not present ($r^2 = 0.15$, $P = 0.13$). Therefore, I considered that, for most of the wolves, the minimum-convex polygons were reasonable estimates of the locations of the actual boundaries of their territories.

The wolves were killed from 3.5 km inside the border of their estimated territory to 6.4 km outside the border, but 41% were killed within 1.0 km (16% of the mean radius) inside or outside of the estimated edge, and 91% were killed within 3.2 km inside or outside (50% of the mean radius) of the edge (Fig. 1).

These results support the contention that wolves run a greater risk of fatal encounters along the edges of their territories than in their centers (Hoskinson and Mech, 1976). Wolves apparently patrol the borders of their territories frequently, and they scent-mark

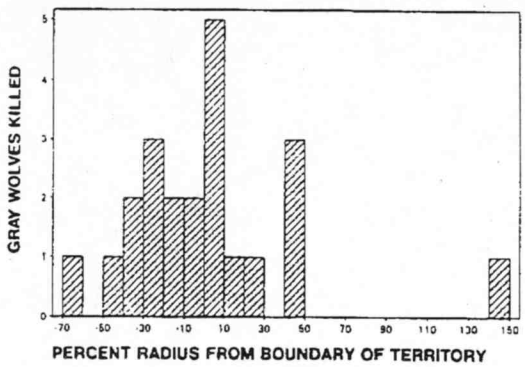

Fig. 1.—Distribution of locations where gray wolves were killed by other gray wolves in relation to edges of their estimated territories. Negative values signify distances inside the territory, and positive values signify distances outside the territory.

the edges about twice as much as the centers (Peters and Mech, 1975). However, the marks must not always keep neighbors away; if they did, fatal encounters would not take place. Furthermore, wolves are known to trespass deep into the territories of other packs (Haber, 1977; Mech, 1977*c*; Peterson, 1977), and the wolves killed ≥6.4 km outside of their estimated territories or ≥3.5 km inside them during this study further attest to this conclusion.

It seems reasonable to conclude from these data that the buffer zone, or zone of contention, along the boundaries of the territories of wolf packs in this study area actually extended ca. 3.2 km inside and 3.2 km outside the estimated territorial border rather than just 1 km in each direction as originally was postulated by Peters and Mech (1975). Conceivably in larger territories, the buffer zones also may be larger. It also is possible that the buffer zone is of fixed width in relation to the perceived edge of a territory and, therefore, independent of the size of the territory. Similar data from a study area with larger territories of wolf packs are required to determine which hypothesis is the case or whether some intermediate relationship exists.

This is the first report showing that any

mammal kills conspecifics along territorial edges. However, until the advent of radiotelemetry, means to determine this kind of information were not available. Even with radiotelemetry, >20 years of data were necessary to obtain an adequate sample during this study. Thus, other carnivores might show similar behavior.

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