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WOLF HOWLING AND ITS ROLE IN TERRITORY MAINTENANCE

by

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(With 7 Figures)
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INTRODUCTION

The wolf *(Canis lupus)* is a wide-ranging social carnivore with a complex spatial organization (MECH, 1972; 1973). The precise manner in which this organization is maintained is unknown, but territory advertisement using olfactory and acoustic modes seems to be involved.

The acoustic mode includes primarily howling. Within a wolf pack, howling may be useful to reassemble separated members (MECH, 1966; THEBERGE & FALLS, 1967), and may communicate information on individual identity, location, and other behavioural and environmental contingencies (THEBERGE & FALLS, 1967). Between packs, however, howling may serve to advertise territory, communicating the locations of packs and thus minimizing contact between them (JOSLIN, 1967).

The objective of the present study was to determine the possible role of howling in territorial maintenance by investigating the responses of wolves in northeastern Minnesota to simulated wolf howling.

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Wolf packs in Minnesota occupy territories of approximately 125 to 310 km^2 (MECH, 1972; 1973; 1974). Little overlap exists between adjacent packs, and boundaries between packs are often distinct, although over long periods they may shift somewhat (PETERS & MECH, 1975). Territories tend to remain stable in size and location over a period of years, and the territory of one of the packs involved in this study, the Harris Lake Pack, has changed little during the past 7 years (MECH, 1977a).

In addition to territorial packs, part of the Minnesota wolf population exists as lone animals (MECH & FRENZEL, 1971). Loners live nomadically in large areas usually encompassing several pack territories and rarely interact except during the breeding season (PETERS & MECH, 1975) or when loosely associating around a kill.

Interpack conflicts leading to the deaths of either resident or intruding wolves (MAHRENKE, 1971; VAN BALLENBERGHE & ERICKSON, 1973; WOLFE & ALLEN, 1973; MECH, 1977b) emphasize the importance of maintaining well-defined territories by indirect means to minimize chances of such encounters. Pack wolves seldom leave their territory under usual conditions (MECH, 1977a), and direct encounters between packs are rare (PIMLOTT *et al.*, 1969; MECH, 1970; PETERS & MECH, 1975). However, direct aggression sometimes serves as a backup system when indirect maintenance fails (MECH, 1977b).

One indirect means of territory maintenance in many mammals, including the wolf, is scent-marking (SCHENKEL, 1947; RALLS, 1971; THIESSEN, 1973; MYKYTOWYCZ, 1974; PETERS & MECH, 1975). The distribution of marks throughout a wolf pack's territory, their frequency of application, and the information that they contain help maintain the wolf pack territory structure (PETERS & MECH, 1975). Although scent-marks advertise an animal long after it has passed, they require direct and close scrutiny, and they fail to inform interested parties of their maker's current location.

On the other hand, vocalizations provide instant information concerning the vocalizer's location from a long distance, and in many species, vocalizations are important in territorial maintenance. JOSLIN (1967) felt that howling could serve this role in wolves, and thus keep packs aware of each others' locations so encounters could be avoided. Of the wolf's four major vocalizations, only howling has the necessary range to be important in long distance communication (JOSLIN, 1967; HARRINGTON & MECH, 1978).

Although direct evidence of the territorial role of howling has been lacking, some circumstantial evidence does exist. Interpack howling sessions may sometimes continue for hours (JOSLIN, 1966; VOIGT, 1973), and in Minnesota, three adjacent packs were heard howling, apparently to each other, each from within its own territory (BRANDENBERG, personal communication). After such sessions, packs often move apart (Rutter & Pimlott, 1968), suggesting that interpack howling occurs in an agonistic context, and thus may be involved in territory maintenance.

The present study, using an experimental approach in a wild wolf population, provides considerably more data about the subject. Through studying elicited howling, we describe the parameters governing interpack howling sessions. What factors affect the responsiveness of one pack answering the howling of another? How does a pack behave in response to alien howling? What is the role of howling in lone, non-territorial wolves? Once these preliminary questions are answered, we attempt to evaluate the role and importance of howling in territory maintenance.

NATURAL HISTORY OF THE WOLF

To appreciate the significance and value of our approach, one must understand the natural history of the wolf.

There are two phases in the activity of a typical wolf pack in Northern Minnesota. During the relatively stationary phase from May through September, the pack's activities are focused around a series of "homesites" where pups are raised (Murie, 1944; Joslin, 1967). For the rest of the year, the entire pack hunts nomadically within its territory and rarely visits particular sites more than a few times. It may travel up to 50 km per day (Burkholder, 1959; Pulliainen, 1965; Mech, 1966) at this time.

Kills of prey usually remain a center of pack activity for several days, depending on: (1) number of wolves, (2) size of the prey, and (3) period since last feeding. A pack of 15 wolves on Isle Royale usually consumed all edible parts of moose (*Alces alces*) by the day after the kill, and within another day abandoned the remains (Mech, 1966). During periods of high prey vulnerability, however, kills may be abandoned after little use (Mech & Frenzel, 1971). At other times, packs and individual members continue to return to old kills, even though little edible material is left. One of our study packs, having little success in hunting, occasionally returned to the same moose kill for more than 4 months.

The breeding season occurs near the end of the nomadic period, from late January to early March, and pups are born in late April and early May (Mech, 1966; Mech & Frenzel; 1971, Mech, unpubl.). Individuals and/or groups of members then radiate out from the den and return later with food to regurgitate to the female and pups (Rutter & Pimlott, 1968).

For 7 to 10 weeks after birth, the pups remain near the den (Mech, 1970). By mid-to-late June they spend most of their time above ground in restricted areas known as "rendezvous sites" (RS), which may be changed several times during summer (Murie, 1944; Joslin, 1967; Voigt, 1973). When a move is made to a new RS, some members of the pack may remain behind, as Voight (1973) and Peterson (1974) also found.

By late September the pups usually are developed enough to travel with the rest of the pack, although there is considerable variation in size and development (Van Ballenberghe & Mech, 1975). The change from the sedentary to the nomadic phase is not abrupt, but occurs gradually, as Ognev (1962) also reported. Once the last RS is abandoned, the pack as a whole will rarely, if ever, use a RS until the next year. However, one or more pack members may occasionally return to a RS during fall and early-winter (Mech, unpubl.). Many of the animals return to the site after becoming separated from the rest of the pack, and may sometimes remain there for several days. The latest use of a RS seen in Minnesota was in late January (Mech, unpubl.).

Wolves generally mature sexually at 22 months (Mech, 1970), although captive animals may be capable of breeding during their first year (Medjo & Mech, 1976). Usually only two age-classes can be distinguished in wolves: pups and adults (including immature yearlings). In this paper, except with animals first marked as pups and therefore of known age, distinction will be made only between pups and older animals. Thus the term "adult" used in this paper is best understood as "non-pup".

STUDY AREA

This study was conducted in the Superior National Forest (SNF) of Northeastern Minnesota (Fig. 1). The terrain is rugged, with conifer or mixed conifer-deciduous forest on uplands, interspersed with extensive swamps, or open water (for details see Ohmann & Ream, 1971).

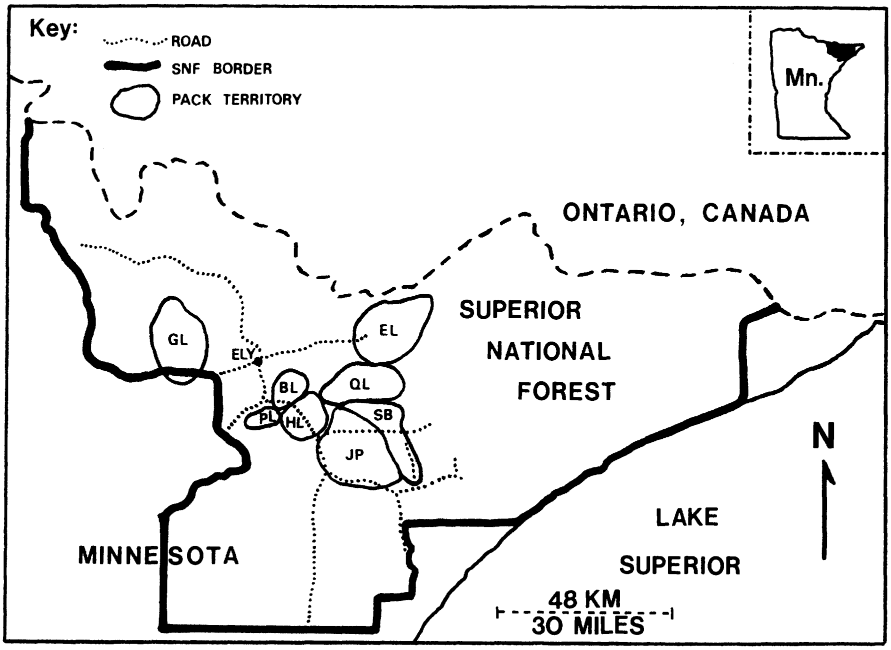


Fig. 1. Locations of wolf pack territories. Pack abbreviations: BL = Birch Lake; EL = Ensign Lake; GL = Glenmore Lake; HL = Harris Lake; JP = Jackpine; PL = Perch Lake; QL = Quadga Lake; SB = Sawbill.

Our primary study area of about 600 km^2 encompassed the territories of the Jackpine (JP) and Harris Lake (HL) wolf packs (Mech, 1973; 1977a). Other packs and lone wolves were studied along roads radiating from the town of Ely (Fig. 1). Harrington spent 638 days in the field, from May 20, 1972 through March 28, 1974, plus three subsequent visits to the SNF, and Mech visited the area periodically throughout the study. We howled to wolves on 412 nights.

The SNF wolf population was estimated at 300 in spring 1972 (Mech, 1973), or about one wolf per 26 km^2 during the study, a figure comparable to the highest densities generally found elsewhere (Pimlott, 1967). From 1969 to 1974 the population decreased

(MECH, 1977b), following a drastic decline of the major prey, the white-tailed deer (*Odocoileus virginianus*) (MECH & KARNS, 1977). Supplementary prey of wolves in the area are moose and beaver (*Castor canadensis*) (STENLUND, 1955; MECH & FRENZEL, 1971; FRENZEL, 1974; VAN BALLENBERGHE *et al.*, 1975).

This study was part of a larger, long-range investigation using radio-telemetry to determine the sociobiology, population dynamics, and ecology of wolves in Minnesota (MECH & FRENZEL, 1971; MECH, 1972; 1973; 1974; 1975; 1977a, b; PETERS & MECH, 1975; VAN BALLENBERGHE & MECH, 1975; SEAL *et al.*, 1975; HOSKINSON & MECH, 1976; HARRINGTON & MECH, 1978).

METHODS

The basic technique of the overall investigation, of which this study was a part, was to live-capture, immobilize, and attach radio-collars (COCHRAN & LORD, 1963) to wolves (KOLENOSKY & JOHNSTON, 1967; MECH & FRENZEL, 1971; MECH, 1974), and then locate them and their packs by aircraft twice a week throughout most of the year and daily in winter when possible. Radio-tagged wolves do not seem to behave differently from others even though some have been radioed for up to 7 years (MECH, unpubl.). Radioed wolves and their packmates were visually observed on about 75% of the times they were located during aerial tracking if snow covered the ground but only 10% of the time otherwise (MECH, 1974).

The primary method used in the present study was to elicit howling from radioed wolves and their associates by "live" human imitation of wolf howls (PIMLOTT, 1960) and then record their responses. Previous work had shown that free-ranging wolves respond to live human imitations as well as, or better than, to playbacks of recorded wolf howling (PIMLOTT, 1960; JOSLIN, 1967) or recorded human imitations (THEBERGE & FALLS, 1967). Also, the apparent ability of wolves to distinguish individual voices (THEBERGE & FALLS, 1967), and their agonistic responses to human howling (JOSLIN, 1967), indicate they regard human howling as produced by strange (alien) conspecifics.

Our primary stimulus (trial) consisted of three to five human howls, each 5 to 6 s long and separated by less than 1 s. We usually began a trial with a "flat" howl, then "breaking" and "flat" howls were alternated for the remainder of the stimulus (Fig. 2). In basic structure, frequency, and frequency variation, the human howls were similar to adult wolf howls recorded in Minnesota (Table 1). Whether the structure, pitch or harmonic emphasis of a wolf howl conveys specific information is unknown, so to avoid complications from unknown information in our howls, we kept their variation as low as possible from trial to trial. Of about 1,900 trials, 80% were solely by the senior author.

The only data used were gathered when we were confident (through radio-tracking) that wolves were close enough to hear us and vice versa. Thus we collected most data in calm (46%) or light wind (46%). Neither wind nor other weather had a significant effect on response rate (HARRINGTON, 1975). Most of the howling was done at night when conditions were quietest, although JOSLIN (1967) and THEBERGE & FALLS (1967) found no differences in responsiveness between day and night.

A howling session was a continuous period of 15 to 120 minutes spent near a radioed wolf during which we attempted to elicit howling. We located and approached wolves from an antenna-equipped truck. We stopped when within hearing range (200 to 1,600 m, as judged by signal strength) and remained near the truck to avoid disturbing the wolves, which seemed unaffected by vehicle noise. Apparently, the wolves also did not often detect our odor, or did not associate it with our howling.

Once an animal was located, we monitored its signal for several minutes to detect possible movement. Then we began the first series of howls. If the wolves did not reply to the first trial within 90 s, we began a second series. Generally if we did not receive a reply after three or four attempts, we left and did not return for at least 24 hours.

If the wolves replied, we waited about 15 minutes before howling again, as PIMLOTT (1960) and JOSLIN (1967) had observed that wolves generally will not howl again for 10 to 20 minutes following a response. After eliciting two or three replies, we left. Usually little more than an hour was spent near a particular wolf during any 24-hour period. Throughout the session, the wolf's radio-signal was monitored to detect any movement toward or away from us.

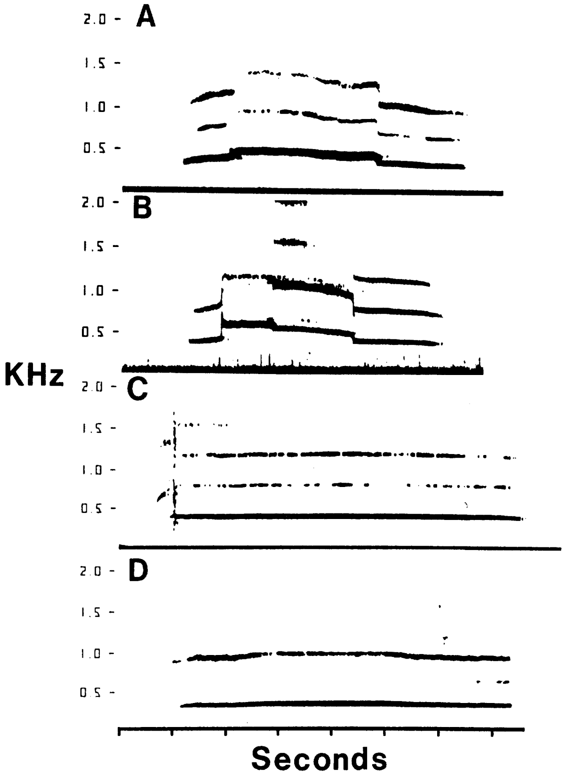


Fig. 2. Comparison of human howls with wolf howls recorded in Minnesota during this study. A) Human "breaking" howl. B) Wolf "breaking" howl. C) Wolf "flat" howl. D) Human "flat" howl.

Howling sites.

All homesite data were gathered around rendezvous sites (RS). Data from areas other than RS were classified as non-rendezvous site (non-RS).

The only important factor that could be identified at non-RS locations was the presence or absence of a kill. Most kills were first observed from the air before we confirmed the wolves' presence there from the ground at night. It was impossible to determine by ground tracking if the wolves were actually at the kill or just near it, so whenever they were in the general vicinity of a kill they were classified as being at it.

Our "No Kill" sample was obtained from two types of situations: (1) when the wolves were travelling as we howled to them, or (2) when, during the day of the howling session, the wolves were seen at the same site from the air, but no kill was observed there. Of

TABLE 1

Comparison of human howls with howls of adult Minnesota wolves

Mean frequency of howl in sample[1]	Human	Wolf 2449 10/12/72	Wolf 2449 7/28/73	Unradioed adults 9/26/72	Unradioed adults 10/6/72	Initial howl of group responses 1972/1973
Highest	359 (5.3)[2]	494 (2.0)	357 (5.2)	365 (1.9)	359 (2.9)	453 (9.5)
	6.2[3]	3.6	3.0	6.9	4.8	6.8
	350 (3.8)	381 (3.5)	355 (4.0)	364 (0.7)	356 (5.5)	392 (8.0)
	4.8	5.6	3.6	6.6	5.3	4.8
Median	346 (7.4)	366 (2.0)	345 (4.3)	354 (3.5)	339 (6.8)	354 (2.7)
	5.5	5.8	3.3	7.4	5.4	4.4
	303 (3.0)	356 (2.2)	322 (2.8)	343 (6.3)	317 (12.2)	314 (8.8)
	6.2	6.8	2.3	5.0	3.7	5.8
Lowest	298 (7.8)	355 (5.5)	319 (5.8)	337 (5.1)	301 (8.5)	296 (7.1)
	6.0	6.1	4.8	5.3	5.1	3.3

1) For each sample, mean fundamental frequency was determined and the four extremes and the median were selected.
2) Mean frequency (Hz), and coefficient of variation (%) in parentheses.
3) Length of howl in seconds.

course, vegetation may screen a kill from the air, or the wolves may be resting several hundred meters from a kill when seen, so the second method is subject to error. For many of the non-RS sessions, inadequate information about the presence of a kill required us to classify the sample as "Unknown". The probability of a kill being present in this sample lies between that of the "Kill" and "No Kill" samples.

Analysis of data.

The wolves' responsiveness to our howling was measured by two parameters, Response Rate per Session (RR/S) and Response Rate per Trial (RR/T). RR/S was the percentage of sessions during which we received replies. RR/S standardized data between different sessions, which might differ greatly in total number of trials, and number of responses to those trials. The rationale behind such a comparison was that the social and environmental context of the wolves' howling site varied little within a session but considerably between sessions.

RR/T was the percentage of trials that were answered *during* a session. RR/T was used to examine differences in responsiveness between sessions with replies. Since RR/T was highly correlated with RR/S, RR/T is only used where it adds to understanding of the data.

Replies were recorded at 38.4 cm per second on a Nagra IV-D tape recorder, using either a parabola-mounted Sennheiser MD-211U dynamic microphone, or a tripod-mounted Sennheiser MKH 805 directional condenser microphone. Recordings were sonagraphed on a Kay Electric Company, Model 7030A Vibralyser, using a 150 Hz filter over the 20-2000 Hz frequency range.

Sonagrams were used to determine the relative number of wolves replying, and their age-classes. Age-class criteria, based on howl length and mean fundamental frequency, were established from a sample of howls from known-age wolves (364 pup and 155 adult howls) (HARRINGTON, 1975; see also HARRINGTON & MECH, 1978). Three classes (pup, adult, unknown) were distinguished such that the probability of misassigning a howl to the first two classes was less than 1%.

Two temporal measures were made of each response, Time to Response (TTR) and Duration of response. TTR was the period between initiation of the trial and the wolves' reply.

WOLF PACK HISTORIES

We studied eight packs of wolves, each having at least one radioed member (Table 2). Six of these packs live adjacent to each other (Fig. 1), but all were not studied simultaneously. Only the Jackpine (JP) and Harris Lake (HL) packs were investigated over an extended period, whereas the other packs were studied from 2 days to 7 months each.

TABLE 2

Background data on wolf packs involved in the present study

Pack	Period studied	Number of months with data	Approximate territory size km^2	Number of wolves (number radioed)	
				Minimum	Maximum
Birch L.	7/73- 9/73	3	100-130	4 (0)	? (1)
Ensign L. 73	1/73- 3/73	3	260	5 (1)	10 (1)
Ensign L. 74	7/73- 3/75	7	260	3 (1)	4 (2)
Glenmore L.	10/72-11/72	1	260	10 (2)	? (2)
Harris L.	7/72- 3/74	20	130-180	2 (1)	5 (3)
Jackpine	6/72- 3/74	22	270	3 (1)	11 (5)
Perch L.	1/74- 3/74	3	65	2 (1)	2 (1)
Quadga L.	2/74- 3/74	1	180	3 (2)	3 (2)
Sawbill	11/73- 2/75	6	130-160	3 (1)	4 (2)

Jackpine Pack.

The JP Pack composition changed during the study, but the basic core consisting of a non-radioed alpha-male and female and their radioed offspring, wolves 2449, 2443, and 2445, persisted from the start of the study until 2 months before the end. After July 1972, 2449 was the only adult radioed; wolves 2443 and 2445 were the only radioed yearlings present in 1973. Table 3 gives the histories of the radioed and other pack members present during the study.

The JP Pack used several RS's each season, and ceased extensive RS use in late September.

Harris Lake Pack.

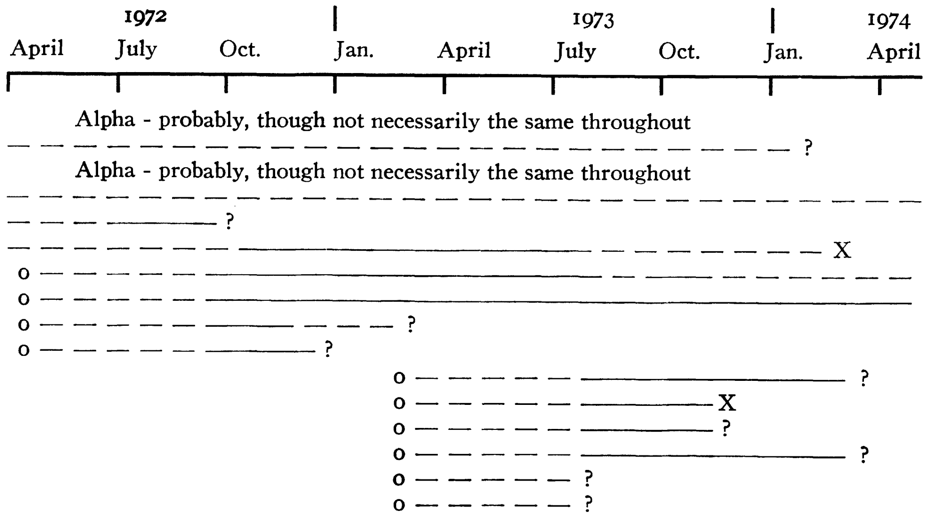
The HL Pack territory remained approximately the same since 1969 through this study (Mech, 1977a). Pack composition was limited to two adults in winter 1971-72, alpha-female 2407 and her mate. Two pups (2247 and 2489), born in 1972, survived through the next winter, with 2489 eventually dispersing from the pack at 22 months of age. Two pups born in 1973, but not radioed, apparently perished by early December of that year (Mech, 1977a). Table 4 details the histories of pack members during the study.

The pack occupied several RS's in 1972, but in 1973 one area served as both the natal den and the RS through August 2. During the next 2 weeks the pups apparently travelled with the adults, spending no more than 3 days at any one site and moving an average of 4.5 km between sites. Unlike the JP Pack, which abandoned its RS's in late September, the HL Pack ceased fulltime use of its sites during August in 1973.

TABLE 3

Histories of Jackpine Pack members

Wolf	Sex	Age
Unknown	Male	Ad
Unknown	Female	Ad
2433	Male	2-yr.
2449	Male	3-yr.
2443	Male	
2445	Female	
2447	Female	
2459	Male	
5063	Male	
5065	Male	
5067	Male	
5069	Male	
Unknown		
Unknown		



Legend: ——— = radio functioning; — — — = wolf present but without functioning radio; o = approximate date of birth; X = approximate date of death; ? = presence with pack unknown.

TABLE 4

Histories of Harris Lake Pack members

Wolf	Sex	Age	1972: April, July, Oct. | Jan. 1973: April, July, Oct. | Jan. 1974: April
Unknown	Male	Ad	Alpha (July 1972) ——— 2499 (July 1973) — — — — — X [a] — — — —
2407	Female	Ad	Alpha (July 1972) ————————————————————————————————
2247	Male		o — — — — — — — — — — ————————————— — — ?
2489	Male		o — — — — — — — — — ——————————— — — ————————————— [b]
Unknown			o — — — — — — — — — — ?
Unknown			o — — — — — ?

Legend: ——— = radio functioning; — — — = wolf present but without functioning radio; o = approximate date of birth; X = approximate date of death; ? = presence with pack unknown.

[a] 2499 was killed in January 1974. A new male, possibly 2247, assumed the alpha position and mated with 2407.

[b] Dispersed from territory in February 1974.

Birch Lake Pack.

Wolves from this pack were monitored for only a short time in 1973, but for 26 days we studied the pack at two RS's. The number of adult members was unknown, and only two pups were detected from howling responses.

Ensign Lake Pack.

Data for the Ensign Lake Pack were available for short periods in 1972-73 and 1973-74. During winter 1972-73 ten wolves composed the pack, but by spring the number had dropped to five. The following winter the pack consisted of only four wolves, including radioed alpha-male 5059.

Sawbill Pack.

The Sawbill Pack consisted of six animals in 1973-74, including a radioed pup, 5097. The next summer an adult male was captured in the territory and found to be 2433, a JP Pack wolf which had dispersed and colonized an adjacent territory. Wolf 5097 and a second male captured in 1974 (5077) evidently were his offspring. The pack included three members in 1974-75: 2433, 5077, and the non-radioed alpha-female.

Perch Lake Pack.

The Perch Lake Pack formed during winter 1973-74, when a pair of lone wolves, including radioed female 2473, established a territory just southwest of the Birch Lake Pack. Data were gathered from them during January, February, and March 1974.

RESULTS

Radioed pack wolves replied to 494 of 1,783 trials (27.7%) (Table 5). Of the replies, 390 (78.8%) were recorded, and 349 were of adequate quality for analysis. Approximately 4,000 sonagrams were prepared from 386 replies. We howled to 10 lone wolves during 29 sessions for a total of 102 trials. Only one of the two replies obtained was of adequate quality for sonagraphing.

There was no evidence that wolves habituated to our howling. First, we obtained similar results for two consecutive seasons. Second, responsiveness declined and increased in both well studied and rarely studied packs, during the same seasons and in the same contexts. Finally, when we howled at JP Pack RS's during 52 sessions in July and August, 1973, no progressive decline or other change in responsiveness was noted; the wolves replied during 17 of 20 sessions in July and all 32 sessions in August.

Response rate at non-rendezvous sites.

The overall RR/S for seven packs was 29.7% ($n = 293$). RR/S varied from month to month at non-RS's and the JP and HL Packs showed the same trends (Fig. 3). Although neither pack sample alone deviated significantly from random, their combined totals did ($G = 25.99$, $P<0.02$). There was a major peak in RR/S in March and another starting in August.

TABLE 5

Summary of data gathered during the present study

Pack	Study period	Site Type	Sessions	Trials Total	Trials No. Successful
Birch	7/18/73- 9/29/73	RS	25	65	44 (67.7%)
Ensign	1/24/73- 3/06/75	non-RS	18	72	22 (30.6%)
Glenmore	10/31/72-11/01/72	non-RS	3	13	4 (30.8%)
Harris	7/27/72- 3/20/74	non-RS	114	401	35 (8.5%)
Harris	7/30/72-10/21/73	RS	32	111	33 (29.7%)
Jackpine	6/28/72- 3/15/74	non-RS	128	518	96 (18.5%)
Jackpine	7/08/72-12/11/73	RS	109	456	233 (51.1%)
Perch	1/11/74- 3/27/74	non-RS	15	76	9 (11.8%)
Quadga	2/21/74- 3/20/74	non-RS	3	11	0 (0.0%)
Sawbill	11/22/73- 2/25/75	non-RS	12	60	18 (30.0%)
Overall totals for packs:			459	1783	494 (27.7%)
Lone wolves			29	102	2 (2.0%)

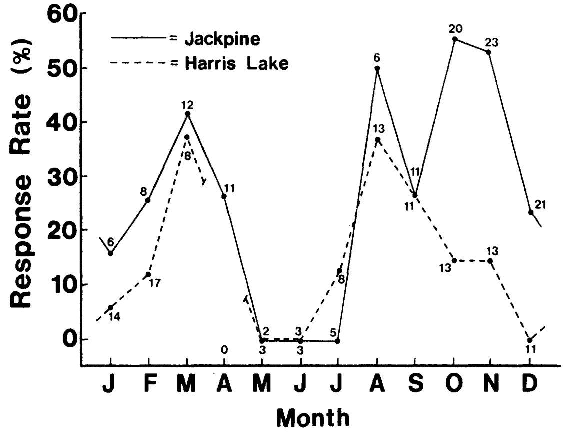


Fig. 3. Seasonal changes in RR/S at non-RS locations. Sample sizes are given for each month.

Response rate at rendezvous sites.

RR/S was investigated around 12 RS's of the JP and HL Packs in 1972 and 1973, and the Birch Lake Pack in 1973. Responses were elicited during 128 of 166 sessions (RR/S = 77.1%), a rate significantly higher than at non-RS's (G = 99.44, P<0.001). Unlike at non-RS locations, RR/S at RS's maintained a similar level from month to month. For RS's, RR/S was consistent within packs for a given year, but differed among packs and years (Table 6).

TABLE 6

Comparisons of response rates at rendezvous sites among packs and years

Pack (year)	RR/S	(n)		G	P
Birch Lake (1973)	100.0	(24)	>	2.220	>0.20
Jackpine (1973)	94.5	(55)	>	7.768	<0.01
Jackpine (1972)	2.4	(29)			
Harris Lake ('72, '73)	40.7	(27)	>	14.79	<0.001
Harris Lake (1977)	85.7	(7)	>	4.894	<0.05

Response rate at kill sites.

Of 22 kills, only one was located at a summer RS, and the RR/S there was similar to that of other RS's. Thus in this section, only non-RS kill data are presented. During 33 sessions near non-RS kills, we attempted to elicit howling in 100 trials (Table 7). Wolves replied during 24 sessions (RR/S = 72.7%) at 18 of 21 kills.

Although RR/S of packs and lone wolves at kills varied from 50 to 100%, there was no significant heterogeneity among the groups ($G = 7.708$, $P>0.2$). The overall RR/S at kills (72.7%), however, differed significantly from the remainder of the non-RS data (34.8%) gathered during the same 6-month period (Table 8). Furthermore, in the non-kill sample, JP and HL Pack data from sessions with only pups or single animals present were excluded, thus increasing RR/S for the non-kill sample.

A more homogeneous sample of kill and non-kill data was prepared for both the JP and HL Packs, by selecting sessions in which both a radio-collared adult and a radio-collared pup, were present. This could only be done during winter 1972-73. For both packs, RR/S was higher at known kill sites, than at sites known, or suspected, not to have a kill (see Methods) (Fig. 4). This difference was significant for the JP Pack ($G_Y = 4.06$, $P<0.05$). As expected, the RR/S at the "Unknown" sites was intermediate, evidently reflecting the presence of undetected kills.

Estimating precisely when a kill was made, and thus how much food was left, was difficult because hours or even days sometimes intervened before we discovered the kill. The data suggest, however, that the wolves' responsiveness diminished as the kill was consumed. During four of five sessions, the JP Pack failed to reply during the second night we visited the same kill, although they had replied on the first night. In addition, the one kill where they replied during two successive nights was of a large male deer which they probably killed shortly before the first session. At a second kill, also made shortly before our first session, they did not reply during the following night;

TABLE 7

Response rate of wolves at kills

		Kill		Response	Number of:[a]	
Pack	Date	No.	Prey	per trial	Adults	Pups
Jackpine	10/25/72	1	Deer	NNRN[b]	1	3+
Jackpine	11/29/72	2	Deer	RNNN	3	3
Jackpine	11/30/72	2	Deer	RNR	3	3
Jackpine	2/08/73	3	Deer	RRNNNNN	2+	2+
Jackpine	3/08/73	4	Deer	NNN	0	1
Jackpine	3/16/73	5	Deer	NNNRNNN	2+	1+
Jackpine	3/20/73	6	Deer	RNN	2+	1+
Jackpine	4/12/73	7	Moose	NNRNNNR	1	2+
Jackpine	4/13/73	7	Moose	NNNNN	1	2+
Jackpine	11/17/73	8	Deer	RRRRRNNRR	3+	2+
Jackpine	11/18/73	8	Deer	NNN	1	2+
Jackpine	11/23/73	9	Moose	RN	1+	?
Jackpine	11/24/73	9	Moose	NNN	1	1
Jackpine	1/10/74	10	Deer	NNRNNR	1+	2+
Jackpine	3/12/74	11	Deer	NRNNNR	3	0
Jackpine	3/15/74	11	Deer	NNNNN	1	0
Harris	1/25/73	12	Moose	RNR	1+	2
Harris	2/02/73	12	Moose	NN	1	1
Harris	2/03/73	12	Moose	NNRR	2	1
Harris	3/06/73	13	Deer	NNNNNN	1	1
Perch	2/25/74	14	Deer	NRNNR	2	0
Ensign	1/24/73	15	Deer	R	2+	2+
Ensign	2/05/73	16	Deer	RR	2+	2+
Ensign	2/06/73	16	Deer	RR	2+	2+
Ensign	2/21/73	17	Deer	RR	2+	2+
Ensign	3/04/73	18	Deer	RRNNR	2+	2+
Ensign	3/04/73	18	Deer	RRN	2+	2+
Sawbill	12/12/73	19	Deer	NN	?	1
Sawbill	12/13/73	19	Deer	NNNN	?	1
Sawbill	12/17/73	20	Moose	NNNRNRNR	2	1+
Sawbill	12/18/73	20	Moose	RRNR	2	1+
(loners)	1/29/73	21	Deer	NR	2+	0
(loners)	1/31/73	21	Deer	?R	2+	0

[a] If a response was obtained, age-class and numbers of replying animals were determined by sonagram analysis. Otherwise the numbers represent radioed animals only. A plus (+) indicates that more wolves probably were present. Yearlings are classed with adults.

[b] N = no response to trial; R = response.

this kill was a fawn, probably completely consumed by the second night. (Of the other three kills, the period between capture and first session was unknown.) During a single session, the highest RR/T was obtained from near a kill known to be less than 4 hours old; the lowest RR/T was obtained after the alpha pair had already abandoned a kill, leaving only a subordinate adult (wolf 2449) and several pups behind.

TABLE 8

Comparison of response rates obtained during sessions at kills with all other non-kill sessions at non-rendezvous site locations

	Kill		Non-kill			
Response rate class	RR	(n)	RR	(n)	G	P
RR/session	72.7	(33)	34.8	(112)	15.064	<0.001
RR/trial	48.0	(100)	38.0	(216)	2.826	0.05<P<0.10

Data are from October 15 through April 15 when all kill data were collected.

In two other packs (HL and Sawbill), replies were obtained only at moose, and not at deer, kills. In both cases, replies were also obtained on more than one night at these much larger prey kills.

Response rate during breeding season.

RR/S increased from early winter through the breeding season into March for both the JP and HL Packs (Fig. 3), as well as for the other, less-studied packs. Because any effect of breeding would be a function of the alpha animals, data from sessions when at least one radioed alpha animal was present were analyzed separately. In each pack the RR/S was higher during and after the breeding season than before. Overall, the RR/S was 7.1% before the breeding season, and rose significantly to 40.0% during and after the season. This difference persisted, even after the data were corrected for possible bias due to kills (Table 9).

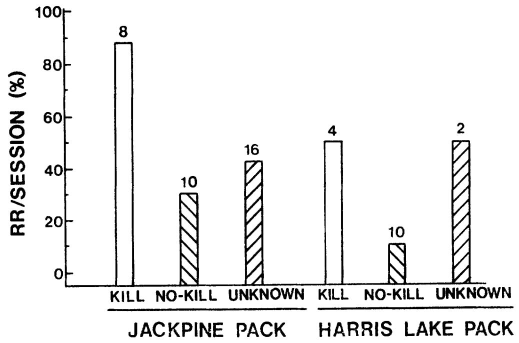


Fig. 4. Relationship between RR/S and the absence or presence of a kill at the pack's non-RS howling site. Sample sizes are given above each bar.

TABLE 9

Response rate of groups with alpha animals in relation to the breeding season

	Before Season [a]		During and After [a]			
Sample	RR/S	(n)	RR/S	(n)	G_Y	P
All sessions	7.1	(28)	40.0	(25)	6.648	<0.01
Minus kill sessions	0.0	(26)	37.5	(24)	10.998	<0.001

[a] Before season = January 1 through February 14; During and after = February 15 through March 31.
Data are combined for the HL, Perch, Ensign and Sawbill Packs.

Response rate of mixed groups.

Within a given pack, the composition of the groups we howled to sometimes varied from session to session (as determined by radio-signals, replies, tracks, and aerial or ground observations). Since RR was greatly influenced by the group's composition, we will consider the two major age-class groupings separately, beginning with mixed-age groups (adults with pups).

Mixed-age groups were studied for two seasons in both the JP and HL Packs. Within each pack, no significant differences in RR/S were noted between years (HARRINGTON, 1975), so data were pooled.

RR/S was highest during summer, when RS's were occupied (Fig. 5). For both packs, peak responsiveness occurred in August, after which RR/S declined to a yearly low in early winter, before increasing into the breeding season, as noted previously. This decline in responsiveness was significant for the better-studied JP Pack ($G = 15.693$, $P<0.02$).

The change in responsiveness appeared related to seasonal factors, since RR/S at RS's and non-RS's was similar within the same month (HL Pack) or between adjacent months (HL and JP Packs) (Fig. 5). In addition, the JP Pack decline in RR/S could not be related to the presence of a kill bias, or observed changes in pack composition (Fig. 6).

Although RR/S of mixed-age groups in both the JP and HL Packs declined from maxima in August to minima in early winter, the HL Pack reached a minimum sooner, as can be seen by comparing the HL Pack's RR/S as a function of the JP Pack's RR/S (Table 10). From July through September, the HL Pack's RR/S ranged between 65 and 78% of the JP Pack's RR/S, but dropped to 39% in October and 26% in November. During February and March, the HL Pack's RR/S rose again to about 80% that of the JP Pack.

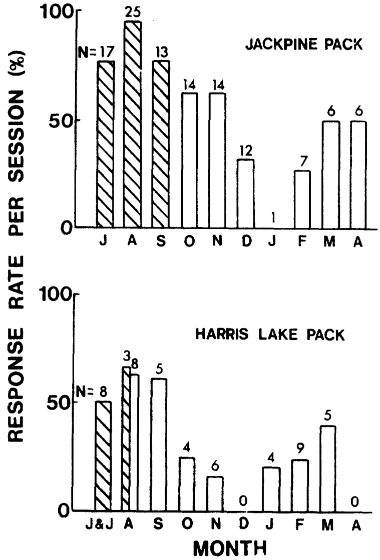


Fig. 5. Seasonal decline in mixed-age group RR/S at both RS and non-RS location. Hatched bars = RS locations; open bars = non-RS locations. Sample sizes are given above each bar.

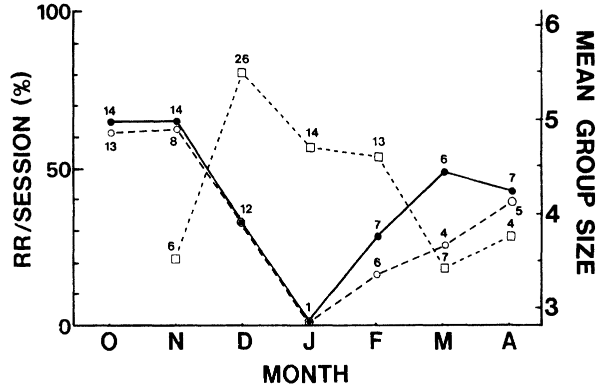


Fig. 6. Relationship between JP Pack RR/S and mean group size as determined by aerial observations. Solid circles = overall RR/S; open circles = overall RR/S minus all sessions associated with known kills; squares = mean group size. Sample sizes are noted above each point.

Age of wolf initiating mixed responses.

The initial howl of mixed group responses was analyzed for length and mean fundamental frequency, and compared with howls from known-age animals to determine whether a pup or adult started the response. Few data were available from other packs, so only those from the JP Pack were used.

TABLE 10

Harris Lake Pack mixed-age group RR/S expressed as a proportion of the Jackpine Pack mixed-age group RR/S

	Jul.	Aug.	Sep.	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.
$\frac{\text{HL RR/S}}{\text{JP RR/S}} =$	0.654	0.692	0.781	0.389	0.260	—	—	0.782	0.800
Sample sizes:									
Harris Lake	8	11	5	4	6	0	4	9	5
Jackpine	17	25	13	14	14	12	1	7	6

Data are from both RS and non-RS locations from July 1972 through December 1973.

Virtually all non-RS mixed group responses were begun by adults (Table 11). The only two responses begun by pups in this sample occurred in early August when the pack was moving between RS's. At RS's, however, pups initiated a significant number of responses, especially in 1973, when they began 94% of them (Table 11).

TABLE 11

Number of mixed-age group responses of the Jackpine Pack initiated by adults and pups in relation to type of howling site

		Age-class of initiator			
Year	Howling site type	Pup	Adult	G_Y 1)	P
1972	Rendezvous site	7	15	5.822	<0.02
	Non-rendezvous site	0	18		
1973	Rendezvous site	51	3	21.564	<0.001
	Non-rendezvous site	2	8		

1) G_Y based on the 2X2 contingency tables outlined in boxes.

Sonagram analysis further indicated that at least one, and often two alpha animals were present during most non-RS mixed-age group replies. In winter 1972-73, beta male wolf 2449 was the only non-alpha adult in the JP Pack. On only one session (n = 17) did he reply without other adults; that reply was one of the shortest recorded for any mixed-age group. On all other occasions, he was accompanied by at least one alpha animal. In six other sessions, both alpha animals were present during replies. In the HL Pack, five of six sessions with replies included the alpha pair, and for the Sawbill pack, all four successful sessions included the alpha pair.

Response parameters of single pack wolves.

Just as it was difficult to determine the exact composition of the groups tested, it was also hard to tell if a radioed wolf was alone. Several times, even though only one radioed wolf was present, several animals responded. However, with additional information from recent aerial sightings or from tracks, or because sometimes most of the pack was found elsewhere, it was often possible to deduce that the radioed animal probably was not accompanied by others. Only data from the JP and HL Packs could be analyzed in this way.

Single pack wolves did not often reply (Table 12) and when they did, they usually howled only once or twice and on 4 of 8 occasions quickly moved away and out of radio contact. Even when they did not respond, they often moved away (48 of 60 sessions). Never did we document a single, non-alpha-male adult pack wolf approaching after we howled.

The highest RR was from the HL Pack alpha male. He was the only radioed adult even to reply when alone, and his RR/T was significant higher than that of the other single wolves (21.6% versus 2.9%; $G = 18.86$, $P<0.001$). Also, during one session he moved toward us while howling, and on another he approached very close without howling.

Two sessions involving non-radioed adults of the JP Pack are also pertinent here. On September 26, 1972, our howling party left the pack's RS after eliciting three responses from the pups and one adult, and drove several kilometers east where adult male 2449 had been alone for several days. In the next hour we tried several times to elicit a response from him, but failed. However, we were answered by two separate non-radioed wolves distant from wolf 2449. One howled only twice during the response of the other, but the second wolf answered several trials and howled 25 to 50 times.

In the second case, another single wolf responded to our howling when alone. On April 12, 1973, we were howling to wolf 2449 and two radioed pups at a kill 2 km from the JP Pack's den. None of the wolves at the kill responded until a distant wolf, between us and the den, responded. Then three or four times when the group paused, this distant wolf, which had remained silent, howled, and the group then resumed its howling.

In both instances, the single howling animal almost certainly was one of the alphas, for they were the only two adults that were not radioed.

Other cases of single wolves replying at non-RS's involved pups and yearlings. Three wolves wore active radioes both as pups and as yearlings. These animals responded alone as pups significantly more often than as yearlings (11.1% versus 1.6%; $G = 4.26$, $P<0.05$). They also responded with more howls per trial answered as pups (10, 9, and 5 howls) than as yearlings (2 and 1 howls).

TABLE 12

Response rate of single radioed pack wolves presumed to be alone during the howling session at non-rendezvous site locations

Wolf	Role	Sex	Sessions with/resp.	Sessions (n)	No. of howls per successful session	Trials (all sessions) Responses	Trials (all sessions) (%)	Trials (all sessions) (n)
Jackpine Pack								
2443	Pup	M	1	(2)	19	2	(28.6)	(7)
							> (9.7)	
2443	Yearling	M	1	(7)	2	1	(4.2)	(24)
2445	Pup	F	1	(5)	5	1	(5.6)	(18)
							> (1.4)	
2445	Yearling	F	0	(14)	—	0	(0.0)	(51)
5065	Pup	M	1	(6)	5	2	(10.5)	(19)
2449	Beta-male		0	(14)	—	0	(0.0)	(46)
Harris Lake Pack								
2247	Pup	M	0	(2)	—	0	(0.0)	(6)
2489	Pup	M	0	(1)	—	0	(0.0)	(2)
							> (1.9)	
2489	Yearling	M	1	(17)	1	1	(2.0)	(51)
2407	Alpha-female		0	(6)	—	0	(0.0)	(20)
2499	Alpha-male		3	(11)	5, 8, 66	11	(21.6)	(51)
Totals			8	(85)		18	(6.1)	(295)

Response rate and pack size.

RR seemed to be correlated positively with pack size, but because of sample heterogeneity among all packs studied, we could compare RR/S for only the JP and HL Packs. With them, sample sizes were adequate for several categories (Table 13). Overall, mixed groups of the larger JP Pack responded significantly more often than those of the HL Pack, and they also responded more often for each category compared. However, when single wolves presumed alone were considered, there was no difference between the packs. Thus the JP Pack's higher RR was evidently influenced by the number of wolves present during the immediate session.

TABLE 13

Comparison of the Harris Lake and Jackpine Packs over several response categories

Category	Harris Lake RR/S	Harris Lake (n)	Jackpine Pack RR/S	Jackpine Pack (n)	G or G_Y	P
Mixed-age groups						
RS's	50.0	(14)	83.9	(56)	4.926	<0.05
non-RS's	36.5	(41)	48.3	(58)	1.345	>0.10 ns
Kills	50.0	(4)	76.9	(13)	0.160	>0.50 ns
Overall	40.7	(59)	66.9	(127)	11.381	<0.001
Single wolves						
non-RS's	10.8	(37)	8.3	(48)	0.146	>0.50 ns

At kill sites, we had data from at least four sessions each for four packs (Table 7). The Ensign Lake Pack was largest (ten wolves), and it responded during all six sessions at kills. The JP Pack averaged six members during the periods kill data were collected; they responded during 11 of 16 sessions (68.8%). The Sawbill and HL Packs were smaller, and both replied on only two of four sessions.

The size of the JP Pack increased from summer 1972 (4 adults, 4 pups) to summer 1973 (5 adults, 6 pups), and RR at RS's also increased significantly during this period (Table 6), as did the proportion of mixed responses started by pups (Table 11). The increase in pack size may have been partly or wholly responsible for the increased RR. By fall, pack size in 1973 had decreased to near 1972 levels, and RR during this period did not differ from 1972.

Recently, we have been able to document a similiar example for the HL Pack. During summer 1972 and summer 1973, the HL Pack consisted of two adults : two pups and two adults : one yearling : two pups, respectively. In summer 1977, however, the pack included two adults, one or two yearlings, and three pups. RR/S at RS's was 46% (n = 13) in 1972 and 42% (n = 19) in 1973, but increased to 86% (n = 7) in 1977.

Influence of pack size was noted with two other response parameters, Time to Response (TTR: p. 11), and howl duration. TTR differed significantly among packs at non-RS's (Anova: $F_S = 5.18$; df = 6,92; $P<0.001$: data in HARRINGTON 1975). Larger packs on the average responded 30 to 40 s after the trial began, whereas smaller groups took longer to respond (Fig. 7). In addition, duration of the group response was at least a minute for the larger groups, but 10 to 15 s less for the smaller groups. Packs with only two non-pup members tended to take longer to respond, and howled for shorter periods when they did respond. With the addition of at least one non-pup in 1973-74, for example, the HL Pack replied 30 s sooner and howled 10 s longer, differing little from the other larger groups (Fig. 7).

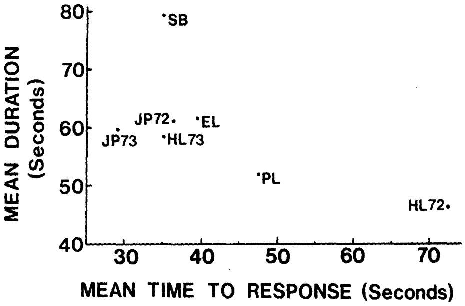


Fig. 7. Relationship between time to response and response duration. Pack abbreviations: EL = Ensign Lake; HL72, HL73 = Harris Lake in 1972 and 1973, respectively; JP72, JP73 = Jackpine in 1972 and 1973 respectively; PL = Perch Lake; SB = Sawbill.

Response rate of lone wolves.

We howled to ten lone wolves and found no differences in their responses. Loners replied during only two of 29 sessions, both when at least two of them were near the same kill. No lone wolf ever replied to us when alone (26 sessions, 92 trials). Pack wolves, when alone, on the other hand, replied to 18 of 296 trials, a significant difference (RR/T: $G = 10.01$, $P<0.05$). Even when only pups and yearlings are considered, single pack members still respond significantly more often ($G = 4.52$, $P<0.05$). Only single pack adults other than alpha males had as low a RR as that of lone wolves.

While lone wolves rarely replied, they did show other reactions to our howling. A lone female once moved away when we howled to her, although generally loners appeared to remain silently in the same area (Table 14). In contrast, single pack wolves, even after replying to us, often moved away (Table 15). Three different lone female wolves approached us closely during separate sessions, as determined from their signals or observed from the air.

General behaviour during howling sessions.

During most howling sessions, the only non-howling behaviour we could assess was movement based on interpretation of radio signals. Most detected movement was away from us (88.3%), and involved the entire group. During approaches, however, only one or two members of the pack usually moved toward us.

Of 165 sessions at 12 RS's we noted seven short-term retreats (p. 26). At 11 of the RS's, the wolves remained despite our almost daily howling nearby for up to a month. Thus the wolves remained at RS's during 95% of the howling sessions.

At non-RS's, movement behaviour could be determined confidently for 280 sessions, during which the wolves remained at or near their original locations on 212 (75.7%). Furthermore, the probability of their staying was correlated with their vocal response. If the wolves replied, they remained 90% of the time (Table 14). On the other hand, if they did not respond, they

TABLE 14

Percentage of sessions wolves remained at or near their original non-RS location [a]

	Vocal behavior during session			
	Response		No response	
Pack	%	(n)	%	(n)
Jackpine	90.6	(43)	68.2	(66)
Harris	77.8	(18)	66.7	(84)
Perch	100.0	(4)	87.5	(8)
Ensign	90.0	(10)	40.0	(5)
Sawbill	100.0	(7)	60.0	(5)
Glenmore	100.0	(3)	—	—
Quadga	—	—	66.7	(3)
Lone wolves	100.0	(2)	86.4	(22)
	G = 5.684 df = 6, P>0.50		G = 7.492 df = 6, P>0.20	
Overall totals:	88.6	(87)	69.4	(193)

G (R *vs* NR) = 14.938, df = 1, P<0.001

[a] Based only on data when movement or lack of movement could be ascertained. On an additional 42 sessions, no such determination could be made.

remained only about 70% of the time. There was no significant heterogeneity among packs in either regard. However, the probability that a pack would remain was significantly higher if it responded than if it did not.

To determine the effect of group composition on movement behaviour, we compared single wolves to groups of two or more, all from the JP and HL Packs. For single animals, there were no significant differences between packs nor between whether they responded or not (Table 15).

Groups of wolves responded similarly from pack to pack. However, groups remained near their original sites significantly more often when they responded and significantly more often than did single responding animals (Table 15). For animals not responding, however, there was no difference between groups and single wolves in whether they remained.

In summary, groups rarely left their location if they replied to us. Otherwise, the probability that either single wolves or non-responding groups would remain was only about 67%.

TABLE 15

Percentage of sessions groups and single wolves remained at or near their original non-RS location

	Vocal behavior during session							
	Response				No response			
Pack	(n)	%	G[a]	P	(n)	%	G[a]	P
Single wolves (from Table 21)								
Jackpine	(4)	50.0	0.000	ns	(40)	70.0	0.008	ns
Harris Lake	(4)	50.0			(29)	68.9		
Totals:	(8)	50.0	0.296	ns	(69)	69.6		
Groups (two or more wolves)								
Jackpine	(40)	95.0	0.282	ns	(25)	64.0	0.024	ns
Harris Lake	(14)	85.6			(41)	65.9		
Totals:	(54)	92.6	14.102	<0.001	(66)	65.2		
Single wolves (both packs)	(8)	50.0	5.738	<0.05	(69)	69.6	0.502	ns
Groups (both packs)	(54)	92.6			(66)	65.2		

[a] G values calculated for figures located within the boxes.

Specific behaviour during sessions-adults.

Return to the rendezvous site.

During three sessions, single adult wolves howled within 1.5 km of RS's. This always occurred when other wolves were howling from the site, so we could not determine whether the single wolves were reacting to us or to their associates at the site. On each of these occasions, however, either the distant wolf or another adult soon returned to the RS. During most other returns to RS's, the returning wolf was not known to have howled prior to its return, so many other returns probably went unnoticed.

Approaches.

Adult pack wolves approached us on at least seven occasions after we had howled repeatedly to them. On four of the occasions, the wolves also howled several times prior to their approach. Because such incidents have rarely been described but bear significantly on the interpretation of our data, we will detail all seven below.

On one night, we howled several times and obtained two replies from the JP Pack. Before our final trial, we noticed that the radioed wolf's signal had become stronger and changed direction. Within 5 minutes we could hear the brush cracking as two wolves approached to within about 7 m of us; neither vocalized.

On a second night, the JP Pack's first response was very faint, so we climbed a ridge to within less than 100 m of the wolves. Most or all of the group answered our first trial, but when we howled again 8 minutes later, only one adult answered. It had moved nearer, and during the next 7 minutes it howled more than 29 times and barked more than 13 times. None of the other wolves, including three pups, vocalized during the encounter. We finally left the ridge and returned to our first location, where we howled again. The entire group replied.

On another occasion, we howled to the Sawbill Pack near what may have been a RS. The pack answered twice during 16 minutes. When we howled again, however, only one animal replied. Initially it was with or near the rest of the group, 400 to 500 m away, but during the course of its response, it moved closer. When about 300 m away, the wolf stopped howling but continued approaching. Within 50 to 70 m of us the wolf stopped, and uttered four short, very low howls, then quickly moved away.

We tested the Sawbill pack again several weeks later, and recorded another approach. We had howled several times without response from one site, so, thinking we might be too far away, we drove down several other logging roads, trying to get closer. Upon arriving again at the first site, 30 minutes later, we found fresh tracks of a wolf on the snow-covered road. They emerged from the woods about 100 m from our howling site, continued past the site and on for another 100 m before returning into the woods. Where the wolf reached the road, it left a scat and a raised-leg urination, an excellent indication of an alpha male (PETERS & MECH, 1975). Our next trial was answered by the pack, in the direction from which the single wolf had come. Our first trial apparently had stimulated the wolf to seek us out.

An approach was also recorded for the Perch Lake alpha pair. Within 15 minutes of the pair's first howling reply, female 2473's radio-signal had become very strong. A passing automobile forced us to move 300 m away, where we howled again an hour later. Both wolves responded from near our original site, and the next morning, we found fresh wolf tracks and much scent-marking for several hundred meters along the road, centered around our first howling site.

Two approaches were recorded for the HL Pack alpha male 2499. The first occurred when he approached toward Harrington from the opposite shore of Harris Lake. During a 2-hour session, he gradually moved closer to Harrington and howled at least 66 times. On the second occasion, he did not vocalize, but his radio signal indicated he moved much closer.

During some of the instances described above, we did not know the identity of the approaching animal. However, on three occasions when the wolves' identities were known, the alpha male was present in each case. On two other occasions, the approaching wolf was either the alpha male or female. None of the other radioed, non-alpha-male adults was ever known to approach us.

Retreats.

We recorded several instances in which packs retreated after our howling. On four nights, the JP Pack retreated up a branch of a creek along its RS, moving 200 to 400 m away. Usually the first one or two responses each night come from the usual RS location, whereas subsequent responses emanated from further and further up the valley. Adults were present during all these retreats.

On one occasion, the Birch Lake Pack left one RS and headed to another about 2 km away during a howling session. The wolves were never again found at the former site, but remained at the latter site throughout the rest of the season through many howling sessions.

Twice one of us observed the HL Pack from the air while the other howled to them from the ground. On neither occasion (non-RS, no kill) did the pack vocalize (although one animal may have barked), even though all members were present. Rather, the group simply arose from sleeping and after a greeting ceremony, moved between 50 and 100 m away, where they lay down to rest again. Short movements such as these may have occurred often, but would not have been detected by radiotelemetry.

Differential Response - Adults versus Pups.

During the summer of 1973, yearlings 2443 and 2445 and a 4-year-old beta male 2449 were radioed in the JP Pack. On eight occasions, even though one or more of these radioed wolves were at, or very near, the RS, they did not howl during one or more replies (as determined by sonagrams). All the howling was done by pups. Six occasions involved 2445, and one each for 2443 and 2449. On the other hand, pups always howled during at least one reply if adults were also howling.

Specific behaviour during sessions-pups.

Approaches.

We were approached six times during howling sessions by pups less than 4-months old. They neither vocalized nor showed any aggressive or submissive behaviour (SCHENKEL, 1947). Rather in each case the pups appeared expectant or inquisitive.

Retreats.

Prior to September, the only pups known to have retreated without adults away from a RS were the HL Pack pups in 1972. On that night (July 30, 1972), we had howled to the two pups for nearly 2 hours, mostly from within 100 m of them, but only one of the pups replied. He interspersed his howls with at least 50 barks and an occasional faint growl. Near the end of the session, we moved away from the pups, at which time the second pup started to respond. Shortly after we retreated, both pups left the site and howled once or twice about 300 m away.

JP Pack pups without adults retreated from us after mid-September. One pup, for instance, moved 100 m or more from us during two of five sessions at a RS. At non-RS's in October and November, single pups moved away during four of six sessions.

Maximum distance wolves replied to howling.

We conducted no systematic studies to determine the maximum distance over which wolves can hear howling, but we did gather circumstantial evidence about the question.

On three occasions, other observers heard wolves howling within a minute of our howling from a distant site. On the first occasion we howled near a HL Pack RS and received no reply. However, we later learned that the Birch Lake Pack had howled at the same time from its RS, 9.4 km away from us. No additional howling was heard from that RS, strongly suggesting that the wolves may have been replying to us.

A similar episode occurred several weeks later when we were howling at another Birch Lake Pack RS. Automatic monitors indicated that two minutes after our first stimulus, wolves howled at both the Birch Lake Pack RS and the HL Pack RS, 10.8 km away. Continuous monitor records showed that the HL Pack had not howled from their RS for over 7 hours previously, suggesting that the wolves were responding to us.

On the final occasion. we howled once near a JP Pack RS, and although no wolves answered from that site, we later learned that wolves had howled at the same minute from another JP Pack RS, 9,5 km away.

On all three occasions, weather conditions were optimal, with calm air. Under similar conditions, the maximum distance we heard wolf howling was 5 km. Thus, while we cannot rule out the possibility that an intervening wolf relayed our howling, neither we nor the distant observers heard such wolves even though they would have been within 5 km of one of us. This increases our confidence that the three instances attest to the ability of wolves to hear howling from at least 9 km away.

DISCUSSION

Context of the responses.

The context in which wolves responded to our howling is crucial to the interpretation of the results, since howling occurs in both intrapack and interpack contexts (Harrington & Mech, 1978). Thus it is important to determine whether the wolves responded as if we were fellow pack members or strangers.

If we were mistaken for a fellow pack member, three predictions would follow: (1) The wolves should approach us, because howling between separated pack wolves results in their reunion (Murie, 1944; Rutter & Pimlott, 1968; Harrington & Mech, 1978). (2) They should reply, for separated wolves frequently respond to the howls of fellow pack members (Rutter & Pimlott, 1968; pers. observation). (3) Groups, especially small ones, should rarely or never respond if all members are present, whereas they should reply if one or more individuals are absent.

However, the following facts strongly indicate that the wolves regarded our howls as those of strangers. Both groups and single animals avoided us. When wolves did approach, it was only one or two, and they often showed agonistic behaviour.

Also, single pack wolves rarely responded or approached. When they did respond, they often howled only once or twice before retreating. In two pairs (Perch Lake Pack, and HL Pack in 1974), replies only occurred when both animals were together. In addition, the JP Pack in 1972, responded on all three nights when evidence indicated that all seven members were together. Finally, pups sometimes approached us during howling sessions, but never after September. Rather, they then usually retreated, even after responding vocally.

Thus, there is no evidence that adult wolves mistook us for fellow pack members and responded accordingly. Apparently we were recognized as "strangers" and responded to in an agonistic, interpack context, just as was JOSLIN (1967). Such a result is not unexpected, for wolves are capable of fine auditory discrimination and probably individual recognition (THEBERGE & FALLS, 1967).

The evidence from pups is less certain. Their approaches may have resulted from mis-identification, or from curiosity, for young pups often approach novel stimuli with little fear (FENTRESS, 1967; MECH, 1970); after 4 months of age, however, they avoid novel stimuli. There was some indication that pups recognized individual voices (HARRINGTON, 1975) and thus evidently did not always differentiate between pack and alien wolves until their behaviour toward novel stimuli changed. Their early approaches, and replies, may have been in the intrapack context of reassembly, whereas their later retreats (and few replies) may have been in the agonistic interpack context shown by adults.

Factors influencing the response rate of pack wolves.

Presence of pups.

Just after a pack abandoned its RS's, the RR of mixed groups was as high as it had been at RS's. In both the JP and HL Packs, mixed group RR/S then decreased within 2 months of RS abandonment. The high RR both at RS's and non-RS's around the time of RS abandonment suggests that a factor unrelated to RS's might be involved. Further, the gradual decline in responsiveness during autumn suggests that this factor likewise changes. Two possibilities emerge: (1) changes in pack composition, and (2) maturation of the pups.

Changes noted in pack composition during fall were the reintegration of subordinate yearlings and other non-pups, effectively increasing pack size, and the increased presence of alpha animals with the mixed groups. In the JP Pack, there was an inverse relationship between RR and both pack size and presence of the alpha-pair. Because a high RR generally is correlated with both increased pack size and the alpha male's presence, RR/S would be expected to increase rather than decline. Therefore the changes noted in pack composition do not appear responsible for the RR decline observed during autumn.

A second possible factor in the autumn RR decline is pup maturation. Responsiveness to howling did decrease throughout the pups' first year, becoming very low by December, but only for pups temporarily alone. During every mixed group response elicited at non-RS's, pups readily responded *if* the adults did. In addition, adults began all mixed group responses once RS's had been abandoned. This last observation suggests that because adults initiate non-RS howling responses, the factor influencing RR must be affecting the adults.

Pup maturation could influence adult behaviour. In captive wolves, adult behaviour toward pups begins to change when the pups are 3 to 4 months old. For example, aggressive behaviour toward adults by the pups is tolerated less as the pups mature (ZIMEN, 1976). Similarly, pups less than 6-8 months old can usually be successfully introduced to strange adults, yet older animals are usually attacked upon such introductions (WOOLPY & GINSBERG, 1967; ZIMEN, 1976). Thus adult behaviour toward pups may be partly dependent on the physical size of the pup. If pups developed either faster or slower than average, appropriate variation should be seen in differences in dates when adult behaviour towards pups would be expected to change.

VAN BALLENBERGHE & MECH (1975) compared the weights of Minnesota wolf pups to a "standard weight" derived from captive pups of similar age. They found considerable differences among pups of different packs. Of importance here, the four JP Pack pups averaged 67% of standard weight in 1972, and the next year four that were captured from a litter of six averaged only 63%. On the other hand, the two HL Pack pups in 1972 averaged 93% of standard. Neither of the two 1973 HL Pack pups were captured but the fact that they began traveling with the adults in August clearly indicated that they too were relatively well developed.

These observed differences in degree of pup development correlated well with the time of decline in mixed group RR/S for the two packs. Generally the faster the pups developed, the earlier RS's were abandoned, and the sooner RR/S diminished. Thus one factor that had an important influence on RR is the presence of young pups. PIMLOTT (1960) reached a similar conclusion when he appraised the effectiveness of the howling technique: "I believe that in this type of work particularly packs with young reply more readily than packs comprised solely of adults."

One adult behaviour that declines as pups mature is degree of protectiveness. During summer, when captive wolves studied by ZIMEN (1976) showed less overall aggression than during the rest of the year, that worker could not approach a pup without eliciting an aggressive response from an adult. Such high levels of protectiveness, however, are not shown by adults toward yearlings or older animals, so readiness to protect pups diminishes as pups mature.

Much adult behaviour during our howling sessions may have functioned in pup protection. The return of adults to RS's, and their occasional retreats with the pups could have served as defensive measures. Approaches by adults to strangers near RS's would help expel these animals. Finally, the RR of mixed groups may reflect the protectiveness of adults toward pups, the decline in RR occurring with a decline in both the readiness of adults to protect the pups, and the need of pups for such protection.

Kills.

A second factor which greatly influenced the RR of adult-pup groups was the presence of a kill at or near their howling site. Groups responded during 72.7% of the sessions when a kill was nearby, but during only 34.8% of the sessions when either a kill was not present or not detected. This difference occurred throughout the entire non-RS period when kills were found. It was particularly apparent between December and mid-February, when the RR/S of mixed groups was otherwise at its yearly low. Thus the presence of a kill greatly increased RR even during a pack's least responsive periods.

Kills are very valuable resources that are not easily replaced. Capturing and killing prey is a difficult and dangerous task; most encounters between pack and prey are unsuccessful (MURIE, 1944; MECH, 1966; MECH & FRENZEL, 1971; HABER, 1973). A decline in the deer population during this study (MECH & KARNS, 1977) reduced the number of available prey, so most kills were fully utilized. Defense of a kill would be expected, for even subordinate captive wolves can successfully defend their food from other, more dominant, individuals (MECH, 1970; ZIMEN, 1976). The high RR at kills probably is related to the defense of that valuable resource.

RR tended to be highest when kills were fresh, and it declined as the amount of food remaining decreased. This suggests that the amount of food remaining directly influenced the RR of the wolves. However, more definitive work on this subject is still required.

Breeding season.

A third factor influencing the RR of mixed groups and mated pairs was the breeding season. The increase in RR during mid-winter correlated with the beginning of the breeding season. In the absence of kills, groups with alpha animals did not reply at all for weeks prior to the breeding season, but their RR increased to 40% during a 10-day period including the peak of the breeding season. For several weeks after, their RR remained high.

ZIMEN (1971, 1976) and KLINGHAMMER (1978) have reported increases in the howling rate of captive wolves around the breeding season. Increases in spontaneous howling during the breeding season have been observed in other canids, including black-backed jackals (*Canis mesomelas*) (SKEAD, 1973), and coyotes (*Canis latrans*) (YOUNG & JACKSON, 1951).

The increased RR reflects a similar increase in aggressive behaviour during the breeding season, and may actually be another manifestation of it. In a captive pack, ZIMEN (1976) found that both intra-pack agonism and aggression toward strange conspecifics peaked in winter around the breeding season.

Social role.

The RR's of single animals correlate with their observed social roles. Alpha males were the most responsive animals, replying on more nights and howling many more times when they did reply. Subordinate pack members replied much less frequently. No other radioed adult was known to reply when alone, including the one radioed alpha female studied (2407). Yearlings replied to only 2 of 126 trials when alone. Lone pups replied slightly more often, but only until December after which their RR was as low as that of yearlings.

Additionally, the importance of the alpha male in influencing RR is suggested by several other observations. First, the increase in RR during the breeding season was correlated with the presence of the alpha animals. In at least three of four packs, the alpha male was present every night a response was elicited, and in the fourth pack, indirect data indicate he was probably present during most, if not all, replies.

Second, on one night the beta male and several 11-month-old pups of the JP Pack did not reply until a distant wolf, either the alpha male or alpha female did. This animal then appeared to "control" the response, for each time the group paused in howling, a distant howl by the single wolf appeared to trigger a further round of howling from the group.

Finally, at non-RS's throughout the year, adults initiated the overwhelming majority of responses. Counts of the number of adults responding in several packs revealed that at least one, and often both, alpha animals were usually present.

Thus an adult wolf usually initiates the responses, the alpha animals are usually present, and an alpha sometimes appears to "control" or "re-initiate" the howling during a response. The higher RR of single alpha males as opposed to alpha females sugests that the alpha male is the decisive factor in determining whether or not a pack will respond to an alien wolf's howls.

The alpha male either controls or initiates much of the behaviour of the pack (MECH, 1970), and during aggressive encounters with strange wolves, the alpha male is the most active (SCHENKEL, 1947). Two chases of strange wolves by the HL Pack reported by MECH & FRENZEL (1971) were pressed by one identifiable alpha animal. On Isle Royale, similar episodes were observed where only one wolf seemed to be particularly intent on the chase (MECH, 1966). Even in captive situations, high-ranking wolves show the greatest aggression toward strangers, whereas low-ranking animals either show fear, apathy, or friendly behaviour. Change in rank of these animals has shown that such behaviour is not attributable to individual differences but to rank itself (ZIMEN, 1976).

The differential response of single pack wolves of various ranks probably is responsible for the significant decrease in RR/S that occurred during early summer. In May, June, and July, 22 of the 25 sessions involved single radioed pack wolves. The only two replies were by two alpha males. Thus the low RR/S seen during this period seems to reflect the overall low response rate of single pack wolves throughout the year.

Pack size.

Generally, the larger the pack, the more likely it was to respond. This influence was shown for four packs at kills, and for the mixed adult-pup groups of the HL and JP Packs under a number of conditions. Pack size was also related to two temporal parameters of group responses; two packs with only two non-pup members took longer to respond and howled for shorter periods than did larger packs. This effect seemed to be a function of immediate group size because single wolves of the JP and HL Packs responded at similar rates, whereas the larger mixed groups of the JP Pack responded much more often than the smaller HL Pack groups.

Pack size could influence RR in two ways. First, each wolf may have a finite probabibility of replying to a stranger. Once any individual initiates a reply, other pack members join in. Thus the probability of a pack reply is merely the sum of individual probabilities; hence, larger packs have greater response rates, despite similar individual probabilities. On the other hand, one or a few pack members may play the role of initiator, and the behaviour, or mere presence, of other pack members influences their response threshold.

The second hypothesis seems more likely, as captive and field observations indicate that only one or a few individuals usually initiate group responses. In captivity, howls initiated by high-ranking animals usually were joined by all the pack, whereas howls initiated by low-ranking animals usually were not (ZIMEN, 1976). In this study, non-RS group responses were initiated by adults, and a number of observations implicated the alpha male in this role. This suggests that within a pack, there is great variability, dependent on age-class and/or social role, in an individual wolf's readiness to initiate a reply to a stranger. However, once a reply is initiated, all, or most, individuals readily join in the howling of their packmates.

Pack size may also influence interpack aggression. Chases of strange animals by packs seen by MECH & FRENZEL (1971) seem to indicate wolves gain self assurance from numbers. In two chases they observed, the lead wolf always stopped two or three times during the chase and allowed the lagging members of its pack to catch up, or it turned back to find them before continuing the chase. ZIMEN (1976) presented suggestive evidence that wolves in a large captive pack reacted more aggressively toward strangers than did wolves in a smaller pack. Thus possibly the higher RR's of larger packs to our howling was another manifestation of such social facilitation in interpack agonism.

Role of howling in territory maintenance.

Among the five proximate factors that most influence RR to alien howling, pack size, social role, and breeding season are closely related to the level of agonism wolves show toward strange animals, indicating that as extra-pack agonism increases, so does RR. This close positive relationship supports the hypothesis that howling is important in territory maintenance.

The remaining two factors, the presence of kills and young, are both resources actively defended by wolves. In addition, they may be among the prime factors ultimately responsible for the evolution of wolf territorial behaviour. According to BROWN (1964), the evolution of territorial behaviour requires (1) competition among conspecifics for resources crucial to reproductive success, and (2) that the resources can be economically defended. As an ecological resource, a deer kill represents approximately one per cent of a pack's yearly energy needs (MECH, 1977a) and is not readily movable. As an evolutionary resource, pups represent a large, seasonal energy investment and are relatively immobile for 3 to 5 months.

The maintenance of both resources requires that the pack retain exclusive control of sites containing them. The fact that the highest RR's obtained during this study were at these two resources provides further evidence that howling plays a major role in territory maintenace. This section considers the details of that role.

Animals gain exclusive use of a terrtiory by overt defense, repulsion by advertisement, or both (WILSON, 1975). In many territorial birds, overt defense often characterizes the resident's response to an intruder's vocalizations (*e.g.* FALLS, 1963; LEMON, 1967; EMLEN, 1972). In addition, the resident's rate of vocalizing (advertisement) usually increases. In several mammals, however, vocalizations facilitate avoidance (BALDWIN & BALDWIN, 1976; WASER, 1975). In the grey-cheeked mangabey (*Cercocebus albigena*), whose spatial organization resembles that of Minnesota wolves, even an intruder's vocalizations usually lead to avoidance, rather than approach (WASER, 1975).

During the present study, resident wolf packs responded to our howling either by remaining where they were or retreating; they rarely approached (less than 3% of sessions). In addition, the few approaches usually occurred after several replies from the resident's original site, following continued vocalization or closer approach of the intruder (which in all such cases was a *single* person). Thus the initial response to an intruder's howling was a vocal reply (advertisement) and not an approach (overt defense). JOSLIN (1967) also noted that approaches only occurred if he howled close to the pack. Thus it appears that from distances beyond several hundred meters, howling apparently helps packs avoid one another.

At least for the wolf, a rationale for the advertisement-avoidance role of howling is apparent. Observed direct encounters between packs are rare (MECH & FRENZEL, 1971; MECH, 1973, 1977a), and when they do occur, typically lead to chases and fighting (MECH & FRENZEL, 1971; MECH, 1972, 1977b; WOLFE & ALLEN, 1973; VAN BALLENBERGHE & ERICKSON, 1973). Thus encounters between packs are dangerous and should be avoided. The expected and observed low frequency of direct encounters between packs strongly indicates that advertisement, not overt defense, is the primary means of day-to-day territorial maintenance. Our data on howling response suggests that the prime importance of howling is such advertisement.

If howling does facilitate avoidance rather than approach, then the low overall RR (29% of sessions) is at first puzzling, for a higher RR would more effectively reduce encounters. An analysis of the costs and benefits associated with replying may help clarify this problem.

The major benefit of replying to the howling of alien wolves apparently is the avoidance of an "accidental" encounter. Accidental encounters have been observed in Minnesota (MECH, unpubl.) and would be most common in the roughly 2 km of territory overlap between adjacent packs (PETERS & MECH, 1975) and when reduced prey availability results in occasional pack trespassing (MECH, 1977a). By howling, resident wolves advertise their position, allowing both resident and intruder to modify their movements to minimize the probability of accidentally meeting.

The potential costs of replying, on the other hand, may be much greater than the amount of energy required to vocalize, because advertisement announces the advertisers' location and may subject them to attack, even by intruding wolves. Several observations have been made in which intruding wolves located and attacked others by following tracks in the snow (MECH, 1972, unpubl.). Howling could also be used in this way. Thus an important potential cost of replying to howling is the possibility of attack.

A pack cannot minimize both accidental and deliberate encounters by any single behaviour: to avoid accidental encounters it should reply, but to avoid deliberate encounters it should remain silent. It could decrease chances of both types of encounters by retreating silently, as wolves did at least one-third of the times when they did not respond during the present study. However, retreating would sometimes mean abandoning a crucial resource. Thus whether a pack replies should depend on the benefits versus the costs of the reply.

If the pack's immediate site contains an important *and* immovable resource, the pack should stay and reply. Accidental encounters will be avoided, and although a deliberate encounter may be facilitated, the benefit gained by retention of the resource may more than compensate for the increased risk. On the other hand, if the pack has no kill or is almost finished with one, and its young are mobile, then the risk of an encounter may be the determining factor, and the pack retreats silently. Generally, the behaviour of the packs during this study appeared to fit the above paradigm. The ultimate effect of such behaviour is that howling responses are not associated with the entire territory, but to specific resources and sites within the territory.

An additional consideration, for which we have no data, could be the location of potentially responding wolves. Virtually all our howling sessions were conducted within the territory of the subject pack; thus we were intruders. The probability of intruders attacking residents should be greater than the probability of attacks from packs howling from outside the resident's territory. PETERS (1978) presented evidence that wolves possess knowledge of spatial relationships within their territory. Thus they are likely to know whether a stranger is howling within or outside their territory, especially if the stranger is relatively close to them, as we were.

Therefore a stranger howling outside the resident's territory represents a low encounter risk so the pack may be likely to reply. If the stranger is intruding, however, the risk of an encounter is greater. Thus a much higher RR may occur among packs in their own territories. Unfortunately, the limits of human hearing and the large pack ranges prevented us from testing the above speculation.

Effectiveness of howling in territorial maintenance.

The effectiveness of howling in territorial maintenance is dependent on (1) the frequency of "spontaneous" howling (*e.g.* not elicited by another pack) and (2) the probability of one pack hearing the howling of another. These will determine the baseline frequency for possible interpack howling interactions.

At present, the spontaneous howling rate is poorly known, especially during the non-RS season, when greater pack mobility increases the importance of avoidance mechanisms. Currently, the only data from the wild are from packs at RS's (VOIGHT, 1973; PETERSON, 1974; HARRINGTON & MECH, in press).

Data on the probability of one pack hearing another, however, are easier to obtain. The pieces of necessary information are (1) the range of wolf hearing, (2) the distance between packs, and (3) the proportion of nights suitable for long-distance sound transmission.

Humans can hear wolf howling at 6.5 km or more in forested areas (JOSLIN, 1967) and 16 km on open tundra (STEPHENSON, unpubl., in HENSHAW & STEPHENSON, 1974). Wolves probably responded to our howling at distances of 9.6 to 11.2 km.

To estimate the proportion of time packs were within 10 km of each other, we measured the minimum daily distances between radioed wolves in the JP and HL packs during the non-RS season (HARRINGTON, 1975: 297). During 13% of the time, these packs were within hearing range of each other. Since each pack is surrounded by four to six others (MECH, 1973), movement away from one neighbour will often bring a pack closer to another. Thus for about 78% of the time (13% times 6 packs), a pack is within howling range of at least one neighbour. Because weather conditions were nearly optimal for sound transmission (calm air or very light winds) during about half the nights of the study (HARRINGTON, 1975), interpack howling interactions were possible on 40% of the nights during the nomadic period.

Furthermore, the probability of one pack hearing another, and the probability of encounters, both increase when packs approach one another at a common border, or when they congregate around winter prey concentrations (PARKER, 1973; MECH, unpub.). Thus the importance *and* effectiveness of howling is greater when accidental encounters are most probable.

Howling and scent marking compared.

Because both howling and scent marking apparently function in territory maintenance, it is useful to compare the two systems. PETERS & MECH (1975) concluded that of four types of olfactory sign made by wolves, raised leg urination (RLU) was "intimately involved in territorial maintenance."

Many similarities are evident between RLU scent marking and elicited howling. For instance, RLU was performed primarily by dominant animals, most often the alpha male, and the rate of RLU increased significantly during the breeding season. Likewise, high RR to alien howling was typical of the alpha male and occurred significantly more often during the breeding season than before. Finally, in areas occupied for any period (kills or RS's), both RLU and RR were high.

In relation to the probability of an encounter between packs, RLU rate increased significantly near borders; thus the distinctiveness of the boundary is enhanced. Similarly, the probability of an interpack howling session is highest when packs are near a common border. Thus both howling and scent marking may remind a pack of its neighbours and the border between them.

TABLE 16

Similarities between raised leg urination (RLU) scent marking and elicited howling rates

Pack	Elicited howling rate[a] (Response rate/session)		RLU rate[a, b] (Sign/kilometer)	
Jackpine	1.00	(47 sessions)	1.00	(30 km)
Perch Lake	0.96	(15 sessions)	0.76	(15 km)
Harris Lake	0.43	(50 sessions)	0.46	(114 km)

[a] The rates are calculated relative to the Jackpine Pack (RR/S = 27.7%; RLU rate = 5 per kilometer).
[b] Data from PETERS & MECH (1975).

A striking similarity between elicited howling and RLU scent marking was the difference in rates of each between packs. PETERS & MECH (1975) studied scent-marking in the same packs during the same period we did. We compared the howling RR's and RLU rates for each pack relative to the JP Pack, which had the highest rates of both (Table 16). The howling data used were those collected at non-RS's during December through March, since all scent-marking data were collected during the same period. In each case, the ranks for each pack were the same for elicited howling and scent marking. The difference between relative RR/S and RLU rate for the Perch Lake Pack may be the result of small sample size, but the rates for the JP and HL Packs, based on adequate sample sizes, can be validly compared. These similarities in rate suggest that a common factor or factors may underlie both behaviours.

At present, the factors related to both behaviours are unknown. However, there are several possibilities. Pack size may be responsible for the difference in rates between JP and HL Packs. However, it cannot be the only factor, for the smallest pack (Perch Lake) was intermediate in rate. Recently, ROTHMAN & MECH (1979) found that newly established pairs (such as the Perch Lake Pack in winter 1973-74) have higher RLU rates than established pairs. Thus higher levels of agonism in new packs may affect the relative rates of scent marking and howling in territorial contexts. Because both elicited howling and RLU are largely a function of the alpha male (this study; PETERS & MECH, 1975), the most logical speculation is that intrinsic and extrinsic factors such as season, pack size, and age of pack probably act through the alpha male in the expression of both behaviours.

Lone wolves.

Lone wolves do not possess territories, but wander widely throughout the wolf population, generally avoiding areas occupied by packs (MECH & FRENZEL, 1971). Packs often chase and attack lone wolves (MECH, 1966; MECH & FRENZEL, 1971). On the other hand, a lone wolf often displays a high degree of tolerance toward other loners; the animals may stay near each other without interacting (MECH & FRENZEL, 1971).

During this study, lone wolves replied during only two sessions, when two or three were at a kill. Otherwise, single lone wolves never replied to our howling. Their low RR parallels their similar low scent-marking rate (ROTHMAN & MECH, 1979).

Because adult howling responses occurred in agonistic contexts suggesting territorial advertisement, lone wolves would not be expected to respond, for they have no territory to advertise. Their behaviour seems to parallel that of most "surplus" animals in a territorial population; they maintain a "low-profile", attracting as little attention as possible and generally trying to avoid territorial animals.

The replies from lone wolves at a kill, however, indicate that even for a lone wolf, a kill is an important resource to defend. In the two responses, however, the group's size may also have contributed to the increased RR, for at least two and possibly three animals were present. It would be interesting to know if a single lone wolf would reply at a kill.

The approaches of the three female lone wolves after we howled suggest a strategy that lone wolves may employ in their interactions with packs and other lone wolves. In every case where a lone female approached, only one person had howled. Thus it is possible that the females were investigating the howler, perhaps looking for a potential mate or the remains of a nearby kill. Single wolves often follow larger packs, usually cleaning up the remains of kills left behind (MECH, 1966, unpubl.). Perhaps by monitoring the howling of pack wolves, they can locate an abandoned carcass to utilize after the pack moves on.

SUMMARY

An experimental study of the role of howling in wolf territory maintenance was conducted in the Superior National Forest, Minnesota. Vocal replies and behaviour of radio-collared wolves in response to human howls were analyzed for eight packs and 10 lone wolves during a 2-year period.

Reply rate varied significantly throughout the year. A mid-winter increase was correlated with the breeding season, especially for groups containing breeding animals (alpha male or alpha female). A second, longer increase in reply rate started in mid-summer, peaked about August, and declined to a low in early winter. The decline in autumn howling response occurred sooner in a pack whose pups developed faster.

Through the year, the howling reply rate was significantly higher among all packs and lone wolves attending prey kills. The more food remaining at a kill, the higher the reply rate was.

For wolves separated from their pack, the howling reply rate was dependent on their age and social role. Among adults, only alpha males ever replied alone, and their reply rate, and number of howls per session, exceeded those of other animals. Alpha males sometimes approached during howling sessions, whereas other adults usually retreated. Younger animals replied more often as pups than as yearlings, and then only during their first 7 months, after which they replied little more than most adults.

Finally, larger packs replied more often than smaller packs.

Specific behaviours noted during howling sessions, including movements away from the howler, indicated that howling was related to interpack agonism. In addition, three of the major factors influencing reply rate also significantly affect the level of agonism toward pack strangers: pack size, social role, and breeding season. The other two factors, kills and pups, are both important pack resources necessitating exclusive occupancy of a site. The high reply rates at sites containing kills or pups constitute strong circumstantial evidence that howling is important in territory maintenance.

During howling sessions, wolves usually remained near their original site after replying, or retreated if they remained silent. This difference apparently was related to the problem of avoiding both accidental *and* deliberate encounters, and to cost/benefit considerations at the wolves' location.

Howling was considered most effective in mediating avoidance in two situations: when two packs approached a common area of overlap, and when a pack returned to an area little used for weeks, in which scent posts would have lost effectiveness in deterring strangers. Both scent-marking and howling apparently are important in spacing. However, they differ in their roles and are complementary, with scent-marking being long-term and site-specific, and howling being immediate and long-range.

Finally, lone wolves which do not possess territories, rarely replied, sharing the "low-profile" behaviour expected of surplus animals in a territorial population.

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ZUSAMMENFASSUNG

Experimentelle Untersuchungen über die Funktion des Heulens in der Erhaltung (Verteidigung) von Territorien bei Wölfen wurden im Superior National Forest, Minnesota U.S.A. ausgeführt.

Heulantworten und das Verhalten von Wölfen, die mit Radiohalsbändern versehen waren, auf menschliche Nachahmungen von Wolfsgeheul wurden untersucht an acht Rudeln und 10 Einzeltieren in einem Zeitraum von zwei Jahren.

Die Antwortrate variierte bedeutend zu verschiedenen Jahreszeiten. Ein Anstieg des Heulens in der Mitte des Winters stimmte mit der Ranzzeit besonders für Rudel mit Elterntieren (Alpha Rüde und Alpha Wölfin) überein. Eine zweiter, länger anhaltender Anstieg in der Antwortrate begann in der Mitte des Sommers, erreichte ihren Höhepunkt im August und war wieder niedrig bei Winteranfang. Der herbstliche Rückgang in der Anzahl der Heulantworten begann früher in Rudeln, deren Welpen sich schneller entwickelten.

Während des gesamten Jahres war die Antwortrate des Heulens bedeutend höher in allen Rudeln und einzelnen Wölfen die sich bei getöteter Beute aufhielten. Je mehr von der Beute übrig blieb, desto höher war die Anzahl der Antworten.

Der Prozentsatz der Heulantworten von Wölfen die vom Rudel getrennt waren hing von deren Alter und Rangordnung ab. Bei Erwachsenen antworteten nur Alpha Rüden wenn sie allein waren. Ihre Antwortrate und Anzahl während eines Versuches war höher als die aller anderen Rudelmitglieder. Alpha Rüden kamen manchmal heran während die Autoren heulten, während andere erwachsene Tiere sich meistens zurückzogen. Jüngere Tiere heulten öfter im Welpenalter als später, wenn sie als Einjährige angesprochen wurden. Nach einem Alter von sieben Monaten verhielten sie sich wie Erwachsene.

Grössere Rudel antworteten öfter als kleinere.

Verhalten während des von Menschen ausgelösten Heulens einschliesslich des sich Entfernens von dem Heulenden, deutet auf feindseliges Verhalten zwischen Rudeln. Weiterhin beeinflussten drei der Faktoren die mit der Heulantwortrate zusammenhängen auch das Verhalten gegen Rudelfremde: Rudelgrösse, Rangstellung und Ranzzeit. Zwei weitere Faktoren, Beute und Welpen, sind wichtige Gründe die exklusiven Besitz eines Gebietes notwendig machen. Die hohe Antwortrate bei Beute und Welpen deuten darauf hin das Heulen wichtig ist für die Erhaltung des Territoriums.

Während der Heulversuche blieben die Wölfe meistens am gleichen Ort nachdem sie geantwortet hatten, oder aber sie zogen sich zurück wenn sie nicht geantwortet hatten. Diese unterschiedlichen Reaktionen scheinen mit zufälligen *und* absichtlichen Begegnungen zusammenzuhängen. Es ermöglicht somit den Wölfen die Vorteile gegen die Nachteile an einem bestimmten Platz zu bleiben, abzuwägen.

Heulen war am wirkungsvollsten, gegenseitiges Vermeiden zu versichern in zwei Situationen: Einmal wenn sich zwei Rudel einem Gebiet näherten wo sich ihre Territorien oder Interessen überschnitten, und zweitens wenn ein Rudel in ein Gebiet zurückkam das sie einige Wochen lang wenig besucht hatten und wo ihre Duftmarken (scent-posts) ihre Wirkung Fremde zu warnen verloren hatten. Duftmarken und Heulen sind anscheinend wichtig für räumliche Trennung von Rudeln. Beide spielen jedoch verschiedene Rollen und ergänzen einander. Dabei ist Durfmarkierung ortsgebunden und langfristig, während Heulen sofort und auf weitere Entfernung hin wirksam ist.

Einzelgänger die keine Territorien besitzen antworteten selten, verhielten sich zurückhaltend wie man es von überschüssigen Mitgliedern einer territorialen Population erwartet.