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CHORUS HOWLING BY WOLVES: ACOUSTIC STRUCTURE, PACK SIZE AND THE BEAU GESTE EFFECT

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CHORUS HOWLING BY WOLVES: ACOUSTIC STRUCTURE, PACK SIZE AND THE BEAU GESTE EFFECT

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ABSTRACT

A variety of structural parameters were measured from wolf choruses recorded in the Superior National Forest, Minnesota, USA. Mean duration of 60s did not vary with pack size or composition. Packs replied to simulated howling after an average of 40s, often interrupting the stimulus howls. Choruses began with simply-structured howls, which became increasingly modulated as the chorus progressed. Little difference in mean fundamental frequency or other howl parameters was found among the choruses from packs of various sizes and compositions. In particular, choruses produced by single adult pairs did not differ from those of larger packs accompanied by pups. The lack of relationship between chorus parameters and pack size or composition indicates there is little useful information concerning a pack's size to be found in its chorus howling.

The observation that chorus howling by adult pairs is often perceived as that of larger groups with pups suggests that chorus structure has evolved to exaggerate the apparent size of the pack, especially those newly-established or otherwise reduced in number. If so, wolf howling choruses may represent a mammalian example of the Beau Geste effect, made particularly viable because of the relative immunity of the signal to probing.

INTRODUCTION

Long-distance vocal interactions between timber wolf *Canis lupus* packs are mediated by howling, particularly the chorus howling of two or more pack members (Mech 1970, Harrington and Mech 1978a, 1979). These choruses are complex and variable structurally (Theberge and Falls 1967, Harrington 1975, Harrington and Mech 1982), and may convey information on pack size (Mech 1970). There is evidence that pack encounters are influenced by pack size, with larger groups generally prevailing over smaller ones (Mech 1966, Mech and Frenzel 1971, Peterson 1977, Zimen 1976, 1982). Thus, information on pack size provided by choruses could determine the outcome of interactions among packs (Mech 1970). However, one would expect communication between competing individuals or groups to be 'deceptive' rather than 'honest' (Krebs and Dawkins 1984). Smaller packs which 'honestly' conveyed information about their size might fare worse than similar-sized packs

which exaggerated or obfuscated that information. Through analyses of physical structure and associated temporal parameters of choruses, the present study sought to determine whether information about pack size is available over the distances normally separating wolf packs.

Several chorus characteristics could convey such information. Choruses are usually preceded by activity directed toward other pack members, including frequent body contact (particularly about the head) and movement about in a tight cluster (Murie 1944, Schenkel 1947, Mech 1970, Zimen 1982). This activity, which continues during the chorus to a lesser degree, may provide mutual stimulation influencing both the initiation and continuation of the chorus. If larger packs generate greater stimulation, then they should reply sooner and howl longer. In interactions between packs, or between packs and lone wolves, a subset of the pack (typically adults and especially the breeding male) is generally most active in engaging strangers (Mech and Frenzel 1971, Harrington and Mech 1979, Zimen 1982). This difference is reflected by higher mortality rates for adults than for pups or yearlings during encounters with strangers (Mech 1977, Harrington and Mech 1979). Thus the number of adults, and not total pack size, may have a more important influence on chorus parameters.

A single wolf usually begins the chorus and is followed after varying intervals by other pack members (Joslin 1967). If wolves can somehow count these individuals as they enter the chorus, such information may provide an indication of absolute or relative pack size. It has been remarked that wolves appear to avoid using similar frequencies during the chorus (Crisler 1958). If so, this characteristic may assist in distinguishing individuals, thus facilitating the counting of voices.

Finally, wolves may acquire information on another pack's size by other means, such as direct confrontations or through olfactory clues left in tracks or by scent marking (Peters and Mech 1975). This information may later be associated with individually distinctive, or signature, howls which come to identify the pack. Then when those particular howls are recognized, the pack's response may be governed partly by previously-acquired information regarding pack size.

STUDY AREA

This study was conducted in the Superior National Forest of northeastern Minnesota, USA (latitude 92°W, longitude 48°N) between July 1972 and March 1975. The forest was characterized by dense vegetation and rugged terrain. Low lying, poorly drained areas often supported dense stands of black spruce *Picea mariana*. Drier upland areas were characterized by dense stands of jackpine *Pinus banksiana* or mixed deciduous-coniferous forest containing white and red pine *Pinus strobus*,

P. resinosa, white spruce *Picea glauca*, balsam fir *Abies balsamea*, aspen *Populus tremuloides*, *P. grandidentata*, and birch *Betula papyrifera*, among others. Understory vegetation, including beaked hazel *Corylus cornuta*, bush honeysuckle *Diervilla lonicera* and mountain maple *Acer spicatum*, was dense and often restricted visibility to 30 m or less. About 15 percent of the forest was covered by open water. Topography was characterized by either long, narrow, steep, parallel-running ridges or low, irregular, round-topped hills with elevations from a few up to 150 m above the intervening lowlands. Further details on the forest vegetation and topography are provided by Ohmann and Ream (1971).

The forest supported a high (approximately one wolf/26 km²) wolf population during the study (Mech, 1973). Wolves have been radio-collared and radio-tracked in the forest since 1968, providing background information on pack size, composition, history, land-tenure system, interpack relationships, and movement patterns (summarized by Mech 1980). The data reported here are part of a larger study concerning the role of vocalizations in spacing among packs (Harrington 1984, 1986, 1987, Harrington and Mech 1978a, 1978b, 1979, 1983).

METHODS

Details concerning methodology are presented in Harrington and Mech (1979). Briefly, radio-collared wolves were located, approached by ground vehicle to within 200–800 m, monitored for several minutes, and then howled to. A series of three to five simulated howls—see Harrington (1975) for details—were presented at 2 min intervals until a reply was obtained or three to five series had failed to elicit a reply. If a reply was obtained, I waited 10–20 min before attempting to elicit an additional reply. In most cases (74%), I left the pack after the second reply and did not return for at least 24 hr. Three replies were obtained on 15% of sessions, and between four and seven on the remainder.

Replies were recorded on a Nagra IV-D tape-recorder at 38.4 cm/s with a tripod-mounted Sennheiser MKH 805 condenser shotgun microphone. All replies were sonagraphed with a Kay Elemetrics 7030A sound spectrograph, using the 20–2000 Hz range with a PF120/1800 filter on the wide setting (effective bandwidth = 37.5 Hz).

Time to reply (TTR) was measured from the beginning of the stimulus series to the first wolf howl. Chorus duration was usually a straightforward measure. Some choruses, however, were preceded by one or more single howls (solo howls). In these cases, the solo howls were excluded and duration was measured from the point where other pack members joined in. In other cases, pauses occurred during the chorus. If these pauses were longer than 3s, they were subtracted. Time of entry (TOE) was the interval between the beginnings of consecutive howls in

the chorus. TOE was measured only for the first five howls of a chorus, if possible. Sometimes, however, sonagram quality prevented me from measuring all five intervals.

The initial howls of all choruses were characterized by mean fundamental frequency, duration, coefficient of frequency variation (CoFV) and coefficient of frequency modulation (CoFM). Frequency was measured every 0.2s using the highest harmonics present and then dividing by the appropriate factor to yield the fundamental. Using these methods, mean error for sounds of known pitch between 290 and 520 Hz was 5Hz (Harrington 1987). From these data, mean fundamental frequency and the CoFV were computed ($\text{CoFV} = (\text{standard deviation} / \text{mean}) \times 100$). The CoFM was a measure of frequency modulation between consecutive 0.2s intervals. The absolute differences in frequency between consecutive intervals were summed and averaged. These averages were then standardized by dividing by the mean fundamental frequency of the howl and then multiplying by 100.

For a sample of 18 choruses, an attempt was made to characterize every individual howl along the four parameters described above. The choruses sampled were selected for their clarity and detail. In addition, other selection criteria included (1) proximity of wolves in chorus (either howling from same location or from sites separated by 100 m or more), (2) presence or absence of pups with the pack, and (3) pack identity, as an attempt was made to analyse the effects of the first two variables within the same pack. Despite the quality of the recordings selected for detailed analysis, some howls could not be characterized because they were obscured by reverberations or by other howls.

Pack size and composition were known from ongoing radio-tracking (Mech 1980). Exact pack size and composition during individual howling sessions, however, was not always known because all pack members were never radio-collared at the same time. We were able to chart some nightly changes in pack size because radioed individuals were absent from the group. During other nights, however, we had no such data. Data will be arranged chronologically following major changes in pack size and composition (details are provided in Harrington 1975).

Frequencies and durations were ln-transformed before parametric statistical tests were performed (Sokal and Rohlf 1969). Non-parametric tests followed procedures in Siegel (1956).

RESULTS

Two packs were relatively accessible throughout the study. One of these (Jackpine) provided 60% of all choruses analysed (Table 1). Therefore, detailed analysis of some chorus parameters will focus on data from this pack alone, while the other five packs will provide supporting evidence.

TABLE 1

Parameters of choruses recorded from wolf packs of various sizes and compositions in the Superior National Forest, Minnesota

Pack	Pack size (total/#adults)	Duration mean \pm SD (N)	Time to reply mean \pm SD (N)	Correlation between duration and TTR	Proportion of stimuli interrupted	Proportion of choruses preceded by solo howls
Birch Lake	6/4+	—	55.7 \pm 14.3 (3)	—	0.00 (3)	—
Ensign Lake	6/4	58.6 \pm 11.2 (7)	20.2 \pm 5.6 (7)	-0.31 (7)	0.14 (7)	0.57 (7)
	10/4+	60.2 \pm 19.3 (9)	39.2 \pm 17.5 (11)	>	0.31 (13)	0.29 (7)
Harris Lake	4/4	66.5 \pm 21.9 (2)	41.5 \pm 33.2 (2)	+0.06 (11)	0.50 (2)	1.00 (1)
	4/2	48.5 \pm 5.5 (4)	52.5 \pm 25.2 (4)	+0.17 (4)	0.00 (4)	0.67 (6)
	4/2	46.2 \pm 12.3 (6)	72.3 \pm 24.7 (9)	+0.23 (6)	0.00 (7)	0.50 (4)
	5/3	63.0 \pm 2.8 (2)	25.5 \pm 0.7 (2)	-0.43 (6)	0.00 (2)	0.50 (2)
	5/3	59.8 \pm 14.5 (9)	25.7 \pm 17.4 (6)	-0.15 (6)	0.43 (7)	0.00 (3)
	2/2	52.5 \pm 3.5 (2)	72.5 \pm 10.6 (2)	—	0.00 (2)	0.00 (1)
Jackpine	8/4	64.6 \pm 16.3 (9)	37.0 \pm 14.2 (9)	+0.48 (9)	0.27 (15)	0.07 (15)
	7/3	60.9 \pm 20.6 (42)	36.5 \pm 19.2 (40)	+0.46* (37)	0.31 (39)	0.39 (51)
	11/5	57.0 \pm 16.8 (21)	28.2 \pm 23.0 (19)	-0.24 (19)	0.43 (21)	0.10 (21)
	9/5	60.3 \pm 13.9 (15)	26.9 \pm 17.4 (19)	-0.06 (15)	0.38 (21)	0.18 (44)
	3/3	56.7 \pm 24.5 (3)	51.0 \pm 11.3 (2)	—	0.00 (2)	0.33 (3)
Perch Lake	2/2	51.2 \pm 38.9 (4)	47.6 \pm 27.3 (5)	> +0.68 (4)	0.17 (6)	0.50 (4)
	4/2	73.6 \pm 21.9 (5)	31.6 \pm 9.9 (7)	-0.21 (6)	0.33 (6)	0.00 (3)
Sawbill	3/3	94.0 \pm 41.0 (2)	43.3 \pm 17.6 (3)	—	0.00 (3)	0.00 (1)
Grand means		59.9 \pm 18.1 (142)	37.1 \pm 22.2 (150)	—	0.28 (160)	0.28 (173)
Correlation between variable and:						
Total pack size—		-0.03, ns	-0.45, ns	+	+0.47, ns	-0.18, ns
Number of adults—		+0.16, ns	-0.49, P < 0.05		+0.51, P < 0.05	-0.03, ns

* P < 0.5

Chorus durations

Choruses varied from 33 to 123s in duration, averaging 60s overall (Table 1). The extensive variation in duration was not correlated with pack size or number of adults in the pack (Table 1). Although packs contained up to 12 members, the longest reply was recorded from a pack of three. Choruses recorded from the two largest packs were often shorter than the overall mean. Within a pack, choruses recorded when one or more adults were known to be elsewhere were not shorter than those recorded when all the adults were present. Finally, within a single night's session, when pack size rarely if ever changed, there was no correlation between the durations of first and second replies ($r=0.15$, $n=30$). An ANOVA indicated that 85% of the variation in chorus duration for the Jackpine pack was attributable to within session factors ($n=17$ nights). Thus pack size was not a determinant of chorus length, and chorus duration did not systematically change during sessions.

Approximately one-third of choruses were preceded by solo howls, usually a single howl (63%) but sometimes including up to six (Table 1). Packs did not differ in the proportion of choruses preceded by solo howls ($G=9.38$, $df=5$, ns), or the number of solo howls occurring per occasion. When more than one solo howl occurred prior to a chorus, most appeared to be produced by a single animal, as judged from the howl's acoustic qualities. During a single session, initial replies were preceded by solo howls 19% of the time ($n=26$). Subsequent replies were preceded by solo howls 35% of the time ($n=54$).

Time to reply

Overall, TTR averaged 40s ($n=106$) and did not vary systematically among packs, although it did correlate marginally with the number of adults in the pack (Table 1), indicating that packs with fewer adults, as a rule, took longer to reply. However, this relationship was only pronounced within one pack (Harris Lake), and with the addition of only one individual in either total pack size (from four to five wolves) or number of adults (from two to three), TTR for this pack became indistinguishable from that of packs of all other sizes.

My stimulus howling was approximately 30s in duration and the packs often replied before my stimulus ended ($x=28\%$, $n=160$). Packs with more adults tended to interrupt more stimuli (Table 1), as they tended to reply more quickly. Joslin's (1966) stimuli were also interrupted during his work in Algonquin Park, Ontario. His lone individual stimulus of 20–30s was interrupted 4% of the time, whereas his longer group stimulus (~70s) was interrupted 23% of the time.

There was no correlation between TTR and chorus duration (Table 1),

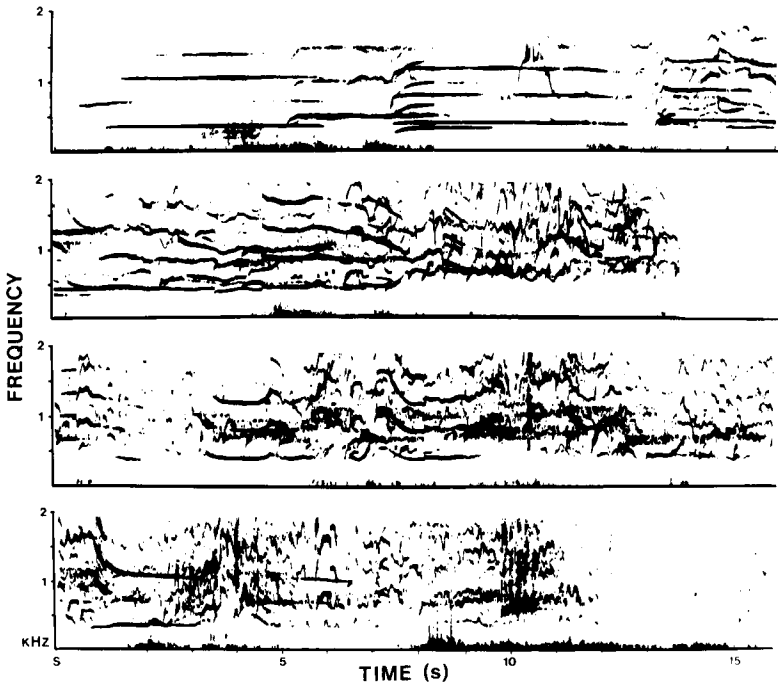


Figure 1. Continuous sonagram of a wolf howling chorus (2 October) recorded in the Superior National Forest, Minnesota. The chorus begins in the upper frame and runs left to right through each successive frame. Ordinate—frequency of howling (0-2 kHz); Abscissa—time in seconds. Pack composition for this chorus was two adults, one yearling and two five-month-old pups.

indicating that packs which replied sooner did not necessarily howl for longer periods of time.

Entry into the chorus

A chorus began with a single howl, which was joined partway through by howls from other wolves (Figure 1). The time interval between howls was longest for the first interval, and became shorter for successive intervals (Figure 2). Accurately determining these intervals became difficult due to reverberations and frequency modulations, which tended to obscure the beginnings of new howls, thus reducing sample size for later intervals. In at least 20 cases, several pack members seemed to enter the chorus *en masse*, but it was not possible to determine when or how many began and thus no measurements were taken. Had I been able to obtain these data, the later intervals would have been shorter than reported here,

suggesting that entry into the chorus is accelerated rather than paced at a relatively constant rate.

If these entries provide information on pack size, then repeat howling by individuals would reduce the accuracy of size estimates. I measured the potential for repeat howling by determining how many wolves had entered the chorus while the first animal was still howling. For a sample of 101 choruses, an average of only 3.0 ± 0.3 wolves had howled before the first individual had an opportunity to howl again.

Structure of howls in the chorus

As a chorus progressed, individual howls became more variable in pitch, although mean pitch of howls did not change systematically (Figure 1, Table 2). The most striking differences were between the first one to several howls and the remainder (Figure 3). Both CoFV and CoFM increased, with the most variable howling recorded in the last portion of the chorus. The correlations between howl position and CoFV and CoFM

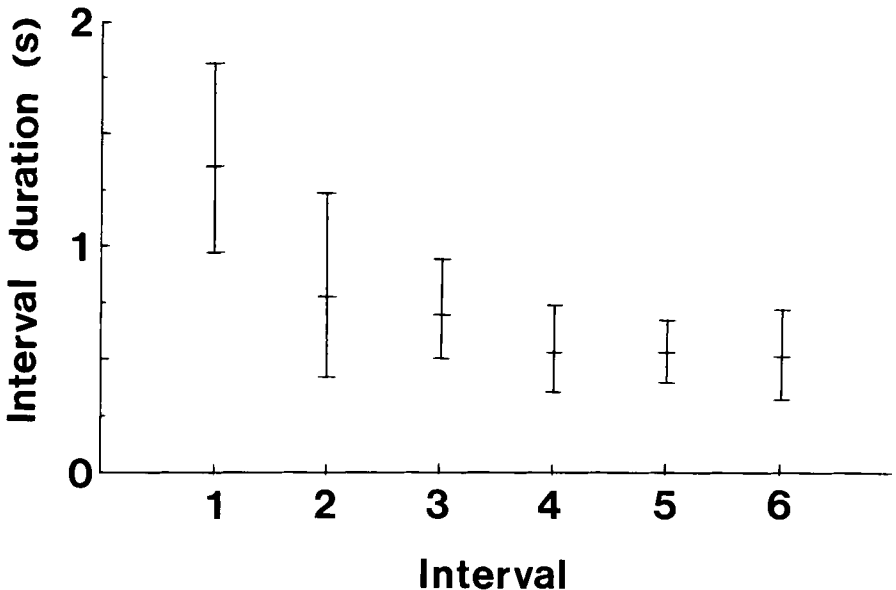


Figure 2. The time of entry of successive individual wolves at the beginning of the chorus. Interval duration is the time in seconds between the beginning of successive howls. Mean duration \pm standard deviation was calculated on log-transformed data and then was back-transformed for presentation. Interval 1 is the period between the first and second howls in a chorus, Interval 2 is the period between the second and third howls, and so on. Sample sizes for the intervals are 97, 97, 92, 83, 65 and 23, respectively.

TABLE 2

Parameters of wolf howls which occurred during choruses that were recorded under a variety of conditions in the Superior National Forest, Minnesota. Fundamental frequencies were ln-transformed before statistics were computed. Values reported below have been back-transformed. Correlations were computed between the variable and the position of the howl in the chorus (from 1 to N). Significant correlations ($P < 0.05$) are indicated by asterisks.

Date and Group Composition	Fundamental frequency (Hz)		CoFV		CoFM		Portions not analysed because of extreme modulation and reverberation	
	mean \pm (1 SD)	(N)	range	r	mean \pm SD	r	r	r
Pups only								
15 July	1006 \pm (794-1276)	(18)	645-1375	-51*	14.0 \pm 8.6	+12	9.8 \pm 6.9	+06 Last 20s (of total 42s)
31 July	880 \pm (694-1115)	(17)	616-1554	-26	13.9 \pm 8.8	+29	7.2 \pm 4.6	+32 Most of last 21s (of total 38s)
31 July	922 \pm (765-1112)	(12)	657-1362	+33	17.8 \pm 8.8	+04	6.2 \pm 3.9	+26 Last 7s (of total 19s)
31 July	933 \pm (719-1210)	(9)	596-1248	+06	17.8 \pm 12.8	+57	5.2 \pm 4.9	+77* Last 13s (of total 20s)
16 August	750 \pm (610-924)	(18)	534-1129	+43	13.4 \pm 9.9	+33	5.7 \pm 4.3	+52* Last 17s (of total 41s)
16 August	728 \pm (653-812)	(24)	552-890	+10	19.9 \pm 9.1	+46*	7.0 \pm 3.6	+47* Last 30s (of total 48s)
13 September	701 \pm (532-922)	(22)	498-1208	+08	25.6 \pm 11.9	+43*	12.8 \pm 7.8	+50* None (entire chorus (35s) analysed)
29 September	653 \pm (496-858)	(26)	397-1033	+23	21.1 \pm 10.5	+48*	10.8 \pm 7.1	+54* 4s near end (of total 52s)
12 October	597 \pm (481-741)	(23)	440-950	+01	19.2 \pm 11.2	+02	8.4 \pm 6.0	+24 3s in middle (of total 38s)
Pups and Adults								
20 July	583 \pm (414-822)	(40)	353-1135	-28	11.6 \pm 7.6	-16	7.5 \pm 6.3	-03 7s near end (of total 56s)
10 September	445 \pm (364-544)	(20)	347-686	\pm 14	8.3 \pm 5.8	+15	4.8 \pm 4.2	+25 None (entire chorus (61s) analysed)
10 September	489 \pm (385-622)	(28)	353-928	-04	10.5 \pm 6.2	+08	2.9 \pm 3.0	+09 None (entire chorus (63s) analysed)
2 October	490 \pm (403-596)	(33)	326-835	+16	12.2 \pm 8.3	+37*	9.0 \pm 10.8	+41* 10s near end (of total 55s)
2 October	455 \pm (367-564)	(33)	332-911	+36*	12.0 \pm 7.9	+50*	5.9 \pm 4.8	+57* None (entire chorus (55s) analysed)
18 December	429 \pm (360-510)	(22)	302-647	+01	19.2 \pm 13.0	-02	7.7 \pm 4.7	+30 5s near end (of total 49s)
12 April	506 \pm (414-618)	(42)	359-834	-17	21.7 \pm 15.2	+14	10.5 \pm 7.3	+27 11s near end (of total 64s)
Adults only								
24 February	467 \pm (359-606)	(53)	328-983	+11	21.4 \pm 11.6	+05	13.2 \pm 6.8	+57* Last 30s (of total 123s)
10 March	528 \pm (427-652)	(15)	360-733	+34	17.8 \pm 8.5	+29	13.0 \pm 5.7	+50* 20s near end (of total 50s)

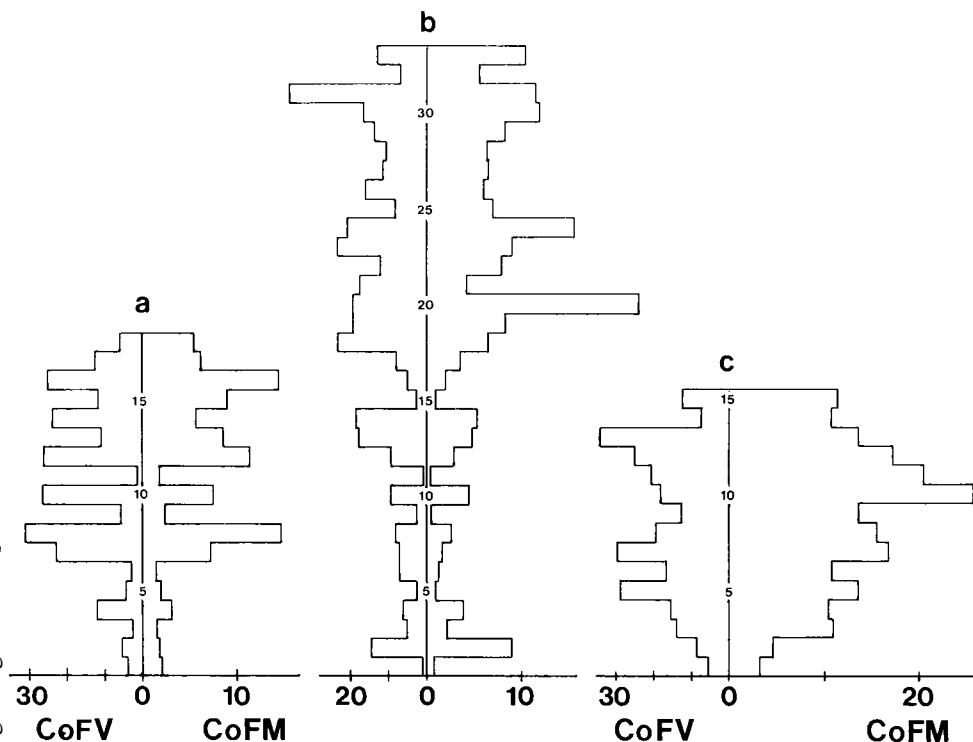


Figure 3. Changes in the Coefficient of Frequency Variation (CoFV) and the Coefficient of Frequency Modulation (CoFM) during the course of three choruses. The position of each howl in the chorus is depicted along the vertical centerline, with the initial howl at the bottom and the last howl at the top. CoFV increases to the left of the centerline, whereas CoFM increases to the right of the centerline. a) Chorus of pups only (16 August). The correlation between howl position and CoFM is significant ($r = 0.52$, $n = 18$). b) Chorus of adults and pups (2 October, Figure 1). The correlations between howl position and both CoFV ($r = 0.50$) and CoFM ($r = 0.57$) are significant ($n = 33$). c) Chorus of adults only (10 March, Figure 6). The correlation between howl position and CoFM is significant ($r = 0.50$, $n = 15$).

are conservative for most choruses because individual howls, especially near the end of the chorus, varied so much in frequency that many howls simply could not be measured even in the highest quality sonagrams. Despite this, five of 18 correlations for CoFV and nine of 18 correlations for CoFM were both significant and positive (Table 2).

The parameters of individual howls in a chorus differed little with regard to presence or absence of pups in a pack. The only significant variation revealed by Analysis of Variation was a higher mean fundamental frequency for howls in the chorus recorded on July 20 when the pups were three months old and weighed only 5–7 kg. Otherwise, the

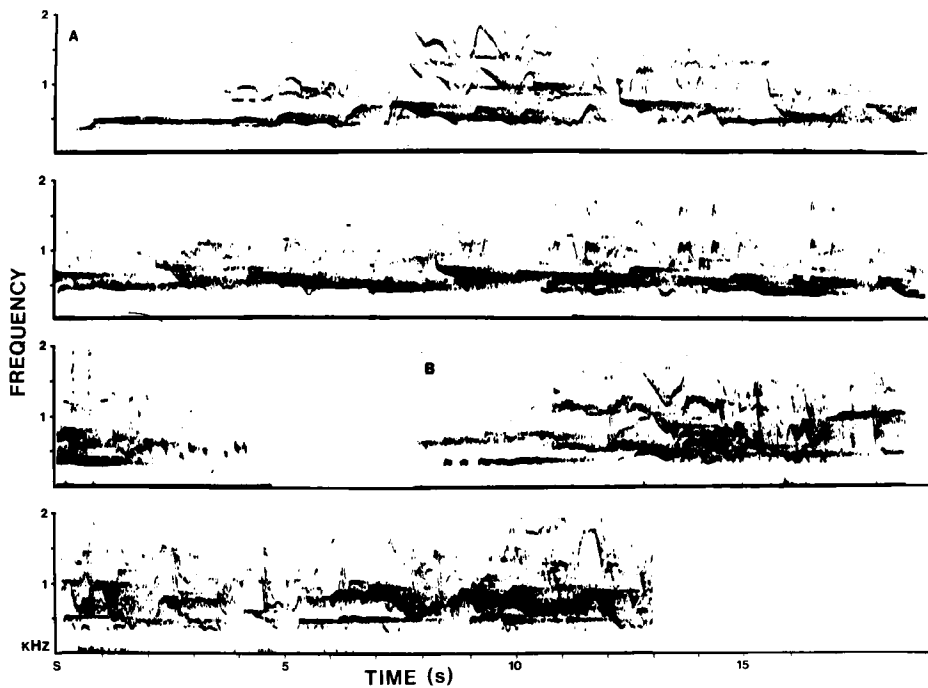


Figure 4. Continuous sonagram of adult wolf choruses recorded in the Superior National Forest, Minnesota. Chorus A was recorded from an established pair (10 March, Figure 3). Chorus B was recorded from a newly-formed pair. Both were recorded during the mid-winter mating period.

overall distributions of mean fundamental frequency, CoFV and CoFM did not vary significantly for any of the other choruses containing either adults only or adults with pups (Table 2). The range of mean fundamental frequencies found in adult-only choruses (Table 2, Figure 4) indicates that adults are capable of and do produce howls of frequencies spanning most of the range typically used by both adults and pups when howling either in chorus (Table 2) or alone (Table 3).

During July, August, September and October, a number of choruses were recorded from groups of pups unaccompanied by adults or yearlings. These choruses followed the same patterns of frequency modulation as did choruses which also contained adults and yearlings (Table 2, Figures 3 & 5). The only difference was that the distribution of fundamental frequencies in the pup choruses was shifted toward a higher frequency range, which progressively declined as the pups matured (Table 2). The lower frequency range (300–400 Hz) of howls typical of adult choruses was missing, as pups of this age probably cannot produce these frequencies (Harrington and Mech 1978a).

The only notable exceptions to the above generalizations concerned

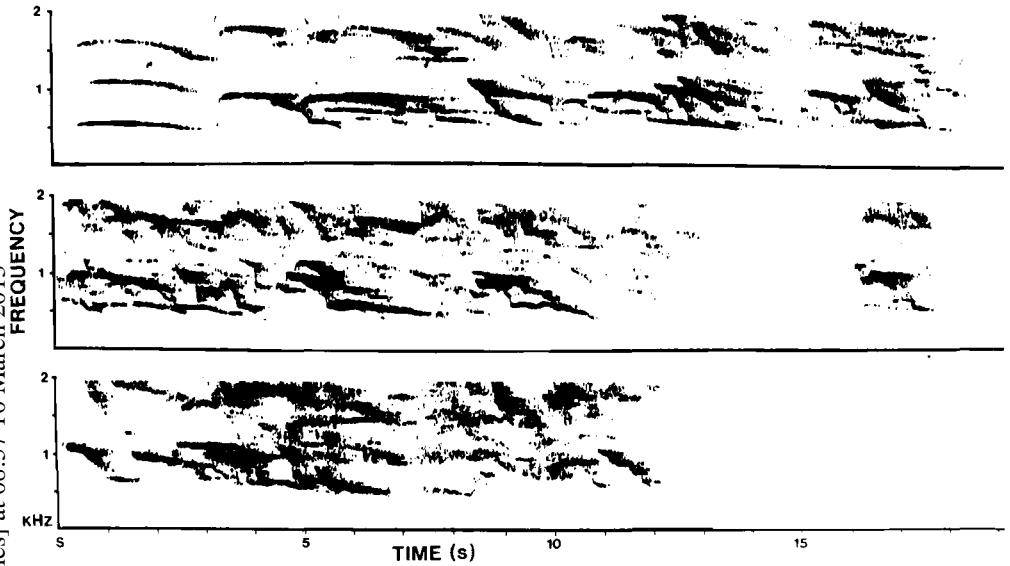


Figure 5. Continuous sonagram of a wolf pup chorus recorded in the Superior National Forest, Minnesota. The litter of 3–4 month old pups contained two males and two females.

packs whose members were not in close physical proximity. Choruses produced on occasions when I knew that pack members were scattered apart, often over distances of a hundred meters or more and in all cases presumably out of sight, did not show the progressive increases in CoFV or CoFM that were typical of packs whose members were howling from the same location (compare Figure 6 with Figure 1). On September 10, a pack (two adults, one yearling, two pups) replied from a series of ridges 0.5 km from me in three or more scattered groups. All choruses recorded that evening were characterized by little variation in CoFV or CoFM throughout the reply (Table 2). These results can be contrasted to howling recorded from the same group three weeks later on October 2 (Table 2, Figure 1). On this later occasion, all five pack members were at the same location, and both CoFV and CoFM showed significant increases during the two choruses recorded that night.

Another exception occurred during a session recorded less than 50 m from the pack (July 20). This group was not radioed and thus I inadvertently approached too close (<50 m) to them. Howling by the adult(s) continued to remain relatively unmodulated throughout the reply, and as a result the correlations between CoFV and CoFM and howl position were not significant. The closeness of my approach possibly influenced this chorus's structure.

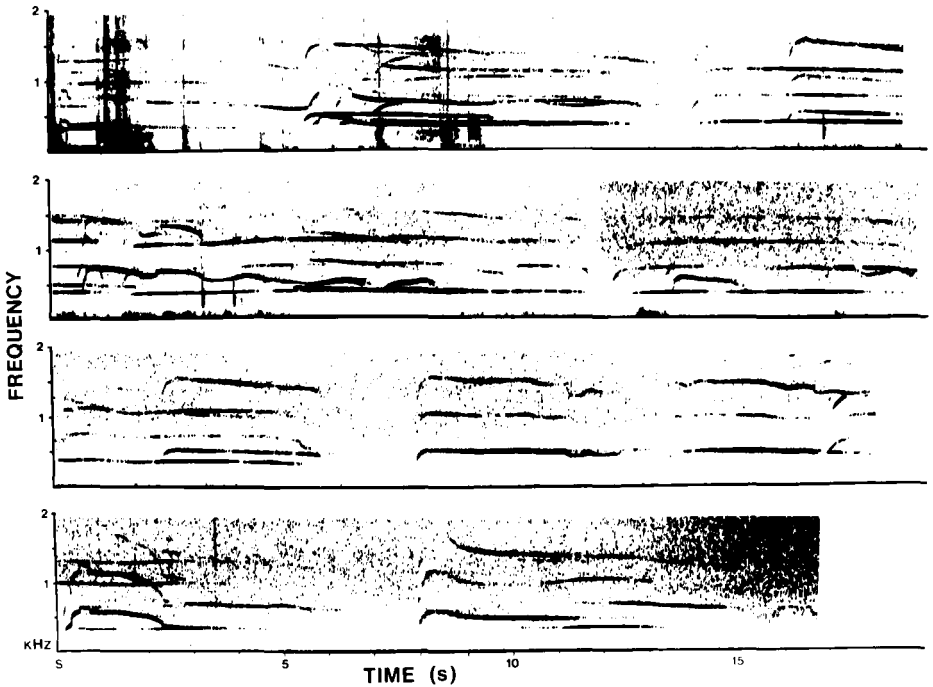


Figure 6. Continuous sonagram of a wolf pack chorus (10 September) recorded in the Superior National Forest, Minnesota. The wolves in this pack (two adults, one yearling, two pups) were not howling from the same site. This recording was made three weeks earlier from the same animals shown in Figure 1.

Characteristics of initial howls

The initial howls of choruses usually had a simple structure and were therefore easy to measure. They may provide "signature" information about individual or pack identity. The initial howls recorded for the Jackpine pack, however, were quite variable in frequency, duration, and structure (Figure 7). In mean pitch, the initial howls spanned the entire frequency range recorded from adults in general (Table 3), and their durations also spanned those of adults in general (Harrington and Mech 1978a). There was also no obvious relationship among the variables measured (fundamental frequency, coefficient of variation, duration), except for a significant positive correlation between fundamental frequency and duration (higher-pitched howls are longer in duration: $r = 0.62$, $n = 39$, $P < 0.001$). Correlations between fundamental frequency and coefficient of variation ($r = 0.01$) and coefficient of variation and duration ($r = 0.11$) were not significant.

This variation found in the initial howls of Jackpine pack choruses could come from two major sources: (1) variation among the howls of an

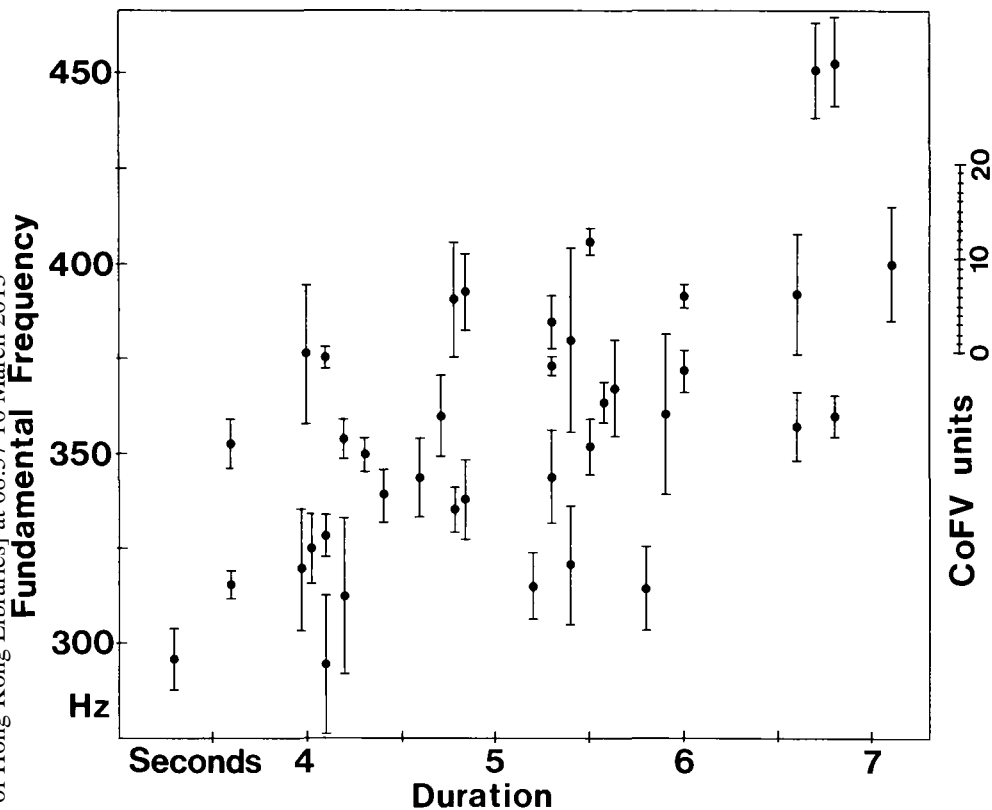


Figure 7. The characteristics of initial howls from choruses recorded from the Jackpine pack in the Superior National Forest, Minnesota. Mean fundamental frequencies (dots) are bounded by lines representing the relative degree of frequency variation, expressed as the coefficient of variation (CoFV). Thus a line centered at 343 Hz and measuring a total of 10 units represents a howl with a mean fundamental frequency of 343 Hz and a coefficient of variation of 10%.

individual wolf, which initiated all the choruses; or (2) variation among the howls produced by several individual wolves, each of which initiated a proportion of the choruses. In the latter case, the particular individual initiating a chorus may be either dependent on pack composition, and therefore only one particular individual initiates choruses for each possible combination of individuals, or independent of pack composition, and thus any individual might initiate the chorus regardless of which individuals are present. In an attempt to eliminate some of these possibilities, I compared the initial howls for the first and second replies recorded during the same sessions from the Jackpine pack. Because wolves were not known to leave the group during a session and therefore pack composition remained constant, initial howls recorded during the

TABLE 3

Parameters of individual howls recorded from wolves which were unaccompanied by other wolves, as a function of the animals' ages

Age class	Sample	Fundamental mean \pm SD	frequency (n)	(Hz) Range
Pup	July	478 \pm 34	(65)	398-588
	July	730 \pm 121	(78)	545-1112
	August	626 \pm 96	(51)	439-865
	October	550 \pm 125	(118)	346-647
	November	513 \pm 90	(58)	360-669
	Mean	580 \pm 136	(370)	346-1112
Yearling		392 \pm 47	(23)	346-507
Adult	A	362 \pm 25	(16)	333-439
	B	399 \pm 27	(50)	360-496
	C	392 \pm 50	(64)	319-510
	D	360 \pm 30	(40)	301-447
	E	358 \pm 33	(58)	295-453
	Mean	377 \pm 41	(228)	259-510

same session should be more similar if the same animal initiates both choruses using its own distinctive "signature". An ANOVA indicated that nearly 70% of the variation is accounted for by within session factors. This suggests one or both of the following: one wolf may initiate all replies during a session, but does so using quite variable howls, or several different adults initiated choruses within a pack and within a session. Whatever the case, there is no evidence that a chorus begins with a specific distinctive "signature" howl. The extreme variation found in initial howls would make it difficult for strange wolves easily to associate individual howls or voices with a specific pack.

Subjective impressions of pack size

Human impressions of pack size have been attempted by counting wolves as they enter the chorus (Joslin 1967). This method requires hearing the initial 5-10s of the reply, and is subject to the same limitations concerning the potential for repeat howling by individuals after the first three have begun howling. These counts must be done at relatively close range over distances much shorter than those normally separating packs. No systematic data have been collected to determine the reliability of pack size estimates based on this method. However, a number of observations indicate that these counts must be viewed with caution (Harrington and Mech 1982). These include the observation that chorus

howling by a single adult pair is often mistaken for that of a pack of four or more adults accompanied by one to several pups. This has been noted historically (*Memoirs* U.S. Grant, cited in Eckels 1939) and by several experienced wolf biologists (described in Harrington 1975).

I have experienced this phenomenon on three occasions with two different pairs. In one case, a pair replied from 600 m. During their reply, I had the distinct impression that four adults were howling, two located at 270°, one at 290° and the fourth at 240°. Several weeks earlier this same pair had replied from a greater distance. My impression on that occasion was of a pack of three to six animals, including pups. Another pair's chorus howling gave me a similar impression. On all three occasions, it was known that no other animals were in the area or in the pack. In addition, all three occasions occurred during the final two months of my study, at a time when I had listened to and recorded over 99% of the howling used in this study. Thus it is unlikely that inexperience could explain this phenomenon.

A more reasonable explanation is based on the effects of intervening environmental features on the propagation of frequency-modulated sounds. Specifically, frequency-dependent reflection from different surfaces will introduce echoes into the sound at the receiver's end (Wiley and Richards 1978). For the relatively unmodulated howls at the beginning of the chorus, the presence of echoes poses little difficulty to the receiver. But as the howls become increasingly modulated, direct sound and echoes become decoupled and the receiver is faced with decoding a complex mixture of direct sound and echo from each animal. In addition, directional information becomes more complex, as direct sound and echoes will differ in their paths to the receiver. At some level of complexity, the receiver may be unable to continue correctly to associate echoes with their direct source. At that point, echoes are now treated as direct sounds with individually, and spatially, distinct sources. The howling of two wolves at one site may then be perceived as that of four or more animals at several different sites.

DISCUSSION

The results clearly indicate that the duration of a chorus gives little useful information regarding pack size. Latency to reply is little better, except in the case of some of the smallest packs which took longer than average to reply. However, packs often replied before I had finished howling, as Joslin (1967) also noted. Since my stimulus was about half as long as a typical chorus, it might be expected that a stimulus chorus of average length (about 60s) would be interrupted about 70% of the time (based on chorus durations and TTR's recorded in the present study). Thus any information on pack size conveyed by reply latency would be virtually useless to the pack that had initially howled.

The results further suggest that counting individuals as they enter the chorus would yield a poor estimate of pack size. Despite the relatively simple structure of the initial howls, these rapidly give way to more variable, frequency-modulated howls which occur in quicker succession or even simultaneously. At the same time, the first animals to reply have ended their howls and now can howl again. Thus it may be possible to easily count the first three animals (assuming both groups are not howling concurrently), but beyond this the count is made more difficult by the increasing complexity of individual howls and the repeat howling of individual pack members. Furthermore, distance-mediated degradation (Wiley and Richards 1978) of the howls would greatly reduce the quality of the signal to be decoded, and thus introduce an element of uncertainty, especially over the distances normally separating packs, i.e. 10 km in summer and 17 km in winter (Harrington 1975).

Distance-mediated degradation would also reduce the usefulness of signature howls which might be associated with past experiences of a pack's size. In addition, the variability of the initial howls, their occurrence without an alerting signal (they themselves may signal the impending chorus), and the overlap between stimulus and response choruses, further reduce the probability that wolves may be using the first howl (or howls) of a chorus to determine pack size. Finally, the observation that humans have mistakenly overestimated the size of even the smallest packs, indicates that it is unlikely that packs can assess the size of their neighbors' packs using the acoustic information provided by choruses. These data converge on the conclusion that choruses do indicate the presence of at least two wolves, but beyond this, there is little reliable information to indicate how much larger than two the group is.

Two alternative hypotheses, that chorus structure has evolved in order to either withhold information on pack size or exaggerate the apparent size of the pack, can now be advanced. The former hypothesis is generally supported from the data presented above. The latter hypothesis of exaggeration receives some support from the finding that humans overestimate pack size, but this occurs only for the smallest packs (i.e. two to three animals). Beyond these small groups, there is no evidence of regular pack size overestimates (and subjective impressions indicate that the largest pack sizes may be underestimated). However, these smallest groups would be the most vulnerable during interpack hostilities, and would receive a significant benefit if their size were often overestimated through their howling. This would be especially true during pack formation, when two wolves are faced with the task of establishing their territory within a mosaic of hostile neighbouring packs. Once their territory is established, the benefit of sounding larger than reality periodically returns when the pack's numbers are reduced by mortality or emigration, though probably not to the same extent as during their initial establishment. A similar exaggeration of apparent size may also occur with scent marking, which serves as the pack's other primary means of

territory maintenance. Peters and Mech (1975) and Rothman and Mech (1979) both found that newly established pairs scent marked at significantly higher rates than did established pairs, and at rates more often found in larger packs.

If chorus structure has evolved to exaggerate a pack's apparent size, then the Beau Geste hypothesis advanced by Krebs (1977) may explain its evolution. Krebs proposed that large song repertoires in the males of some bird species may have evolved because they increased the apparent density of resident territorial males and thus deterred the immigration of non-resident males. Males with larger repertoires were thus more successful in deterring settlers than those with smaller repertoire. The Beau Geste hypothesis has been criticized on a number of theoretical grounds, among these being (1) the evolutionary spiral of deception (i.e. small lies must be followed by increasingly larger lies to remain effective as the trait spreads in the population) and (2) the vulnerability of deception to probing (i.e. immigrants which had to see and not just hear the residents could easily unmask the fraud).

For wolf chorus howling, the structural parameters which may exaggerate pack size are indeed widespread, which would seemingly diminish any genetic benefits of the deception, as all packs would sound larger than life. However, it is likely that there is an upper limit to perceived pack size, governed by the capacity of the wolf's short term auditory processing system. For humans, the limits of short-term memory are between five and nine items (Miller 1956); similar limits would be expected for wolves. My own subjective impression is that packs of five to seven wolves sound no different than packs of 10 to 12 individuals, and the data in Table 2 support this conclusion. Thus the size of the lie may be finite: packs can only sound so large. It is also likely that the effect of the deception decreases as pack size increases. Thus the perceived increase in size is largest for the smallest packs. In this manner, all packs may benefit from the exaggeration of numbers, but only on a periodic basis when their numbers are small (and they are consequently most vulnerable).

The deception may also be relatively immune to probing due to the potentially high costs associated with closely approaching a neighboring pack. Wolf packs do not frequently meet, but when they do, chases are inevitable and fighting resulting in mortalities is common (Mahrenke 1971, Mech and Frenzel 1971, Mech 1977, Harrington and Mech 1979). Thus a pack which attempts to verify its neighbor's size by probing risks triggering a potentially fatal attack should the probed pack be larger. Usually, a pack tolerates the proximity of another pack it cannot see (Harrington and Mech 1979), thus leaving the deception intact. Probing occurs rarely (< 5% of occasions) and has only been noted in response to the howling of a single stranger (Harrington 1987).

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