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AN ANALYSIS OF HOWLING RESPONSE PARAMETERS USEFUL FOR WOLF PACK CENSUSING

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Abstract: Gray wolves (*Canis lupus*) were studied from April 1972 through April 1974 in the Superior National Forest in northeastern Minnesota by radio-tracking and simulated howling. Based on replies during 217 of 456 howling sessions, the following recommendations were derived for using simulated howling as a census technique: (1) the best times of day are dusk and night; (2) July, August, and September are the best months; (3) precipitation and winds greater than 12 km/hour should be avoided; (4) a sequence of 5 single howls should be used, alternating "flat" and "breaking" howls; (5) trials should be repeated 3 times at about 2-minute intervals with the first trial at lower volume; and (6) the trial series should be repeated on 3 nights as close to each other as possible. Two censuses are described: a saturation census and a sampling census.

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Because wolves inhabit large areas, censusing them is difficult and expensive, and in many areas, impossible. Techniques used have been winter aerial tracking and observation (Stenlund 1955), aerial radio-tracking and observation (Mech 1973), and simulated howling (D. H. Pimlott, unpubl. rep., Midwest Fish and Wildl. Conf. 22, 1960; Theberge and Strickland 1978). The last technique may have considerable potential subject to certain conditions. In addition to censusing packs, replies to howling have been used to estimate pack size, composition, and home range (Joslin 1967, Pimlott et al. 1969, Voigt 1973). However, to date an adequate analysis of factors influencing the results of simulated howling has not been conducted. The present study used a radio-collared wolf population (Mech 1979) to evaluate the factors influencing the use of howling for censusing.

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STUDY AREA AND METHODS

This study was conducted in the Superior National Forest in northeastern Minnesota, between April 1972 and April 1974. The topography is generally flat, with numerous low ridges supporting mixed deciduous-conifer forest, interspersed with extensive black spruce (*Picea mariana*) bogs and open water (Mech and Frenzel 1971).

Wolves were trapped and radio-collared, and information on pack size, affiliation, home range, homesites, and movements was obtained via twice-weekly aerial locations, and daily locations when possible during December through March (Mech 1979).

Radio-collared wolves were radio-lo-

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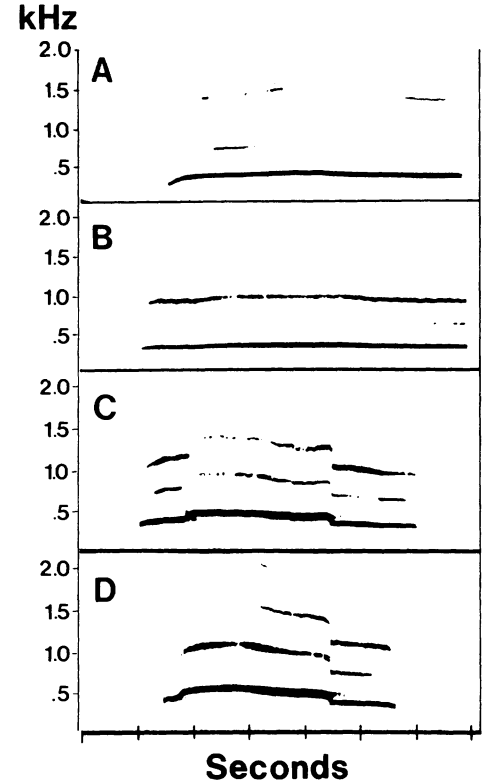

Fig. 1. Human-simulated wolf howls used during this study. A and B are "flat" howls; C and D are "breaking" howls.

cated (AVM, Champaign, Ill., LA12 receiver) from the ground and approached to within 0.2–1.0 km. The animal's signal was monitored to determine general activity. We only howled to animals thought to be stationary, using stimuli described below. Replies were recorded via a Nagra IV-D tape recorder at 38.4 cm/s. If there was no reply, a 2nd trial was attempted 2–5 minutes later. If no reply occurred after 3–5 such trials, the session was terminated, and the wolf was left for at least 24 hours. Often 3 days or more elapsed before we relocated the wolf.

Individual packs were studied from 1 to 22 months. Mean monthly sample size

Table 1. Howling reply rate of radio-collared wolves as a function of stimulus type, pack size, and location.

	Type of stimulus howl			
	Single		Group	
Pack location and size	%	*N*	%	*N*
Overall	27	1,526	32	272
At homesites				
2 small packs[a]	45	154	24[c]	34
1 large pack[b]	50	371	54[c]	90
Away from homesites				
2 small packs	9[c]	425	8[c]	61
4 large packs	20[c]	576	30[c]	87

[a] Includes 2 or 3 adults and/or yearlings.
[b] Includes 4 or more adults and/or yearlings.
[c] Differences ($P < 0.05$, G test) between small and large packs.

is the average number of sessions per pack per month studied. The Harris Lake (HL) and Jackpine (JP) packs yielded about 78% of the data; the remaining data were derived from 6 other packs.

The stimuli were 2 human imitations of wolf howling. Single stimuli were produced by 1 person (Harrington), and consisted of alternating "flat" and "breaking" howls (Fig. 1), each 5–6 seconds long, separated by a pause of 1–2 seconds. Thus a single trial lasted 20–30 seconds. Group stimuli consisted of 2 or more people howling concurrently, although normally 1 person began the stimulus, with the others joining in after several seconds. The typical length of a group trial was 30 seconds. Further details are given by Harrington and Mech (1979).

If a reply was obtained, we waited 15–20 minutes to avoid the refractory period (Pimlott, unpubl. rep., 1960) before attempting further trials. On 1 occasion, however, we tested the influence of our howling location on the refractory period. Our team split into 2 groups. One attempted to elicit howling every few minutes from 1 site. The other group, 150 m away but equidistant to the wolves, did not howl until immediately after the pack had replied for a 4th time to the first group.

"Time to response" was measured from the beginning of the stimulus to the wolves' reply. Reply rate was determined on a per-trial and a per-session basis. Reply rate per trial was used to assess the effectiveness of the 2 stimulus types. Reply rate per session was used to assess the influence of seasonal, meteorological, circadial, lunar and other environmental or biological factors. Two-tailed *G* tests (Sokal and Rohlf 1969), were used for statistical tests, with a probability level of 0.05.

Locations for the JP and HL packs from (1) all aerial and ground radiolocations, (2) radiolocations during all howling sessions, and (3) radiolocations during howling sessions with wolf replies, were plotted on 1:62,500 scale topographic maps. Home range areas were calculated after connecting the outermost locations (Mohr 1947). The ratio of (3) to (2) indicates the degree of underestimates of home range area based solely on howling replies.

RESULTS

Stimuli

Overall, there was no difference ($P > 0.05$) in reply rate to single and group stimuli (Table 1). However, small packs replied less ($P < 0.05$) than large packs to both types of stimuli away from homesites, and to group stimuli at homesites. Reply rates for small and large packs were similar only at homesites when single stimuli were used.

Packs often did not reply to the 1st trial. During 217 successful howling sessions, the 1st stimulus was answered only 68% of the time. After the 2nd trial, 86% of the groups had replied, and this increased to 95% after the 3rd trial. Further trials had only insignificant effects. The average time for a pack's reply was 30.0 seconds ($N = 262$). Less than 9% of the replies occurred after 60 seconds, and only 1.5% took more than 90 seconds.

When wolves were within 100–200 m, responses were best elicited if we howled at a low volume. During sessions when both "normal" and "low" volume howls were presented, 35% ($N = 40$) of the normal howls were answered, whereas 70% ($N = 23$) of the low volume howls elicited replies ($G = 7.13$, $P < 0.50$).

During our 1 test of the refractory period, the group that periodically attempted to elicit replies obtained them only after periods of 14, 20, and 15 minutes. The 2nd group then howled immediately after the last wolf reply, and the pack answered within 45 seconds.

Other Factors

Sky condition (clear, partly cloudy, cloudy, overcast) and precipitation (none, rain, snow) had no ($P < 0.3$ in both instances) effect on reply rate. Wind did influence reply rate, but only away from homesites. The reply rate was higher ($G = 6.64$, df $= 1$, $P < 0.01$) for calm air than for the 3 wind speed classes.

Responsiveness to simulated howling varied ($P < 0.05$) throughout the year; a short-lived peak occurred during the breeding season and a more prolonged peak during summer and fall (Fig. 2). Data from the least responsive pack (HL) indicated that the 2 peaks were equivalent, but the larger pack was much more responsive during summer and fall.

Packs differed greatly in their responsiveness (Fig. 2). After a single howling session in July, for example, the probability of discovering the least responsive pack (HL) was only 0.3, whereas most

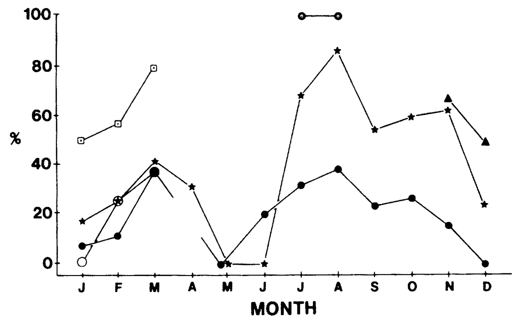

Fig. 2. Seasonal differences in reply rate to human-simulated wolf howling. Reply rate is the percent of nights (sessions) replies were obtained. Pack and mean monthly sample size: ★ = Jackpine pack (21), ● = Harris Lake pack (13), ⊡ = Ensign Lake pack (6), ▲ = Sawbill pack (4), ○ = Perch Lake pack (5), ⊛ = Birch Lake pack (12). Superimposed points indicate same values for 2 packs.

other packs were at least twice as likely to be heard after a single session.

Considerable diurnal differences in howling reply rate were found (Table 2). Differences between dusk and night were small, but the response rate at homesites was lower ($G = 5.49$, df = 1, $P < 0.05$) during the day. This difference further increased ($G = 6.52$, df = 1, $P < 0.05$) once wolves began traveling nomadically. Neither the phase of the moon nor the visibility (or light) of the full moon affected the reply rate.

Home Range Size

Although howling sessions were conducted over significant portions of pack home ranges (48–93%; $\bar{x}$ = 67%), replies were obtained only from much smaller areas, especially during summer when most were from homesites (Table 3).

DISCUSSION

Packs of different size vary in their responsiveness to simulated howling (Harrington and Mech 1979). A valid censusing technique must reduce these differences to ensure that all packs are

Table 2. Diurnal effects on howling reply rates of radio-collared wolves.

	At homesites		Away from homesites	
Time	Percent reply	*N*	Percent reply	*N*
Day	62	39	17	54
Dusk	78	23	37	41
Night	81	105	33	194
G	5.57		6.71	
P	≈0.05		<0.05	

likely to be located. The procedures outlined below are intended to both maximize the probability of replies, while also equalizing reply rates among packs.

Stimuli

While slightly less effective than group stimuli, single stimuli should be used because they reduce the difference in reply rate between large and small packs. If censusing is done in summer or early fall when packs occupy homesites, the differences in reply rates among packs should be minimal.

When single stimuli are used, the type of howl may be crucial. A preliminary analysis of single wolf howling distinguished "flat" from "breaking" howls (Fig. 1), each probably being modal representatives along a graded continuum (Harrington 1975). The relative effectivness of these 2 howls for eliciting replies is unknown, but captive wolves replied more readily to "breaking" howls (F. H. Harrington, unpubl. data). For now, we recommend alternating "flat" and "breaking" howls with 5 howls per trial.

Packs did not always answer the 1st trial during a session, but most had replied by the 3rd. Therefore, 3 trials, separated by about 90 seconds, should be made at each census location.

If wolves were close, we obtained

Table 3. A comparison of home range size of wolves as determined by radiotelemetry and howling replies.

Season, pack, and year		Home range size (km²) as determined by: All radio-locations	Locations during howling sessions	Replies during howling sessions
Jun–Sep				
Harris Lake	1973	131.6	65.4	19.4 (29.7%)[a]
Jackpine	1973	186.9	151.2	35.6 (23.5%)
Oct–Apr				
Harris Lake	1972–73	170.3	81.5	40.4 (49.6%)
Harris Lake	1973–74	183.0	87.4	34.4 (39.6%)
Harris Lake	1972–74	183.0	111.9	54.3 (48.5%)
Jackpine	1972–73	243.0	199.7	146.4 (73.3%)
Jackpine	1973–74	238.1	221.1	173.0 (78.3%)
Jackpine	1972–74	273.9	265.6	241.0 (90.7%)

[a] Percentage of area within which replies could have been obtained.

higher rates when we howled at lowered volume, possibly because loud howls are intimidating and may inhibit replies. Thus the 1st trial should be conducted at a low volume. If no reply is obtained, additional trials may be conducted at high volume to maximize range. Similar recommendations were made by Pimlott (unpubl. rep., 1960).

The distance between howling sites is important with regard to optimizing the area of coverage in the time available. Sites too closely spaced may provide good coverage but waste time, whereas sites too widely spaced may miss wolves. The effective range of vocalizations is 1 consideration in optimizing spacing. Under optimal conditions, we have heard replies at distances over 5 km; circumstantial evidence indicates that wolves replied to us at distances up to 10 km (Harrington and Mech 1979). Normally, however, 3.2 km appears to be the maximum human range of hearing howls, especially during summer, when packs sometimes frequent low-lying bogs, and interference from other natural sounds (running water, vocalizing animals, etc.) is common (Pimlott, unpubl. rep., 1960). A spacing of 3.2 km between sites is recommended. Local conditions such as topography and vegetation should be taken into consideration.

Our study suggests that wolves probably are refractory to howling (Pimlott, unpubl. rep., 1960) only if both humans and wolves remain at the same locations. Movement to a site several kilometers away should eliminate effects of previous replies, so it does not appear necessary to stagger sites (Pimlott, unpubl. rep., 1960) during surveys conducted on the same night.

Packs do not reply every night. During both peak reply periods (Fig. 2), the lowest reply probability was about 0.3. To ensure that replies are obtained from most packs at least once, surveys should be repeated for 3 nights over the same route. If possible, these nights should be consecutive to minimize complications due to pack movements between nights.

Other Factors

The major influence of weather appears to be its effect on sound transmission. Reply rates were lower during winds than in calm air. Responses obtained during moderate wind were only from nearby packs. Because locations of wolves would be unknown during censuses, work should be suspended when winds exceed 12 km/hour. Rain increases ambient noise, and snow is a good sound absorber; therefore both should be avoided (Pimlott, unpubl. rep., 1960). Packs reply less often during daylight. Censusing should be done between dusk and dawn.

The reply rate is high enough to use the howling technique during the midwinter breeding season, and from midsummer through early fall (Fig. 2). Seasonal differences in pack movements and composition seem to us to make the latter period more advantageous for censusing. In contrast to winter, homesites comprise the focus of summer pack activity (Joslin 1967, Pimlott et al. 1969, Harrington and Mech 1978), and pack movements are short and infrequent. Most homesites are used for at least 3 consecutive days (Joslin 1967, Voigt 1973, Harrington and Mech 1979).

One caution should be considered in summer censusing. Packs usually occupy only 1 homesite at a time, especially small packs with only a few pups. However, large packs may sometimes occupy 2 homesites concurrently, particularly from late July through September (Harrington and Mech 1979). In our study, packs occupied more than 1 homesite on 8 of 143 days. Although relatively uncommon, multiple homesite use could inflate estimates of pack numbers. When more than 1 homesite was used, however, only 1 appeared to be of primary importance. Secondary homesites could be recognized by: (1) their location near another homesite that contained several pups with adults ($\bar{x}$ = 3.8 km; N = 2); (2) presence of only 1 or 2 pups (12 of 12 nights); and (3) the absence of adults (10 of 12 nights). Such splitting occurs most often as homesites are gradually abandoned and 1 or 2 pups lag behind (Harrington 1975, Harrington and Mech 1982*a*). Since both lagging pups and their packs are responsive to howling at this time (Harrington and Mech 1979), the potential for overestimating pack numbers increases after September.

Limitations of the Howling Technique

Detecting Social Units of Varying Sizes.—The howling technique may be biased towards detecting larger packs, since they seem most responsive. This bias can be reduced by using single stimuli and by censusing during summer and early fall. Adults accompanied by pups are more responsive than the same adults alone (Pimlott, unpubl. rep., 1960; Harrington and Mech 1979), so the howling technique would be less sensitive to packs unsuccessful in producing young. Lastly, the howling technique is almost totally insensitive to detecting lone wolves (Harrington and Mech 1979).

Determining Pack Size and Composition.—Pack replies have been used to obtain estimates of pack size and age-class composition (e.g., Joslin 1967, Pimlott et al. 1969). Pack size is usually estimated by counting each individual as it joins the chorus (Joslin 1967) and composition is determined by the relative pitch of various individuals' howls.

We have found that: (1) only the first 2 or 3 animals enter the chorus on a staggered basis, whereas the rest of the pack enters en masse, making them difficult to count (Harrington 1975); (2) subordinate adult and pup howls consist of rapid frequency modulations (yipping and yapping), adding to the chorus's complexity and making it nearly impossible to distinguish individuals, even from sonagraphs of excellent recordings (Harrington 1975); (3) some subordinate pack adults may not howl during an elicited chorus and thus are not counted (Harrington and Mech 1979); and (4) all pack members are unlikely to be present, especially during summer (Harrington and Mech 1982*b*). On 4 occasions, howling judged by experienced observers to be that of 3–5 wolves, in some instances accompanied by 2 or more pups, was actually from adult pairs alone. Because censuses typically involve only 1 or 2 contacts with a pack, the above considerations indicate that estimates of pack size and composition based on elicited howling should be viewed with extreme caution.

Determining Home Range Size.—Howling replies have been used to determine pack home ranges (Joslin 1967, Pimlott et al. 1969, Voigt 1973). Serious problems are inherent in this technique. Our determinations of home range area based on howling replies were gross underestimates, especially in summer (Table 3). This was because adult wolves seldom reply when traveling alone, or in small groups, away from homesites (Harrington and Mech 1979). Howling replies may accurately delineate the area receiving most use from both adults and pups, but will grossly underestimate the area used by adults away from homesites.

Censusing Methods

Two types of censusing approaches based on the above considerations are proposed. The "saturation census," requiring good accessibility, would be an attempt to locate all packs within a limited area, such as a preserve or national park. For the saturation census, a grid of lines at approximately 3-km intervals should be established, with each intersection consituting a census station. The exact station location can be modified to take advantage of, or avoid, pertinent environmental factors. The area censused each night should be roughly square to maximize the number of potential trials with each pack. This area should be censused on 3 consecutive nights (when possible) before an adjacent area is covered.

The "sampling census" is an attempt to estimate the number of pup litters surviving in a large area in late summer. It involves (1) howling at a large number of randomly selected areas, (2) determining the approximate mean area of coverage from the census sites, (3) calculating the ratio between number of replies received and total area covered, and (4) projecting that ratio to the entire census area.

Two main problems must be confronted with this type of census. First, it may be difficult to reach some of the selected census area. However, in raising their pups, wolves do not avoid gravel roads, rivers, trails, or other possible human travel routes, even though they do avoid concentrations of human residences. This behavior means that such routes can be used to expedite the sampling, and that sample sites occurring in inaccessible locations can be discarded. Although the sample is no longer truly random, we do not believe the results will be biased to any appreciable extent. Obviously there must be enough accessible routes well distributed throughout the census area to allow a large enough number of sites to be sampled.

The 2nd problem is that the final estimate for the area to be censused is critically dependent on the estimated mean radius of coverage of the howling from each sample site. This distance depends on topography and vegetation and on the hearing abilities of the census takers. For each study area, census takers must conduct their own tests to determine the mean effective radius of their howling. This can be done through testing groups of wolves located by simulated howling.

Because it is impossible to obtain accurate estimates of the number of wolves replying, the sampling census only indicates the number of packs or of litters of pups produced. During population declines, or scarcity of winter prey, some of these litters may perish in early winter after the census (Van Ballenberghe and Mech 1975). Nevertheless, the census would still indicate the number of breeding packs inhabiting the area. Furthermore, it should also allow year-to-year comparisons, and thus indications of population trend in any given study area.

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