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ARTICLE

Howling activity of free-ranging wolves (*Canis lupus*) in the Białowieża Primeval Forest and the Western Beskidy Mountains (Poland)

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Abstract We investigated spontaneous howling by radio-collared wolves *Canis lupus* inhabiting the Białowieża Primeval Forest (BPF), eastern Poland, and elicited howling behavior in wolves of the BPF and the Western Beskidy Mountains, southern Poland. Over half (58%) of all spontaneous howls recorded throughout a year occurred in the period from July to October, with a peak in August. The daily pattern of vocal activity by wolves was characterised by a peak between 1800 and 0000 hours, which coincided with the first (dusk) peak of wolf mobility. Wolves howled from the core areas of their territories and not from the peripheries. Howls served as communication between temporarily separated pack mates (43% of cases), after re-union (18%) and before setting out for a hunt (22%). Very few spontaneous howls (2%) were targeted at a neighbouring pack. Wolves responded to human-simulated howling in June–September, with a peak in August (reply rate: 39%). The duration of elicited howling increased significantly with group size: howls by single wolves or pairs lasted, on average, 34–40 s, whereas those of five to seven wolves (including pups) had an average duration of 67–95 s, with a maximum length of nearly 4 min. In the populations of Polish wolves studied here, spontaneous howling served primarily for intra-pack communication. Nonetheless, the high reply rate to howling simulation showed that – if necessary – wolves readily advertised their presence in a territory to strangers.

Keywords *Canis lupus* · Elicited howling · European wolves · Intra-pack communication · Spontaneous howling

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Introduction

Wolf howling occupies an important role in inter- and intra-pack communication (Joslin 1967; Theberge and Falls 1967; Harrington and Mech 1978a, b, 1979; Dekker 1985; Harrington 1987; Nikolskii et al. 1986; Nikolskii and Frommolt 1989; for review, see: Harrington and Asa 2003). Within packs, howling serves as a long-distance contact call, facilitating reassembly (Harrington and Asa 2003). Among packs, howling is a communicative signal that helps residents and intruders avoid confrontations and residents maintain territories (Harrington and Mech 1979).

Most studies of wolf howling have relied on the use of recordings or live human imitations as stimuli to elicit responses. Studies in North America (Harrington and Mech 1979) revealed that human imitations of howling are treated by adult wolves as an intruder's call and that the main reason for replying is to keep the strange wolf at a distance. Pups under 4 months of age, however, appear to treat human stimuli as howls of other pack members and readily reply to them. The high rate of replies by adults in the summer was thought to be related to the greater protectiveness of a pack towards young pups during that period (Harrington and Mech 1979). A similar late summer–early autumn peak of elicited howling has also been reported from the Northern Apennines, Italy (Gazzola et al. 2002) and from Russia (61% in August, Nikolskii and Frommolt 1989). In addition to the summer peak, Harrington and Mech (1979, 1982), in their studies on radio-collared wolves, found a secondary, winter peak (during mating season) of responsiveness to simulated howling.

However, data on spontaneous howling remain scarce. Most of the data available has been collected from occasional opportunistic observations during wolf tracking expeditions throughout the year or from systematic monitoring programmes in the spring and summer only, when packs spend much of their time at the den and rendezvous sites due to pup-rearing (Harrington and Mech 1978a; Nikolskii et al. 1986). Harrington and Mech (1978a), who studied spontaneous howling by wolves during the pup rearing season, found a significant increase in howling frequency around the beginning of August. These researchers felt that this increase represented a growing need for long-range intra-pack communication as pups became more mobile as well as an increasing demand for long-distance advertisement (inter-pack communication) to avoid encounters with strange wolves. They predicted that the howling rate should remain high or even increase during the fall and winter, when packs abandon their homesites and begin to travel over their entire territories (Harrington and Mech 1983). Unfortunately, to date, there have been no systematic studies of spontaneous howling for most of the year, when packs travel extensively throughout their territories.

We present data on both spontaneous howling by wolves that were studied by radio-tracking throughout the year in the Białowieża Primeval Forest (BPF), eastern Poland and howling elicited by stimulated howling in two populations – that from the Białowieża Primeval Forest and the second from the Western Beskidy Mountains, southern Poland. Our aim was to investigate: (1) daily and seasonal variation in wolf howling rates; (2) the social context of howling; (3) response rates by wolves to stimulation; (4) duration of howls in relation to the number of vocalising wolves.

Study areas

The BPF (52°30′–53°N, 23°30′–24°15′E), eastern Poland, is one of the last natural woodlands in the lowlands of temperate Europe. It is located on the Polish-Belarussian border and comprises mixed and deciduous tree stands of spruce (*Picea abies*), pine (*Pinus silvestris*), oak (*Quercus robur*), hornbeam (*Carpinus betulus*), black alder (*Alnus glutinosa*), ash (*Fraxinus excelsior*), lime (*Tilia cordata*) and maple (*Acer platanoides*). Most of the Polish part of the BPF (530 km^2) is a commercially exploited forest managed by the State Forests; the remainder (100 km^2) forms the Białowieża National Park (BNP), with a small (47 km^2) zone under strict protection. The BPF harbours a rich community of ungulates, including European bison (*Bison bonasus*), moose (*Alces alces*), red deer (*Cervus elaphus*), roe deer (*Capreolus capreolus*) and wild boar (*Sus scrofa*), as well as two species of large predators, the wolf and the lynx (*Lynx lynx*). In 1996–1999, three to four wolf packs (15–18 individuals in total) inhabited the study area. The population density was 2.3–3 wolves/100 km^2, and the territories of the packs covered an area of 137–323 km^2 (Jędrzejewski et al. 2002). For more information on the BPF, see Jędrzejewska and Jędrzejewski (1998).

The Western Beskidy Mountains (WBM; 49°23′–49°53′N, 18°45′–19°48′E), southern Poland, are located in the western range of the Carpathian Mountains, near the Polish-Slovakian and Polish-Czech borders. The region includes the Silesian and Żywiec Beskidy ranges. Mountain ridges are cut by deep river valleys, and the altitude varies from 300 to 1725 m a.s.l. Most of the area is covered by spruce forest with admixtures of beech (*Fagus sylvatica*), fir (*Abies alba*), black alder, ash and sycamore (*Acer pseudoplatanus*). Most of the forests are commercially exploited. The study was conducted in an area of approximately 300 km^2. The ungulate community consists of red deer, roe deer and wild boar, whereas the guild of large predators includes wolf, lynx and brown bear (*Ursus arctos*) (Nowak et al. 2005). In 1997–2001, four packs (14–23 wolves in total) lived in the study area. The population density was 2.2–3.2 wolves/100 km^2, and the territories of packs covered an area of 98–227 km^2 (Nowak 2002; Nowak et al. 2005).

Materials and methods

Data on spontaneous howling by wolves were collected by means of radio-tracking the wolves in the BPF during the period 1994–1999. Twelve wolves belonging to four packs were live-trapped and radio-collared (for details, see Jędrzejewski et al. 2001). Radio-tagged wolves were located by triangulation 2–5 days per week by following forest roads with a vehicle or bicycle. In addition to daily locations, sessions of 2–9 (usually 4–6) days of continuous radio-tracking were conducted with locations taken at 30-min (March 1994–December 1996) or 15-min intervals (January 1997–September 1999) (Jędrzejewski et al. 2002). Observers followed the wolves from a mean distance of 0.94 km (Theuerkauf and Jędrzejewski 2002). During 390 days of continuous radio-tracking, 136 spontaneous howls by wolves were heard. In 115 cases, observers noted the time of the howl in detail, and in 93 cases the context of howling was described based on the wolves' behaviour prior to and after howling (movements, kill remains found, prior and consecutive radio-tracking, consecutive snow tracking, known pack composition, etc.). We made an effort to cover all packs and the entire year with a similar intensity of continuous radio-tracking; monthly samples varied from 19 days in December to 55 days in February, and averaged 32.5 days per month (standard error: 2.5).

Data on elicited howling were collected mainly in the WBM between 1997 and 2001 using human-made howl imitations (Joslin 1967), which consisted primarily of a 'single' (rather than 'group') stimulus (Harrington and Mech 1982). Weather permitting (calm nights without rain), one person emitted three 6- to 7-s-long howls, separated by 2- to 3-s-long breaks, in open places (e.g. summits, forest roads, clearcuts). In total, each trial lasted about 35 s. If we did not elicit a response within 2 min, a second trial of howls was produced, followed by a third one if necessary. In the WBM, howling sessions were conducted on 163 days, during all months of the year. In total, we obtained 61 replies from wolves on 24 days. For all replies we recorded the date, time of initiation and length of the howl. We assessed the number of replying adult wolves and the presence and number of pups on the basis of live aural analysis of the replies as the wolves howled or subsequent analysis of recordings of the replies.

In the Augusts of 1997, 1998 and 1999, we conducted 17 sessions of stimulated howling in the BPF in situations when radio-collared wolves were located nearby. Field helpers were placed in the forest at a distance of 1.5 km from each other in order to hear the replying wolves. One or two howlers emitted stimuli, as described above. The time was noted and the number of wolves was estimated for each reply.

Results

Seasonal and daily rhythms of wolf howling activity

Overall, spontaneous howling by wolves in the BPF was heard at a mean annual rate of 0.35 howls/day, with monthly rates ranging from 0.14 howls/day in November to 0.78 howls/day in August. However, as these figures are underestimates of actual howling rates (see Discussion), we presented them as relative measures (percentages) corrected for unequal listening effort. The monthly distribution of spontaneous howling (Fig. 1) significantly differed from a homogenous pattern (G=30.10, df=11, p<0.01; G-test for homogeneity of percentages). Up to 58.4% of all howls recorded throughout the year were heard in July–October, with a peak in August (18.8%). The vocal activity of the wolves was low to moderate in November through June (3.4–6.8% monthly). Such a seasonal rhythm of wolf spontaneous howling corresponded well to their response rates to stimulation in the WBM (Fig. 1). Wolves answered human 'howling' in June–September only, with a peak in August (responses to 39.4% of stimulation). Moreover, amongst 17 stimulated howling sessions conducted in the BPF in August (1997–1999), wolves responded to stimulation in 12 cases (70%) and kept silent in only fives cases (30%).

The daily pattern of wolf vocal activity in the BPF is presented on the background of total activity of radio-collared animals, recalculated from Theuerkauf et al. (2003) (Fig. 2). In general, the wolves showed a high level of mobility during the whole day. However, two peaks of activity(wolves were active more than 50% of the time) were recorded: at dawn (0400–0800 hours) and dusk (1800–2200 hours). During the mid-day hours (1000–1600 hours) the wolves were active less than 40% of the time. The daily pattern of wolves' vocal activity had only one peak, at 1800–0000 hours. Very little howling was recorded during the daytime, from

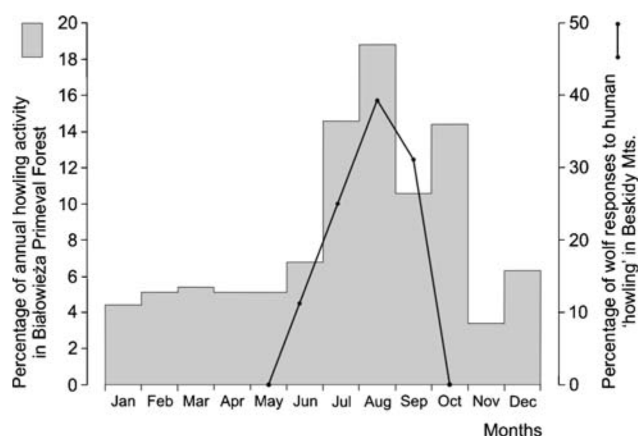

Fig. 1 Annual pattern of spontaneous howling activity of radio-collared wolves (*Canis lupus*) in the Białowieża Primeval Forest (BPF), eastern Poland (*grey bars*; n=136 howls) and response rates by wolves to human 'howling' in the Western Beskidy Mountains, southern Poland (*black line*)

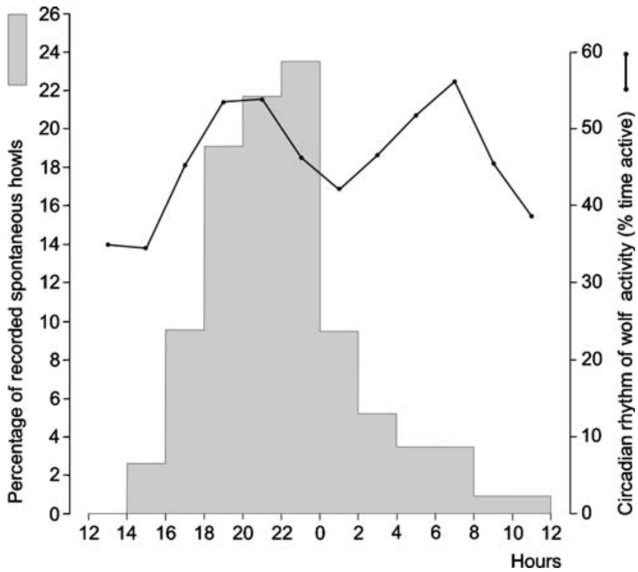

Fig. 2 Spontaneous howling (*grey bars*; *n*=115 howls) in relation to daily rhythm of activity of wolves in the BPF (*black line*; recalculated from Theuerkauf et al. 2003)

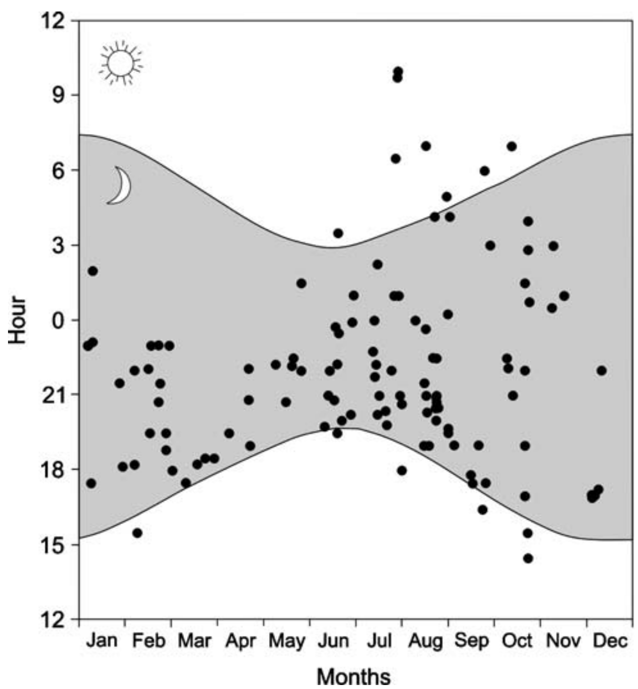

Fig. 3 Cases of spontaneous howling by wolves in BPF in relation to day- and night-time throughout the year

0800 to 1600 (Fig. 2). The daily pattern of wolves' howling was significantly different from a homogenous distribution over 2-h periods (G=165.47, df=11, p<0.001).

We plotted the incidences of spontaneous howling in relation to day- and night-time throughout the year (Fig. 3). The evening peak of howls usually occurred just after sunset. Daytime howls (heard after sunrise) were recorded only in June–October.

Spatial distribution of spontaneous howls in wolf territories

In two neighbouring packs in BPF, all of the recorded howls were mapped in the territories estimated to be the Minimum Convex Polygons (MCPs), which contained 100% of the locations collected from the spring of 1998 until the spring of 1999 (annual territories). Wolves howled from the central parts of their territories (where the den for breeding was also located) and not from the peripheries (Fig. 4). Although the size of the whole territories was 213 and 285 km^2, respectively, howling was recorded only on an area of 68 and 32 km^2, respectively, comprising 32 and 11% of the total area. For these two packs, the polygons delimited by 100% of the howling records were equivalent to MCP75% (pack on the right in Fig. 4) and MCP50% (pack on the left) of the radio-tracking locations.

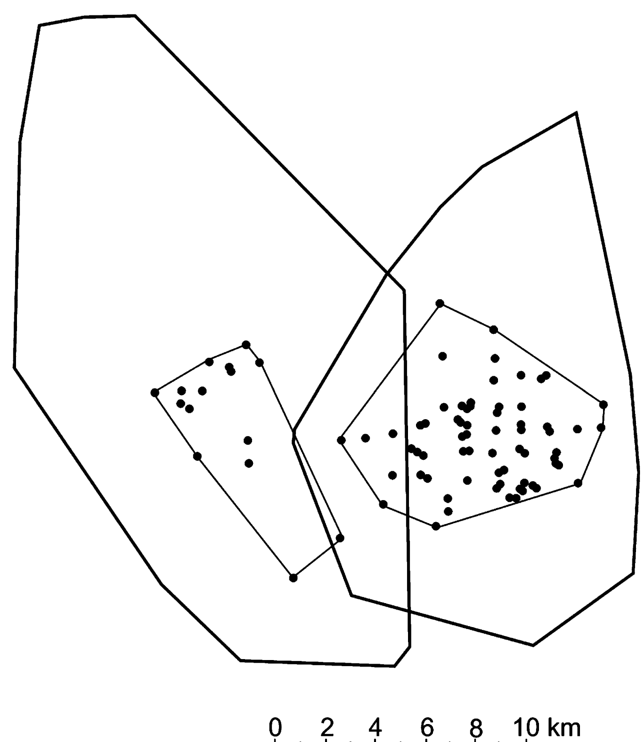

Fig. 4 Distribution of spontaneous howling in territories of two wolf packs in BPF in 1998–1999. Wolf territories (Minimum Convex Polygons with 100% of radio-locations) are according to W. Jędrzejewski and co-workers (unpublished data). Inner polygons enclose an area with 100% of the recorded howls

Duration of elicited howls in relation to group size

The duration of the 56 elicited howls varied from 15 to 210 s and averaged 67 s (SE: 5). Wolves usually joined the chorus howl one by one, with some time lag after the first vocalising animal. The number of wolves in a howling group (range: 1–7) explained 31% of the observed variation in the log-transformed duration of a howl (Fig. 5). The regression line showed that howls of single wolves and pairs lasted, on average, 34–40 s, whereas those of packs with five to six wolves (always including pups) were longer, typically averaging 67–95 s (Fig. 5).

Social context of howling

For the data collected in the BPF, circumstances accompanying cases of spontaneous howling allowed us to interpret the social and behavioural context in 93 cases (ten cases remained unclear). Throughout the year, 43% of howls served as communication between members of the same pack that were temporarily separated (Table 1). Such situations included long-distance communication between wolves before their re-union in the woods (compare Murrie 1944, p 106; Mech 1966, p 66), howls by pups and/or a subadult wolf at the den when adults were absent and howls by adults returning to rendezvous sites. Howls of the whole pack that were emitted after re-union comprised 18% of all recorded vocalisations. In 22% of the cases, the pack howled when setting out for a hunt, and in 5% of the cases they howled at a fresh kill. Very few howls (2%) involved direct communication between neighbouring packs (Table 1).

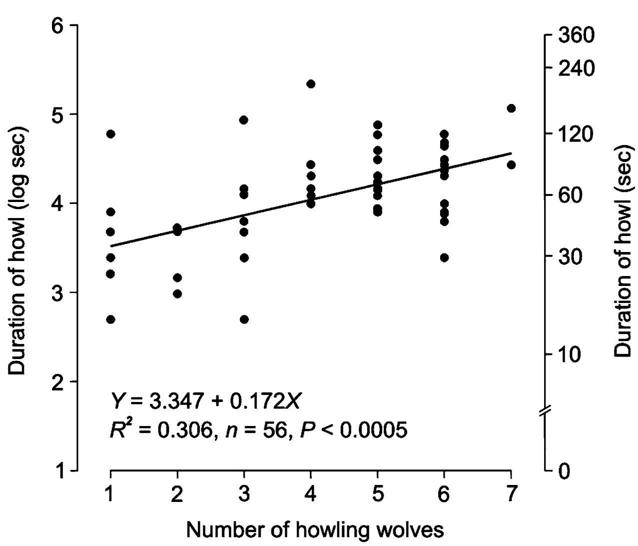

Fig. 5 Duration of elicited howls [n=46 cases from the Western Beskidy Mountains (WBM) and ten from the BPF] in relation to the estimated number of howling wolves

Table 1 Interpretation of social and behavioural context of spontaneous howling by wolves in the Białowieża Primeval Forest, eastern Poland, based on data from continuous radio-tracking

Interpreted role of howling	Percentage of recorded howls
Communication between two parts of the same pack	43
Including:	
Long-distance communication between two groups of the same pack prior to re-union	*23*
Pups and/or helpers at the den communicating with other pack members	*16*
Adults locating the pups prior to re-union	*4*
Before setting out for a hunt	22
After re-union of temporarily split pack	18
At a fresh kill	5
Long-distance communication between adjacent packs	2
Undetermined	10
Total	103 (100%)

In the Beskidy Mountains, some casual behavioural observations were made during howling stimulation sessions. Twice the ‘howling’ observers were approached by responding pups (visual observation). In three cases, first a single wolf or a wolf with pups responded, and then the whole pack replied from a long distance, moved towards the observers or returned directly to the resting place with the pups and howled. Twice the whole pack retreated during howling (consecutive howls heard from increasingly longer distances). In one case, the ‘howling’ observers were silently approached by a pack (visual observation).

Discussion

Despite the large and systematic effort to record vocal activity of wolves under natural conditions, the data collected here are underestimates of the actual rates of spontaneous howling. First, the audibility of the howls (usually 1–2 km) was lower than the range of the radio-telemetry signals (up to 3 km; Theuerkauf and Jędrzejewski 2002). Secondly, weather conditions (wind and rain) were important factors hindering the audibility of howls. Finally, and most importantly, a large number of the locations was determined by observers following the wolves in a vehicle. This means that the observers were usually able to hear the howling only when they got out of the vehicle for

2–5 min at 15- or 30-min intervals. However, all of these factors causing underestimate of wolves' vocal activity did not vary in any systematic way among seasons or time of the day. Therefore, we believe that the relative temporal changes in the intensity of spontaneous howling by wolves in the BPF are well reflected in our results.

Our study has documented that wolf howling, a long-distance vocal communication, serves various functions. The spatial and temporal distribution of the howls (vocalisations occurred most often in the core areas of the territories in July–October, when pups were 2–6 months old) strongly suggest that intra-pack communication prevailed over inter-pack signalling such as territory advertising or warning against strangers. Indeed, howling was infrequent in April–June, as if the wolves were reluctant to disclose the location of a breeding den and small pups. A possible explanation for why the territoriality function of wolf howling was less important than intra-pack communication is that not all pack territories in BPF were surrounded by other territories. Nonetheless, the fairly high response rate by wolves to simulated howling showed that whenever facing the risk of unknown intruders, wolves can readily and immediately advertise their presence in a territory.

In the dense forests of both Białowieża and the Beskidy Mountains, the wolf howls were usually audible (to humans) up to 1–2 km. This is a rather short distance compared to maximal values of 10 and 16 km reported by Harrington and Mech (1978b) and Henshaw and Stephenson (1974) for North American forest and tundra, respectively. But there again, the territory size in Poland is much smaller than those in the forest zones of North America (Jędrzejewski et al. 2001).

Our results did not confirm the prediction by Harrington and Mech (1978a) that the howling rate should remain high or even increase during the fall and winter. In our study, howling frequency was high in the summer and early autumn, but it decreased significantly in the late autumn and remained relatively low throughout the winter and spring. This suggests that high howling activity is connected with pup rearing and plays an important role in intra-pack communication during that period. In late autumn, when pups travelled with the hunting pack, spontaneous howling significantly decreased. In Minnesota, USA, Harrington and Mech (1982) found a second peak in wolf vocal activity during the mating season (in March), we did not find this peak during our study period. On the other hand, our study showed infrequent but regular howling in the early denning period (May–June), whereas the wolves studied by Harrington and Mech (1982) kept largely silent during that time. One possible explanation for these differences may be the respective methods used. While we recorded spontaneous howls, Harrington and Mech (1982) studied reply rates to human-stimulated howling. Thus, in the latter study, the inter-pack context of howling was being deliberately provoked, which may have made wolves both more ready to reply during the breeding season as well as more reluctant to reply during the early denning period.

Wolves howled mostly from the central parts of their territories. A similar pattern was revealed in studies on distribution of scent marks by wolves (Zub et al. 2003), where marks were concentrated in ''hot spots'', such as in the vicinities of the breeding dens. This result corresponds well with those of previous studies in which wolf howling, similarly to scent marking, was considered to be an important mode of territory maintenance through advertisement (Harrington and Mech 1979).

According to Harrington and Mech (1982), a precise count of those wolves howling in a large group is difficult, but the recognition of two to three individuals joining the chorus in sequence is possible. Moreover, there is a clear difference in the frequency and duration of sound produced by adults and pups younger than 6 months (Harrington and Mech 1978b; Harrington 1986; Nikolskii et al. 1986). Therefore, howling stimulation has been used successfully as a method of estimating wolf numbers and the composition of packs (Theberge and Pimlott 1969; Theberge and Strickland 1978; Zimen and Boitani 1975; Ciucci et al. 1997; Ciucci and Boitani 1999). We found that our estimates of wolf numbers based on howling generally corresponded well to the data on pack size and composition obtained by radio-telemetry and/or snow tracking.

The average duration of elicited howling in our study was similar to that found in Minnesota (Harrington and Mech 1979) and shorter than that observed in Canada (Joslin 1967). Contrary to our study, Harrington (1989) found that, in Minnesota, the mean duration of chorus howls by wolves did not vary with pack size or composition. The longer duration of howling by larger groups, as recorded in Polish wolves, may be explained by the pattern of group howling observed both in captive (Zimen 1976) and free-living wolves (Joslin 1967; Harrington and Mech 1979). At the beginning, wolves join the chorus howl one by one, first the dominant wolf and then two to three other individuals. Thus, more wolves in a group may stimulate each other to longer or repeated howling.

In conclusion, our study provides data showing that the wolves howled most intensely between July and October, usually at dusk and at night, and in the core areas of their territories. Spontaneous howling by wolves served primarily as an intra-pack communication. Nonetheless, high response rate to howling simulation suggested that – if necessary – wolves readily advertised their presence in a territory to strangers.

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