Behavioral and ecological implications of seasonal variation in the frequency of daytime howling by Yellowstone wolves

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Long-distance vocal communication exists in many group-living carnivores. Understanding its behavioral and ecological significance suffers from few quantitative studies in undisturbed, wild populations. In Yellowstone National Park, Wyoming, United States, we examined seasonal changes in occurrence of wolf howls and howling replies based on more than 11,000 unsolicited howls given over a 10-year period. Howling was 5-fold most frequent in the pre-breeding and breeding seasons. Pack howls primarily, but also single howls, were most common during these seasons. Answers during these seasons were predominately interpack howls. These howling peaks correlated with elevations in estradiol, testosterone, and luteinizing hormone reported elsewhere. Following the breeding season, overall howling abruptly decreased through March and April, although howling at den sites was frequent, particularly in April and May. Howling frequency remained low all summer, during which time answers switched abruptly and almost exclusively from interpack to intrapack. Single howls stimulated distant pack members to answer with increasing frequency as the summer progressed. Although not independent, the frequency of both total howls and interpack howling rose throughout the fall. We relate these seasonal changes in total howling and interpack answers largely to breeding and spacing behavior in pre-breeding and breeding seasons, and intrapack answers to pack cohesion in other seasons. Because our results may reflect a high-density, unexploited wolf population, comparative studies under other conditions would be useful.

Key words: *Canis lupus*, communication, howl, vocalization, wolf, Yellowstone

Most group-living canids (dingoes, *Canis lupus dingo*; coyotes, *Canis latrans*; red wolves, *Canis rufus*; gray wolves, *Canis lupus*; and eastern wolves, *Canis lycaon*), hyaenids (spotted hyenas, *Crocuta crocuta*), and felids (African lions, *Panthera leo*) engage in long-distance vocal communication. Detailed studies of their undisturbed behavior are few because they all are somewhat elusive and require large study areas. Current understanding of wolf howling is based on "evidence that ranges from speculative through anecdotal to quasi-experimental" (Harrington and Asa 2003). Our objective was to examine seasonal changes in the frequency of occurrence of wolf howls and howling replies to understand better their behavioral and ecological significance. By relating the seasonality of howling to other seasonal changes in wolf behaviors, we hoped to contribute insights into both the triggers and the consequences of howling.

The limited literature on seasonality in wolf howling is inconsistent. Mech and Boitani (2003), based on Peters and Mech (1975), reported for wolves in the Upper Great Lakes Region of North America that "territorial advertisement and defence [including howling] tend to peak during the breeding season." Studies of captive Mexican wolves (*C. l. baileyi*—Servin 2000) and Great Plains wolves (*C. l. nubilus*—Klinghammer and Laidlaw 1979) reached similar conclusions. Nonetheless, research on wild wolves in southern Europe (Gazzola et al. 2002) and in Poland (Nowak et al. 2007) showed that howling peaked in the summer and fall, with no increase whatsoever in the pre-breeding and breeding seasons. The former study used recordings to stimulate howling. In Minnesota, where human imitations were used to elicit howls, the peak also was not during the breeding season but in October and November (Harrington and Mech 1979), with a secondary peak in March. These studies involved few packs (2 to 3) in comparatively low-density populations, with only 1 or 2 years of data. Small sample sizes may not have reflected population-level patterns due to differences in pack age, sex

ratio, and social composition, or a limited number of potential breeding partners.

Two broad categories have been advanced for the long-distance vocalizations of wolves: inter- (between) pack howls consisting largely of territorial advertisement and defence (spacing behavior) and mate attraction; and intra- (within) pack howls involving coordination of movements, reunion, and bonding within social units (summarized by Harrington and Asa 2003). The functions of howls of both categories are aided by the potential for recognition of individual wolves via their howls (Theberge and Falls 1967; Palacios et al. 2007).

We hypothesized a peak in interpack howling during the pre-breeding and breeding seasons, largely based on an expected influence of reproductive hormones. Coyotes (Gese and Ruff 1998), dingoes (Corbett and Newsome 1975; Corbett 1995), and some populations of wolves (Peters and Mech 1975; Klinghammer and Laidlaw 1979; Servin 2000) have marked peaks in long-distance vocalizations in the reproductive season, and all are monestrous. In contrast, seasonality does not occur in the whoops of spotted hyenas (K. Holekamp, Michigan State University, pers. comm.) or in the roars of African lions (Schaller 1972), both of which are polyestrous.

Seal et al. (1983, 1987), Packard (2003), and Kreeger (2003) have outlined seasonal changes in reproductive hormones in wolves. Estradiol surges during proestrus in February then drops precipitously at the end of proestrus and early metestrus (pregnancy) in late February or early March, then drops more slowly until May and remains low all summer. Testosterone remains at its seasonal high from December through March, then it, too, drops until June and remains low all summer. Luteinizing hormone, involved in testosterone production, follows the same pattern as testosterone.

Strengthening our prediction about a pre-breeding and breeding peak in interpack howling was a corresponding high level of territory-related interpack aggressive encounters at that time. In Yellowstone National Park, Wyoming, United States, a marked peak in the distribution of 292 such recorded encounters occurred in those seasons (Quimby et al. 2015).

The literature gave us less basis for predicting the frequency of intrapack howling. Intrapack howling requires separation of pack members. In an Alaskan wolf population, pack cohesion dropped throughout the summer (Peterson et al. 1984). In Yellowstone, Metz et al. (2011) reported that pack cohesion was greater in winter than in summer. Therefore, although reasons for these seasonal differences in pack cohesion were not defined, we predicted greater intrapack howling in summer. Nonetheless, any extrapolation from other studies about pack cohesion may be uncertain. A comparative analysis of winter pack cohesion among 6 widely separated North American wolf populations showed little similarity (Theberge and Theberge 2004).

Materials and Methods

We studied the fully protected, high-density wolf population in the northern range of Yellowstone National Park using no artificial stimuli to elicit howls. In 28,735 h of field observations, one of us (R. McIntyre) recorded place, time, and other information on all howls he heard. Every day without exception between 1 January 2001 and 31 December 2010, he began field observations at daybreak, averaging 7.9 h per day. Often, wolves were inactive at midday, at which time he took a break (not included in the above hours of field time), resuming in mid to late afternoon and through the crepuscular period until dark. No data were collected after dark.

The extensive, open, shrub-steppe ecosystem of the study area provided excellent opportunities for observation. Park roads provided access, and ongoing research on other aspects of wolf ecology and behavior made relevant information available on individual identities of wolves, pack structures, locations, and movements (Smith et al. 2015). From 4 to 8 packs of wolves were on Yellowstone's northern range almost every day. The population varied from 72 to 99 wolves/1,000 km^2 (Smith et al. 2015).

McIntyre had wolves within sight the vast majority of his hours in the field. He used radiotelemetry to locate wolves and to know where to observe, and he had radio contact with at least a dozen revolving volunteer "wolf watchers." Periodically, he was assisted by other personnel at Yellowstone conducting research on wolves with telemetry equipment.

All observations were made with a spotting scope directly from park roads or pullouts or from nearby promontories. Wolves were normally 1 to 3 km away. If closer, McIntyre, who often was in official park uniform, controlled visitors so that disturbance did not influence wolf behavior and park rules against harassment of wildlife were followed.

McIntyre recorded a running commentary of all wolf behavior with a voice recorder, and later transcribed his observations. All data used in our analyses were extracted from the transcriptions. Most howls could be assigned to specific packs based on telemetry identification or visual markings. Thus, our analysis frequently could distinguish howling wolves as pack or non-pack members. To avoid bias, only howls heard by McIntyre were used, and not those reported to him by others. We calculated monthly averages of howls heard per 100 h of field time.

Several rules and definitions were applied to extract the data based on what we believed to be normal, or the most commonly observed behavioral patterns based on McIntyre's > 40,000 h of observation. We defined a "howl" as 1 or a sequence of howls (typically 5–20 per wolf but sometimes more) followed by at least 5 min of silence by the wolves that howled. A "single howl" was 1 or a sequence of howls given by 1 wolf, typically temporarily away from its pack but occasionally with pack mates who remained silent. A "pack howl" was a sequence, or chorus, by > 1 pack mate within ½ km of each other. Howls were "spontaneous" if not known to have been elicited by other howling wolves. An unknown number of howls may have been misclassified if initiated by wolves howling beyond McIntyre's hearing. We assume constancy in this bias across types of howls.

An answer to a howl was considered to be another "howl," if it came from more than ½ km away and within 5 min. We classified answers as given by single wolves or packs, and by

pack mate(s) or foreigner(s), or unknown. "Foreigners" were member(s) of another pack than that of the individual(s) who initiated howling, most often an adjacent pack but sometimes a seasonally migratory or temporarily roving pack from the park's interior or from beyond park boundaries. We used the term "initiator" to designate the identity of wolves that elicited an answer, and assessed their status as single wolves or packs.

All howls or a sequence of howls were given a score of 1. When the word "continuous" or "on and off" or related terms appeared in McIntyre's notes, we added another score (i.e., counted them as 2), or occasionally a third score if noted as such a third time. Such additional scores were rare, affecting less than 1% of all records.

We also noted if howls in spring and summer were at den sites or rendezvous sites. Such sites were under direct observation at distances that did not disturb the wolves. Wolves were considered at one of these sites if within ½ km, an arbitrary but consistent distance that allowed for yearly comparisons. Rendezvous sites were under-ranked because of our occasional uncertainty. We noted if pups initiated pack howls or howled alone.

We examined departure from randomness in the pattern of seasonal howling using a 1-way analysis of variance (ANOVA) in which howls per 100 field hours was the response variable and months the explanatory variable. The years were included in the initial models, but had insignificant effects on the average howls per 100 field hours and hence were excluded from the final model. To assure no model assumptions were violated, we determined that the residuals passed the Shapiro–Wilk test ($P > 0.05$) and there were no obvious patterns in the residual plot. We used R for all statistical tests.

We also examined departures from randomness in 7 paired comparisons in the yearly patterns of various subcategories of howling (i.e., single wolves versus packs, or packmates versus foreigners). To test for significance between and within these subcategories, we used 2-way ANOVAs with howls per 100 field hours as the response variable and both months and subcategories of howls as explanatory variables. Again, the years were included in the initial models, but had insignificant effects on the average howls per 100 field hours and hence were excluded from the final models. We used Shapiro–Wilk tests and residual plots to assure no model assumptions were violated. To fully illustrate differences in patterns, we report each of these ANOVA test results with its 3 F-values: "F subcategory," which is a test of significant difference in average monthly howls per 100 hours between the 2 subcategories across the year; "F month," which is a test of significant difference occurring in at least some months within each subcategory; and "F interaction," which is a test of significant interaction or relational pattern between the 2 subcategories. For simplicity, we refer to these 3 F-values as $F1$, $F2$, and $F3$, respectively.

The research was conducted under annual scientific permits issued by the U.S. National Park Service, and met guidelines for the use of wild mammals in research approved by the American Society of Mammalogists (Sikes et al. 2016).

RESULTS

Of 11,742 howls, 5,879 were pack howls, 4,287 were single howls, and 1,576 were uncertain; 2,289 howls were answers. As a 10-year average, howling was heard every 2.4 h of field time.

Seasonal variation in howling.—Seasonal variation in howling was considerable, following a consistently similar pattern in frequency of occurrence each year (Fig. 1). The difference among months was highly significant ($F_{11,107} = 27.0$, $P < 0.001$). The monthly average number of howls per 100 h for the pre-breeding season (December and January), and the breeding season (February) peaked at 69 and 72, respectively. Howling declined sharply through the post-breeding season (March),
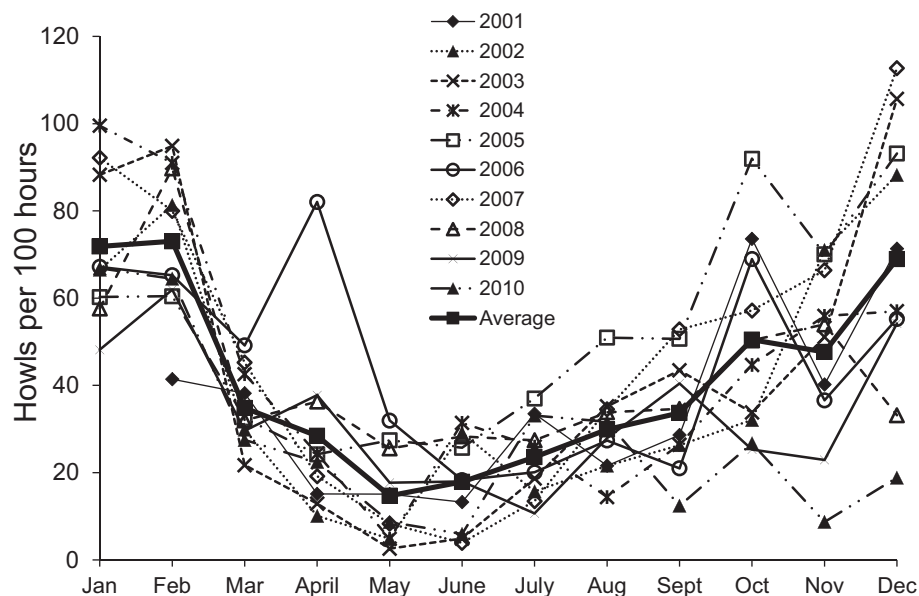

Fig. 1.—Yearly consistency in the monthly pattern of wolf (*Canis lupus*) howls on the northern range of Yellowstone National Park, Wyoming, over 10 years 2001 to 2010. All howls (*n* = 11,742) were unsolicited.

denning (April), and when pups were at dens (May). The number of howls in May averaged only 20% of those in January. Howling increased incrementally through the summer when pups were resident temporarily at various rendezvous sites, and in fall when pups began travelling with the pack, rising to a second but lower peak in October, when the number of howls was 69% of those in January (Fig. 1).

Over the 10 years of the study, only 2 major inconsistencies broke this pattern. Howls in April 2006 were abnormally frequent, represented by the highest data point shown for that month (Fig. 1). In that month, a trespassing pack invaded the den site of a resident pack and exhibited many days of aggressive behavior, preventing the resident pack from bringing food to the den site. The pups eventually starved (Smith et al. 2015). The other inconsistency was a low number of howls noted in September, November, and December 2010, shown as the lowest point for those months (Fig. 1). During this period, some packs dissolved and some new packs arose to take their places. Uncertainty in the population over trespassing wolves or pack affiliations may have influenced frequency of howling. Removal of these 4 outlier points reduces the overall monthly variability but the overall pattern is obvious and statistically significant even with these points removed (Fig. 1).

Total howls consisted of both pack howls and single howls, which followed similar seasonal patterns of frequency of occurrence (Fig. 2). The patterns for pack and single howls differed significantly ($F1_{1,216} = 24.8$, $P < 0.001$; $F2_{11,216} = 21.1$, $P < 0.001$; $F3_{11,216} = 2.6$, $P = 0.003$). Pack howls were more frequent than single howls in November through January and again in March. A large increase occurred in single howls in December, January, and February. Removing answering howls did not affect the patterns, and patterns for the 2 categories still differed significantly.

Answering howls.—The 2,289 answering howls represented 19.5% of all howls. Answering howls followed the same consistent patt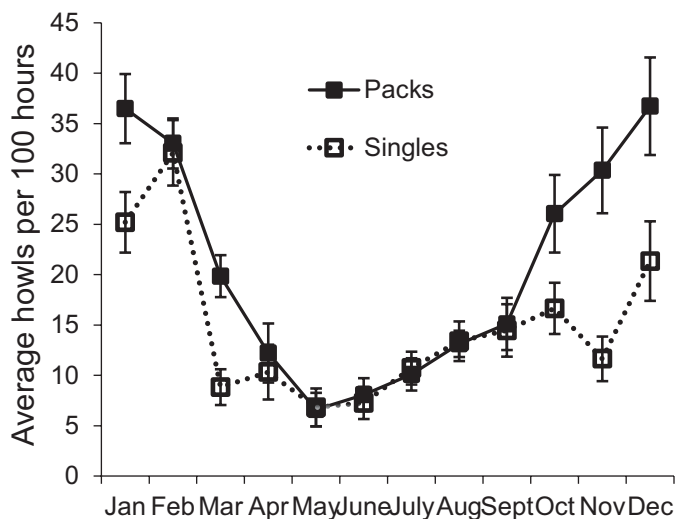ern of seasonality as did spontaneous howls, although with less dramatic differences between seasons (Fig. 3). Average means and monthly variation differed significantly ($F1_{1,216} = 480.8$, $P < 0.001$; $F2_{11,216} = 24.9$, $P < 0.001$). The 2 subcategories did not show interaction effects. The mean monthly contribution of answers to total howls ranged between 13% and 23%, being marginally greatest in months where total howls were greatest—December, January, and February.

Answers by packs versus single wolves.—Answers were given predominately by packs (967 times or 67.8%) compared to single wolves. Their monthly patterns differed significantly ($F1_{1,216} = 40.0$, $P < 0.001$; $F2_{11,216} = 9.9$, $P < 0.001$; $F3_{11,216} = 3.0$, $P = 0.001$). While packs and single wolves answered at close to the same proportions in summer, packs answered more frequently than single wolves in October through March (Fig. 4).

Packs initiated answers (896, 63.1%) significantly more often than single wolves (524, 36.9%; Fig. 5; $F1_{1,216} = 27.2$, $P < 0.001$; $F2_{11,216} = 12.5$, $P < 0.001$; $F3_{11,216} = 3.0$, $P = 0.001$). Packs and single wolves initiated answering howls in similar proportions in summer but packs initiated more answering howls from October through March, with the exception of February (Fig. 5).

Answers by pack mate(s) versus foreigner(s).—Where answering wolves could be identified, they were pack mates (874, 57.9%) more often than foreign wolves (635, 42.1%). These answering rates, too, showed marked seasonality ($F1_{1,216} = 19.7$, $P < 0.001$; $F2_{11,216} = 10.9$, $P < 0.001$; $F3_{11,216} = 5.9$, $P = 0.001$). Answers by foreigners were consistently rare throughout the denning and summer season (Fig. 6). Instead, almost all answers during summer were by pack mates, especially from May through September. Foreign answers increased dramatically in October, November, and December (Fig. 6).
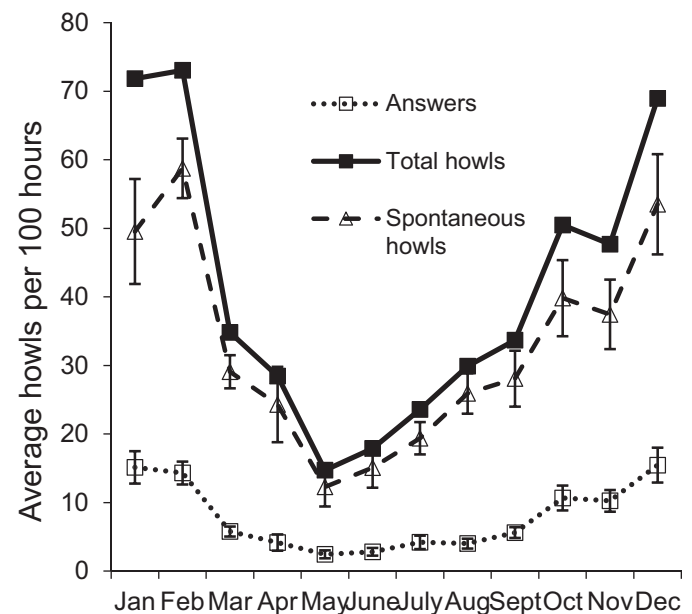

Fig. 2.—Monthly variation in pack versus single wolf (*Canis lupus*) howls on the northern range of Yellowstone National Park, Wyoming, 2001 to 2010. Averages plus standard errors (*n* = 10,166).

Fig. 3.—Relative monthly contribution to total wolf (*Canis lupus*) howls of spontaneous howls versus answers to wolves' howls on the northern range of Yellowstone National Park, Wyoming, 2001 to 2010. "Total howls" is the same line of monthly means over the 10 years as in Fig. 1. All howls (*n* = 11,742) were unsolicited. Averages plus standard errors.

Throughout the year, foreign answers (single and pack combined) were initiated most frequently (454 times or 73.8%) by howls from packs compared to howls from single wolves, but monthly differences existed only for October and November (Fig. 7; $F1_{1,216} = 24.3$, $P < 0.001$; $F2_{11,216} = 17.5$, $P < 0.001$; $F3_{11,216} = 2.3$, $P = 0.001$).

Answers from pack mates (single wolves and packs combined) were initiated slightly more frequently (442 times or 54.8%) by howls from other distant pack mates than by howls from distant single members of the same pack ($F1_{1,216} = 6.3$,

$P < 0.001$; $F2_{11,216} = 6.1$, $P < 0.001$; $F3_{11,216} = 4.1$, $P = 0.001$), with the greatest differences in August and December (Fig. 8).

Spring and summer howling at den and rendezvous sites.— Between April and August, 470 howls were recorded when pups were present at dens (327) or rendezvous sites (143; Table 1). Pups were confined to dens in April, and the 106 howls heard in that
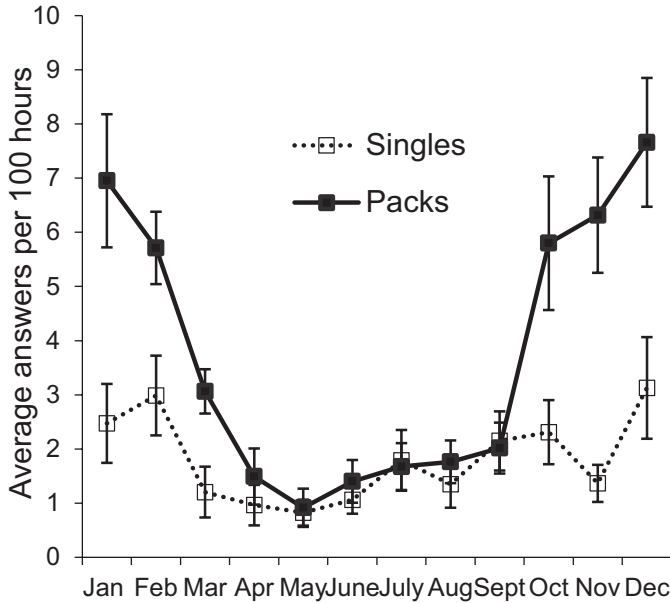

Fig. 4.—Relative monthly contribution to answers of single wolves (*Canis lupus*) versus packs on the northern range of Yellowstone National Park, Wyoming, 2001 to 2010. Averages plus standard errors (*n* = 1,965).
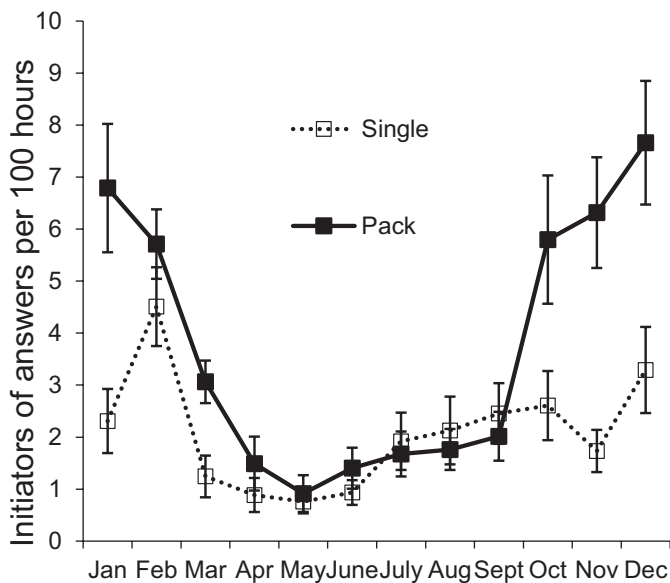

Fig. 5.—Relative monthly contribution of single wolves (*Canis lupus*) versus packs as initiators of answers on the northern range of Yellowstone National Park, Wyoming, 2001 to 2010. Averages plus standard errors (*n* = 2,050).
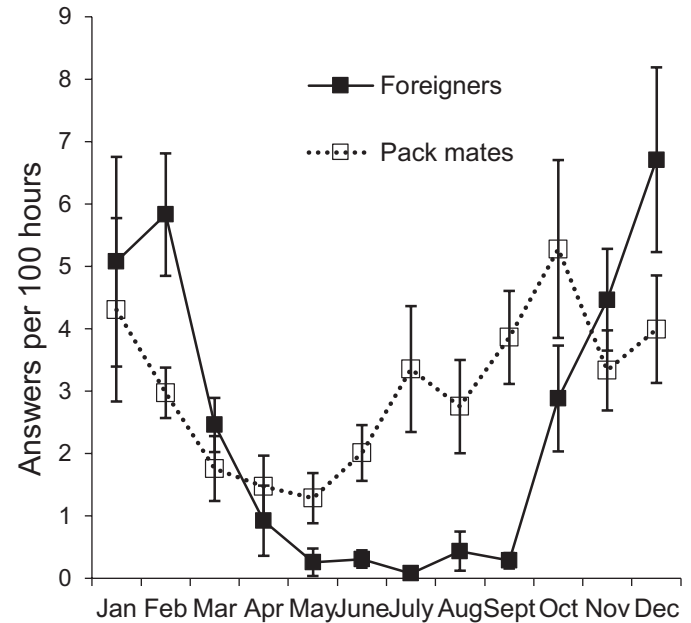

Fig. 6.—Relative monthly contribution to answers to wolf (*Canis lupus*) howls by foreigners (interpack) versus pack mates (intrapack) on the northern range of Yellowstone National Park, Wyoming, 2001 to 2010. "Foreigners" are non-pack members. Averages plus standard errors (*n* = 1,958).
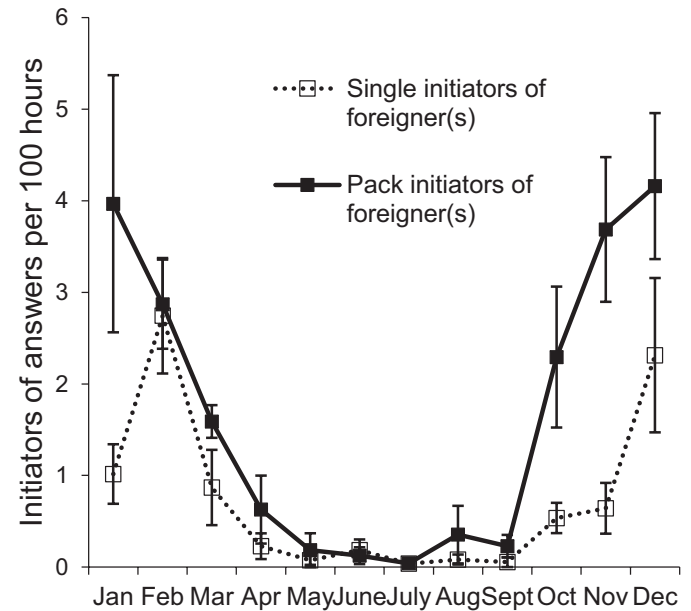

Fig. 7.—Relative monthly contribution of wolf (*Canis lupus*) packs versus single wolves as initiators of answers by foreigners on the northern range of Yellowstone National Park, Wyoming, 2001 to 2010. "Foreigners" are non-pack members. Averages plus standard errors (*n* = 946).

month were all by adults. In May, adults were the first to begin 90% of the 80 howls at den sites, and in June 82% of the 81 howls at den sites. By July, with roughly one-half of the howling being at den sites and one-half at rendezvous sites, adults still were the first to begin more than one-half of the howls recorded (67% of 119). In August, howls where pups were the first to begin predominated (74% of 68), almost all at rendezvous sites rather than at den sites. In August, packs sometimes used temporary resting sites for a few hours versus more lengthy stays at rendezvous sites. In addition, pups sometimes travelled with their packs in August.

From May through August, pup howling at den or rendezvous sites constituted 2%, 7%, 13%, and 9% of total howls heard anywhere in the study area (Table 1). During these months, total howls increased, and the contribution of pups to this increase was 42%, 70%, and 55% in May-to-June, June-to-July, and July-to-August, respectively.

DISCUSSION

Pre-breeding and breeding seasons were characterized by a dramatic peak in total howls as hypothesized (Fig. 1), and packs
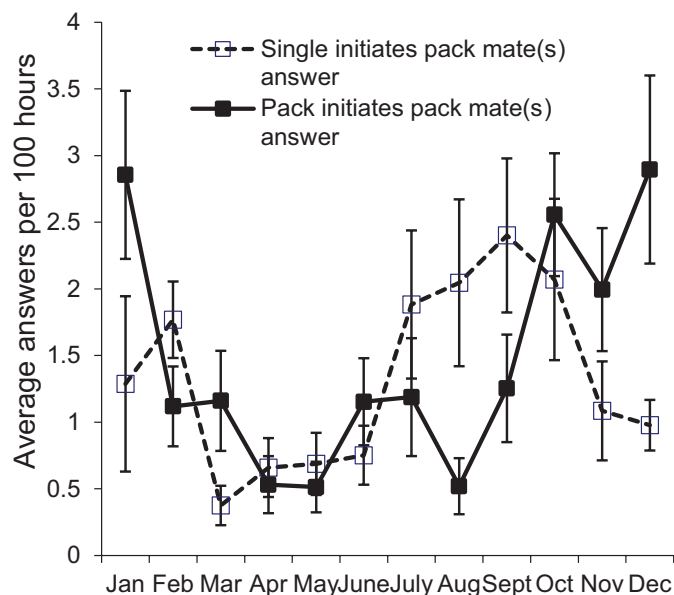

Fig. 8.—Relative monthly contribution of wolf (*Canis lupus*) packs versus single wolves as initiators of answers by pack mates on the northern range of Yellowstone National Park, Wyoming, 2001 to 2010. Averages plus standard errors (*n* = 606).

contributed more than single wolves (Fig. 2). Answering howls also peaked in the pre-breeding and breeding seasons (Fig. 3). Packs initiated howls from other wolves more than did single wolves (Fig. 5). Similarly, answers were given by packs more than by single wolves (Fig. 4). Answering wolves were foreigners (interpack howling) more than pack mates (intrapack howling; Fig. 6). Packs initiated answers from more foreigners (Fig. 7) and more pack mates (Fig. 8) than did single wolves.

In summer, significantly less howling occurred (Fig. 1), with pack and single howling contributing approximately equally (Fig. 2). Howling increased as summer progressed, as predicted. The greatest proportion of answers occurred in May and June (Fig. 3). Packs and single wolves initiated other wolves to answer about equally frequently (Fig. 5). Similarly, answers themselves were given approximately equally by packs and single wolves (Fig. 4). Answering wolves were predominately pack mates rather than foreigners, representing a major switch from the winter (Fig. 6). Packs and single wolves initiated the very small amount of foreign howling about equally (Fig. 7), but single wolves initiated most pack mate howling, especially in summers (Fig. 8).

Our study assessed howling during crepuscular and daylight hours, allowing observations of wolves who howled and individual identification. Wolves howl most frequently at crepuscular times or after dark (Joslin 1967; Pimlott et al. 1969; Theberge 1974; Theberge and Strickland 1978; Harrington and Mech 1979). We do not know if seasonal patterns of nighttime howls differ from those of daytime howls because no similar study exists for comparison.

Seasonal howling and space use.—The seasonal switching in relative importance of interpack versus intrapack answers was dramatic (Fig. 6). This switch is relevant to our hypothesis that interpack howling would peak in the pre-breeding and breeding seasons, reflecting heightened territorial and mating behavior and peaks in annual levels of estradiol in females and testosterone and male luteinizing hormone in males, as reported by Seal et al. (1979, 1987), Packard (2003), and Kreeger (2003). In summer, howling, like reproductive hormones and interpack aggression, was greatly reduced, with interpack answers having dropped by more than 80%.

Mech and Boitani (2003) wrote that "a wolf pack's territory and home range are the same, since the defended territory is the home range." The concepts of "territory" and "home range" have a history of inconsistent use, possibly from being

Table 1.—Spring and summer wolf (*Canis lupus*) howling at den and rendezvous sites in the northern range of Yellowstone National Park, Wyoming, United States, 2001–2010. "Adults" and "Pups" indicate howls that either were given by this category alone, or who howled first and were joined by others at the den or rendezvous site.

Month	Dens		Rendezvous sites		Total
	Adults alone or first	Pups alone or first	Adults alone or first	Pups alone or first	
April	106	0	0	0	106
May	72	8	0	0	80
June	66	15	10	6	81
July	45	10	35	29	119
August	4	1	14	49	68
Total	293	34	59	84	470

extremes of what actually may exist in various degrees, and thus no consensus exists for a single, precise definition of home range (Powell 2000). Nonetheless, in Yellowstone, the imperative of foreign wolves to interact territorially was considerably reduced in summer, based both on interpack howling reported here, and on interpack aggression (Quimby et al. 2015).

Possibly the seasonal differences in howling were influenced by more than reproductive hormones, such as by movements relevant to pup care or hunting. Because throughout the summer, some lower level of aggressive interpack encounters did occur, and lower levels of the reproductive hormones still existed, degrees of causality are impossible to determine.

Intrapack howling.—Intrapack howling increased as summer progressed (Fig. 6), as predicted. Our prediction was based on the premise that decreasing pack cohesion would trigger howling as wolves, relying less on rendezvous sites, attempted to locate one another. However, in winter, when pack cohesion in Yellowstone was reportedly higher than in summer (Metz et al. 2011), intrapack howling was unexpectedly high (Fig. 6). Thus, the proposed link between intrapack howling and pack cohesion needs more study, specifically with an analysis of the extent of monthly separation of pack members using radiocollared wolves. Such data could be extracted from Yellowstone Park's files over the same years as our howling study.

Howling at den sites.—The denning season (March, April, and May) represents a transitional or intermediate period in space use, reflected in both our howling data and in reported aggressive encounters (Quimby et al. 2015). Despite the drop in howling, we noted 178 howls given by adults at or very close to den sites during those months. Howling at den sites seems risky with 6 recorded attacks by foreign packs in Yellowstone resulting in the deaths of 13 resident adults and an unknown number of pups. More wolf-caused deaths have occurred in April than in any other month (Smith et al. 2015).

If such a high level of killing at den sites was a norm in wolf populations, and howling acts as an attractant, then natural selection would tend to purge it. Den-site killing on Yellowstone's northern range may have been influenced by an exceptionally dense wolf population. No den-site killing has been recorded in Yellowstone's interior where wolf density has been lower. Further data on the frequency of both howling and den-site killing on Yellowstone's northern range would be worthwhile with the current, much lower wolf population density.

Single versus pack howling.—Single and pack howling showed very similar seasonal trends and levels from January through September, but pack howling predominated from October through December (Fig. 2). Single howling was most common in the pre-breeding and breeding seasons. Single howling has mate-finding potential, given its possibilities for individual recognition (Theberge and Falls 1967; Palacios et al. 2007). Consistent with a mate-finding function, most single answers occurred during the pre-breeding and breeding seasons as well (Fig. 4). However, a proportion of this single howling also served intrapack functions, as illustrated by intrapack answers (Fig. 8).

Pack howling, rising rapidly in October and peaking as well in pre-breeding and breeding seasons (Fig. 2), showed a strong link to territorial behavior throughout that period with an increase in foreign answers. However, pack howling functioned in intrapack howling during that period, also (Fig. 8).

Generality of this study.—Several studies of howling mentioned in the introduction showed different patterns. Ours, however, involved considerably larger sample sizes as well as less human interference and a non-exploited population. Environmental or social conditions may have differed, however. Our results may reflect specific ecological conditions at Yellowstone such as the largest elk herd in North America (Peterson et al. 2014), which may have influenced time spent hunting.

Limiting the generalization of our results is the considerable flexibility in seasonal space use by different wolf populations. For example, some wolves follow migratory caribou (Stephenson and James 1982; Musiani et al. 2007) or deer (Forbes and Theberge 1995; Theberge and Theberge 2004). In the latter case, wolves were more strongly territorial in summer than in winter. Nonetheless, our results lay a groundwork for comparative studies of howling, particularly in wolf populations where human exploitation may have reduced density and altered social structure, and hence altered the ecological role that howling may play.

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