Triggers and consequences of wolf (*Canis lupus*) howling in Yellowstone National Park and connection to communication theory

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Abstract

Animal vocal communication is rife with concepts that, while important, are difficult to evaluate in nature. Particularly interesting is their application to large social mammalian carnivores characterized by year-long, loud vocalization. Here, we quantified triggers and consequences of 504 wolf (*Canis lupus* Linnaeus, 1758) howl events in Yellowstone National Park observed across 16 years. We related our results to two general theories of animal communication: that vocalization is more about communicating emotional/motivational states than a purposeful transfer of detailed information and that flexibility in use of long-distance vocalizations has been important to overall behavioural plasticity and advanced sociality in non-human primates and large social carnivores. In our study, half the howl events were triggered by 12 different environmental or social situations, most of which generated levels of anxiety. The remainder were non-triggered, apparently motivated internally but in contexts that reflected basic adaptive drives such as bonding and pack coordination. Approximately half of all howl events elicited either a change in sender activity or responding howls or travel from distant wolves, which we quantified. Wolf howling was inconsistent (low percentage of occurrence) in most behavioural contexts, hence demonstrating flexibility and social discrimination in its use. Thus, both theories were strongly supported.

Key words: wolf, *Canis lupus*, howling, Yellowstone, vocal communication

Résumé

La communication vocale chez les animaux fait appel à des concepts qui, bien qu'importants, sont difficiles à évaluer en milieu naturel. Leur application à de grands mammifères carnivores sociaux qui produisent de fortes vocalisations tout au long de l'année est particulièrement intéressante. Nous quantifions les déclencheurs et conséquences de 504 épisodes de hurlement de loup (*Canis lupus* Linnaeus, 1758) observés sur 16 ans dans le Parc national de Yellowstone. Nous relions nos résultats à deux théories générales de la communication animale, à savoir que les vocalisations tiennent plus de la communication d'états émotionnels/motivationnels que du transfert volontaire d'information détaillée et que la souplesse dans l'utilisation de vocalisations de longue portée est importante pour la plasticité comportementale globale et la socialité avancée chez les primates non humains et les grands carnivores sociaux. La moitié des épisodes de hurlement étudiés ont été déclenchés par 12 situations environnementales ou sociales distinctes, dont la plupart ont produit de l'anxiété. Les autres évènements n'avaient pas de déclencheurs, leur motivation étant apparemment interne, mais dans des contextes qui reflètent des pulsions adaptatives de base comme la formation de liens affectifs et la coordination de la meute. Environ la moitié des épisodes de hurlement ont induit soit un changement de l'activité de l'émetteur ou des hurlements ou déplacements de loups éloignés, que nous avons quantifiés. Les hurlements de loups n'étaient pas cohérents (faible pourcentage de survenue) dans la plupart des contextes comportementaux, ce qui démontre que leur utilisation est souple et fait preuve de discrimination sociale. Les résultats appuient donc fortement les deux théories. [Traduit par la Rédaction]

Mots-clés : loup, *Canis lupus*, hurlant, Yellowstone, communication vocale

Introduction

Loud, year-long vocalizations characterize large social mammalian carnivores. Among these species, vocalizations are the least understood of their set of typifying social be-

haviours: coordinated hunting of large prey (Kruuk 1972), alloparenting (Montgomery et al. 2018), multi-generational social units, and group territoriality incorporating fission–fusion dynamics (Aureli et al. 2008). Despite difficult logistics

in collecting field data, the topic needs more research considering that "the successful functioning of a society is entirely dependent on its communicatory system" (Schaller 1972).

The accepted generalization for wolf howling is that it functions in "reunion, social bonding, spacing, and mating" (Harrington and Asa 2003). Drawn from field research (Joslin 1967; Theberge 1975; McCarley 1978; Harrington and Mech 1979, 1983; Theberge and Theberge 1998; Nowak et al. 2007) and from captive studies (Theberge and Falls 1967; Klinghammer and Laidlaw 1979; Schassburger 1987, 1993; Tooze et al. 1990), this generalization is very similar to those made for loud, year-long vocalizations that characterize other large social mammalian carnivores: African lion (*Panthera leo* (Smith, 1858)) (Schaller 1972; Grinnell and McComb 2001; Gray et al. 2017), spotted hyena (*Crocuta crocuta* (Erxleben, 1777)) (Theis et al. 2007; Gersick et al. 2015), African hunting dog (*Lycaon pictus* (Temminck, 1820)) (Kingdom 1977; Robbins 2000), and dingo (*Canis lupus dingo* Meyer, 1793) (Newsome and Coman 1987; Corbett 1995; Déaux et al. 2016).

Our study objective was to build on the above listed functions to determine in what environmental and social contexts howling was used in the daily life of wolves and with what consequences and consistency. In doing so, we hoped to not only better understand how howling contributes to their adaptive behaviour but to relate howling to two relevant theories of animal communication: (1) that vocal communication is more about communicating emotional/motivational states than a purposeful transfer of detailed specific information (Dawkins and Krebs 1978; Owings and Morton 1998; Freeberg et al. 2012) and (2) that flexibility in the use of long-distance vocalizations has been important to overall behavioural plasticity and to advanced sociality in both non-human primates and large social carnivores (Aureli et al. 2008). These theories are important components in understanding the gap "that separates us from other animals" (Suddendorf 2013).

A prediction of the first hypothesis is that behaviour accompanying loud vocalization in wolves should clearly reflect emotions and motivations. It does so for general wolf behaviour, perhaps more so than in any non-primate mammal (Bekoff 2007), expressing emotions through facial and body positioning (Schenkel 1947), as well as in various short-range vocalizations including growls, whines, yelps, and squeals (Schassburger 1987, 1993; Coscia et al. 1991; Harrington and Asa 2003).

"Motivation" encompasses internal "needs" or "drives" such as hunger, territoriality/mating, physical comfort, caregiving/soliciting, contagious behaviour, and seeking/exploratory behaviour (Scott 1963; Panksepp 1998; Panksepp and Biven 2012; Zechowski 2017). Among these, we gave contagion ("allelomimetic behaviour") special attention because many wolf population studies have used recordings successfully to locate animals. Contagion, "an innate propensity to copy" (Scott 1963), enhances social bonding, social coordination, and synchrony of emotions (Spinka 2012), thus allowing "group members to behave as a cohesive unit" (Avital and Jablonka 2000).

Relative to the second hypothesis concerning vocal flexibility, from research on non-human primates, Cheney and Seyfarth (2018) postulated that in species with small repertoires and little acoustic modification [such as the wolf], vocal flexibility can be measured as the advanced capacity to either express or withhold vocalization [vocalization consistency] according to social contexts. Flexibility in the use of loud vocalizations has been described for all four of the other species: spotted hyena (Kruuk 1972; Smith et al. 2012; Holekamp and Benson-Amram 2017); African wild dogs (Fox 1975); dingo (Déaux et al. 2016), and African lion (Pfefferlea et al. 2007). For example, both spotted hyenas and African lions exhibit low response rates to distant whooping or roaring of only 32.4% for the former (Mills 1990) and 25% for the latter (Schaller 1972). Similarly, in our previous wolf censuses, we frequently knew that radio-collared wolves were present but did not answer our imitations or recordings (Theberge and Strickland 1978).

So, although inconsistency in sound signals runs against efficiency of information transfer (Bradbury and Vehrencamp 2011), we hypothesized that we would find much inconsistency in the use of howling by wolves. However, we expected to be able to identify different extenuating circumstances as potential sources of inconsistencies, for example, distraction by various intensive activities or the influence of sensitive locations such as dens or when trespassing. Alternatively, we would have to attribute inconsistencies to intangible and unmeasurable sources such as capabilities and complexities of social discrimination, that is, decisions to howl or not influenced by the relationship of the sender to receiver. Such discrimination representing a component of behavioural flexibility may have considerable adaptive significance for a species like the wolf with complex movements based on shifting pack dynamics (Gersick et al. 2015). The wolf's potential to make such decisions is strengthened by evidence that howling provides information on both individual and pack identity (Theberge and Falls 1967; Tooze et al. 1990; Palacios et al. 2007; Zaccaroni et al. 2012; Root-Gutteridge et al. 2014, Déaux et al. 2016).

Throughout our study, too, we paid attention to identifying not only events, but also the pattern, building on our results in a previous paper (McIntyre et al. 2017) that showed a 5-fold increase in howl events in pre-breeding and breeding seasons compared with the rest of the year and a parallel shift of answers from interpack to intrapack.

Going into this study, therefore, we expected that wild wolf howling would express inconsistency (flexibility), across a range of contexts, with contributing factors being either a mix of tangible environmental explanations or if inexplicable, being subtly, socially induced. We expected, too, to identify evidence of considerable emotional/motivational expression concurrent with howling.

Materials and methods

We studied a wolf population varying between 34 and 98 wolves in 5–7 packs inhabiting approximately 1000 km[2] of Yellowstone National Park's Northern Range. Immigration and emigration occurred freely. The study area provided ideal conditions for our observation-based study: mountainous terrain but with open shrub–steppe ecosystems covering expan-

sive valley floors, lower slopes, and alluvial fans; predominantly low willow riparian vegetation along Lamar River and other watercourses; only limited aspen vegetation due to browsing and aridity; high rocky outcrops and ridges used as travel routes by wolves; and about 90 km of road access. Aiding our study, too, was collaboration with Park biologists conducting other wolf studies.

Fieldwork encompassed 21 sessions between 2001 and 2016, with 11 in September or October (hereafter called "fall") over 79 days and averaging 11 h per day to total 869 h, and 10 sessions in January, February, or early March (hereafter called "(pre)breeding season" to encompass both pre- and during breeding) over 109 days and averaging 8 h per day to total an almost equal 872 h. The study took place in daylight hours because of need for visual observation.

We located wolves by telemetry under annual permits issued by Yellowstone's Office of Research and by observations largely through spotting scopes. Park rules prohibited human howling, or use of playbacks, or approach beyond the proximity of roadways. Most days not only were Park staff monitoring wolf locations, but additionally 5–15 reliable volunteers with whom we had periodic radio contact were searching visually from private vehicles. Thus, we usually had reasonable knowledge of wolf locations within observational distance. Once located, we stayed with them as long as possible, moving when they moved or were reported elsewhere. We recorded and monitored distant howls with a sensitive Telinga microphone and parabola with auditory sensitivity exceeding human hearing.

We amassed 504 "howl events". A "howl event" was defined as one or more howls given by either a single or group of wolves over any length of time until ended by 5 min of silence. This 5 min period while arbitrary was chosen because most howling, even with answers, ended within 5 min, thus providing discreet parcelling.

An "answer", defined in the same way as a howl event, was included in the same howl event if it occurred within the 5 min of the sender's howls. Answering howl(s) by non-pack mates were termed "foreigners". When uncertain, we omitted the event.

While an "answer" was independent of any subsequent travel by sender or receiver, we employed the term "response" in one analytical context to measure a frequency of howling and (or) travel when receivers were known by us to be present — in sight, or gave answering howls, or through telemetry — and again occurred within 5 min of the sender's howl.

We further defined three other types of howl events:

1. "Prolonged" — howling that extended for 15 min or more without any 5 min breaks and thus still falling within one howl event, including either unanswered howling or back-and-forth howling, analyzed separately. We set this parameter subjectively to isolate it from more normal events that involved one set of howls by sender(s) and one set of answering howls by receiver(s) with nothing more. The validity of this divide was confirmed in our data with 68% of events that involved answers fitting this norm.

2. "Yip–yap" — a variant, each animal giving repeated series of short, fast, high-pitched, loud, juvenile-like howls, and yip–yaps, often occurring during intense "rally" or "scrum" with individuals clumping, jumping, and rolling together.

3. "Bark–howls" — howls beginning with, or incorporating, barking.

Triggers of howl events were identified from observed environmental or social contexts immediately preceding or accompanying howls. They are described as they appear in the Results section. One, however, required a different methodological framework: "delayed influence of distant howling foreigners", which occurred periodically over several hours when foreigners stayed distant but close enough to motivate back-and-forth howling. Here, we accepted a triggering howl up to an hour earlier, derived from examining a declining rate of answers with time: 0–20 min after the first event ($n = 33$); 21–40 min ($n = 7$); 41–60 min ($n = 6$). This "series howling" was too important and obvious to ignore (7 series constituting 44 howl events) and occurred only when both senders and receivers remained relatively stationary.

Non-triggered howl events were identified when nothing was evident that caused wolves to howl, either any preceding change in pack behaviour or any environmental or social influence. On occasion, we possibly missed hearing distant wolves that the pack under observation did hear. However, wolves hearing distant wolves commonly turned and conspicuously oriented themselves towards the sound. When we were uncertain, we checked with telemetry, visually, or by radio contact with observers after the event. Helping verify that we were able to separate triggered from non-triggered with consistency, our results showed significant differences in several measures. Events where topography or vegetation hindered evidence were excluded. To understand contextual differences between triggered and non-triggered howl events, we compared three measures: position in territory, activity immediately preceding the event, and location. Position in territory was subdivided into core, periphery, or outside (i.e., trespassing). Arbitrary definitions were "core", being more than 3 km within territory boundaries as mapped using 95% minimum convex polygons in Yellowstone Wolf Project Annual Reports (Smith et al. 2001–2016); "peripheral", being inside but within 3 km of territory boundaries or outside within 1 km; and "trespass", being more than 1 km outside territory boundaries.

Activity was classified as (*i*) "stationary" — bedded, standing, walking around slowly, or feeding. These were grouped because pack members often showed them simultaneously; (*ii*) "slow travel" — wolf(s) walking, pausing, sometimes briefly lying down; (*iii*) "fast travel" — wolf(s) trotting or running; and (*iv*) "milling" — wolves moving in a tight, seemingly random pattern in a small area, obviously scenting the ground or coming together after being spread out.

Location was separated into carcass site, den site, rendezvous site with repeated use, temporary resting site where wolves stopped for up to 24 h, local lingering site used for briefer stops or travel.

Turning to consequences of howl events, we defined them as occurring during or within 5 min of the end of howling. They were categorized as (*i*) change in activity of the sending wolf or pack or (*ii*) "answer" (howl alone) or "response" (travel with or without howl) by a receiver. "Receiver" was defined as being more than 1 km from the sender(s), because we considered wolves within 1 km to be together especially in these open, high-visibility habitats, and up to 3 km as the outer auditory distance chosen after repeated experience of watching and hearing howls in different conditions. Identities of receiver(s) as pack mates or foreigners were determined by sight, telemetry, and knowledge of pack compositions.

"Contagious howling", although possibly operating in any answer, was only identifiable by us in one context: in intrapack howl events when a single wolf's first few howls spread into a pack howl, but only when in a non-triggered situation, i.e., those that were not confounded by an environmental trigger that could have started the other pack members' howling irrespective of the influence of the initiator. We calculated an intrapack contagious howling index by calculating the percentage of all non-triggered howl events where all or several pack members joined in, with events where only one wolf in the pack howled and the rest remained silent.

Statistical analyses in this paper involved χ^2 tests when warranted to assure sample size sufficiency for drawing conclusions. Sample sizes differed in various comparisons due to specific unobtainable data but are always provided. Vocalization consistency was measured as percentages of occurrence in various pools of specific data — the higher the percentage, the greater the consistency. Data were entered into a Microsoft Access database to facilitate analysis.

In this paper, we commonly used the term "wolf(s)" when referring to a single wolf or several, not knowing which was the case or wanting to include both. Similarly, we use the term "sender(s)" and "receiver(s)".

This study involved no auditory or physical interference with wolves' behaviour, a requirement of our annual U.S. Parks Service research permits, and hence no need for further animal ethics approval.

Results

Chart 1 provides a navigational guide.

From the pool of 504 howl events, 464 had sufficient data to be classified as either "triggered" by an observable environmental or social situation (50.6%), or "non-triggered" (49.3%).

Triggered howl events

Three broad categories of triggered events occurred approximately equally: presence of foreign wolf(s) 37.7%, intrapack dynamics 32.0%, and disturbance 30.5%. These three categories were each subdivided into four subcategories (Fig. 1). Just 4 of these 12 subcategories accounted for 72% of all triggered events: "delayed influence of distant howling foreigners", "road disturbance" when vehicles and (or) people on roadway blocked wolf movements, "left behind" when wolves, often pups, were left most often at den or rendezvous sites, and "close encounter with foreign wolves" within a few hundred metres and aware of each other.

The remaining eight subcategories were each represented by fewer than 7% of events. "Pack travelling when some members lag behind" occurred either as a pack left a site (eight events), or when strung out while travelling (seven events). In both situations, leaders or a wolf near the front stopped, looked back, and howled, often repeatedly. "Interpack wolf(s) chase" usually involved howling by the wolf being chased just after the chase ended. The chasers were larger packs. "Disturbance alien" twice involved a dog, once a horse, and 4 times a low-flying radio-tracking plane.

In all subcategories of triggered howl events, wolves exhibited elevated levels of excitement by alert postures, raised or wagging tails, orientation towards a cause often with wolves bunching up or running.

Consistency of howling in foregoing triggered situations

Eight of the 12 triggered subcategories in Fig. 1, those showing a bar for "no howl", allowed us to quantify consistency. The four excluded subcategories were rejected because the howls themselves were necessary for our recognition of the situation; thus, their inclusion would have biased the comparison. Summing howls and no howls showed the former occurring in 57% of these 235 triggering situations.

Singles versus packs in triggered situations

The ratio of pack to single howls in triggering situations was 0.61/0.391 ($n = 235$). Figure 1 shows that pack howls dominated over singles in all major subcategories.
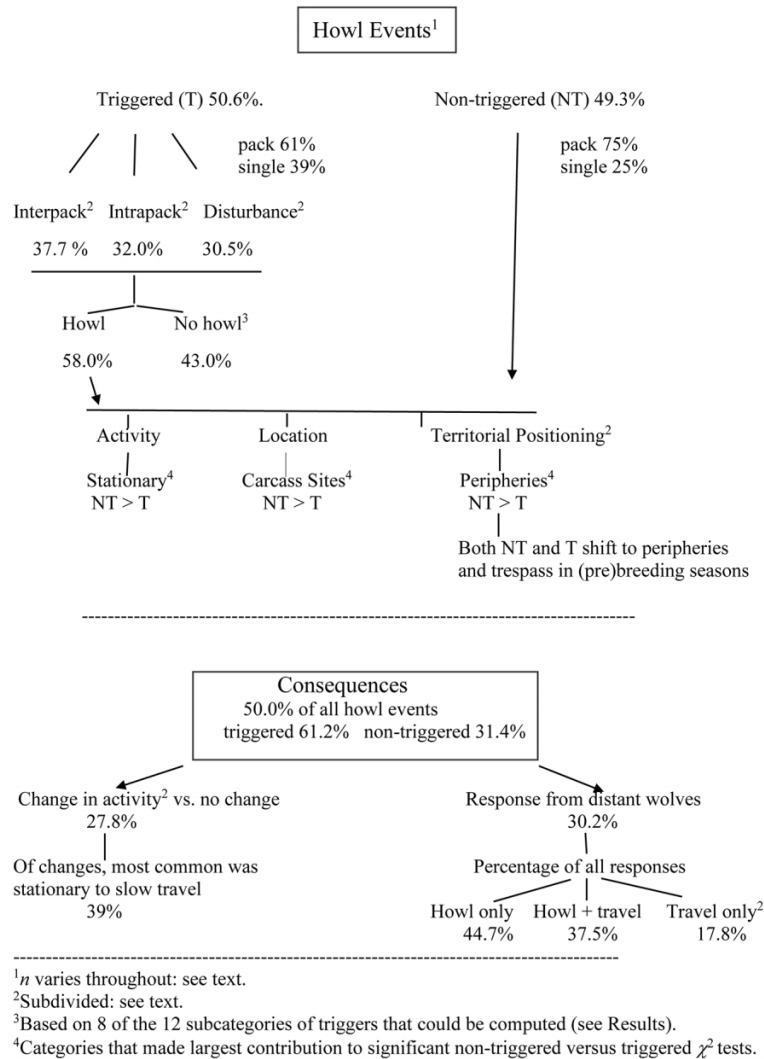
Non-triggered howl events

The additional 229 howl events (49.3%) took place with no obvious trigger, due either to some internal motivational processes or some subtle social context we could not discern. They generally were initiated with limited excitement, often by stationary, bedded wolves. The proportion of pack to single howls, 0.75/0.25, was significantly greater than in triggered howls just reported above (χ^2 test, $\chi^2_{[1]} = 10.4$, $p < 0.001$, $n = 464$).

Because the origins of these non-triggered events were less clear, we compared their context with triggered events in several ways. We found significant differences in activity ($\chi^2_{[3]} = 41.2$, $p < 0.001$, $n = 443$), location ($\chi^2_{[5]} = 39.0$, $p < 0.001$, $n = 448$), and territorial positioning ($\chi^2_{[2]} = 11.2$, $p < 0.01$, $n = 444$) due, respectively, to more than expected non-triggered howl events when wolves were stationary, at carcass sites, and in territory peripheries.

Regarding territorial positioning, the initiation of both non-triggered and triggered howl events shifted significantly with season. They changed from central parts of territories in fall to peripheral and trespass in (pre)breeding season ($\chi^2_{[2]} = 27.1$, $p < 0.001$, $n = 220$, and $\chi^2_{[2]} = 32.1$, $p < 0.001$, $n = 224$, respectively) (Fig. 2). Noteworthy in Fig. 2 is the high amount of trespass howling, occurring in a total of 102 events (23%), of which 90 (88%) were in (pre)breeding season. Generally, single wolves contributed much less than packs but followed the pack trends.

Chart 1. Flow chart of major results.

Howl Events[1]

Triggered (T) 50.6%.   Non-triggered (NT) 49.3%

pack 61%   pack 75%
single 39%   single 25%

Interpack[2] Intrapack[2] Disturbance[2]
37.7 %   32.0%   30.5%

Howl   No howl[3]
58.0%   43.0%

Activity   Location   Territorial Positioning[2]
Stationary[4]   Carcass Sites[4]   Peripheries[4]
NT > T   NT > T   NT > T

Both NT and T shift to peripheries
and trespass in (pre)breeding seasons

Consequences
50.0% of all howl events
triggered 61.2%   non-triggered 31.4%

Change in activity[2] vs. no change   Response from distant wolves
27.8%   30.2%

Of changes, most common was   Percentage of all responses
stationary to slow travel
39%

Howl only   Howl + travel   Travel only[2]
44.7%   37.5%   17.8%

[1]*n* varies throughout: see text.
[2]Subdivided: see text.
[3]Based on 8 of the 12 subcategories of triggers that could be computed (see Results).
[4]Categories that made largest contribution to significant non-triggered versus triggered χ^2 tests.

Consequence

Change in activity

In a pool of 439 howl events, a change in activity by the sending wolves occurred in 111 (25.3%). Most common was change from stationary to slow travel, occurring in 48 or 43.2% (Fig. 3). Also illustrated is an almost equal propensity for these changes to occur in silence, without the coordinating influence of a howl.

Response (howl and (or) travel) to howling by distant wolves

This second type of consequence occurred in 152 (30.2%) of the 504 howl events, and of these 152, predominant were answering howls with no travel in 44.7% followed by answering howl plus travel in 37.5%, and travel with no howl in 17.8%.

Amalgamating the two foregoing categories, travel occurred in 84 of the 152 response events, or 55.3%. These 84 travel events represent 16.7% of the total of 504 events.

Finally, examining 79 of the 84 travel events in more detail (5 were rejected due to observational uncertainty), most common was travel of receiver(s) to sender(s) in 50%, followed by sender to receiver in 28% (for more detail see Fig. 4).

We also noted 99 howl events representing 19.6% of the 504 events where distant wolves, known to be present by us, did not respond. While this figure is partly a function of our situational good fortune, it importantly documents a lower end of a range where known receivers chose to remain silent.

Amalgam of the two types of consequences

Let X be the probability of change in sender(s) activity in response to a howl and Y be the probability of a distant response to a howl. From our data, we estimated X to be 111 out of $439 = 0.25$ and Y to be $152/504 = 0.3$. Assuming these two events are conditionally independent in a howl event, then we would expect the probability of no consequence to be $1.0 - [(1 - X)(1 - Y)] = 0.52$. Conversely, our data indicate that only half the howl events had an observable consequence.

Fig. 1. Frequency of the 12 different triggering howl situations, with inconsistency shown by no howls given in these situations (n = 464).
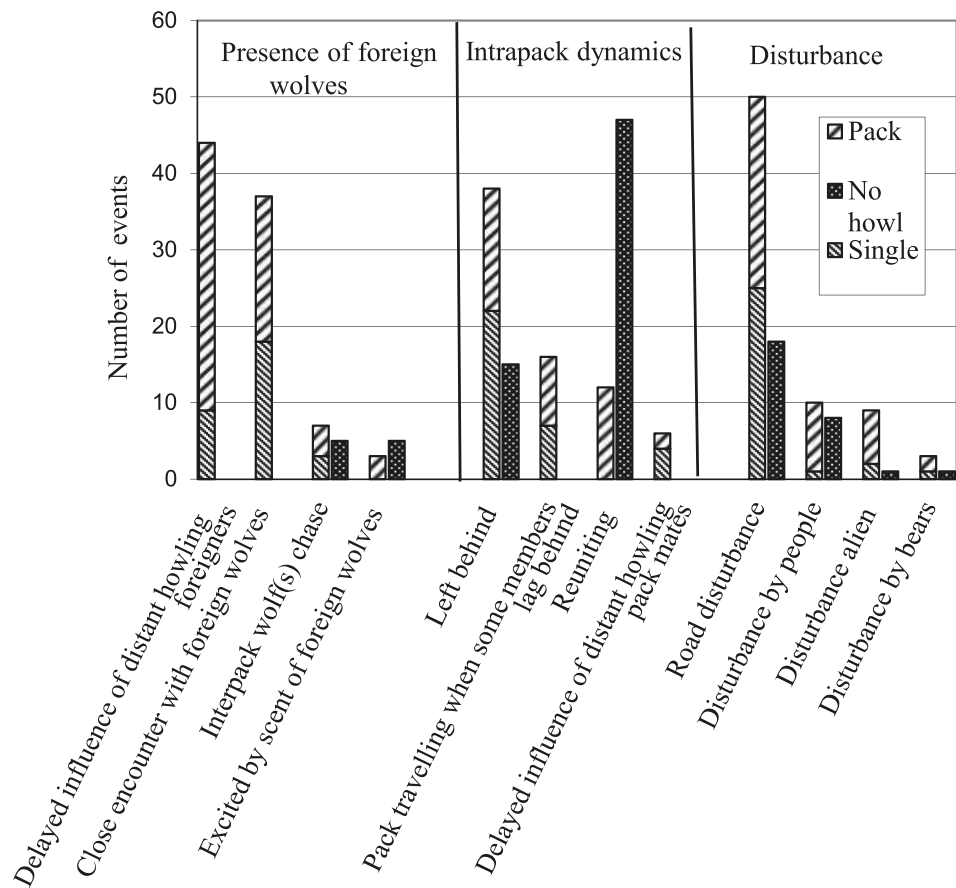

Fig. 2. Territorial positioning showing significant shift by both triggered and non-triggered howl events outward from core in fall (n = 157) to periphery and trespass in (pre)breeding season (n = 287).

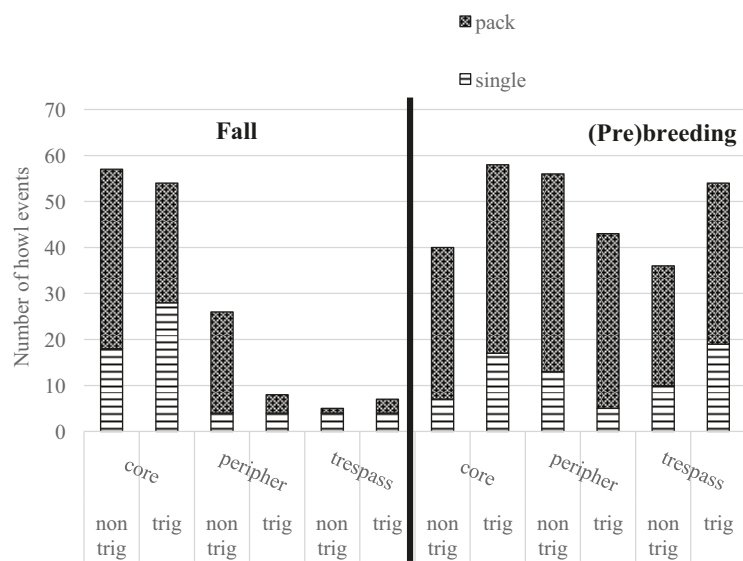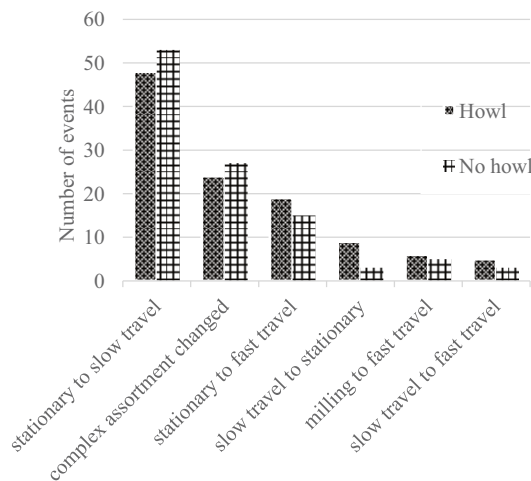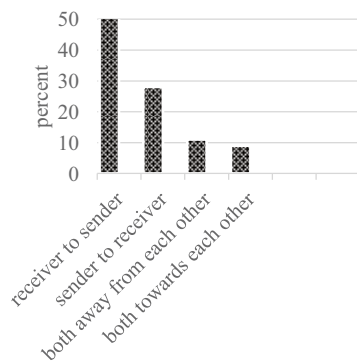**Fig. 3.** Frequency of howl events accompanying various changes in activity, with inconsistency shown by no howls in these situations ($n = 122$).

Fig. 4. Percentage of howl events eliciting travel either by sender or receiver. Data points describe independent howl events ($n = 79$).

Relations between triggers and consequences

Out of 434 howl events with sufficient data, the two most common trigger/consequence pairings were events with no discernable trigger and no discernable consequence at 32.7%, and events with both discernable triggers and consequences at 32.0% (Fig. 5). Lumping, the sum of the two triggered groupings had significantly more consequences, 61.7% ($n = 227$) than did the sum of the two non-triggered groupings, 31.4% ($n = 434$) ($\chi^2_{[1]} = 39.8$, $p < 0.001$). That greater contribution by triggered events to consequences included both changes in activity, 61.2%, and response from distant wolf(s), 78.3%.

Prolonged howl events

Fifteen percent ($n = 76$) of all 504 howl events were prolonged. Singles initiated 55% and packs 45%. Both contributed most in the (pre)breeding season at 76% and 68%, respectively.

In the fall, 95% of prolonged events were initiated in territory cores. In contrast, in the (pre)breeding season, fewer events were initiated in territory cores, 44%, and more in territory periphery or trespass situations, 56%.

Fig. 5. Overview. Percentage of howl events with or without triggers and with or without consequence ($n = 434$).
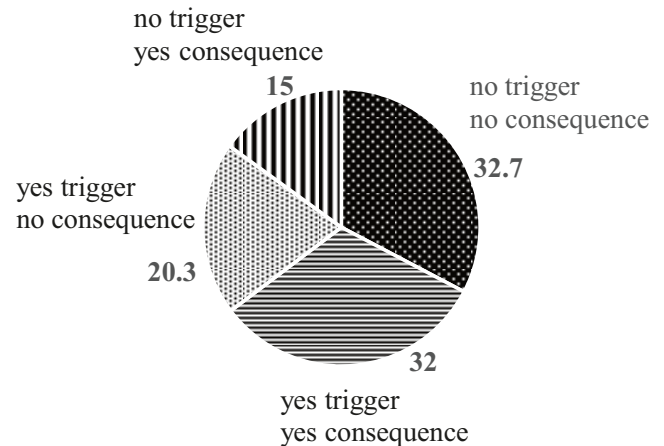
No answer occurred in 54% of prolonged howl events. In these events, even with no reinforcing answers, longevity of the event for singles was 61 ± 40 min, $n = 20$, and for packs 40 ± 20 min, $n = 21$.

Contagious howling

We calculated a "contagion index" with 195 events in which pack members within 1 km of the initial sender members joined in 170 times and pack members remained silent 25 times for an index value of 0.87.

Yip–yap howl events

In these events of high excitement, pack members typically formed a knot of jumping, wiggling animals mostly with elevated tails. As wolves assembled, participants, including even alphas, typically exhibited a change from normal howls to short, higher pitched, juvenile puppy-like howls. After several minutes, wolves either fell silent or reverted to normal howls as they disengaged. These scrums were easily identifiable by sound alone.

Of the 344 pack howls, 90 (26%) involved yip–yap. Of these 90, after removing 11 uncertain events, 52% were triggered and 48% were non-triggered. The 52% were dominated by exciting situations, especially delayed influence of distant howling foreigners (13 events), close encounter with foreign wolves (6), road disturbance (5), and reunion (4). The 48% non-triggered were initiated at non-existent or low levels of excitement.

Change of activity occurred in 36% of yip–yap events, which was not significantly different from that shown by pack howls that did not include yip–yap. Similarly, the 41% of yip–yap events that generated a response from distant wolves was not significantly different from that generated by non-yip–yap events. Only 18% of yip–yap events occurred in trespass situations, and all except two were in the (pre)breeding season.

Bark–howl events

Most were triggered with high-level agitation: 14 close encounters with foreign wolves, 10 close-in disturbances by humans/bears/dog, 4 interpack wolf(s) chases, and 1 each of single pup left behind and intrapack aggression. Another five were non-triggered.

Discussion

Vocal inconsistency — behavioural flexibility

Howling in almost all contexts was inconsistent, with percentages of occurrences normally falling well below 75% (Chart 1).

Thus, our data strongly support our hypothesis that wolves would express howling inconsistently across most contexts. As per Introduction section, to evaluate the potential sources of these inconsistencies, we considered two alternatives: (1) the influence of various extenuating circumstances such as distraction by location or overriding activities, or if unexplainable, (2) the influence of intangible reasons such as social discrimination based on complex social relationships. We found only limited evidence for the first alternative. Howling seemed relatively independent of activity except for more than expected non-triggered versus triggered events when wolves were stationary or at carcass sites, but in both cases, only to a minor degree (Results section). Wolves involved in our study even howled periodically at dens, the presence of pups notwithstanding (McIntyre et al. 2017). Even the risk associated with trespass was not an overarching influence that prevented howling, occurring in 23% of all howl events. Finally, in none of the 12 subcategories of triggered howl events (Fig. 1) did we ever identify extraneous reasons why they remained silent.

Exceptions to inconsistencies were limited to two short-interval contexts where wolves never howled: when on a chase or when making or initially feeding on a kill. Also, near-exceptions were the two highest percentage occurrences in the study: contagious answering by nearby pack mates at 87% and trespass howling in the (pre)breeding season at 88%, expressing, respectively, internal reflexive or hormonal motivational underpinnings.

Turning to the alternative explanation for inconsistencies, we now considered the significance of intangible influences, specifically social discrimination. As referenced in the Introduction, this explanation effectively turns the negative of inconsistency into the positive of adaptive flexibility through decision-making of whether or not to howl based on social discrimination. Selective benefits may accrue to intrapack, social positioning related to age, sex, kinship, breeding status, familiar or less familiar associates, dominant/subordinate relationships, temporary alliances, and potential mates (normally non-kin). Such connections may influence pack operations such as coordination, cooperation, division of labour, leadership, threat-resolution, and dispersion. Social discrimination could also occur at the inter-pack level, especially in northern Yellowstone where pack territories overlap and dispersal between neighbouring packs commonly occurs (Smith et al. 2001–2016). As such, neighbouring packs will often know each other well (may sometimes be related), and this familiarity could affect movements, decisions to answer, or changes in activity after hearing howls.

While we arrive at social discrimination for wolves after finding limited evidence for its alternative explanation, doing so conforms with conclusions drawn by Cheney and Seyfarth (2018) from their research with non-human social primates that equates inconsistency with flexibility, and that, in turn, is reflective of social context (social discrimination) (Introduction section). Justifying the relevance of their conclusions beyond primates to the large social carnivores is the concept that their shared advanced sociality may have been substantially advanced by their vocal flexibility and complexity (Theis et al. 2007; Aureli et al. 2008; Freeberg et al. 2012; Holekamp and Benson-Amram 2017).

Direct evidence for the importance of flexibility based on social discrimination came from our earlier research with a captive wolf under controlled experimental conditions (Theberge and Falls 1967). With us out of sight, it repeatedly and without fail answered Mary's howl but never John's, even when we both howled a steady middle C, making the distinction on sonograph-distinctive sound harmonics. The wolf had a different social relationship with each of us: friendliness and appeasement with Mary, agitated and wary with John caused by re-location, thereby clearly showing flexibility in answering based on its social relationships. It seems safe to assume that Yellowstone wolves, indeed all wolves, would have this same natural ability.

Emotional/motivational states versus direct information transfer

For information transfer to exhibit necessary reliability and repeatability for even rudimentary "referential communication" (Wheeler and Fischer 2012), howling would have had to exhibit greater consistency than we found. Instead, our evidence with wolf howling supports the contention that signalling emotional/motivational states rather than a purposeful transfer of specific information provides the basic underpinnings of non-human animal vocalizations (Dawkins and Krebs 1978; Owings and Morton 1998; Freeberg et al. 2012).

Summarizing our results, the most prevalent expressions of excitement occurred in anxiety-generating contexts, which characterized about half of all howl events. They occurred in adverse circumstances that scaled from disturbing up to threatening, even to agonistic, especially in the "presence of foreign wolves" (Fig. 1), being understandable in this population where interpack wolf killing has been a major source of mortality (Smith et al. 2001–2016). Included in anxiety-generating contexts were 11 of the 12 categories of all triggered howl events (Fig. 1) except for "reunion", and most bark–howl and yip–yap events. All the foregoing invariably invoked excitement and arousal exhibited by posture and movements, (as described in Results section). Howling appeared to help resolve these situations by spreading awareness, consolidating or in some cases scattering pack members, presenting and coordinating an intimidating front, or reassembling wolves after the event. Highly excited and anx-

ious wolves commonly exhibited largely agonistic behaviour with elements of flight or fright oriented towards the source of anxiety.

Yip–yap howl events, while commencing either when wolves were excited, or when more passive in non-triggered situations, always appeared as joyous gatherings of positive valence as individual pack members joined the scrum. They clearly exhibited emotional contagion (Avital and Jablonka 2000).

Most bark howl events were caused by very threatening experiences and intense agonistic ambivalence. However, five (14%) were non-triggered with no strongly emotive environmental explanation. Their motivation is unclear, being either due to internal arousal or unidentifiable circumstances.

Most non-triggered events were initiated less emotively; however, they appeared to involve internal motivational states as evident from consequent activity or movement. Such howling likely reflected a range of internal needs (Scott 1963) such as hunger, when a pack howl initiated travel that resulted in a kill, or territoriality, shown by peripheral or trespass howling, or aggression with bark–howling, or auditory exploratory behaviour, demonstrated by unanswered prolonged howling, or by howling, especially by singles, that resulted in pack reassembly. Our "contagion index" of 87% also reflected an internal need, but contagion was likely part of many distant wolf(s) answers that we could not reliably measure. Contagion isolated from auxiliary roles of other motivational states has been difficult to identify, and thus "our understanding of its development and social dynamics is still very poor" (Provine 1996).

Similar to wolves howling when excited, spotted hyenas commonly whooped then too (42% of 181 bouts) (Theis et al. 2007). Also, like wolves using bark–howls in extreme alarm, both wild dogs and dingoes gave several variants of barking in disturbing contexts (Corbett 1995; Robbins 2000; Déaux et al. 2016). And equivalent to our 49.3% non-triggered wolf howls, spotted hyenas gave "spontaneous whoops" in 50.3% of 181 event (Theis et al. 2007), and African lions roared spontaneously in 75% of 300 episodes (Schaller 1972).

Our results, therefore, align abundantly with a broad literature. Ever since Darwin (1872), the fundamental importance of emotion and motivation has been reconfirmed repeatedly (Etkin 1964; Seyfarth and Cheney 2003; Scherer 2009; Altenmueller et al. 2013; Fitch and Zuberbuhler 2013; Fischer 2017; Zechowski 2017). Goodall (1986) wrote that "the production of sound in the absence of appropriate emotional state seems almost an impossible task", and Suddendorf (2013) stated that "most animal vocalizations seem to be under emotional rather than cognitive control". Mammals and humans share similar neurochemicals that underlie emotional/motivational states (Bekoff 2012).

Territorial positioning related to seasonal pattern in howling

Here, our data add a territorial-positioning explanation for a distinctive seasonal pattern in wolf howling that we identified in an earlier paper (McIntyre et al. 2017). That pattern described a significant shift in answering howls from almost exclusively being intrapack throughout most of the year, including fall, to almost exclusively being interpack in the (pre)breeding season. The new information in our present paper is the evidence of a reason why — a change from howling predominantly from territorial cores in the fall, where receivers would most likely be packmates, to territorial peripheries and trespass, where receivers would more likely be foreigners. Underlined in both sets of data are the seasonal importance of howling to territoriality with its functions of defence and mate securement.

Ancillary comments on howling functions

Spacing must be considered howling's ultimate function, because all howling serves indirectly and inescapably as a broadcast. While this role of spacing has been deduced before (Introduction), here we quantified it to the extent possible. We documented movements as a consequence of howling in 16.7% of all 504 howl events. These movements predominately brought wolves together (Fig. 4). This 16.7% is undoubtedly minimal due to movements undetected by us or happening beyond our methodological 5 min limit. But also, spacing between packs is most likely accomplished by howling that curtails movements, influencing them as information "taken under advisement" — places to go to or avoid up to 48 h later (Theberge and Theberge 2004).

Regarding other functions as per Harrington and Asa (2003), bonding was obviously on display in the yip–yap howl events, which occurred in 26% of all pack howls. However, bonding was also highly probable for many or even most of the non-triggered pack howl events through the influence of contagion. Possibly without contagion, answering howls would be few, thus limiting its adaptive value, an important area for more research.

The role of howling in pack coordination was exhibited by 25.3% of 439 events when it precipitated a change in activity, and also when packs were travelling and some members lagged behind (Fig. 1).

Finally, howling accompanied reuniting pack members in 20% of 59 events. However, they reunited in silence in the remainder (Fig. 1).

Summary conceptual interpretation of wolf howling

Howling is fundamentally a periodic expression of emotions, most commonly some level of anxiety, which can be loosely triggered by external events, or almost equally is motivated by internal needs. Howling is highly flexible, expressed, or withheld in almost all environmental and social situations based largely on inferred sensitivity to social relationships. It functions proximally in mating/territoriality, social bonding, pack coordination, and reunion, but ultimately in spacing. It accomplishes these five functions by the conveyance of meaning through context that is interpreted by receivers, rather than being a transfer of specific information through signal variation, as far as is presently known.

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Data generated or analyzed during this study are available from the corresponding author upon reasonable request.

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