



Wolf howls encode both sender- and context-specific information

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Loud, long-distance calls serve varied functions across animal species including marking territory, attracting mates and signalling one's identity. Here, we examined the types of sender- and context-specific information encoded in the howls of captive timber wolves, *Canis lupus*. We analysed 913 howls from nine individuals across three packs and investigated whether howl structure varied consistently as a function of phenotypic factors (age class, sex, pack and identity of the caller) in addition to the context in which the call was produced: specifically, whether the call was produced in a 'spontaneous' context just after sunrise or was 'elicited' by the absence of a group member. Calls were correctly classified by individual identity and production context, but not by any other factors. Principal components analyses indicated that individual differences were primarily associated with frequency-based measures, whereas acoustic variation between production contexts was associated with a variety of frequency-, intensity- and energy-based measures. Recognition of individual differences in vocalizations is likely to be important for navigating social relationships in wolves and further work is required to determine which life history factors may shape these individual differences. Differences resulting from production context are suggestive that these howl variants may serve different functions. The extent to which these individual and contextual differences are understood by receivers remains an open question.

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Given their often obvious and striking nature, the long-distance vocalizations of animals have received considerable empirical research interest over the years (Gustison & Townsend, 2015; Hauser, 1996; Bradbury & Vehrencamp, 1998). From the infrasonic rumbles of African elephants, *Loxodonta africana*, to the songs of whales or birds, long-distance or 'loud calls' have been shown to serve a range of mating and territorial functions. For example, the loud calls of gibbons (*Hylodytes* spp.) play a role in negotiating and advertising territory among male–female pairs (Geissman, 2002), while the songs of many bird species are important in attracting females and even stimulating ovulation (Catchpole & Slater, 2003). The loud calls of social mammals, such as lions, *Panthero leo*, and

chimpanzees, *Pan troglodytes*, have also been shown to serve multiple adaptive functions, such as signalling territories while maintaining contact and mediating cohesion with group members (Grinnell & McComb, 2001; Notman & Rendall, 2005). Analysis of the acoustic structure of these vocalizations and subsequent playbacks have helped shed further light on how exactly these calls have their effects. For example, the loud roars of red deer, *Cervus elaphus*, have long been known to represent sexually selected signals, being produced more frequently during the rutting or mating season (Clutton-Brock & Albon, 1979). Through applying a source-filter framework to the analysis of their roars it has additionally been shown that honest, accurate information on body size is cued through filter-related acoustic parameters, or formants, with larger males having more dispersed formant frequencies in their roars (Fitch & Reby, 2001). What is more, both males and females attend to this information and use it to modify their mating/fighting-based decisions with males avoiding and females approaching larger-sounding roars (Charlton, Reby, & McComb, 2007; Reby et al., 2005).

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A number of studies have now shown that long-distance vocalizations have the potential to cue an array of sender-specific, phenotypic information including the caller's identity (Barbary macaques, *Macaca sylvanus*: Fischer, Hammerschmidt & Todt, 1998; chacma baboons, *Papio ursinus*: Fischer, Hammerschmidt, Cheney, & Seyfarth, 2001; Fischer, Metz, Cheney, & Seyfarth, 2001; Dolphins: Sayigh, Esch, Wells, & Janik, 2007; chickens, *Gallus gallus domesticus*: Kent, 1987; meerkats, *Suricata suricatta*: Townsend & Manser, 2011), sex (Charlton, Zhihe, & Snyder, 2009b; Rendall, Owren, Weerts, & Hienz, 2004), age (Charlton et al., 2009b) and group membership (Crockford, Herbinger, Vigilant, & Boesch, 2004; Vehrencamp, Ritter, Keever, & Bradbury, 2003). In addition to this, some species also encode more dynamic motivational, behavioural and/or contextual information in their loud calls. Encoding of contextual information in animal vocalizations, such as black-capped chickadees, *Poecile atricapillus*, expressing information about the size of a predator in their alarm calls (Templeton, Greene, & Davis, 2005), has received considerable research attention over the years, partly due to its ostensible similarity to the highly context-specific nature of human language and the potential implications for understanding its evolutionary origins (Townsend & Manser, 2013; cf. ; Wheeler & Fischer, 2012). Furthermore, the capacity for both sender- and context-specific information to be encoded in a single call type has additionally been demonstrated (Briefer, Vannoni, & McElligott, 2010; Cornec, Hingrat, Robert, & Rybak, 2015; Lemasson, Boutin, Boivin, Blois-Heulin, & Hausberger, 2009; Theis, Greene, Benson-Amram, & Holekamp, 2007; Volodin, Sibiryakova, & Volodina, 2016). For example, male giant pandas, *Ailuropoda melanoleuca*, dynamically modulate the fundamental frequency (rate of vocal-fold vibration in the larynx) of their bleats to reflect their motivational state, increasing it when alone in order to broadcast their quality to potential mates (Charlton, Keating, Rengui, Huang, & Swaisgood, 2015), whereas other acoustic features signal the size and sex of the individual (Charlton, Zhihe, & Snyder, 2009a). Indeed, the multi-encoding of static and dynamic features in a single call may, alongside sequentially combining vocalizations (e.g. Outtarra, Lemasson & Zuberbuhler, 2009), represent an additional mechanism by which animals can maximize the expressive power of a limited vocal repertoire (Manser, Seyfarth, & Cheney, 2002). Here, we follow up existing work investigating whether this capacity is present in howls, the stereotypical loud call of wolves.

As with other social mammal loud calls, wolf howls are thought to function to mediate spacing within their groups (Mazzini, Townsend, Virányi, & Range, 2013; Mech & Boitani, 2010). This is likely to facilitate contact not only between separated group members but also between groups (Mech & Boitani, 2010; Nowak et al., 2007; Zaccaroni et al., 2012). Recent research has begun to shed light on the proximate mechanisms by which these effects come about, demonstrating, for example, that the acoustic structure of howls can be used to accurately predict individuality (Palacios, Font, & Márquez, 2007; Root-Gutteridge et al., 2014) and group membership (Zaccaroni et al., 2012). Interestingly, previous work has also suggested that wolves produce howls in subtly different contexts: howls occur at increased rates spontaneously after sunrise (Gazzola, Avanzinelli, Mauri, Scandura, & Apollonio, 2002; Harrington & Mech, 1982) and when faced with the temporary absence of group members (hereafter 'elicited' howls), both in the wild (Mech & Boitani, 2010; Nowak et al., 2007) and in captivity (Mazzini, Townsend, Virányi, & Range, 2013). Furthermore, individuals have also been shown to howl more often when separated from closely affiliated individuals (Mazzini et al., 2013). However, until now it was unknown whether calls produced in these different contexts also systematically differ in their acoustic structure. We therefore extended this body of work using a

substantial data set to investigate whether, in addition to more static, individual-specific information types, wolf howls can also encode external, context-specific information.

Specifically, we examined the influence of various phenotypic attributes of callers and accompanying behavioural contexts on the acoustic structure of timber wolf howls. In line with the findings discussed above, we investigated the extent to which howls vary between individuals (Palacios et al., 2007; Root-Gutteridge et al., 2014) and packs (Mech & Boitani, 2010; Zaccaroni et al., 2012). Furthermore, in light of the consistent differences in size between the sexes (females are on average a third smaller than males, MacNulty, Smith, Mech, & Eberly, 2009) and the impact this has on vocal tract anatomy (Taylor & Reby, 2010), we expected to find sex-specific influences on overall acoustic structure of howls. Similarly, we also predicted that the howls of adult (24+ months) individuals would differ from those of juveniles (5–24 months) due to differences in size resulting from maturation. Regarding context, we determined whether howls produced in a spontaneous (just after sunrise) or elicited (by the temporary absence of a pack mate taken for a walk by care staff) context were acoustically distinct from one another.

METHODS

Study Site and Subjects

All howls were recorded at the Wolf Science Center (WSC) in Ernstbrunn, Austria. Thirteen wolves, kept in three different packs, were subject to behavioural observations and acoustic recording (Table 1). All individuals were born in captivity from lineages originating in North America but came from different locations in North America and Europe. All were hand-raised in peer groups at the Wolf Science Center after being separated from their mothers in the first 10 days after birth (for details see Range & Virányi, 2014). Puppies were bottle-fed and, after 3–4 weeks, hand-fed with solid food. All individuals had continuous access to humans for the first 5 months of their life. After 5 months, the wolves were integrated into established packs of the previous generations. We broadly defined two age categories in line with accepted definitions from the literature (Mech & Boitani, 2010). Adults were classified as individuals that were at least 2 years of age. Juveniles were classified as individuals that were between 5 months and 2 years of age. The wolves participated in training and/or cognitive and behavioural experiments at least once a day and, hence, still had frequent social contact with humans (Range & Virányi, 2011). The enclosures of each of the three packs range over 4000–8000 m². They are equipped with trees, bushes, logs and shelters and water for drinking is permanently available. The wolves receive a diet of meat and dry food. All raising and keeping procedures of wolves at the Wolf Science Center are in line with the animal protection law in Austria (Tierversuchsgesetz 2012–TVG 2012). No special permission for use of animals (wolves) in such sociocognitive studies is required in Austria. The relevant committee that allows research on animals without special permission is Tierversuchskommission am Bundesministerium für Wissenschaft und Forschung (Austria).

Data Collection

Wolf howls were recorded with a directional microphone (ME66/K6 and a MZW66 pro windscreen, frequency response 40–20 000 Hz ± 2.5 dB; Sennheiser, Old Lyme, CT, U.S.A.) attached to a solid-state recorder (Marantz PMD 661), sampled at a frequency of 44.1 kHz. All howls were recorded at a distance of 1–10 m. Comments by the observer documenting the howling individual or the context were simultaneously recorded with a

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