



Disentangling canid howls across multiple species and subspecies: Structure in a complex communication channel



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ABSTRACT

Wolves, coyotes, and other canids are members of a diverse genus of top predators of considerable conservation and management interest. Canid howls are long-range communication signals, used both for territorial defence and group cohesion. Previous studies have shown that howls can encode individual and group identity. However, no comprehensive study has investigated the nature of variation in canid howls across the wide range of species. We analysed a database of over 2000 howls recorded from 13 different canid species and subspecies. We applied a quantitative similarity measure to compare the modulation pattern in howls from different populations, and then applied an unsupervised clustering algorithm to group the howls into natural units of distinct howl types. We found that different species and subspecies showed markedly different use of howl types, indicating that howl modulation is not arbitrary, but can be used to distinguish one population from another. We give an example of the conservation importance of these findings by comparing the howls of the critically endangered red wolves to those of sympatric coyotes *Canis latrans*, with whom red wolves may hybridise, potentially compromising reintroduced red wolf populations. We believe that quantitative cross-species comparisons such as these can provide important understanding of the nature and use of communication in socially cooperative species, as well as support conservation and management of wolf populations.

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1. Introduction

The genus *Canis* comprises several species and subspecies that share many ecological and behavioural similarities (Bekoff et al., 1981). Most are apex predators, and although some hunt in packs and others alone, all species are strongly social, living in groups ranging in size from a handful of close family members, e.g. coyotes *Canis latrans* (Bekoff, 1977), to large groups of 20 or more animals, e.g. Ethiopian wolves *Canis simensis* (Sillero-Zubiri and Gottelli, 1994). For humans, one of the most familiar canid behaviours is the howl, a long-range communication channel (i.e., a mode through

which communication can occur) thought to play a role both in territorial advertising and in group cohesion (Theberge and Falls 1967; Harrington and Mech, 1979; Harrington, 1987). Howling is most familiar in grey wolves *Canis lupus* (Harrington et al., 2003), but all species in the genus produce howl-like vocalisations in addition to other, shorter range communication, such as barks, yips, and growls (Cohen and Fox, 1976). These diverse short-range vocalisations are thought to mediate much of canid social behaviour (Yin and McCowan, 2004; Siniscalchi et al., 2008), such as maintaining dominance relationships, but it has been speculated that howling too plays a role in inter- and intra-group dynamics (Harrington and Mech, 1979; Jaeger et al., 1996; Gese, 2001). Support for this hypothesis includes recent studies showing that wolves recognise the howl vocalisations of familiar individuals, and that howls show affective changes in response to the removal of individuals from the

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group (Mazzini et al., 2013; Palacios et al., 2015). In addition, individual differences in howls have been found in other canid species, e.g. coyotes (Hallberg, 2007), and dingoes (Déaux and Clarke, 2013).

Canids of all species pose a number of management and conservation challenges. As apex predators, canids have a major influence on prey populations, and changes in canid numbers can result in trophic cascades (Elmhagen and Rushton, 2007; Beschta and Ripple, 2009). Some species, such as the Ethiopian wolf (Sillero-Zubiri and Gottelli, 1994) and the red wolf *Canis rufus* (Paradiso and Nowak, 1972) are critically endangered, whereas the grey wolf *C. lupus* is frequently in conflict with human populations due to livestock depredation (Sillero-Zubiri and Laurenson, 2001), and golden jackals *Canis aureus* and domestic dogs *Canis familiaris* are considered to be significant reservoirs of rabies (Seimenis, 2008; Davlin and VonVille, 2012). Management of these issues requires an in-depth understanding of the behavioural ecology of these species and subspecies, which would appear to be incomplete without an understanding of the role of long-range vocal communication. In addition, phylogenetic relationships in the genus as a whole are unclear (Bardeleben et al., 2005; Koepfli et al., 2015), with most component species being capable of producing fertile hybrids, and there is considerable lack of agreement over the status of several grey wolf subspecies and populations (Chambers et al., 2012). As a result, the possible role of vocal behaviour as an isolating factor (or otherwise) between populations is important for the conservation of genetic diversity in subspecies that, while genetically compatible, maintain considerable phenotypic adaptation to their local habitats (Chambers et al., 2012).

Partly because of the lack of agreement on the taxonomic status of many canid species and subspecies, and partly for reasons of simplicity, in this paper we will use the term “species” as a shorthand for “species and subspecies”.

Early studies of canid howling behaviour emphasised qualitative descriptions of howl types (McCarley, 1975; Cohen and Fox, 1976; Tembrock, 1976; Lehner, 1978) and overall acoustic characteristics, such as mean fundamental frequency and frequency range, as well as modulation shape measures (Theberge and Falls, 1967; Tooze et al., 1990). Multiple variables describing changes in the frequency and amplitude of the howl over time can be used for individual discrimination, among which important discriminative variables are the mean, maximum, and coefficient of variation of the fundamental frequency, and the amplitudes of the various harmonics (Root-Gutteridge et al., 2014a,b). However, there are reasons to consider that information exists in the precise frequency modulation of wolf howls, as well as in simpler acoustic characteristics. Firstly, howls are predominantly narrow-band vocalisations, meaning that most of the acoustic energy is concentrated at a small range of frequencies at any one time. Further, this well-defined frequency varies throughout the course of the howl (Fig. 1). This “frequency modulation” is known to be used to encode information in other species with similar vocalisations; particularly bottlenose dolphins *Tursiops truncatus* (Janik and Slater, 1998; Quick and Janik, 2012), in which individual identity can be reliably extracted from the frequency modulation patterns of whistles (Kerstenbaum et al., 2013). Frequency modulation is an effective encoding technique in terrestrial communication (Wiley and Richards, 1978), and in addition, considerations of signal transmission indicate that long-range communication in an absorptive environment (e.g. forest) would tend to favour narrow-band frequency modulation over other encoding modalities (Henry and Lucas, 2010). Therefore, we consider it appropriate to analyse the frequency modulation of canid howls in a similar way to that of dolphin whistles, to test for characteristic differences between species and populations.

A few studies have examined frequency modulation in canid howls, e.g. in coyotes (Hallberg, 2007) and Iberian wolves (Palacios et al., 2007), by defining stereotyped modulation patterns such

as, “rising”, “step down”, and “warble to flat”. However, these arbitrary categories may not be perceived as distinct units by the focal animal (Kerstenbaum et al., 2014), and are potentially subject to selective bias by researchers focusing on “interesting” spectral patterns. Therefore, a thorough analysis of frequency modulation must include (a) a quantitative measure of howl similarity (Deecke and Janik, 2006), and (b) a quantitative and objective method for grouping howls into distinct howl types, without relying on subjective interpretation. The latter requirement is particularly acute, as a quantitative comparison between the vocal behaviours of different populations is problematic if both repertoires include vocalisations that are qualitatively of a different nature. For example, comparing the howls of one population to the barks of another would be an unproductive effort. Therefore, an alternative paradigm is required that takes into account the partitioning of a vocal repertoire into distinct types, whether arising from functionally different mechanisms (such as howls and barks), or whether being discrete variations of the same functional mechanism (such as different notes in a bird song). We propose that, where multiple distinct vocalisation types are used with overlapping repertoires between populations, the only meaningful way to compare behaviour is to compare the vocalisation type histograms, rather than compare the individual vocalisations. This approach has also been carried out in previous studies of birdsong syntax (Jin and Kozhevnikov, 2011). In essence, we interpret the howl type usage histograms as a “fingerprint” of vocal behaviour.

In this work, we define and implement a howl similarity metric, as well as an automated clustering technique, and analyse a large database of over 2000 howls from 21 different species of canids. We classify these howls into distinct types, and compare the relative use of this global repertoire by different populations, thereby testing for objective differences that distinguish between different species. Our results show a diversity of different howl types between species and, although we do not explicitly test for contextual reference in canid howling, we cannot exclude the possibility that specific howl types may be more common in some behavioural contexts than others.

2. Methods

We collected a database of canid howling recordings from a wide range of sources. Altogether, we collected 6009 howls from 21 distinct species, from 207 sources. Recordings were made both of captive and wild animals. The number of sources for each species varied from one (dingo *C. lupus dingo* or *C. familiaris dingo*, status unclear, Tibetan wolf *C. l. chanco*, and others) to 20 (eastern timber wolf *C. l. lycaon*). However, we excluded all species with only a single source to avoid confounding individual distinctiveness with species distinctiveness, providing a dataset with 13 distinct species from 131 sources. Of these, 2005 howls were considered to be of sufficient quality for further analysis (no overlapping howls, sufficient signal strength). A breakdown of the recordings is given in Table 1. For each howl, we traced the frequency modulation using a combination of manual and automatic extraction tools, using an image-processing ridge tracker (Kerstenbaum and Roch, 2013), or by fitting the harmonic peaks to a Lorentzian function (Root-Gutteridge et al., 2014b). Each analysis was reviewed by both AK and HRG for validation.

Once the frequency modulation of the howls had been recorded, we compared every howl pairwise to generate a 2005 × 2005 matrix of howl similarity/dissimilarity. We used dynamic time warping (DTW) (Kruskal, 1983) to deliver a quantitative metric of this distance (or dissimilarity) between every pair of howls. Dynamic time warping has been widely used for comparing fre-

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