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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.

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 (Kershenbaum 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 (Kershenbaum 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 (Kershenbaum 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-

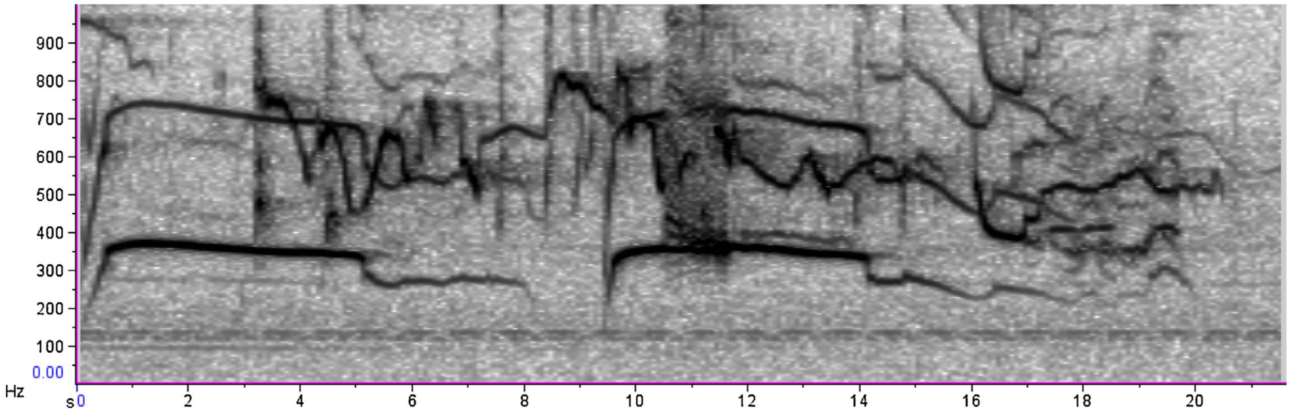

Fig. 1. Example spectrogram of multiple wolves howling.

Table 1
Number of howls, and number of recording sources (packs) for each of the species in the database.

Canid species	Common name	Reference	Number of howls	Number of sources
C. aureus	Golden jackal		28	3
C. latrans	Coyote		187	4
C. rufus	Red wolf	Chambers et al. (2012)	79	4
C. lycaon or *C. l. lycaon*	Eastern wolf	Chambers et al. (2012)	510	20
C. lupus	Grey wolf			
C. l. occidentalis	Mackenzie Valley wolf	Chambers et al. (2012)	127	8
C. l. baileyi	Mexican wolf	Chambers et al. (2012)	31	2
C. l. arctos	Arctic wolf	Chambers et al. (2012)	26	7
C. l. lupus	European wolf	Nowak (1995)	65	13
C. l. signatus	Iberian wolf	Vilà et al. (1999)	25	3
C. l pallipes	Indian wolf	Nowak (1995)	175	7
C. l. lupaster	North African wolf	Rueness et al. (2011)	33	5
C. familiaris or *C. l. familiaris*	Domestic dog(as companion animal)		375	53
C. hallstromi or *C. l. hallstromi*	New Guinea singing dog	Koler-Matznick et al. (2003)	344	2

quency data such as these, particularly in the analysis of dolphin vocalisations (Buck and Tyack, 1993; Deecke and Janik, 2006; Sayigh et al., 2007). The DTW algorithm allows the time points of each sampled frequency measurement to vary freely, until an optimum match between the two curves is achieved. The amount of time-axis distortion necessary to achieve this match is then taken as a measurement of the quantitative difference between the curves.

Using the dissimilarity matrix obtained by DTW, we applied the *k*-means unsupervised clustering algorithm to group the howls into natural clusters based on their similarity. We chose the appropriate number of clusters using a combination of cluster purity, measured as the mean cluster silhouette value (Rousseeuw, 1987), and stability using a bootstrap technique; repeatedly applying the clustering to a random subset of 90% of the howls, and measuring similarity of the clustering results using normalised mutual information (Zhong and Ghosh, 2005).

We then examined the usage of each of the different howl types by the 13 different species. As multiple recordings were obtained from the same individual, or from individuals within the same pack, potential issues of pseudoreplication arise if howls are directly compared to each other; howls from the same individual are likely to be more similar to each other than howls from separate individuals or from different packs. Therefore, rather than analysing howl difference distributions directly, we examined only differences in the use of different howl types, by calculating the proportion of howls $P(t)$ that belong to each howl type t, for each species: $P(t) = n(t)/N$, where $n(t)$ is the number of howls of type t for a particular species, and N is the total number of howls from that species. This provides a "fingerprint" of howl type usage, which can then be compared between species. We calculated the sum of squared differences Δ between the howl type histograms of different sources (packs) within each of the 13 species:

$$\Delta(a,b) = \sum_{t}^{T} \left(P_a(t) - P_b(t)\right)^2$$

where $\Delta(a,b)$ is the sum of square differences between sources a and b, $P_a(t)$ and $P_b(t)$ are the incidences of howl type t in sources a and b respectively, and T is the total number of distinct howl types for this species.

To test the ability of the howl type usage fingerprint to identify canid species, we measured the sum of squared differences Δ between each source (pack) and the mean histograms of each of the 13 species (with the target source excluded), and recorded which species was most similar to the target source as indicated by the lowest value of Δ. From this we constructed a confusion matrix showing the classification of each of the sources, whether to the correct species type or to an incorrect species.

We then used an exact test (Fisher, 1925) to estimate the significance of the similarity within a species. We randomised the howl type distributions 10^5 times within each species by reordering the incidences $P(t = 1 \ldots T)$ randomly, and recalculated $\Delta'(a,b)$ to generate a null distribution of sum of squared differences. We then calculated the proportion of randomised differences Δ' that were less than the measured intra-species difference Δ. We also identified the most common howl type in each species and examined various exemplar howls of this type, as an illustration of what may be a typical howl type for this species.

Finally, we examined more closely the similarity in the howling behaviour of three sympatric species, the red wolf, eastern timber wolf, and coyote. Red wolves and coyotes hybridise in the wild,

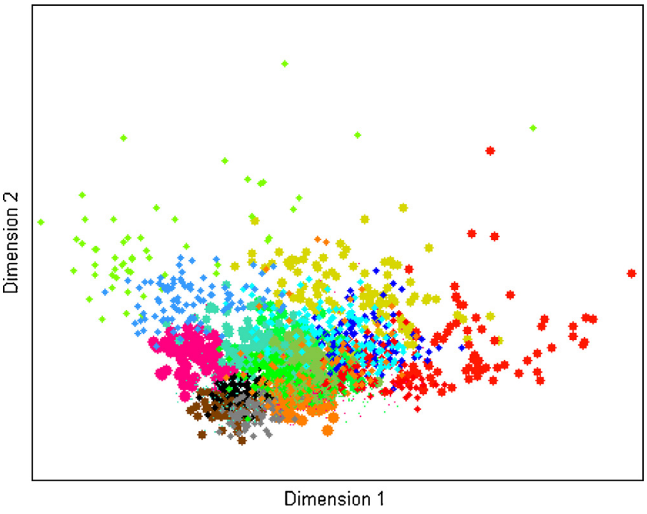

Fig. 2. Multidimensional scaling of the 2005 × 2,005 howl distance matrix into two dimensions. Each point is a howl, and points closer together are more similar than those further apart. Colours indicate *k*-means clustering assignment. The size of each point is for ease of visualisation only. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

which poses a threat to reintroduction programs for the critically endangered red wolf (Hinton et al., 2013; Gese et al., 2015). The eastern timber wolf *C. l. lycaon*, is considered a subspecies of grey wolf, but whose taxonomic status is unclear, and is considered to be very closely related to *C. rufus*, if not conspecific (Wilson et al., 2000; Koblmuller et al., 2009; Chambers et al., 2012). We tested for significant differences between the howls of these three species, to determine whether howling behaviour may potentially provide a form of behavioural isolation, or alternatively encourage admixing and introgression. We reclustered the DTW data, using only howls from the red wolf, coyote, and eastern wolf. We then repeated the sum of square difference analysis, comparing the red wolf-coyote-eastern difference to a null distribution generated by randomising the order of the histogram of howl types, as well as comparing the histogram fingerprints between sources, as with the full data set.

3. Results

Applying multidimensional scaling (Cox and Cox, 2000) to the full 2005 × 2005 matrix of howl distances found 37 significant dimensions, which were then passed to the *k*-means clustering algorithm. Analysis of silhouette values in *k*-means led to 21 distinct clusters (howl types). Fig. 2 shows the howl distance matrix reduced to two dimensions (for visualisation), with cluster assignment indicated. The clustering appeared robust; 99.3% of all howls were classified with posterior probability >0.5. Bootstrapping and re-clustering with 90% of the data produced a normalised mutual information in comparison to the full data set of 0.760 ± 0.033, i.e., 76% of the cluster assignment information was retained even when applying the algorithm to a reduced data set.

Within-species comparisons show that for the eastern timber wolf, the domestic dog, the coyote, the red wolf, the North African wolf *C.l. lupaster*, and the Arctic wolf *C. l. arctos*, howl type usage was more similar among sources of that species than would be expected by chance (Table 2). This indicates that in these species, the different sites from which recordings were taken showed a species-specific pattern of howl type usage.

The use of each howl type, adjusted for overall howl use frequency, for each of the species show species-specific fingerprints (Fig. 3). The red wolf and coyote share howl type 3 as the most common; the European *C. l. lupus* and Iberian *C. l. signatus* wolves share type 5; and the Mackenzie Valley *C. l. occidentalis*, Indian *C. l. pallipes*, and Mexican *C. l. baileyi* wolves share type 7. Each other species has a distinct call type that is most commonly used, relative to its overall usage in the sample database. Apart from these distinctive howl types, the different species have different repertoire diversities, with for instance the North African wolf making use of many fewer howl types than the golden jackal, despite being represented by a similar overall number of sources and howls (Fig. 3). One qualitative trend noticeable from the exemplar howls (chosen as those nearest to the cluster centroid) is that the smaller species (red wolf, coyote, New Guinea singing dog, domestic dog, golden jackal) favoured howls that ended with a sharp drop in frequency, whereas larger species (arctic wolf, eastern timber wolf, European wolf, Mackenzie Valley wolf) used howls with much less frequency modulation, particularly at the end of the howl (Fig. 4), although this may be an artefact of the lower fundamental frequency used by larger species.

The confusion matrix for the identification of species by source, and the results of the species identification assessment (Tables 3A and B) shows that the coyote, Arctic wolf, and North African wolf all were well identified by howl usage fingerprint comparison, with identification of the red wolf and Mackenzie Valley wolf also higher than expected. The New Guinea singing dog *C. l. hallstromi*, domestic dog, golden jackal, and North African wolf appeared to form a cluster of similar howl usage types, and the coyote and red wolf seem to form a separate cluster, with heavy use of

Table 2
Exact test of similarity of howl type use within each species. The *p*-value represents the proportion of randomised trials where the mean difference between sources within a particular species was less than the actual mean difference within the species. Starred values are significant at 5%.

Species	*p*		Number of sources
Golden jackal	0.718		3
Coyote	0.019	*	4
Red wolf	0.007	*	4
Eastern timber wolf	0.014	*	20
Mackenzie Valley wolf	0.955		8
Mexican wolf	0.891		2
Arctic wolf	0.006	*	7
European wolf	0.237		13
Iberian wolf	0.935		3
Indian wolf	0.144		7
North African wolf	<0.001	*	5
Domestic dog	0.003	*	53
New Guinea singing dog	0.899		2

Table 3A
Classification success by comparing howl type usage histograms as fingerprints. The% correct column indicates how many recording sources (animal packs) were correctly identified as their particular species when compared to all other sources in the database. The best guess column indicates which species were most frequently identified as the most similar species to the target source.

Species	% correct	Best guess
Golden jackal	33.3	Domestic dog
Coyote	50	Coyote
Red wolf	25	Red wolf, Coyote, Domestic dog, Arctic
Eastern timber	5	Arctic
Mackenzie Valley	25	Mackenzie Valley, Indian
Mexican	0	Red wolf
Arctic	57.1	Arctic
European	0	Mackenzie Valley
Iberian	0	Eastern timber, European, Mackenzie Valley
Indian	0	Mackenzie Valley
North African	40	North African
Domestic dog	13.2	North African
New Guinea singing dog	0	Domestic dog, North African

type 15 howls (which only seem to be used by 3 other species, and at very low frequency).

In the reduced analysis of just red wolf, coyote, and eastern timber wolf, there were a total of 776 howls, 510 eastern timber wolf, 187 coyote, and 79 red wolf. Applying multidimensional scaling to the full 776 × 776 matrix led to 42 significant dimensions, and 11 *k*-means clusters. All howls (100%) were classified with posterior probability >0.5, and bootstrapping followed by reclustering led to a normalised mutual information of 0.706 ± 0.059. With these data, the red wolf and coyote also showed significant similarity between the different sources (packs) of the same species ($p = 0.006$ and $p = 0.009$ respectively), whereas the eastern timber wolf was only

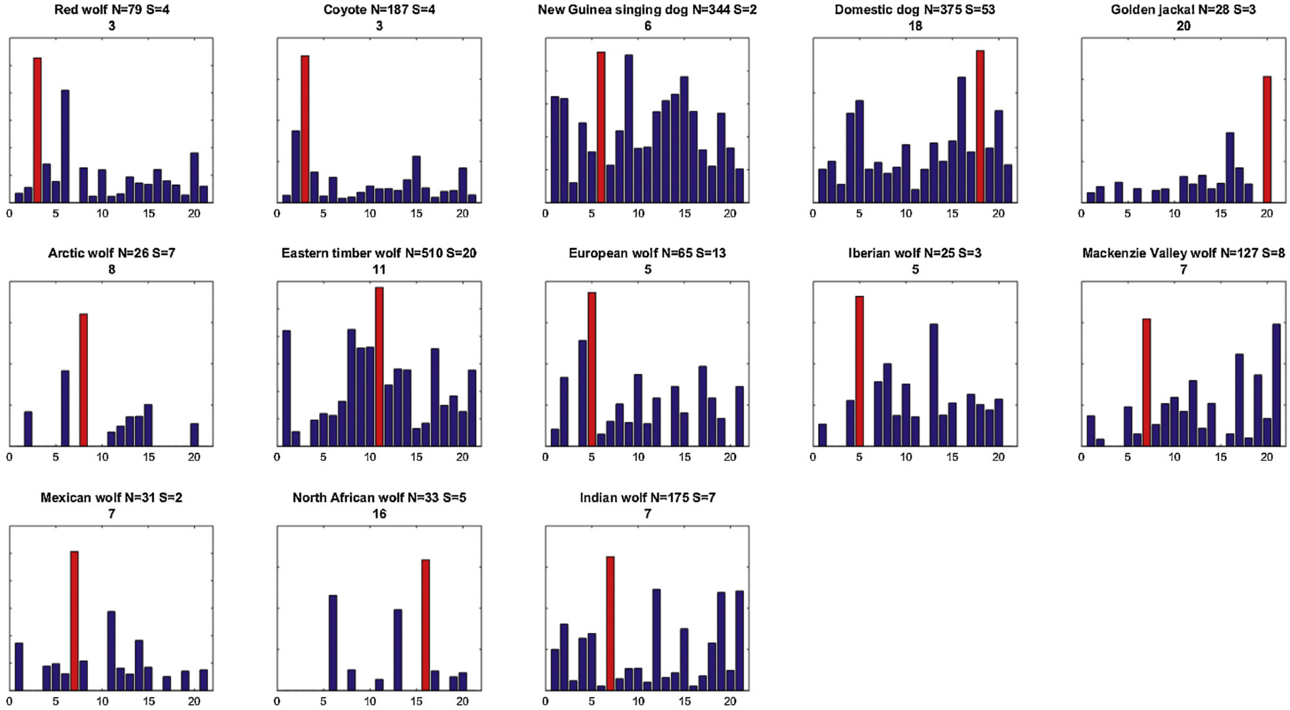

Fig. 3. Howl use histograms for each of the 13 species, showing the relative use of each of the 21 howl types, adjusted for overall howl type frequency. Red bars show the most commonly distinctive howl type for each species, with the index number of that type appearing above each histogram. *N* indicates the number of howls, and *S* indicates the number of sources. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

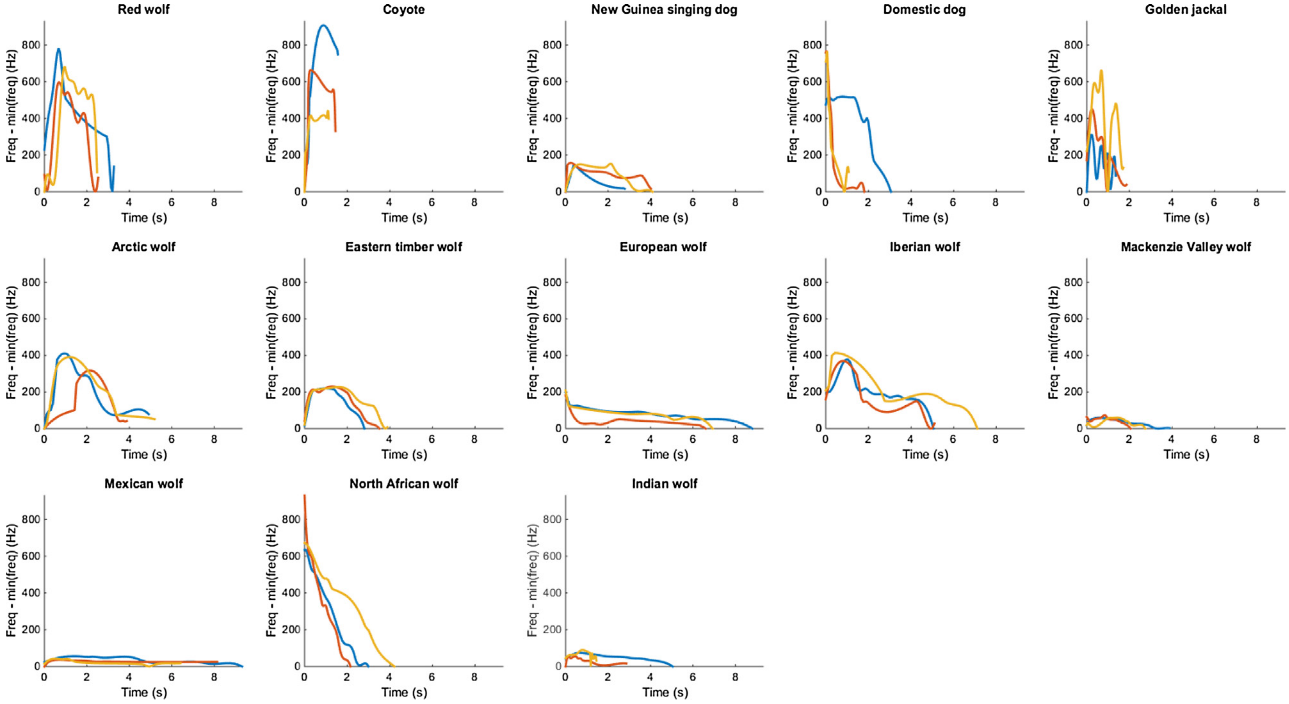

Fig. 4. Three examples of the howls of the particular howl types identified as characteristic of each species, and represented in Fig. 2 by the red bars. Note that the howls within a type are similar in a dynamic time warping sense, although they may vary somewhat in length. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 3B
Confusion matrix showing the number of sources identified as each species type.

		Predicted species												
		RW	COY	NGSD	DD	GJ	ARC	ETIM	EUR	IBER	MV	MEX	NAFR	IND
Actual species	RW	1	1		1		1							
	COY	1	2									1		
	NGSD				1								1	
	DD	3	3	1	7	4		3	8	3	2	2	9	8
	GJ				2	1								
	ARC		1	1			4							1
	ETIM	3					5	1	1	3	4			3
	EUR		2		2		2			2	3	1		1
	IBER							1	1		1			
	MV	1			1			1	1		2			2
	MEX	1								1				
	NAFR	1		1		1							2	
	IND		1		1				1		4			

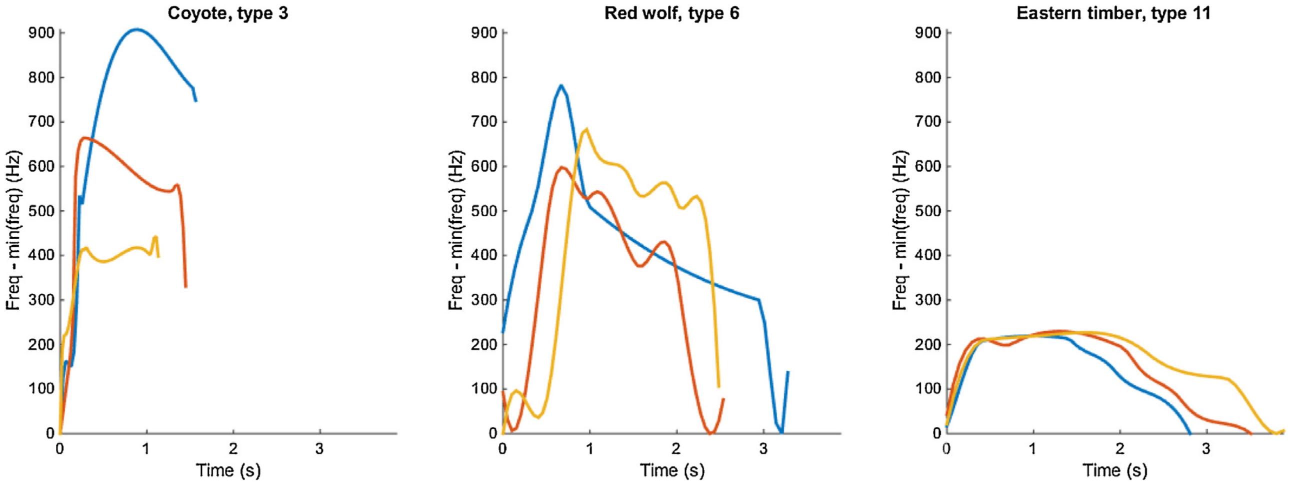

Fig. 5. Examples of coyote howls of type 3 (left), red wolf howls of type 6 (middle) and eastern timber wolf howls of type 11 (right). Type 6 howls are rarely used by coyotes and eastern timber wolves, but commonly used by red wolves, and may represent an intermediate form. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

marginally significant ($p = 0.052$). Comparison of the howl type fingerprints showed that the coyote was well identified from most sources (3 out of 4 sources correctly identified), whereas the red wolf and eastern timber wolf were often misclassified one as the other, with the red wolf identified as eastern timber wolf in 2 out of 4 sources, and eastern timber wolf as red wolf in 6 out of 20 sources. Red wolves and coyotes share their most common howl type – type 3–which is rarely used by timber wolves. Red wolves will often use howl type 6, which coyotes and timber wolves rarely use, and may be intermediate in characteristics between coyote (type 3) and timber wolf (type 11) howls, by being lower in frequency and less frequency-modulated (Fig. 5).

4. Discussion

In this study we analysed over 2000 howls from 13 different species and subspecies belonging to the genus *Canis* around the world. Using dynamic time warping as a quantitative measure of howl dissimilarity, we applied an objective unsupervised clustering algorithm to group the howls into distinct howl types. The *k*-means algorithm produced 21 clusters that were stable to bootstrapping, and that probably represent genuine howl type categories, which we define without the need for subjective description of howl characteristics.

Each population recorded made different use of these 21 howl types, with many species/subspecies having a particular howl type that was characteristic of that species/subspecies. Within six of the species – the eastern timber wolf, the domestic dog, the coyote, the red wolf, the North African wolf, and the Arctic wolf – a statistically significant similarity existed in their howl type usage. Further, we found that individual populations of five of the species – coyote, red wolf, Arctic wolf, North African wolf, and Mackenzie Valley wolf – could be identified using the howl type histograms of the remaining populations in the data set.

In general, we conclude that canid howling is not an arbitrary signal, but possesses species-specific information, which may reflect adaptive and/or neutral processes of isolation.

We also performed a more detailed analysis of the howls of three American canids – the red wolf, the coyote, and the eastern timber wolf – because of the conservation importance of hybridisation between the critically endangered red wolf and the coyote, as well as continuing disagreement over the phylogenetic relationship between the red wolf and both the coyote and eastern timber wolf. We found that coyote and red wolf howl type usage differs significantly, which could be a useful tool for managing red wolf conservation in the face of competition from sympatric coyotes. Red wolf howling was similar to that of eastern timber wolves, further complicating the challenge of red wolf introduction both at the southern end of its range (coyotes) and at the northern end (eastern). In contrast, red wolves and coyotes share their most common howl type, whereas red wolves will often use howl type 6, which coyotes and timber wolves almost never use. The intermediate nature of howl type 6 may provide potential evidence of hybridization between these species.

We note in passing that the smaller species – the red wolf, domestic dog, New Guinea singing dog, golden jackal – show a greater diversity of howl types than the larger species, and are similar to each other in their howl type usage. We lack sufficient data to examine this further; however, this phenomenon could be due to peculiarity of the habitat or niche of these smaller species, or could be due to a different emphasis on long and short range communication between larger and smaller species, differences in the vocal production mechanism in different sized species, or a different emphasis on the social role of howling.

Given the diverse and non-arbitrary nature of howl differences, it is natural to ask whether variations in howl structure reflect referential or context-specific information. Early studies of wolf communication pointed out that different vocalisation types (e.g. howl vs. growl, yelp, etc.) were associated with different behavioural contexts (Cohen and Fox, 1976; Tembrock, 1976), but stopped short of suggesting that particular features within howls themselves represented certain arousal states or environmental contexts (Theberge and Falls, 1967; Lehner, 1978). More recent studies have begun to address this question in dingoes (Déaux and Clarke, 2013), as well as dogs (Faragó et al., 2014), and there is some evidence that vocal communication may be used in *Canis* to coordinate hunting activity (Muntz and Patterson, 2004). Experimentally, it has been shown that howl modulation patterns convey individual identity, and that animals attend to this information (Palacios et al., 2015). Thus, individual identity in howl structure is more than just an epiphenomenon, and may be of relevance to conservation and management programs (Llaneza et al., 2005; Terry et al., 2005; Brennan et al., 2013; Hansen et al., 2015). Depredation of livestock by coyotes (Knowlton et al., 1999) and wolves (Sillero-Zubiri and Laurenson, 2001), in particular, is a cause for concern, but attempts to use vocalisation playbacks as active deterrents have largely been unsuccessful (Gable, 2010).

Our results have shown clear differences in howl structure between populations. Whether populations in geographical proximity represent separate species, subspecies, or otherwise, it seems clear that distinct ecotypes exist. The presence of discrete differences in vocal behaviour suggests that consideration should be given to conservation of populations such as *C. rufus* and *C. lupus lycaon*, even if genetic isolation does not exist. Recent studies have shown multiple examples of dialects not just in birdsong (Kroodsma, 2004), but also in multiple mammalian taxa including rodents (Slobodchikoff and Coast, 1980; Gannon and Lawlor, 1989), primates (de la Torre and Snowdon, 2009; Thinh et al., 2011; Meyer et al., 2012), and hyraxes (Kershenbaum et al., 2012). Our study adds to recent work showing dialectic differences between the howls of wolves in Europe and North America (Palacios et al., 2007), and fits into an increasingly important trend of understanding the proximal causes and ultimate significance of dialectic variation (Lameira et al., 2010).

In the case of the critically endangered red wolf, hybridisation with coyotes represents the largest threat to reintroduced populations (Hinton et al., 2013; Gese et al., 2015). Although howling behaviour has long been identified in *Canis* as a mechanism for separating competing populations (Harrington and Mech, 1979; Jaeger et al., 1996; Gese, 2001), and vocal behaviour as a mechanism for genetic isolation in other mammalian taxa (Braune et al., 2008), to our knowledge no studies have addressed the question whether vocal differences can act to reduce interspecific hybridisation in *Canis*, or may in fact be the result of past hybridisation. Coyotes fail to respond to stimuli of wolf howling (Petroelje et al., 2013); detailed analysis of *C. rufus* recordings have uncovered non-howl vocalisations that have not been reported in *C. latrans* (Schneider and Anderson, 2011); and the behavioural responses of individual wolves vary according to the familiarity of playback howls (Palacios et al., 2015). All these findings raise the possibility that vocal differences between *C. rufus* and *C. latrans* may have conservation significance. Our work adds to this body of evidence, and should encourage further investigation of the possibility of behavioural isolation between these populations.

Our study made use of data sources of widely varying size and quality—something inevitable when integrating recordings from around the world and from species of greatly varying abundance. We have endeavoured to minimise the statistical artefacts arising from this imbalance, and have been careful to use the recording source (essentially, a single pack) as the unit of comparison. Some pseudo-replication may remain, as we cannot ensure that the proportion of howls in each type is constant for a species. However, in most cases there are insufficient howls from specific individuals to look at how the pattern varies by individual within species. In addition, it is possible that differences between populations reflect differences in contextual stimuli. Despite these statistical limitations, we believe that such broad comparative studies have great value in understanding behaviour across a wider taxonomic basis than just the species, and we hope that this utility compensates somewhat for the patchy nature of the data sources.

Automatic clustering using unsupervised algorithms is potentially problematic, as the presence of computer-identified clusters does not guarantee that these elements have cognitive significance for the animals involved. Indeed, we have no mechanistic indication that canids perceive and compare howls in a way similar to our dynamic time warping. To date, what we know is that wolves detect changes in the fundamental frequency of howls outside their natural range of variability, and changes in the frequency modulation pattern of howls (Palacios et al., 2015). However we feel confident that DTW provides a useful comparative tool, because consideration of acoustic propagation would indicate that frequency modulation of howls is likely an important encoding technique in long-range communication. Also, we took care to evaluate our clustering results using multiple metrics, and assessing their stability in the face of bootstrapping, to maximise confidence that the howl type partitions did, in fact, represent a division of howls into realistic howl types.

This study has involved only correlative analyses, but we believe that this kind of quantitative categorisation of vocalisation types is necessary before carrying out manipulative and playback experiments. Being armed with an objective set of howl types, or a methodology for arriving at such a definition, allows researchers to test the cognitive significance of different howl compositions, and look for potential behavioural correlates, such as territorial advertising and group cohesion. Any experimental work with critically endangered species such as the red wolf can be problematic, but we hope that with a firmer understanding of the vocal behaviour of these animals, it will be possible to design experiments that will benefit the conservation and management of this and other species.

5. Conclusions

Howling is a social communication process that is likely of major importance in the overall behaviour of all canid species. A deeper understanding of their social behaviour is not possible without a framework within which to understand their vocal behaviour. In particular, quantitative and objective assessment of howling is highly preferable to subjective interpretation by humans, who lack the auditory and cognitive instruments of the focal animals. Techniques such as ours providing quantitative comparisons are important for any future experiments to investigate functionally referential elements to the canid howl repertoire, which would be a highly significant finding for two reasons. Firstly, the role of vocal communication in mediating social behaviour in canids may contribute to understanding the evolution of human language (Seyfarth and Cheney, 2014). To our knowledge, no animal species other than humans possess any form of true language, not even any form of "proto-language". Therefore, it has been problematic to explain the evolution of human language as a continual progression from "non-language" to "language", through increasing adaptive advantage at each step (Tomasello, 2008). The presence of complex referential communication in species that must cooperate to survive was probably a crucial step in the evolution of language (Jackendoff, 1999). Understanding the communication systems of extant social species is essential to understanding the potential evolutionary trajectories to more complex communication that have occurred in the past, eventually leading to human linguistic abilities. Although taxonomically distant from early hominids, wolves and other canids show remarkable parallels with humans in, for example, social behaviour, intelligence, and vocal communication (Miklósi, 2014). Further understanding of canid social communication could serve as a model system for the evolution of more complex vocal communication and language. Secondly, canid conservation and management can benefit from acoustic methods for surveying and assessing population size and health/genetic purity (Llaneza et al., 2005; Brennan et al., 2013), which can be difficult using traditional methods, particularly when snow is absent (Blanco and Cortés, 2011). Active acoustic deterrence has also been suggested as a tool in the control of animal movements for mitigating wolf conflict with farmers (Gable, 2010), but such techniques cannot be successfully implemented without understanding the message being transmitted. Therefore, clearer and quantitative techniques for the description of the long-range communication of canids could have multiple benefits for the conservation and management of these species: through understanding the processes controlling behavioural isolation, identifying populations by remote surveying, and active techniques to reduce human-animal conflict.

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