Barking and mobbing

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ARTICLE INFO

ABSTRACT

Barking is most often associated with the domestic dog *Canis familiaris*, but it is a common mammalian and avian vocalization. Like any vocalization, the acoustic character of the bark is likely to be a product of adaptation as well as an expression of the signaler's internal motivational state. While most authors recognize that the bark is a distinct signal type, no consistent description of its acoustic definition or function is apparent. The bark exhibits considerable variability in its acoustic form and occurs in a wide range of behavioral contexts, particularly in dogs. This has led some authors to suggest that dog barking might be a form of referential signaling, or an adaptation for heightened capability to communicate with humans. In this paper we propose a general 'canonical' acoustic description of the bark. Surveying relevant literature on dogs, wild canids, other mammals and birds, we explore an alternative functional hypothesis, first suggested by [Morton, E.S., 1977. On the occurrence and significance of motivation-structural rules in some bird and mammal sounds. Am. Nat. 111, 855–869] and consistent with his motivational-structural rules theory: that barking in many animals, including the domestic dog, is associated with mobbing behavior and the motivational states that accompany mobbing.

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1. Introduction

Barking is a universally recognized hallmark of the domestic dog, *Canis lupus familiaris*. From the casual human listener's standpoint, barking seems readily distinguishable from other vocalizations. But the terms "bark" and "barking" are often used in the scientific literature without a precise definition of a bark's structure. The function of this vocalization is variously analyzed as an alarm call (Cohen and Fox, 1976; Tembrock, 1976; Lehner, 1978; Schassburger, 1987, 1993; Harrington and Asa, 2003); a territory-marking signal (Lehner, 1978; Cohen and Fox, 1976); a rally call (Schassburger, 1987; Cohen and Fox, 1976); or an indicator of motivational state (Morton, 1977; Bleicher, 1963; Tembrock, 1976). Coppinger and Feinstein (1991) argue that dog barking is a developmental artifact with no intrinsic function; Yin and McCowan (2004), Yin (2002) and Feddersen-Petersen (2000) speculate that barks may have referential content; and Pongrácz et al. (2005) suggest that barks are co-adapted signals between dogs and humans.

Several descriptions of the acoustic properties of barking and other canid vocalizations have appeared in the recent literature: Reide and Fitch (1999) looked at correlations between vocal tract anatomy and vocalization in the dog; Riede et al. (2001) and Riede et al. (2005) examined harmonic-to-noise ratios in the bark; Yin and McCowan (2004) carried out an extensive analysis of the acous-

tic character of barking in 10 adult dogs of 6 breeds, looking at the interaction of multiple parameters. In our laboratory we made sonograms of barking and other vocalizations of several breeds at various ages, examining tonal and noisy qualities.

Despite this recent attention there does not yet appear to be a common and useful definition of the acoustic structure of the bark. We offer one here, acknowledging that barking is a highly variable phenomenon: Yin and McCowan (2004) and many others provide ample evidence of individual differences in dogs; Mitchell et al. (2006) do the same for the coyote. Casual listeners readily conclude that individual dogs bark differently in different circumstances, and that different breeds have distinctive barks. Dog barks resemble other calls, described as "woofs," "yelps" or "cries." Some investigators treat them as functionally related graded variants of a single call-type. But we show that the bark nonetheless has basic, largely invariant structural properties which distinguish it systematically from other signals. Moreover, by taking into account this distinctive acoustic character – a generalized form that can be termed "canonical" because it occurs not only in the domestic dog and related canids but also more widely in mammals and birds – we are able to propose a functional explanation for barking as well as an account of its contextual variability.

2. Acoustic features of barking

Sounds are generally characterized along three acoustic dimensions—frequency, amplitude and duration. Within each dimension, certain parameters capture the acoustic nature of particular signals.

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These parameters include the following (with abbreviations we will adopt in later discussion).

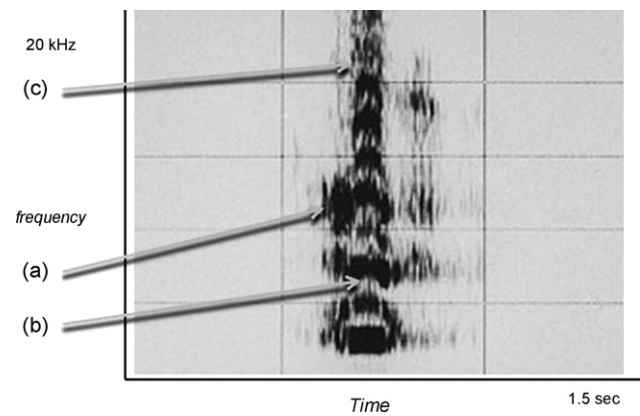| Frequency	
Tonality	T
Noise	N
Mean Pitch	MP
Frequency Modulation	FM
Amplitude	
Relative Amplitude	RA
Abrupt Onset	AO
Duration	
Pulse Duration	PD
Pulse Repetition	PR

3. Frequency

The frequency or pitch of a sound is determined by the rate of periodic oscillation (vibration) of some structure (e.g. laryngeal vocal folds in mammals) disturbing a medium such as air; it is measured in cycles per second or Hertz (Hz). Slow vibrations sound low in pitch, fast vibrations sound high. This rate depends on anatomical and physiological factors (e.g., vocal fold length and thickness), which vary in individuals. Vibration rate in many animals is also under voluntary control, thus it can vary from production to production in a single call-type, as well as over time within a single signal.

Tonality (T). Tonal vocalizations are produced by structures that vibrate periodically (regularly). A *tonal* sound may be a simple wave, exhibiting a single frequency. This basic rate of vibration is the *fundamental frequency* (F0), which gives rise to the perception of the sound's relative *pitch*. But in the majority of biological systems, the oscillating structure generates a complex wave with a series of harmonic overtones in addition to F0. The overtones are integral multiples of F0. Harmonic overtones in particular frequency ranges may have differing levels of energy; such bands are referred to as *formants*. Harmonic complexity and formant structure contribute to the overall auditory impression of a sound—its *timbre*. The timbre of a simple-wave (or narrowband) tonal sound is often described as "pure"; the more harmonically complex (or broadband) the tonal sound, the richer its timbre as perceived by a (human) receiver.

Barking typically contains a tonal component in which the fundamental frequency and a set of harmonic overtones, usually broadly distributed over the spectrum, are discernible in the signal (Bleicher, 1963; Lehner, 1978; Morton, 1977; Pongrácz et al., 2005). This tonality may persist throughout the call, occur only in a portion of the signal, or may be masked by noise (Fig. 1); in some cases, a tonal component is absent.

Noise (N). Noisy sounds are generated by structures that vibrate irregularly (aperiodically), producing complex waveforms with components at many non-harmonically related frequencies. By definition noisy signals do not have a single fundamental frequency, but *dominant* frequencies – regions of the acoustic spectrum with the greatest energy – may produce an impression of relative pitch in noisy sounds. Noise is often *broadband*, with frequency components in a wide range of the acoustic spectrum, or *narrowband*, concentrated in a particular frequency range. Noise may co-occur in a signal with harmonically related tonality (Fig. 1).

Barking is described in the literature as a noisy signal containing multiple non-harmonically related frequencies over a broad range of the spectrum (Bleicher, 1963; Lehner, 1978; Pongrácz et al., 2005; Schassburger, 1987). Some writers do not distinguish the bark from the yelp (Feddersen-Petersen, 2000), but the yelp is purely tonal with no noisy components. Our view is that the presence of noise (typically though not always co-existing with a tonal component) is a diagnostic feature of the canonical definition of a bark (Fig. 2).


Fig. 1. Bark of an adult male malamute dog. The abrupt onset is characterized by an initial noisy burst (a); it is followed by a tonal component (b) with frequency modulation evident in multiple harmonics; and some broadband noise (c) can be seen throughout much of the signal, particularly in the upper frequencies. The barks shown in this and the other two figures are illustrative of the phenomenon under discussion and were chosen for those characteristics. They are not directly comparable.
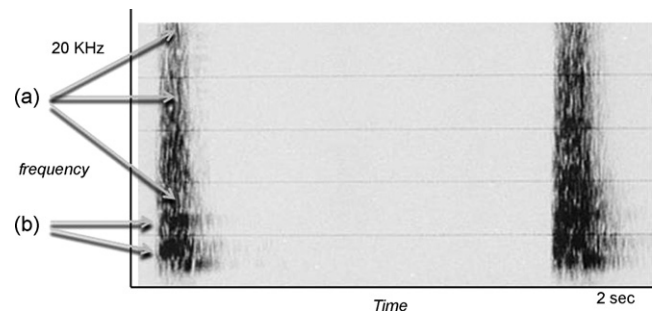
Fig. 2. Two barks from an adult female Anatolian guarding dog. Left: broadband noise (a) occurs along with two distinct tonal harmonic components (b). Right: noise dominates throughout the frequency range, with little if any tonality evident in the signal.

Noise is characteristically present throughout the signal, or a noisy period can precede a tonal period (Fig. 3).

Mean Pitch (MP). Pitch is the perception of frequency. Both tonal and noisy signals give an impression of pitch. In tonal signals pitch is often a direct function of the fundamental frequency (F0), the base frequency at which the vocal folds are vibrating. Pitch may also be determined by harmonics in the upper frequency range that have greater acoustic energy than the fundamental (formant regions), hence pitch may be relative with respect to F0. In
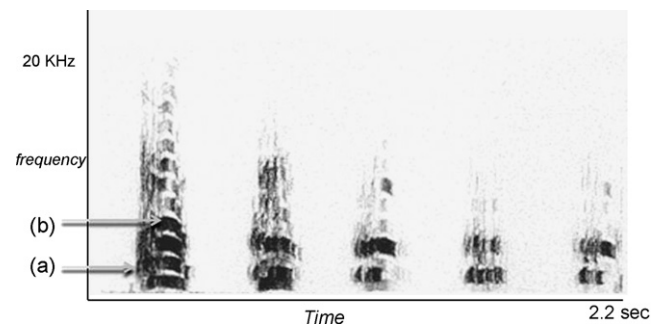
Fig. 3. Pulse repetition in an adult female Maremma guarding dog. This series of barks is characterized by regularly timed inter-pulse intervals, and decreasing amplitude. Note also the abrupt onset and initial noisy component (a) in the first pulse, followed by a predominantly tonal frequency-modulated period (b) with multiple harmonics.

noisy signals the dominant frequency, or the frequency range at which the most energy is present, also creates an impression of pitch. For our purposes we define mean pitch as the mean fundamental frequency in signals containing tonal components and the mean dominant frequency for signals that lack tonal components.

Barking is highly variable in pitch. Feddersen-Petersen (2000) reports F0 values varying from 120 to 1640 Hz, and dominant frequency values ranging from 200 to 2360 Hz in 6 breeds; Bleicher (1963) reports a dominant frequency range between 200 and 3000 Hz. Sales et al. (1997) report a dominant frequency range of 250–4000 Hz in the barking of kenneled dogs. This variation is likely a function of the size, age and breed of an individual; it may also relate to the animal's motivational state (Morton, 1977). Moreover, individual barks themselves typically vary in frequency (FM). In general, barking is described in the literature as relatively high-pitched. Bleicher (1963) reports a mean fundamental pitch of 650 Hz. In our own lab (Clemence, unpub. 1992) the fundamental frequencies of 25 randomly sampled barks from each of 86 individuals (recorded on a Sony Professional Walkman recorder with a Sony 0–15 kHz omnidirectional microphone) were extracted in MacSpeech Lab II (GW Instruments, Camridge, MA) and analyzed in Statview (SAS Institute, Cary, NC). We found an average fundamental frequency of 715 Hz (SD115).

Frequency Modulation (FM). The frequency (hence relative pitch) of a given tonal vocalization can vary over time (Fig. 3). These modulations can be considerable, with rapid shifts in F0 over many hundreds of Hz, or more gradual. Because harmonic overtone structure is integrally related to F0, modulation will affect these upper frequencies as well. Although a very small degree of FM, or jitter, is present in most biologically generated tonal signals, some signals are relatively "steady-state" or monotone, and exhibit minimal modulation.

The bark often has a characteristic "chevron-shaped" modulated frequency contour, with a relatively rapid rise and fall. Yin and McCowan (2004) report frequency ranges of 766 Hz and higher within a single bark; Schassburger (1987) also reports a wide intra-signal frequency range. Monotone barks occur in some individuals, but some degree of FM is the general rule.

4. Amplitude

Amplitude is a function of the amount of energy in the signal as emitted by the sender. It is not a constant, and may vary over time within a signal, or when a call is repeated at brief intervals. Moreover, amplitude decreases with distance by the inverse-square law, therefore a signal heard 10 m from its source would be significantly louder than if it were detected at 100 m. Amplitude can also be strongly affected by external factors such as environmental conditions and habitat obstacles as well as internal factors such as available respiratory volume and muscle effort.

Relative Amplitude or Loudness (RA). Given that loudness, like pitch, is a perceptual phenomenon and that this perception is affected by the extrinsic physical factors noted above, it is appropriate to think in relative terms such as "softer" or "louder" when characterizing amplitude. There is general agreement in the literature that barking is a relatively loud signal (Lehner, 1978; Sales et al., 1997; Tod et al., 2005).

Abrupt Onset (AO). A signal can reach its maximum amplitude gradually or suddenly. Sounds that are described as having an *abrupt* onset are characterized by a steep "rise-time" for amplitude. Some AO signals are produced by a build-up and rapid release of pressure resulting in a very brief broadband burst of noise at the beginning of the signal, often perceived as click-like. Non-AO signals have a gradual rise-time.

Barks are reported to have abrupt or explosive onsets (Scott and Fuller, 1965; Lehner, 1978; Schassburger, 1987; Robbins and McCreery, 2003).

5. Duration

Duration is the time aspect of the signal, i.e. the period during which the signal is emitted. The duration of biological signals may be as brief as a few milliseconds, as long as several seconds or even several minutes.

Pulse Duration (PD). The energy expended in a call may occur in a single "pulse" of some length. For comparative purposes we define the duration of a call in terms of the time in which a *single pulse* is active.

A single bark is a short event, lasting from 100 to 500 ms (Scott and Fuller, 1965; Tembrock, 1976; Lehner, 1978; Schassburger, 1987; Robbins and McCreery, 2003; Yin and McCowan, 2004).

Pulse Repetition (PR). Calls with pulse repetition may repeat with short silent inter-pulse intervals. The absolute duration of pulse-repeating calls is longer than the basic value of PD for that call. The *rate* of PR is a function of the number of individual pulses per unit of time.

Dogs typically bark serially, with very short silent inter-pulse intervals, which may vary in length both within and between animals. The rate of repetition can be very high: Scott and Fuller (1965) for example report a cocker spaniel barking at 900 pulses per hour. Increased barking rate, i.e., shorter pulse-interval, appears to be correlated with increased arousal level (Gould, 1983). But PR is not an invariant property of barking: it is a "canonical" and typical feature of domestic dog vocalization, although single barks (pulses) do occur in dogs. It is also important to note that PR increases informational reliability (redundancy) as well as the perceptual salience of a signal.

6. The canonical form of the bark

What, then, are the acoustic features that distinguish the bark from other types of vocalizations? We maintain the bark is a signal that is always abrupt in onset and short in duration. It may exhibit both tonality and noise in some degree; is relatively high-pitched; is subject to frequency modulation; is relatively loud; and is subject to rapid repetition. Taken together, these properties uniquely define the bark. *We are aware of no other vocalization described in the literature that generally exhibits all of these features.* For simplicity of exposition, we treat each of the acoustic parameters described above as *binary*—marked either [+] or [−] depending on whether it is present or meets a particular threshold value for that parameter (granting that certain features are subject to variation). In this framework the "ideal" bark may be described schematically as in Table 1.

We refer to this as the *canonical* bark—a specific range of intrinsic acoustic properties and possibilities that define a particular signal type occurring in the dog, related canids, and many other mammals and birds. Of course not every observed instance of the bark will exhibit all of these characteristics. We do not intend the notion of "canonical bark form" to suggest that barking is a stereotyped phenomenon, in the way that many alarm calls or care-soliciting signals may be stereotyped. The domestic dog bark is highly variable with respect to some of the features noted above, as Yin and McCowan (2004) and many others have observed. Some of these variations arise from intrinsic anatomical differences between individuals. Animals can also alter components of the signal under particular motivational or behavioral conditions. For instance, the binary feature [+PR] in Table 1 indicates that pulse repetition is a typical realization of the canonical bark. Indeed it may be a common behav-

Table 1
Comparison of canonical barking with other Canis vocalizations.

Vocalization	T	N	MP	FM	RA	AO	PD	PR
Bark	+	+	+ (≥600 Hz)	+	+ (≥70 dB)	+	−(<500 ms)	+
Whine	+[a,f]	−[a,f]	+[a,d,g]	+[a]	−[b]	+[a,b]	+[d,f]	+[a]
Yelp	+[f]	−[f]	+[b,e]	+[f]	+[a,b]	+[e]	−[c,f]	+[b]
Growl	−[e,f]	+[a,f]	−[b,f]	−[a,b,c]	−[b]	−[c,e]	+[c,d]	−[a]
Howl	+[a,f]	−[a,b,f]	−[d,f,g]	+[h]	+[b]	−[b]	+[a,d,f]	+[i]
Woof (huff)[2]	−[b,e,f]	+[b,e,f]	−[f]	−[b]	−[b]	−[b]	−[b,f]	−[b,i]

[a] Cohen and Fox (1976).
[b] Lehner (1978).
[c] Tembrock (1976).
[d] Feddersen-Petersen (2000).
[e] Bleicher (1963).
[f] Schassburger (1987).
[g] Theberge and Falls (1967).
[h] Mitchell et al. (2006).
[i] Lord (pers. obs.).

ioral outcome. But whether a given animal emits a repetitive signal, or the actual rate of repetition, will depend on specific conditions of its production.

It is also important to separate the terms "bark" and "barking." To us, "a bark" is an ideal signal type that generally fits the canonical form in Table 1, and is distinct from other calls in an animal's repertoire. But by "barking" we mean the actual engagement of this signal type in behavior—and it is here that significant variation can arise.

As noted above, other calls described in the literature differ from the bark in just one or two canonical features. It is not surprising that vocalizations like the bark, yelp, huff and cry share a degree of perceptual similarity to human observers and all may be referred to as "barks" (even reports in the literature may fail to distinguish amongst them, e.g., Feddersen-Petersen, 2000). Moreover, because of the inherent variability of signals in actual behavior they may appear to grade into one another. A particular bark with little or no discernible tonality and relatively low amplitude may not be readily distinguishable from a woof. A beagle cry or bay that is made with some small degree of noise and a relatively short pulse duration may not be readily distinguishable from a bark; a bark made with little noise may be difficult to distinguish from a yelp. Graded signals are not uncommon in mammalian vocal-behavioral systems (Marler, 1967). We discuss this question further along with motivational conflict in the acoustic structure of mobbing calls.

7. Who barks?

Barking, as defined above, is not unique to the domestic dog. It is reasonably common in a variety of taxa. Signals consistent with canonical barking are found in numerous non-canid mammalian species including distantly related carnivores, cervids, primates and rodents, and are common in avian species. The presence of barking in the vocal repertoire of the wild canids is not surprising, on the uncontroversial assumption that domestic dogs and their wild counterparts share a relatively recent common ancestor. But phylogenetic homology (rather than analogy) is not likely to be the explanation for the occurrence of barking calls in distantly related mammals or birds. A broader comparative approach helps to understand the nature of an apparent convergence, and also helps to explain the function and biological history of the barking signal. The examples in Table 2, as well as our general conclusions about the occurrence of barking calls, are based on inspection of calibrated spectrograms (sonograms) and acoustic descriptions that have appeared in the literature.

8. Wild canids

Barking is reported in the vocal repertoire of almost all the wild *Canidae* (Cohen and Fox, 1976), including wolves (Cohen and Fox, 1976; Schassburger, 1993; Feddersen-Petersen, 2000; McCarley, 1978), coyotes (Lehner, 1978; Mitchell et al., 2006; McCarley, 1975), foxes (Cohen and Fox, 1976; Frommolt et al., 2003; Murdoch et al., 2008; Brady, 1981; Darden and Dabelsteen, 2006), jackals (Tembrock, 1976), African wild dogs, *Lycaon pictus* (Robbins, 2000), bush dogs, *Spethos venaticus* (Brady, 1981), dingos (Corbett, 2004), and New Guinea singing dogs (Koler-Matznick et al., 2003; Brisbin et al., 1994). Virtually identical to domestic dog barking in its acoustic character, each species appears to exhibit a somewhat narrower range of variability in tonality/noise and mean pitch. For example, wolf barking is often (but not always) relatively noisy and low-pitched (Cohen and Fox, 1976; Schassburger, 1993; Feddersen-Petersen, 2000). This reduction in acoustic variability can be expected given that, unlike the domestic dog, adults within wild canid species tend to be similar in size and shape.

9. Other mammals

The literature on mammalian vocal behavior is replete with examples of vocalizations that display the acoustic features we ascribe to canonical domestic dog barking. Representative cases among primates are reported for squirrel monkeys, *Saimiri sciureus* (Winter et al., 1966), the black-and-white ruffed lemur, *Varecia variegata* (Pereira et al., 1988), female chacma baboons, *Papio ursinus* (Fischer et al., 2001), and Garnett's greater bush baby, *Otolemur garnettii* (Becker et al., 2003). Digweed et al. (2005) describe an alerting signal in the white-faced capuchin monkey, *Cebus capucinus*, as "shorter and more plosive (abrupt-onset)" than a related alarm call, "giving it a conspicuously bark-like quality". It is typically given repeatedly in protracted bouts of calling. The capuchin signal is both noisy and tonal.

Reby et al. (1999a) note that "most *Cervinae* species bark", however, only a few have been described with enough detail to be categorized as canonical barking. The barking vocalization of both the Indian muntjac, *Muntiacus muntjac* (Wiles and Weeks, 1981; Oli and Jacobson, 1995), and Chinese muntjac, *Muntiacus reevesi* (Yahner, 1980), match our definition. Roe deer barking also corresponds with the acoustic characterizations of barking (Reby et al., 1999b).

Additional mammalian examples in diverse taxa include red squirrels, *Sciurus vulgaris* (Greene and Maegher, 1998) and tree shrews, *Tupaia belangeri* (Schehka and Esser, 2007). Mammals such as the meerkat, *Suricata suricatta* (Graw and Manser, 2007;

Table 2

Characteristics of the bark in non-canid mammals and bird species.

Species	T	N	MP	FM	RA	AO	PD	PR	Context
Canonical bark	+	+	≥600 Hz	+	≥70 dB	+	<500 ms	+	Conflict/mobbing
Squirrel monkey (yap)[1,2]	+	+	≥600 Hz*	+	NA	+	100–250 ms[1]	+	Mobbing[1]
Black-and-white ruffed lemur (pulsed squawks)[3]	+	+	≥600 Hz*	+	"High amplitude"	+	<400 ms	+	Squawk at potential predators; approach and squawk in response.[3]
Chacma baboon (female loud bark)[4]	+	+	≥600 Hz*	+	Mean 69 dB	+	~200 ms	+	Do use in mobbing (response varies depending on context, look for eliciting stimuli)[4]
Garnett's greater bush baby (bark)[5]	+	+	589 Hz	+	"Loud"	+	~400 ms	+	NA
White-faced capuchin (alerting call)[6]	+	+	≥600 Hz*	–	"Loud"	+	<150 ms	+	Non referential predator call and mobbing call[6]
Indian muntjac (bark)[7,8]		+	588 ±43 Hz[8]	+	"Loud"	+	620 ms ± 64 ms[8]	+	Potential predator (usually when it can't tell what is coming)[7]
Chinese muntjac (bark)[9]	+	+	670–1120 Hz	+	NA		270–510 ms	+	Novelty (hypothesized to interrupt predator)[9]
Roe deer (bark)[10]	+	+	1600–2500 Hz	–	"Loud"	+	<500 ms*	+	Unknown disturbance (hypothesized Predator deterrence)[11]
Red squirrel (bark)[12]	+	+	3000 Hz	+	"Loud"	+	20–400 ms	+	Potential terrestrial predators
Tree shrew (high arousal threat squeak)[13]	+	+	2313–2413 Hz	+	"Loud"	+	<70 ms	+	Conflict[13]
American crow (inflected caw)[14]	+	+	"High pitched"	+	"High amplitude"	+	<200 ms	+	Owls, hawks and humans[14]
Southern lapwing (mobbing call)[15]	+	+	>1000 Hz*	+	NA	+	<500 ms	+	Mobbing[15]
Black-capped chickadee (mobbing call)[16]	+	+	>2000 Hz	+	NA	+	<400 ms	+	Mobbing[16]
Mexican chickadee (mobbing call)[18]	–	+	3000 Hz*	–	Loud*	+	200 ms*	+	Mobbing[18]
Red vented bulbul (low pressure alarm call)[17]	+	+	>940 Hz	+	NA	+	~100 ms	+	Potential threat[17]
Blue jay (mobbing call)[18]	+	+	2000 Hz*	+	Loud*	+	400 ms*	+	Mobbing[18]
Titmouse (mobbing call)[18]	+	+	1000 Hz*	+	Loud*	+	220 ms*	+	Mobbing[18]
Western tanager (Mobbing call)[18]	+	+	2200 Hz*	–	Loud*	+	100 ms*	+	Mobbing[18]
Red-breasted nuthatch (Mobbing call)[18]	+	+	1500 Hz*	+	Loud*	+	400 ms	+	Mobbing[18]

1 Winter et al. (1966); 2 Fichtel et al. (2005); 3 Pereira et al. (1988); 4 Fischer et al. (2001); 5 Becker et al. (2003); 6 Digweed et al. (2005); 7 Wiles and Weeks (1981); 8 Oli and Jacobson (1995); 9 Yahner (1980); 10 Reby et al. (1999a); 11 Reby et al. (1999b); 12 Greene and Maegher (1998); 13 Schehka and Esser (2007); 14 Yorzinski et al. (2006); 15 Walters (1990); 16 Hurd (1996); 17 Walters (1990); 18 Kroodsma (2004).

* Estimates based on spectrogram.

Manser, 2001), raccoons, *Procyon lotor* (Sieber, 1984) and Gunnison's prairie dogs, *Cynomys gunnisoni* (Kiriazis and Slobodchikoff, 2006), are reported as displaying vocalizations that seem to match barking, but are not described in enough detail to categorize them definitively. We suspect that a similar degree of variability may be characteristic of barking behavior in general—for reasons that will become clear in our discussion of the function of barking.

10. Birds

While the descriptive term "barking" is usually associated with mammals, signals with the canonical features of barking occur widely in birds; the onomatopoetic label "barking" is often used to describe them. Avian barking shares the features [+AO, +RA, +PR, +FM, −PD], but as is the case with dogs and other mammals the values of [N] and [T] (harmonic-to-noise ratio) and mean pitch [MP] are variable. Many authors (e.g. Marler, 1955; Leger and Carroll, 1981) have noted this convergence on canonical barking features across a wide range of avian species, especially in the context of predator-avoidance behavior. Morton (1977) notes the acoustic (and motivational) similarity between mammalian barking and certain avian calls.

Among the numerous birds in many taxa that exhibit barking are the American crow, *Corvus brachyrhynchos* (Yorzinski et al., 2006); the lapwing, *Vanellus vanellus* (Walters, 1990); the black-capped chickadee, *Parus atricapillus* (Hurd, 1996; Ficken et al., 1976); and the red-vented bulbul, *Pycnonotus cafer* (Kumar, 2004). Additional examples, from Kroodsma (2004), include the blue jay (*Cyanocitta cristata*); the tufted titmouse, *Baeolophus bicolor*; western tanager, *Piranga ludoviciana*; the Mexican chickadee, *Poecile sclateri*, and the red-breasted nuthatch, *Sitta canadensis*. A number of other birds appear to bark, but lack detailed acoustic descriptions—such as the Carib grackle, *Quiscalus lugubris* (Griffin et al., 2005); the greater racket-tailed drongo, *Dicrurus paradiseus* (Goodale and Kotagama, 2006); the recently discovered Ecuadorian antpitta, *Grallaria ridgelyi* (Krabbe et al., 1999); and the gray catbird, *Dumetella carolinensis* (Hurd, 1996).

11. Why barking?

Animals produce sounds for many reasons. Some are communicative signals involving a transfer of information between a sender and a receiver that confer a selective advantage on both. These may be heritable products of natural selection, e.g., innate alarm or care-soliciting calls. But animals also produce vocalizations that have no primary adaptive communicative value for a sender or receiver. Biological sounds may arise, for instance, as a by-product of a normal physiological function such as relaxed breathing. Canid moans may be sounds of this sort (Koler-Matznick et al., 2005). Likewise, sounds such as yelps and moans may be emitted by animals in the context of acute pain because a common mid-brain region, the periaqueductal gray (PAG), aids aspects of vocalization as well as pain reception and modulation (Behbehani, 1995). In such cases there is often no receiver, and no significant functional advantage is gained by vocalizing. But even without an intrinsic communicative function, these vocalizations may sometimes adventitiously produce a beneficial response, as when a loud yelp of pain from a prey animal incidentally provokes a startle response in a predator, allowing the prey animal to escape. Thus they may be become exaptations in the sense of Gould and Vrba (1982) and Gould (2002). Exaptations arise when an existing adaptive trait or developmental outcome is recruited (or "co-opted") to a new and perhaps quite distinct functional end with no intervening process of selection. Finally, wholly novel signals may be learned as a consequence of experience (and perhaps "culturally" transmitted).

The wide-spread occurrence of the barking signal across many (unrelated) taxa may thus be plesiomorphic, i.e., an evolutionary trait that is homologous within a particular group of organisms but not unique to members of that group. Alternatively, it may be a consequence of convergent selection pressures or exaptive solutions. Or, multiple explanations may be at work in different taxa.

12. Function of barking

Barking occurs in a remarkable range of contexts, and barking has been described as a "hypertrophied" behavior in dogs compared with the wild canids (Cohen and Fox, 1976). They bark near feeding time and they bark, sometimes incessantly, when left alone. They bark when it is time for a walk, they bark at approaching human strangers, on recognition of familiar humans, at cars (both familiar and unfamiliar) coming up a road, at sudden changes in the environment (wind noise, a bright moon, detection of an odor of interest), in the presence of conspecifics and non-conspecifics alike, and in many situations where there does not appear to be an eliciting environmental signal. Some dogs will bark in a particular location, daily, over years, with no evident external stimulus. And barking itself – or sounds like the hooting of an owl – may be the stimulus, as one animal triggers a chain response of barking in others.

The apparent multiplicity of contexts associated with dog barking might seem to mitigate against assigning any single function to barking. This (among other observations) led Coppinger and Feinstein (1991) to doubt that dog barking represents a single adaptive consequence of natural selection. Certainly there are cases of single animal signals serving multiple functions in multiple contexts. Bird song is a prime example, playing both territorial and reproductive roles – excluding males while attracting females – in many species (Searcy and Nowicki, 2008). Nevertheless it is unusual for a single animal signal to have as wide an array of distinct contextual triggers as dog barking. The multiplicity of contexts has suggested to some researchers (including Feddersen-Petersen, 2000; Pongrácz et al., 2005, 2006; Yin and McCowan, 2004; Yin, 2002) that dog barking might possibly function as a form of referential communication, with each context having an acoustically different bark, both intra- and inter-specific (between dogs and humans) (see Section 20 for further discussion).

13. Mobbing behaviors

We propose here a simpler functional explanation—barking is a signal associated with *mobbing behavior*. Its canonical acoustic shape and contextual variability are consequences of the functional requirements and motivational states that underlie mobbing.

Widely reported in birds and in many mammals, mobbing is defined as a form of cooperative anti-predator behavior (Caro, 2005). It is elicited by the approach of a predator or an unknown stimulus, including unfamiliar members of the same species or other species: more generally, an "intruder". Mobbing involves multiple group behavioral responses and is characterized by conspicuous displays: rapid and abrupt movement, and on occasion joint physical attack (Table 2). It is typically initiated by a single individual who has first detected an intruder, and is signaled by means of vociferous and conspicuous vocalization. Mobbing calls are received by both the intruder and the sender's conspecifics (Klump and Shalter, 1984). Conspecifics may respond by approaching the sender, joining in the production of the mobbing vocalization, and repeatedly approaching and withdrawing from the intruder. The intruder's approach (often predatory) behavior is interrupted.

Mobbing tends to occur in situations where the animal has *conflicting motivations*: when an individual is motivated to escape but also to stand its ground (e.g., when a parent, at a den site with offspring, confronts a predator). Conflict can also be elicited when the animal is not fearful enough to run (e.g., when an intruder is detected but has not yet come closer than the animal's flight distance, or there is not enough information to determine the threat of the intruder), or when it is physically constrained in some way and cannot engage in normal approach/withdrawal responses. Therefore, mobbing calls may regularly occur in situations of conflict that are not in response to actual or even perceived predators (See Section 19 for further examples).

14. The acoustic structure of mobbing calls

Why then have so many different species converged on barking-like signals in mobbing contexts? The literature suggests two possibilities. First, from a functional acoustic standpoint, mobbing vocalizations need to be highly salient and easily localized. Marler (1955) observed that mobbing calls tend to be characterized by wide frequency-spectra ([+N] and/or [+FM] in our terms), sharp onset [+AO], brief duration [−PD], high amplitude [+RA], and rapid and persistent repetition[+PR]. All these characteristics are well-suited for detection and localization by conspecifics and also for attention by the intruder. Ficken and Popp (1996), in an acoustic analysis of 52 mobbing calls in passerine birds, report considerable variation in the details of acoustic structure of calls across species but virtually all are readily detectable and localizable. The majority of these calls share all or most of the acoustic properties of canonical barking.

Second, there is a motivational basis for the acoustic structure, illuminated by the motivation-structural (MS) theory of Morton (Morton, 1977; Owings and Morton, 1998). MS theory holds that factors shaping internally motivated vocalizations have phylogenetically deep adaptive roots, and that close-contact signals sub-divide along two major acoustic axes: harshness (harmonic-to-noise ratio), and frequency. The end-points of these axes reflect specific groups of motivational states. High frequency and tonality (without noise) correlate with affiliative behaviors, including appeasement, submission and care-solicitation, all of which are associated with *approach* on the part of the receiver. Low frequency and noise (with no tonal component) correlate with aggressive behaviors, including dominance and threat, and are associated with *withdrawal* by the receiver. Morton supports his hypothesis with a survey of vocalizations from a large variety of birds and mammals. Although factors such as sensory and ecological constraints on perceptibility and transmissibility may sometimes take precedence, Morton's motivational rules have been largely supported by further research on both birds and mammals, including the canids: Cleveland and Snowdon (1982), Sieber (1984), August and Anderson (1987) and Robbins and McCreery (2003), among others.

MS rules potentially impose significant constraints on signal form: high-frequency vocalizations, for example, are functionally inconsistent with aggression, since this form tends to attract rather than deter a threat to the signaler by encouraging approach. By the same logic, low-frequency noisy vocalizations are inconsistent with care-solicitation behavior. But, crucially for our purposes, the MS model predicts that there can also be signals that tend toward the midpoints of the two motivational axes—e.g., which rise and fall in frequency, and/or which are not exclusively tonal or noisy. The bark is a signal of precisely this sort. Morton (1977) suggests that such "composite" or "midpoint" forms indicate motivational conflict:

"Presumably, a sound indicating ambivalence, such as occurs in mobbing behavior (e.g., Andrew, 1961), may acquire a steep slope

so as to become nearly a pulse if selection pressure derived from the sound's function favors qualities that enhance the sender's location by the receiver (Marler, 1956). . . In mammals, the intermediate structure tends to be frequency constant but still short or abrupt, and the sounds are termed *barks* or *grunts*. For both birds and mammals, this sound type indicates the sender is indecisive (i.e., it may either go toward or away from or become more or less aggressive or appeasing toward the stimulus), usually because the stimulus is too far from the sender for it to make an adaptive response" (p. 861–862).

A motivationally ambivalent composite signal like barking is thus ideally suited to mobbing (Owings and Morton, 1998). It may be viewed as directed at two different receivers: conspecifics and intruders. A tonal component [+T], and higher pitch [+MP] encourage the approach of conspecifics (and also non-conspecifics who convergently recognize the signal) to join in the collective deterrence behavior. A noise component [+N] and lower pitch [−MP] encourages withdrawal in an intruder. Along with perceptually salient features such as abrupt onset [+AO], high amplitude [+RA] and pulse repetition [+PR], these characteristics are also likely to attract and engage an intruder's attention, a condition under which predatory sequences are often disrupted (Clark, 2005; Woodland et al., 1980; Zuberbühler et al., 1999).

This motivational perspective also explains variation in the bark itself (Owings and Morton, 1998). An animal always has some motivation for signaling and the character of its vocalization is often a reflection of motivational state. But a bark is by its nature a reflection of conflict—a struggle between differing motivational states. The conflict can be significant, e.g. between hostile (lower pitch and more noise) and soliciting (higher pitch and less noise). Moreover, it can be expressed while in a state of higher arousal (with high pulse repetition, high amplitude, high pitch), or of lower arousal. The degree of conflict itself can even vary. We suspect that some features of the bark, such as its invariantly abrupt onset and short duration of individual pulses, may not be directly related to motivational state. But those acoustic characteristics that are indeed correlated with motivation can vary together (or separately) and can fall anywhere along their individual scales, generating a high degree of potential variability. By contrast, the bark's canonical form and potential for variation are distinct from signals such as the care-soliciting, high-arousal yelp (pure tonal, high pitch, high amplitude) and the low-arousal but aggressive woof (entirely noisy, low amplitude, low pitch). These relatively invariant vocalizations have fixed functions and do not signal conflicting degrees of hostility, solicitation or arousal.

15. Mobbing in wild *Canis*

If the dog bark is homologous with mobbing calls we would expect that dogs' closest relatives would bark in mobbing contexts. Therefore the genus *Canis* is of particular interest. All members of the genus *Canis* (including dogs) are karyotypically identical and can reproduce fertile offspring with one another (Chiarelli, 1975). Although the origin of the dog is continuously debated, it is obvious that the form evolved recently from some generalized species of *Canis* (Coppinger et al., 2009).

Though he does not explicitly call it a mobbing vocalization, Schassburger (1987) suggests that wolf barking might function to signal a "call to arms of distant pack members" and to elicit the "withdrawal of intruders". McNay (2002) conducted a review of wolf-human interactions in Alaska and Canada from 1900 to 2001, and found that in all cases where wolves were documented as defending either a den or rendezvous site, they barked loudly. He also notes that wolves often ran towards and then away from humans near dens. These descriptions closely fit the classical

picture of mobbing behavior, and are strongly suggestive of motivational conflict.

Lehner (1978) reports that when coyotes are approached at their den sites they typically use the "woof", a low amplitude noisy signal that induces pups to hide, and then run a considerable distance from the den site and bark repeatedly. Lehner also suggests that coyote barking occurs during hunting, agonistic interaction and in territorial displays, but his descriptions are not specific enough to determine if the vocalizations fit the canonical form of the bark as we have defined it, or if they are associated with mobbing-like behavior.

While descriptions of the context of barking in jackals are not detailed, barking is regularly reported at the den site. Loveridge and Nel (2004) report that black-backed jackals (*Canis mesomelas*) bark when threatened at the den site. Estes (1991) reports that golden Jackals (*Canis aureus*) will growl and bark when they sense danger near the den. Moehlman (1983) states that a single adult jackal (either black-backed or golden) at a den can protect pups from intruders by growling and barking.

16. Mobbing in domestic dogs

A fundamental question about barking in the domestic dog is why it is so much more frequent than in other members of *Canis*. In light of the mobbing hypothesis advanced here, we rephrase the question: Why do dogs seem to be (or to perceive themselves to be) so frequently beset by intruders? In one respect, the answer seems transparent: mobbing is induced when intruders approach places like den sites (a territory) where escape behavior is inhibited or impossible. It could be argued that the domestic environment dramatically increases the number of situations that elicit mobbing and its associated vocal behavior (Convergent with Yin, 2002).

As noted earlier, mobbing vocalizations are produced when an animal is in conflict, unable to escape an intruder (real or perceived). For wolves this tends to occur when they are in the presence of their offspring and threatened by an intruder. Dogs are routinely confined or constrained with no opportunity for escape. Kept in a kennel, a crate, a house, a fenced yard or tied up, they cannot run from approaching unfamiliar "intruders", who are virtually omnipresent in human environments. The relatively close living quarters of captive dogs thus facilitates group vocal response to a mobbing signal, accounting for the cacophony that often follows the initial barking of a single animal. It should be noted that free-living "village dogs" in non-western societies, described by Coppinger and Coppinger (2001), are not constrained or confined and exhibit much lower levels of barking. Boitani et al. (1995) noted that free-ranging village dogs rarely barked or approached humans or strange dogs except in the core of their territories. Ortolani et al. (in press) found village dogs in Ethiopia significantly more likely to vocalize if approached while in a house or constrained than when approached on a street.

The less fearful an animal, the more likely it will hold its ground (Stankowich and Coss, 2007) and produce a mobbing vocalization rather than a simple alarm call and flight (Knight et al., 1987). Calling rates increase with decreasing distance to a predator (Curio and Regelmann, 1985). The shorter an animal's flight distance – that is, the closer an animal allows an intruder to get – the more likely it is to mob and vocalize.

The relationship between decreased flight distance and increased barking is also supported by the work of Belyaev (Trut, 1999) who bred Siberian silver foxes (*Vulpes vulpes*) specifically for decreased flight distance in order to improve their tractability during handling. After 30 generations the offspring from this line of foxes displayed many unexpected morphological and behavioral phenotypes associated with domestic dogs, including reduced flight distance. They also exhibited a significantly increased tendency to bark, compared with non-selected animals.

Graw and Manser (2007) suggest that along with deterring predators, mobbing may also allow animals to approach and inspect novel stimuli to determine if they are threatening. By mobbing, they not only avoid being surprised by an actual predator, but they can also inspect the intruder. Curio et al. (1978) has shown that the target of mobbing in captive European blackbirds is culturally transmitted. A "teacher bird", which appeared to be mobbing a non-threatening novel object, taught the native birds to mob non-threatening objects. Other species such as capuchin monkeys (Digweed et al., 2005) have been regularly observed to mob animals that do not resemble known predators.

The hypothesis is that barking (as a component of mobbing behavior) enhanced the fitness of the canid ancestor and is retained in descendent populations of dogs. Hence barking, or at least the disposition to bark, must be genetically transmitted. In our own observations of congenitally and profoundly deaf dogs, we see evidence that the form of the bark itself is inherited. These animals first exhibit barking behavior at precisely the same developmental stage as normally hearing animals, and they participate in barking bouts with other dogs which are essentially indistinguishable from that of normal dogs of the same breed and size.

However, we do not believe that selection pressure has led to hypertrophied barking in the dog. Rather, the increased frequency of dog barking is a consequence of a domestic environment (in which conflict and novel stimuli are commonplace) and the process of domestication. Not only are dogs more likely to be placed in a conflicting situation as a result of being artificially restrained, but dogs are also more likely to place themselves in a conflicting situation. As noted earlier, decreased fear of novelty – which occurred during the domestication and/or development process – encourages mobbing behavior. Because dogs are less likely to run from novelty than wolves, dogs are more likely to put themselves in a conflicting situation even when they have the option of escape. These factors not only have an immediate effect on the display of barking behavior in the adult, but also on its development.

Adult behavioral complexes including social behaviors such as mobbing first begin to appear during the juvenile period between approximately 4 and 8 weeks. At onset, these patterns occur out of context, and may be performed along with components of behavioral sequences persisting from earlier periods in ontogeny (Burghardt, 2005). Juvenile "play" has been interpreted as the mixing and repetition of motor patterns during this developmental period (Coppinger and Smith, 1990; Burghardt, 2005). By experimenting with onsetting behavioral motor patterns, juveniles learn combinations that are rewarding when performed in specific contexts.

Earlier display can lead to greater frequency of a display (hypertrophy). While the onset of barking in dogs and wolves is the same (dogs, 18–24 days: Ohl, 1996; Bleicher, 1963; wolves, 11–28 days: Frommolt et al., 1988; Harrington and Asa, 2003; Lord, pers. obs.) the frequency of display is also dependent on environmental factors. Decreased fear and increased exposure to novelty would give dogs more opportunity to incorporate barking into other behavior sequences increasing the likelihood that barking will be more broadly represented in the adult behavioral repertoire. In recent observations in our lab, both wolf and dog pups participate in raucous barking during play, although it occurs with much more regularity in the former. In addition, dogs, like any other canid, can learn to use any behavior in a new situation provided that it is reinforced. It is likely there are numerous circumstances that induce conflict in the dog and elicit barking and subsequent attention from human beings.

17. Other perspectives

The mobbing hypothesis offers a simple structural and functional account of barking behavior in dogs, related canids, and other mammals and birds. This is important, given the recent attention in the literature to hypotheses that attribute greater complex (cognitive) functions to barking in the domestic dog. We have noted the considerable evidence that the acoustic structure of dog barking varies with context; some authors have further suggested that such variation may have a referential function. Feddersen-Petersen (2000), Yin (2002) and Yin and McCowan (2004) all address this question directly or indirectly. Several authors (Pongrácz et al., 2005, 2006) argue that barking has context-specific effects on both canine and human receivers, and speculate that barking was an adaptation to canid-human communicative requirements during the course of canid domestication. Because these approaches include some of the most extensive and acoustically detailed investigations of barking to appear in the literature in recent years – and because they offer accounts that compete with the mobbing hypothesis as general explanations for barking – we discuss them in some detail.

18. Referential communication

Biological signals may be components of functional behavior, expressions of an organism's internal state, or they may in some cases be *referential* signs that relate to an event or property of the external world. Referential signals are emitted under the stimulus of particular objects or events, and therefore will vary with context (Evans, 1997). Such signals are adaptive for both the sender and receiver (Marler, 1967), providing information about the world that can facilitate an adaptive response (Seyfarth and Cheney, 2003). By contrast, non-referential signals are adaptive for the sender and may initiate an adaptive change in the receiver's behavior, but neither the signal nor the response is specific to a particular eliciting stimulus or context (although the signal may vary with the nature and intensity of the sender's internal state).

19. Is (any) mammalian barking referential?

Referential alarm calls have been reported in the literature. Seyfarth and Cheney (2003) observed that vervet monkeys have acoustically distinct alarms for predatory mammals, birds and snakes. Similar claims have been made for a number of other mammal and bird species (Marler et al., 1992; Evans, 1997; Hauser, 1997). The white-faced capuchin produces two acoustically distinct antipredator calls: one is elicited by avian predators and the other by potential terrestrial predators. The avian call – acoustically dissimilar to the bark – appears to be referential, while the terrestrial call, a bark-like signal, does not (Digweed et al., 2005). The avian call is produced only when the monkey sees low flying or diving birds that resemble predatory raptors. The barking call is produced in a much broader array of contexts including to potential terrestrial predators and non-threatening mammals such as coatis and peccaries that do not resemble predators or conspecifics. It may be noted that these cases do not fit the standard picture of mobbing contexts. Rather, they are all potentially conflicting situations in which the animal may not know what reaction is called for (on approach of an unknown conspecific group) or may not be able to retreat (when constrained by humans or a large number of other animals). Thus the internal state of the caller is much the same as in a mobbing situation. The response to the bark call is also variable and depends upon the eliciting stimuli. On some occasions monkeys respond by running away; on others they respond by mobbing. In both cases monkeys first confirmed the threat visually before producing a response (Digweed et al., 2005; Fichtel et al, 2005). Thus, barking does not signal conspecifics to mob, but attracts the attention of conspecifics who need to see the eliciting stimuli before respond to it. Except for dogs (see below), there is no claim in the literature for barking being referential.

20. Is dog barking referential?

Several authors (Feddersen-Petersen, 2000; Yin, 2002; Yin and McCowan, 2004) noted that the acoustic structure of dog barking varied with context. Feddersen-Petersen noted different subsets of subcategories in the repertoires of different breeds, but most significantly found that warning, threat, and play-fighting barking was relatively noisy, while play-solicitation barking was more tonal. Yin (2002) found that the acoustic structure of barking varied with context: play and isolation barking were higher in frequency and more tonal than disturbance barking. Yin and McCowan (2004) found that disturbance barking was low-pitched and noisy, with little modulation; isolation and play barking were high-pitched, tonal, and more highly modulated. They also found that inter-bark intervals of disturbance barking were shortened. (In some cases the inter-bark interval was so short it was unperceivable to the human ear, producing what the authors referred to as 'superbarks').

While these works contribute to the data on signal variability, they do not provide evidence that barking has a referential function. The contextual cases are entirely accounted for by Morton's rules and arousal levels. Moreover, the behavioral contexts in which barking occurs in these studies are consistent with the mobbing hypothesis and auxiliary assumptions about development and exaptation.

Pongrácz et al. (2005) examined whether humans could determine the context of a given barking sequence in a playback experiment. The authors played recordings of barks from 19 dogs all from a single breed, the Mudi. The barks were recorded in six distinct situations: presence of a stranger; "schutzhund", where a trainer acted menacingly and encouraged the dog to bite a padded arm band; going for a walk; isolation; presence of a ball; and "play". Human subjects, split into three groups (mudi owners, other dog owners, and non-owners) listened to 3 different barking sequences from each context (for a total of 18 barks). They were asked to rate the level of aggressiveness, fearfulness, despair, playfulness, and happiness of the barking on a scale from 1 to 5, and to categorize each barking into one of the six situations in which the barking was originally recorded.

The authors found that each group was able to assign the barks to their appropriate categories approximately 40% of the time, this rate is better than chance (or 16.67% or 3 out of 18 cases). By combining the data of all three groups Pongrácz et al. found that 58.33% of stranger barks, 48.15% of the schutzhund barks, 23.15% of the walk barks, 47.22% of the alone barks, 25% of the ball barks, and 37.04% of play barks were categorized correctly. The authors conclude that dog barking has been selected to communicate information to humans, and suggest a process of co-adaptation between dogs and humans in the course of domestication.

The ability to guess the context of a dog's barking with 23.15% – or even 58.33% – success may be statistically significant, but certainly does not suggest that barking is a co-adaptation between dogs and humans, let alone that it is systematically referential. Rather we may conclude from the authors' data that Morton's rules – plesiomorphic in the mammals – were at work both for dogs and humans. In other words these results show that humans can discern that barks are generally more fearful or more aggressive, but they cannot tell what stimuli is eliciting the bark, therefore they cannot respond adaptively without further visual information.

Pongrácz et al. (2006) went on to investigate whether humans were in fact using Morton's rules to identify the emotional

content of barking. The same three groups of listeners were used as in the previous paper (mudi owners, other dog owners, and non-owners). The investigators recorded barks from the same six situations (stranger, dog attacks human, walk, alone, ball, and play). However, these barks were then rated as having high, medium, or low pitch and high, medium or low levels of noisiness. The barks were placed into one of nine subsets based on these characteristics (e.g. high pitch, low noisiness; high pitch, medium noisiness; high pitch, high noisiness). Ten barks from each subset were played back with either short, medium, or long interbark intervals. This arrangement resulted in 27 different structural possibilities, which were played to the human subjects for rating. Human subjects were once again asked to rate barking on a scale of 1–5 for the same five emotional components (aggressiveness, fearfulness, despair, playfulness and happiness). The results showed that the importance of structural components to human listeners varied with context (e.g. "aggression" scores relied on pitch and inter-bark interval, while "despair" relied on pitch, inter-bark interval, and tonality). In every case, emotional ratings were consistent with Morton's rules. It is unclear how anthropocentric emotional categories such as despair and happiness fit into Morton's continuum of aggression/affiliation.

Be that as it may, these results provide little basis for the claim that there was selection for diversification of barking in dogs or for referential content in those barks, either through selection by humans for more understandable dogs or as an adaptation of dogs to increase their ability to cooperate with humans.

In summary, Yin (2002), Yin and McCowan (2004), and Feddersen-Petersen (2000) offer evidence that dog barking can vary contextually. They show that robustly distinct barks (differing from one another in noise/tonality ratio and inter-pulse interval, or pulse-repetition rate) occur in distinct interactional and social settings, including interactions with humans. Pongrácz et al. (2005, 2006) show that humans can pick up on some of these contextual differences in playback studies. While the authors are all careful to allow that these differences may arise from differing "affective" or motivational states (just as Morton would predict), they also nevertheless suggest that contextual variations in the bark may be "intentional", i.e., representing information *about* the context, rather than simply signaling the internal state of the sender in a particular context. Yin and McCowan (2004:353) write that "Co-variation between context and bark structure suggests that dogs may perceive *meaningful* [our emphasis] differences between contexts and adjust their barks accordingly" and Pongracz et al. (2006:238) write that their "results do not exclude referential communication".

We would argue that these studies do not provide evidence that barking in the dog supports a referential hypothesis, or that dog vocalization has evolved to be a special case.

21. Conclusion

We have hypothesized that barking is associated with the functional requirements and motivational states that underlie mobbing (i.e. conflict, as suggested by Morton, 1977; Owings and Morton, 1998). In wild *Canis* barking occurs in this mobbing context. In dogs, the underlying motivational state associated with barking occurs on a daily basis. This increase in conflicting motivations leads directly to increased barking as well as a greater developmental propensity for the behavior. This mobbing hypothesis offers a conceptually and empirically simple account of the structure and the function of barking in the domestic dog and in a wide variety of other species. Experiments testing for differences in development, eliciting stimuli, and environment on the quality, frequency and sequencing of dog barking would be valuable.

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