

Did Neanderthals and other early humans sing? Seeking the biological roots of music in the territorial advertisements of primates, lions, hyenas, and wolves

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Group defense of territories is found in many gregarious mammalian carnivores, including lions, dwarf mongooses, suricates, canids, and hyenas. In these species, group members often mark territory boundaries and direct aggressive behavior towards alien conspecifics found within the territory (Boydston, Morelli, & Holekamp, 2001). Middle Pleistocene hominids such as Neanderthals occupied an ecological niche similar to the larger of these carnivores (Stiner, 2002), and so could be expected to share with them a suite of behavioral traits. Complex, coordinated vocalizations that function, at least in part, to advertise the group defense of a territory is one behavioral trait exhibited by several social carnivores, as well as many other gregarious animals, including primates. Hagen and Bryant (2003) proposed that the evolution of human music and dance was rooted in such coordinated auditory and visual territorial advertisements, an hypothesis we develop and expand upon here. In essence, human proto-music might have been functionally analogous to the howling of wolves.

If music has an evolved function, it is most likely as some sort of signal. Putting the possibility of deception aside, this means music encodes information that is in the fitness interest of performers to send, and listeners to receive. But what could a song, especially one without words, tell us that we do not already know?

In a sexually reproducing species, a vocal signal can advertise both location and ‘quality’ to members of the opposite sex. Singing in male birds, for example, is often used to attract females, and aspects of song quality appear to correspond with mating success (Catchpole & Slater, 1995). Darwin (1871) astutely suggested this might also explain the evolutionary origins of human music, a suggestion recently taken up by Miller (2000).

Although mate choice could well have played a role in the evolution of human music, it cannot easily explain several of music’s most important characteristics. Music is often performed in circumstances, such as funerals, that have little directly to do with mating; it is frequently directed towards adult members of the same sex; it exhibits rhythm, presumably to synchronize group performances; and it is, in most cases, the cooperative product of a group, something not easily explained by individual competition for mates. If music and dance were instead rooted in the territorial advertisements of coalitions, all of these would have straightforward

explanations (Hagen & Bryant, 2003).

In Hagen and Bryant, the territorial roots of music and dance were sketched, with most of the focus on the attributes that make them effective coalitional signals. Here, we explore music’s possible territorial roots in depth, providing the background non-biologists will need to follow the argument. Building on the work of Geissmann (2000), we argue early humans, as gregarious territorial primates and social hunters, probably evolved complex, coordinated vocalizations.

At some point, we believe, a unique feature of human social organization co-evolved with increasingly synchronized vocal and instrumental displays. Thus did the calls of human ancestors, which were probably functionally analogous to chimpanzee pant hoots or wolf howls, evolve into the music of modern humans.

Territoriality

A broad and diverse range of organisms, including bacteria and numerous invertebrate and vertebrate species, are territorial (Baker, 1983; Maher & Lott, 2000; Smith & Dworkin, 1994). Although biologists have employed a number of definitions of territoriality, the oldest and most common is: defense of an area to exclude other animals, using physical force, threat, or advertisement (Maher & Lott, 1995). In some cases, the defended area has sharp, well-defined boundaries; in others it broadly overlaps with the territory of other individuals.

Territoriality is far from ubiquitous. Many animals occupy a home range they do not defend; others retain first access to, or dominate, a resource, but do not prevent others from using it too; still others, such as some flocking birds and schooling fish, traverse large, undefended expanses of land and ocean

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(Maher & Lott, 1995).

To account for variation in territoriality, biologists have produced a number of related theories grounded in the presumption that retaining exclusive access to essential and limited resources like food, mates, and shelter often yields substantial fitness benefits. When those benefits outweigh the costs of defending the resource – what biologists term *economically defendable territories* – organisms should tend to evolve territoriality (Adams, 2001). The crux, of course, is understanding how benefits and costs vary for different organisms in different environments, where the term ‘environment’ encompasses both physical and social dimensions.

Maher and Lott (2000) reviewed a large number of studies exploring the ecological determinants of territoriality among vertebrates, restricting their review to studies of within-species variation in territorial behavior. As expected, a variety of ecological factors had a significant impact on territoriality. Across studies, Maher and Lott identified 20 such factors, including eight related to food, four to other types of resources, and another eight to, e.g., population density, habitat features, predation pressure, and so on. Although a comprehensive theory of territoriality has yet to emerge, these results support an evolutionary approach to territoriality as an evolved response to challenges posed by the physical and social environment.

The bourgeoisie

In nature, it has been observed that current territory residents have a distinct advantage when fighting intruders, or, better yet, their territory ownership often remains completely uncontested, a remarkably consistent and striking pattern. This ‘prior-residence’ effect has been found in taxa ranging from sea urchins to mammals (Kokko, López-Sepulcre, & Morrell, 2006). One of the first applications of evolutionary game theory aimed to explain the effect using a simple model with two behaviors, fight (Hawk) and retreat (Dove), and two roles, owner and intruder (Maynard Smith & Parker, 1976). The ‘bourgeois’ strategy – fight only when in the owner role – was found to be an evolutionary stable strategy (ESS; an ESS is an important criterion for an evolutionarily ‘plausible’ strategy). One interesting feature of the bourgeois strategy is that it is successful even though it is not related to fighting ability or any other advantage. It is, in essence, a *convention*. In the U.S. if two automobiles reach a four-way intersection at the same time, the convention is the auto on the right has the right-of-way to proceed through the intersection first. Although each driver has an incentive to proceed first, each has bigger incentive to avoid a collision. By agreeing on a convention, any convention, for the right-of-way, all drivers avoid the large cost of a collision, albeit at the smaller cost of ceding right-of-way half the time (on average).

Similarly, by agreeing on the convention that intruders always retreat, animals avoid the cost of fighting, albeit at the cost of ceding territory half the time when in the intruder role (but keeping it the other half the time when in the owner role).¹ Under certain assumptions, a bourgeois convention can be maintained in a population even when intruders are

moderately better fighters than owners (Hammerstein, 1981). Related models consider multiple owners (neighbors) who have conflicts over territory boundaries but might have a common interest in allying against intruders (Getty, 1987; Pereira, Bergman, & Roughgarden, 2003; Leiser, 2003), so-called ‘dear enemies.’

For our purposes, however, it is the prior-residence effect itself, not its explanation, that is most important.

Territorial advertisements

Given the prior-resident effect, it is clearly in the interest of owners to advertise their residence in a territory. By so doing they deter intruders who might exploit the territory’s resources, and they reduce the likelihood of an encounter with an intruder which might lead to a costly fight. Not surprisingly, territoriality and advertisement go hand-in-hand.

As has long been recognized, many territorial species advertise their ownership by scent-marking boundaries and other prominent territory locations (Hediger, 1949). Strong-smelling urine, feces, or secretions from special glands are rubbed or deposited where intruders are likely to encounter them. Male house mice, for example, mark their territories with urine containing individually-specific patterns of major urinary proteins (MUP). These proteins are non-volatile, thus creating a persistent mark. Because individual mice express a stable combination of MUPs (typically 7-12) in urinary scent marks, and because MUPs are highly polymorphic, the marks are reliable indicators of individual identity, allowing owners to, e.g., distinguish their own marks from those of intruders. Chemical communication is the only known function of MUPs, which also bind species- and sex-specific volatile ligands (Nevison, Armstrong, Beynon, Humphries, & Hurst, 2003). Like many signals, scent-marks appear to have multiple functions. In addition to territorial advertisement, these include attracting mates, signaling overt aggression and dominance, and indicating health and other aspects of quality (Gosling & Roberts, 2001; Ralls, 1971).

Acoustic signals are another obvious and widely used means to advertise residence. A number of mammals produce acoustic vibrations by drumming, most commonly using their feet, but in some cases their heads or teeth. The majority of drumming mammals are rodents, but drumming is also observed in primates, carnivores, deer, rabbits, elephant shrews and marsupials (Randall, 2001). As with scent-marking, several functions have been ascribed to drumming, territorial advertisement prominent among them. The banner-tail kangaroo rat, for example, spends most of its time on, or inside, a large dirt mound where it has stored as much as 100 liters of seeds. It advertises its presence on the mound

¹ The anti-bourgeois strategy – fight only when in the intruder role – is also an ESS. Yet the anti-bourgeois strategy is extremely rare. Several solutions have been offered to explain the rarity of the anti-bourgeois strategy, most proposing some consistent owner advantage. See Kokko et al. (2006) for a brief review, and for an alternative approach involving frequency-dependent population feedback effects differentially affecting the strategies of owners vs. intruders.

by footdrumming spontaneously during the night, as well as in response to the footdrumming of neighbors and during mound challenges (Randall, 1984).

Vocalizations, however, are probably the most prevalent form of acoustic territorial advertisement. A subclass of these exhibit a sequence of notes – continuous sounds with a distinct frequency – of such clear and recognizable patterning they are often referred to as songs.

Bird song

Singing is particularly common in birds, especially the passerines, which constitute about half of all bird species. The territorial function of bird song was noted over two hundred years ago, became widely recognized by the 1920's, and by the 1970's was seen by some as perhaps the most important function of singing in birds (Catchpole & Slater, 1995). In temperate regions male birds usually must acquire and hold a territory in order to attract females and successfully breed. The seasonal increase in male song production coincides with the onset of male aggression towards other males and the occupation of territory. Males sing vigorously at male rivals, with such vocal duels often escalating into overt aggression (Catchpole & Slater, 1995). (It has recently been recognized that females sing much more frequently in tropical than in temperate species; see Slater & Mann, 2004, for discussion.)

Catchpole and Slater (1995) review two types of evidence that singing, in part, indeed serves a territorial function. The first involves a number of experiments in which a bird is temporarily removed from their territory, and their ability to sing surgically eliminated. In these experiments, a small portion of the hypoglossal nerve, which enervates the syrinx, is severed, or the thin membrane of the interclavicular air-sac is punctured. Control birds are also removed from their territory, anesthetized and operated on, but their singing ability is left intact. Altered birds and controls are then returned to their territories. Other than loss of singing ability, altered birds do not seem to suffer any physical impairment.

Several such experiments found songless males suffering dramatically more territorial intrusions by rivals relative to controls (in some cases, nearly triple the rate), involved in more fights, compensating for loss of singing with increased visual displays, and more likely to lose their territories or places in leks to other males.

Surgical impairment of singing ability raises the obvious concern some other, unknown capacity of the birds is also impaired, and this unknown factor is responsible for the experimental results. An alternative experimental approach was therefore developed that replaced male territory holders with loudspeakers playing back the putative territorial songs. Control conditions included areas with no speakers, and others with speakers playing back a non-bird sound (e.g., a tin whistle).

Several of these experiments found experimental areas were avoided for long periods, often days, whereas control areas were occupied within a few hours. Eventually, however, with no real bird to defend the experimental area, it was

occupied despite the loudspeaker playback.

Group territoriality and coordinated vocalizations

In and of themselves, territorial advertisements exhibit two of three properties of human music not easily explained by mate choice. First, they are used in territorial conflicts, roughly analogous to the political and military contexts of much human music (Hagen & Bryant, 2003). Such contexts have little directly to do with mating. Second, they are aimed at territorial intruders, which, unlike the target of most sexual signals, are often adult members of the same sex. Yet territorial advertisements are not necessarily performed by groups, the third key feature of human music eluding an easy explanation under the sexual selection hypothesis. In species in which territory is held by a group, however, advertisements often consist of coordinated vocalizations by group members that appear to be signaling group strength.

Group living is expected when benefits such as cooperative hunting, parenting, or defense outweigh costs such as increased competition for local resources or exposure to pathogens. Alternatively, a heterogeneous resource distribution might cause animals to form groups (Alexander, 1974; Johnson, Kays, Blackwell, & Macdonald, 2002). The theoretical issues surrounding the evolution of group cooperation are complex, but it is nonetheless frequently observed in nature (Hammerstein, 2003). Not surprisingly, territorial animals living in groups often cooperate in territorial defense, including the advertisement of ownership. Both the North American and Eurasian beaver, for example, live in family groups where males and females of all ages mark territory boundaries at scent mound sites near the water's edge (Campbell, Rosell, Nolet, & Dijkstra, 2005; Rosell & Nolet, 1997).

Coordinated acoustic signals are found in diverse taxa ranging from insects to apes, with some of the more spectacular coordinated vocalizations produced by birds. According to one review, about 3% of bird species are known to produce duets – complex, highly coordinated and temporally overlapping and/or alternating songs usually sung by male-female pairs (Hall, 2004). Duets occur in phylogenetically diverse bird species, indicating independent evolution (and thus a widely-encountered, important selection pressure). Duetting is much more common in the poorly-studied tropical species than in the well-studied temperate species, which probably explains why it has only recently begun to attract sustained attention from evolutionary biologists.

Hall (2004) reviewed the evidence for a variety of proposed functions for duetting, including signaling mated status to rivals (a form of territorial advertisement, where the 'territory' is one's mate), commitment to the relationship, and (physical) territory ownership. All three hypotheses found some support. Summarizing across species and across studies using various methodologies (e.g., model birds, loudspeaker replacement, zoo observations, and observations of unperturbed behavior in the wild), the evidence for physical territorial advertisement includes the fact that most species produce loud, easily located duets which are capable of being

heard for some distance beyond the territory of the singers. Duets are performed from prominent places, during dawn border patrols, in countersinging interactions with neighbors, and in response to intrusion and playback. Spatial proximity of duetters increases the threat perceived by intruders, and duetters distinguish the duets of neighbors from unfamiliar duets, responding more aggressively to duets by strangers. In all species tested, both sexes respond to intrusions, and in some the sexes have been shown to coordinate their response.

Many predictions of the territorial advertisement hypothesis remain to be tested, as Hall rightly cautions. Nevertheless, among birds the evidence is strong that duetting, in part, is joint territorial advertisement by a mated pair who share a fitness interest in defending their territory.²

As we will discuss shortly, the coordinated vocalizations of primate and carnivore taxa defending territory in groups also appear to be a form of territorial advertisement. If human ancestors defended territory in groups, a compelling case could be made they, too, probably evolved some form of coordinated vocal advertisement of territory ownership. And that, arguably, could be one of the roots of music.

Middle and Late Pleistocene *Homo*

In the comparative method, insights into the traits of one species are sought in comparisons with closely related species, which are expected to share traits by descent, and/or which occupy similar ecological niches, and therefore should evolve similar adaptations. We will take both approaches here. First, though, it is important to identify which human taxa to focus on.

The genus *Homo* emerged in Africa towards the end of the Pliocene and the beginning of the Pleistocene, roughly 2 million years ago (MYA), expanding into Eurasia shortly thereafter. Sometime between 1.5 and 0.8 MYA *Homo* diverged into at least two branches. The smaller-brained, more primitive branch – *H. erectus* – persisted in Asia until about 70,000 years ago. We will refer to early members of this branch as early *Homo*. The larger-brained branch, our focus, is known mainly from Africa and Europe (Stringer, 2003). We will refer to them as humans.

The taxonomy of the human branch is still quite unsettled. Early forms are variously referred to as *H. antecessor* or *H. heidelbergensis*, whereas later forms are referred to as *H. neanderthalensis* in Europe and *H. rhodesiensis* in Africa. *H. sapiens* is widely thought to have evolved from an African population of this large-brained branch sometime after 250,000 years ago (Stringer, 2003). We will refer to early populations of this branch (e.g., *heidelbergensis*, *antecessor*, *neanderthalensis*, *rhodesiensis*) as Middle Pleistocene, or early, humans, and to *H. sapiens* itself as Late Pleistocene, or modern, humans.

Neanderthals, in all likelihood, were not ancestors of modern humans, but they are a well-studied European population of Middle Pleistocene humans that was probably cognitively and behaviorally similar to the much less well-understood Middle Pleistocene African population that did give rise to

modern humans. This assumption is supported by the fact that the Levallois technique – a sophisticated method of stone tool manufacture used by Neanderthals – appeared almost simultaneously in Europe, Western Asia and Africa c. 300 KYA (Roebroeks, 2001). When necessary, we will therefore draw upon Neanderthal data.

Phylogenetic proximity: primate models

Humans are primates. If primates were rarely territorial, or if territorial primate species did not advertise territory ownership, our argument would be deeply undermined. Mitani and Rodman (1979) conducted one of the first comparative studies of primate territoriality. They noted primates, a large and diverse clade, were convenient subjects for such a study because, unlike birds and ungulates, primates maintain relatively stable home ranges (not necessarily defended) and stable intergroup relations throughout the year. Mitani and Rodman constructed a simple index of defensibility, $D = d / \sqrt{4A/\pi}$, where d is the average day range (distance traveled in one day), and A is the area of the home range (the denominator thus approximates the width of the home range). When $D \geq 1$, they reasoned an animal was able to adequately patrol, and thus defend, a home range. Among 33 primate groups, they found 19 had values of $D \geq 1$, and 13 of these (68%) were territorial. Most non-territorial groups had values of $D < 1$, whereas none of the territorial ones did. They explain the exceptions (non-territorial groups with $D \geq 1$) by noting the ability to patrol a territory is a necessary, not sufficient, condition for territoriality, and other factors will need to be taken into account to explain why some species that could adequately patrol territory do not defend it. (See Lowen & Dunbar, 1994, for an improved model.)

Loud calls

Males in most territorial species produce loud calls that are good candidates for territorial advertisements. Phylogenetic reconstruction of these long-range calls in 158 primate species indicates the presence of male long-distance calls is the ancestral state (Wich & Nunn, 2002). Wich and Nunn (2002) found the carrying distance of male long-distance calls correlated with the size of the home range, consistent with the role of male long-distance calls in defending mates, attracting mates, and defending territorial resources. Loss of territoriality tended to be associated with loss of long-distance calling, an association which was significant, but not

² Long-tailed manakins appear to be an exception to our claim that mate choice is unlikely to explain cooperative displays of complex, coordinated music and dance. An alpha and beta pair of males attracts females to leks with highly coordinated duets and dances (Trainer, McDonald, & Learn, 2002), but, despite years of practicing together, the pair do not jointly defend territory or cooperate in any other known way (David B. McDonald, personal communication). In fact, only the alpha mates. However, as females tend to remain loyal to lek 'perch-zones' after alpha male turnover (Trainer et al., 2002), it could be the pair cooperates to defend its position at the lek perch-zone itself.

perfect. For example, 93% of territorial species had long-distance calls, whereas only 50% of non-territorial species did.

Because measures of male intra-sexual competition were not associated with the evolution of male long-distance calls, mate defense does not appear to be one of their functions, leaving mate attraction, territorial advertisement, or perhaps some other function as viable hypotheses. A recent review of primate loud calls, however, found little evidence they function in mate assessment or attraction. Instead, evidence to date indicates long-distance vocalizations function to maintain spacing between individuals or groups; in other words, they serve a territorial function (Delgado, 2006).

Geissmann (2000) suggested the evolutionary roots of human music are to be found in these primate long range calls (see Ujhelyi, 1996, 2000, for an argument rooting language, rather than music, in these calls). Geissmann's hypothesis is strengthened by clear evidence chimpanzees, one of our two closest relatives, not only produce long range calls, but also combine drumming and loud vocalizations in coordinated group displays that appear to play an important role in agonistic intergroup relations.

Chimpanzee group territoriality and advertisement

Among primates, our closest relatives are the apes, and chimpanzees and bonobos are sister species. Of the latter, chimpanzees are much better-studied in the wild than bonobos (Stanford, 1998), so bonobo data will only be briefly discussed.

Although early studies had concluded chimpanzees were not territorial, over two decades of research has firmly established male chimpanzees actively and aggressively patrol and defend their territory in groups (Herbinger, Boesch, & Rothe, 2001). A detailed study of communities in the Tai chimpanzee population (Herbinger et al., 2001, and references therein) found males in one community invested time and energy to defend territory at least twice a month by patrolling borders or locating neighbors. Encounters were dangerous, occasionally resulting in death. It is therefore not surprising chimpanzees, like other species, appear to advertise territory ownership.

During both within- and between-community interactions, chimpanzees produce a species typical call, the pant hoot, that can be heard over distances of 1-2 km. Between-communities, it is produced during border patrols and encounters with neighbors. Within-communities, it is produced when traveling, approaching or meeting members of other parties, arriving at feeding sites, nesting, and during conflicts (Crockford, Herbinger, Vigilant, & Boesch, 2004). Interestingly, chimpanzees also drum by pounding on tall buttress roots of trees with hands and feet, producing an acoustic signal that can travel over 1 km. Even more interesting, drumming is often integrated with pant hoots (Arcadi, Robert, & Mugurusi, 2004).

In Tai, when auditory contact with a neighboring community was made, community members advanced towards their

opponents 86% of the time, coming into visual contact 48% of the time. When visual contact was not made, opponents usually drummed for up to one hour, which Herbinger et al. (2001) interpret as serving to mark territory and signal group number and strength.

Pant hoots have also been experimentally shown to play an important role in territoriality, including the signaling of group strength. Wilson, Hauser, and Wrangham (2001) conducted an experiment in the Kanyawara chimpanzee community demonstrating the coordinated, group nature of chimpanzee territorial advertisement. They played back the recorded pant hoot of a single, extragroup male to parties of chimpanzees under different conditions. Variables included the number of adult males in the party and the location of the party (near the center or boundary of their territory). Male chimpanzees responded dramatically to the playback, orienting towards the loudspeaker and becoming aggressively aroused. When in small parties (1-2), males approached the loudspeaker in 5 of 9 trials, but only countercalled in 1 trial, presumably because they lacked 'military strength.' When in parties of three or more, however, males countercalled in 12 of 13 trials, and the chorus involved most or all of the males present, with occasional female participation. Location did not affect response.

Bonobos also produce loud calls during agonistic intergroup interactions. When two subgroups come into close proximity, they engage in very long exchanges of *Hooting* and *Composed barks* before eventually moving apart (Bermejo & Omedes, 1999). Bonobos also drum (see Fitch, 2006, for a brief review of drumming in the great apes).

Singing primates

Geissmann's proposal that human music is rooted in primate long-distance calls is further supported by the fact that about 26 non-human primate species in four genera, *Indri*, *Tarsius*, *Callicebus* and *Hylobates*, produce loud, patterned vocal sequences of notes meriting recognition as songs. This amounts to about 11% of primate species or 6% of primate genera. Because these genera are distantly related, singing appears to have evolved independently in each one. In singing species, both males and females sing. Perhaps relatedly, all singing primates have monogamous mating systems, and most exhibit male-female duets. This pattern is also found in many bird species, where, however, singing is much more common than in primates (Geissmann, 2000).

One of the singing clades, our lesser-ape 'cousins' the gibbons (*Hylobatidae*), are, after the great apes, our closest relatives. Gibbons diverged from the other apes (orangutans, gorillas, chimpanzees, and the human lineage) about 15-18.5 million years ago (Raum, Sterner, Noviello, Stewart, & Disotell, 2005). In contrast to songs in many songbirds, gibbons largely inherit rather than learn their songs (Geissmann, 2002).

Monogamous pairs of gibbons maintain exclusive territories, vigorously defending them from intruders (Mitani, 1990; Reichard, 2003), in at least one case with lethal consequences (Palombit, 1993). Observations and experiments

confirm singing and duetting play an important role in territorial defense, in addition to other possible functions. In more than 10 cases, for example, Kappeler (1984) observed non-resident gibbons reacting to the song bout of a resident female by immediately fleeing the area without being detected. Loudspeaker playback experiments (Mitani, 1990) found mated pairs of Bornean gibbons had a strong tendency to respond to duet playbacks near the center of their territories, a weaker tendency to respond to playbacks near territory boundaries, and essentially no tendency to respond to playbacks outside their territory.

Summarizing the primate data: many primate species are territorial; primate territoriality is strongly influenced in a predictable fashion by fundamental ecological variables related to resource acquisition and monitoring, supporting an evolutionary approach; males in most territorial species produce long-distance calls appearing to serve, in part, as territorial advertisements; one of our closest relatives, the chimpanzee, defends territory in groups, and produces loud choruses of pant-hoots, often combined with drumming, in intergroup agonistic encounters; our other closest relative, the bonobo, also produces loud calls during agonistic intergroup interactions; and some primates, including lesser apes, produce songs and duets that play an important role in territorial behavior.

Convergences: social carnivores

A second tack within the comparative approach is to explore adaptive convergences among distantly related species occupying similar ecological niches. What ecological niche, then, did early humans occupy? Although there is widespread agreement meat-eating was of increasing importance to early *Homo* during the late Pliocene and early Pleistocene, c. 2 MYA, there is considerable debate whether this was mainly due to hunting or scavenging (Brantingham, 1998; O'Connell, Hawkes, Lupo, & Blurton Jones, 2002). There is much less debate, however, that by the late Middle Pleistocene, c. 250 KYA, early humans regularly hunted big game.

The emergence of social carnivory in Homo

Here we briefly summarize Stiner's review of the archaeological evidence of meat eating in *Homo* (Stiner, 2002), touching at a few points on the work of others.

A *guild* is a group of animal species exploiting the same class of food resources in similar ways. The large-bodied predator guild of Africa and Eurasia included big cats, hyenas, and canids. Hominids invaded this guild c. 2.5–2 MYA. Though lacking speed or 'built-in' weaponry, these bipedal apes might have been able to successfully compete with large-jawed carnivores for ungulate prey, in part, by exploiting the remarkable efficiency of stone flakes and hammers to extract meat and bone marrow from scavenged limb parts. This meant early *Homo* probably interacted regularly with sizable predators.

Resource partitioning is a predicted outcome of interspecific competition among guild members. One analysis of

the distribution of prey body parts (e.g., heads, limbs) transported by various predators such as wolves, hyenas, and hominids suggested hominids invaded the predatory niche in an ecological 'slot' between top predators like wolves and confrontational scavengers like the spotted hyena. Top predators have early access to complete fresh carcasses and so concentrate on body parts with significant exterior meat, whereas confrontational scavengers concentrate on large, fresh, marrow-containing bones or heads. Plio-Pleistocene hominids appeared to concentrate on limbs, which comprise both meat and marrow (Brantingham, 1998).

Be that as it may, there is currently little evidence *Homo* was a regular big game hunter until the appearance of early humans c. 250 KYA. At this point in the archaeological record there is a distinct shift in patterns of association between humans and archaeofaunal assemblages. In Eurasia at least (where the archaeological record is far better known), a number of late Middle Pleistocene sites have rich deposits of human-modified ungulate bones in clear association with stone artifacts, a marked contrast to the murky record at older locations.

An analysis of faunal assemblages associated with these early humans reveals a predation pattern focused on immediate access to prime-aged adult ungulates. This distinguishes them from other ambush hunters, like lions and tigers, that hunt non-selectively, and from cursorial (running) hunters like wolves and spotted hyenas that target juvenile, elderly, and diseased animals. It also distinguishes them from Late Pleistocene humans who hunted a much broader range of species. Because many ungulates in the faunal assemblages were large and dangerous, the foregoing pattern indicates early humans were cooperative hunters, similar to lions, wolves, hyenas, and wild dogs (Roebroeks, 2001).

Physiologically, early humans were presumably omnivores, yet plant remains are poorly preserved in the archaeological record. From faunal remains alone the extent to which early humans relied on large herbivores, and thus occupied an ecological niche similar to large-bodied social carnivores, remains an open question. Ratios of stable isotopes of carbon and nitrogen found in bone collagen, however, are reliable indicators of an individual's average diet over the course of several years. $\delta^{15}\text{N}$ values increase with trophic level, with the highest values found among top carnivores. $\delta^{13}\text{C}$ values help discriminate between marine and terrestrial sources of protein, as well as forest vs. open environments. By comparing the stable isotope ratios of early humans with herbivores, scavengers, and top carnivores from the same ecosystem, it is possible to establish their position within the ecosystem. Several Neanderthal specimens have now been compared with associated herbivores and carnivores. Neanderthal values cluster near, yet above, those for sympatric lions, wolves, foxes, and hyenas, and far above those for omnivorous bears and herbivores (Bocherens, Drucker, Billeliou, Patou-Mathis, & Vandermeersch, 2005; Richards et al., 2000). Neanderthals were, with little doubt, accomplished social hunters at the top of the food chain.

Stiner makes a forceful case, worth quoting, for the centrality of carnivory in human evolution (Stiner, 2002, p. 5):

In stark contrast to modern nonhuman primates, humans and many carnivores frequently (a) cooperate in the care and stashing of infants, (b) transport food over long distances, (c) cache food, (d) share food well beyond the boundaries of propinquity, and (e) systematically process large bones for the soft tissues they enclose. The predatory behaviors of nonhuman primates have absurdly few dimensions if compared to the ways of wolves, wild dogs, spotted hyenas, and certain other carnivores.

Given the strong hand social carnivory appears to have played in shaping a suite of human behavioral traits, it remains, then, to be determined whether large-bodied social carnivores sympatric with early and modern humans tend to be territorial and, if so, whether they advertise territory ownership using coordinated vocal signals.

Territoriality in sympatric social carnivores

The Eurasian predator guild to which early humans belonged included three large social hunters in addition to humans: lions (*Panthera leo*), spotted hyenas (*Crocuta crocuta*), and grey wolves (*Canis lupus*).³ All four predators lived in caves, often the very same ones (at different times, of course!), and exploited very similar prey species. One faunal study of Upper Pleistocene cave sites, for example, found an essentially complete overlap in species exploitation patterns of humans and spotted hyenas. The single wolf sample differed from the human and hyena sample, however, with fewer red deer and more rabbit. Although wolves heavily exploit ungulates when not denning, this cave sample was a wolf den, which ungulates avoid (Stiner, 1992).

A closer look at each species reveals other similarities, including territoriality and advertisement.

Lions.

Like early human ancestors, the genus *Panthera* originated in Africa sometime before c. 3.5 MYA. The oldest known lion-sized *Panthera* fossil was discovered at Laetoli, Tanzania, a site famous for preserved footprints of a bipedal hominid dated to about the same period (3.7 MYA). The first definitive lion fossil (*P. leo*), from Olduvai, another key East African hominid fossil site, dates to 1.87-1.7 MYA. Like *Homo*, lions subsequently dispersed out of Africa. By the Middle Pleistocene, c. 500 KYA, lions were found throughout Africa, Europe, the Middle East, Siberia, and much of southwestern Asia; by 122 KYA, they were found throughout North America, and by c. 70-10 KYA, perhaps northern parts of South America as well. No other large land mammal other than humans has ever had a comparable range (Yamaguchi, Cooper, Werdelin, & Macdonald, 2004, and references therein).

Based on analyses of lion paleoecology, sociobiology, and depictions in cave art, Yamaguchi et al. (2004) conclude Pleistocene lions were group-living, so their behavior should resemble modern lions. Modern lions live in prides of 1-18 adult females and their dependent offspring, along with a

coalition of 1-9 males. Small (1-2 females) and large (≥ 10 females) prides fare poorly due to between- and within-group competition, respectively. Prides persist for generations, with females jointly defending territories against other females and infanticidal males. Territory size varies with overall food availability but not the number of females in the pride (Packer et al., 2005).

Lions of both sexes advertise their territory by roaring, and the number of distinct roars is used to gauge (and presumably to signal) the strength of a pride. Lions respond differently to simulated intrusions (loudspeaker playback of roars) according to a number of factors, including sex, composition of the defending pride, and the number of roaring individuals in the playback. Key findings of playback studies are that in a low-density population, female lions only aggressively approached the simulated intruders when they outnumbered them, whereas in a high-density population, females approached even when the odds of winning were low, probably due to higher competition for resources (Heinsohn, 1997, and references therein). Similarly, male coalitions, who are defending their access to females, cooperatively responded to simulated intrusions, decreasing the latency of response time as coalition size increased relative to the number of simulated intruders (Grinnell, Packer, & Pusey, 1995).

Spotted hyenas.

Contrary to their popular conception as scavengers, spotted hyenas are primarily hunters. Like lions, the evolution of the spotted hyena also roughly parallels human evolution. The earliest fossils date to c. 3.5 MYA in east Africa, with at least three subsequent waves of migration to Eurasia during the Plio-Pleistocene (an Asian origin, however, remains a possibility). Although the 'cave hyena' – the now extinct Eurasian variety of spotted hyena – exhibits some morphological differences with the African variety in body, cranial, and dental dimensions, genetic data do not support the existence of a distinct species or even subspecies (Rohland et al., 2005). Hence, the behavior of modern spotted hyenas may well reflect the behavior of Pleistocene African and Eurasian populations.

Extant spotted hyena populations live in large, stable female-dominated clans with a median size of about 50 individuals. Although spotted hyenas usually hunt alone, cooperative hunting is not infrequent. Serengeti clans have a unique 'commuting' system whereby individuals from one clan are allowed to commute unmolested along recognized thoroughfares through neighboring territories to hunt migratory prey. Nevertheless, clans in these and other populations actively and cooperatively defend exclusive territories by scent marking, defecating at latrines, patrolling, aggressively expelling non-residents, clashing with neighboring groups, and giving loud 'whooping' calls (Hofer & East, 1993a, 1993b).

Whoops serve a number of functions differing by age, sex, and resident status. Between clans, females use whoops during territorial clashes with neighbors, when rallying group

³ The African guild included wild dogs, *Lycaon pictus*, but not grey wolves.

members to defend communal resources against outsiders, and to deter potentially infanticidal non-clan members from approaching cubs at the communal den (East & Hofer, 1991).

Grey wolves.

Grey wolves evolved from the Eurasian species *Canis etruscus* c. 700 KYA, and subsequently expanded their range to North America in several waves of migration across the Bering Land Bridge (Vila et al., 1999). Wolves typically live and hunt in packs comprising a breeding pair, their maturing offspring, and unrelated individuals (Schmidt & Mech, 1997). Wolf packs defend large, exclusive territories with scent-marking, aggression, avoidance, and howling. In many cases, territories are stable year-around, but in others, wolf populations follow migratory herds for hundreds of kilometers, establishing temporary territories for several months at a time. Direct encounters between packs are rare, but when they occur, they often lead to fatalities (Harrington & Mech, 1983).

Like lions and spotted hyenas, wolves advertise their presence with a loud vocal signal (howls). Howls by both individuals and multiple pack members (chorus howls) are influenced by factors such as presence of young, a kill, pack size, and pack composition (Harrington & Mech, 1979). Although a study using human howling to simulate an intruding wolf found the relative location of intruder vs. the pack had no impact on howling responses, the strong attachment of wolves to particular sites probably explains why howling nevertheless successfully serves to promote interpack avoidance and exclusive territories (Harrington & Mech, 1983).

Proto-music

It is time to draw together the two comparative threads: humans as primates, apes, and a sister species of the chimpanzee. And humans as social hunters belonging to the same predator guild as lions, hyenas, and wolves.

As primates, it would not be at all surprising for early humans to be territorial (see Cashdan, 1983; Dyson-Hudson & Smith, 1978, for evidence of territoriality in contemporary hunter-gatherers) and to advertise territory ownership with a loud, distinctive call. Furthermore, as group-living apes and close relatives of the chimpanzee, it would not be surprising for early humans to mark territory and signal group strength with a chorus of loud vocalizations combined with drumming. And, as apes with strong male-female pair-bonds, it would not be out of the question for early humans to produce complex songs and duets serving, in part, to defend territory. Based on our primate heritage, a human proto-music consisting of a loud, distinctive vocal chorus of calls, perhaps with drumming, is, as Geissmann (2000) argued, entirely plausible, and even expected.

A similar conclusion follows from a comparison with fellow members of our Pleistocene predator guild. As large-bodied top predators cooperatively hunting big game, early humans were likely to be territorial and to mark territory and signal group strength using loud, coordinated vocalizations analogous to roars, whoops, and howls.

Group performance of loud vocal calls serving territorial and other functions is a compelling candidate for a human proto-music. If animals respond to territorial intruders with something like what humans experience as anger, and the intruders with something like fear, then proto-music would also be intimately associated at least two powerful emotions, much as music is intimately associated with many powerful emotions. Thus, although we differ greatly on details, we agree with Mithen (2005) that proto-music played an important role in the lives of Neanderthals and other early humans.⁴

This putative proto-music lacked several features of modern human music, however. There is little reason, for example, for it to have exhibited rhythm, synchronization, or extensive variation. To explain these features of music, additional selective forces must be identified. We propose two.

The first selective force derives from the distinction between multiple owners (neighbors, or 'dear enemies') and intruders (also termed 'floaters'). It often observed that owners respond less aggressively to the intrusions or advertisements of neighbors than to those of strangers (Getty, 1987; Leiser, 2003, and references therein). In territorial disputes, neighbors pose less of a threat because they already possess territory. Though boundaries might be disputed, there is little incentive for an owner with sufficient territory to pay the cost of evicting a neighbor from the neighbor's own territory. Floaters, on the other hand, pose a grave threat to owners because floaters do not possess territory, and so have an incentive to take over a seemingly undefended territory. This distinction requires owners to be able to recognize known neighbors from strangers. Otherwise owners risk over-responding to a neighbor, or failing to respond to a strange floater attempting to assert ownership.

Identity, then, emerges as an important feature of territorial advertisements, and this requires variation. Many primates, as well as lions, hyenas, and wolves, advertise ownership with a combination of signals, including vocalizations and scent-marks. As discussed earlier, it has been shown that mouse scent-marks, and probably other mammalian scent-marks, contain individually specific proteins serving to establish identity. Something about humans and the human ecological niche, however, might have prevented the evolution of scent-marking. Perhaps it was our orthograde posture, which kept our noses away from the ground, or a reduced sense of smell (but see Shepherd, 2004, for an argument that humans have a superb sense of smell).

Whatever the reason for the lack of scent-marking in modern humans (and presumably early humans), the need to advertise not only ownership but identity, remained. If vocalizations had to assume the role of scent marks in establishing identity, they would have had to evolve sufficient patterned variation to serve as reliable signals of identity.⁵ Interest-

⁴ In a book-length treatment, Mithen (2005) argued that the increasingly complex lives of human ancestors required an increasingly complex yet 'holistic' vocal communication system, which he identifies as music. We, in contrast, use a comparative approach to argue for the likelihood of the described proto-music. Space precludes a more detailed comparison of the two hypotheses.

⁵ The identity afforded by individually-specific proteins is

ingly, chimps in closely neighboring communities actively modify their pant hoots to create community-specific calls (Crockford et al., 2004).

A loud, vocal signaling system with enough potential for group-specific variation would probably still not need rhythm and its ability to synchronize the vocalizations of large groups. Among singing primates, rhythm is unique to humans (Geissmann, 2000). As we explain next, this signature feature of music could be accounted for by a correspondingly unique aspect of human territorial defense and a consequent group-analog of sexual selection.

Alliances and the evolution of music

Within-group cooperation and between-group competition are found in numerous mammalian species, including primate species. Humans are nearly unique, however, in that groups often form *cooperative* relationships with other groups (Rodseth, Wrangham, Harrigan, & Smuts, 1991).

Cooperation at the group level is nearly unprecedented. Among the approximately 200 species of primates, only hamadryas baboons and humans are known to form cooperative group-level alliances (Cheney, 1987). Yet hamadryas group-level alliances are limited to close male kin. Much like a segmentary lineage system (e.g., Evans-Pritchard, 1940), a one male unit (OMU) comprising a single male and his harem of females can ally with one or more closely related OMUs to form a clan; clans, in turn, can ally to form bands. Larger groups more successfully compete for resources against smaller groups (Colmenares, Esteban, & Zaragoza, 2006; Kummer, 1968).

Humans are apparently unique in their ability to form close, highly cooperative intergroup relationships in the absence of consanguineal ties. Across human societies, the modal pattern is one of male kin forming alliances with other groups of male kin, usually via an exchange of females. Intergroup cooperation is a foundation of the complex, region-wide social structures characterizing humans. As Rodseth et al. (1991, p. 236) put it in their comparative study of primate social organization, “the breakthrough in human social organization...is *intergroup affinity*” (emphasis in the original). And it is intergroup affinity that underlies the human pattern of territory defense, as groups often call on allies to help deter or respond to enemy intrusions and attacks (e.g., Chagnon, 1968).

The rarity of group-level alliances in the primate world is probably rooted, at least partially, in the problem of identifying those groups with sufficient agent-like properties to serve as viable cooperative partners. Game theoretic models of cooperation assume that the players all possess a number of properties enabling them to engage in strategic interactions. For individuals as such, these assumptions are usually warranted (e.g., all their body parts are able and willing to work together). The same is not true of groups. Unlike individuals, the agent-like properties of groups in a cooperative species can range the gamut from spatial aggregations of individuals who do not know each other and have no willingness or

ability to work together, to highly cooperative groups.

We will refer to a group of individuals who are willing and able to cooperate on complex tasks as a *coalition*. Coalitions have agent-like properties and can thus serve as cooperative partners. The problem then becomes how to discriminate between coalitions and non-coalitions, and also how to discriminate among coalitions of varying quality. For even when a newly formed coalition is willing and able to work together, its performance is unlikely to match a coalition that has worked together for months or years. To give a contemporary example, despite assembling the top players in the league, ‘All-Star’ sports teams, which come together to play one game with almost no practice time, rarely play as effectively as regular teams.

Hagen and Bryant (2003) argued music and dance were reliable signals of coalition quality. A group display of complex, group-specific songs and dances synchronized by rhythm could only be produced with weeks or months of practice, reliably signaling the group must have been willing and able to work together for at least that amount of time. Yet songs and dances could be performed for, and assessed by, potential allies in minutes or hours at the feasts where alliances are usually forged (there as been a resurgence of anthropological interest in the sociopolitical dimensions of feasting; for overviews, see Bird & Smith, 2005; Hayden, 1995; Potter, 2000; Wiessner & Schiefenhovel, 1996). Consistent with this hypothesis, Hagen and Bryant showed variation in music synchrony predicted perceptions of music quality, which, in turn, predicted perceptions of coalition quality.

Choosing allies based on musical prowess would spark an evolutionary ‘arms race’ between coalition members with an interest in producing ever more convincing signals of coalition quality, and potential allies with an interest in better discriminating between performances of coalitions of different quality, leading, eventually, to the rich coalition signaling system we call music.

Our hypothesis does not specify when, exactly, music evolved. Because we propose that music and alliances co-evolved, under our hypothesis music should have appeared whenever alliances did, probably sometime after the human lineage diverged from chimpanzees, c. 6-7 MYA (but see Mithen, 2005, for discussion of the physiological and archaeological clues of the emergence of music over human evolution).

If coalitions are the group-analog of agents, then music might also serve as the group-analog of emotional signaling by individuals. Just as individuals signal certain strategic states like anger, joy, or sadness to social partners with a variety of emotion-specific facial signals (Ekman, 1971), coalitions could signal group-level analogs of anger, joy, or sadness to allies and enemies with performances of angry, joyous or sad music (Hagen & Bryant, 2003). At news of an enemy intrusion, for example, a coalition might sing an

founded on a combinatorial system involving 20 amino acids (themselves coded for by DNA, another combinatorial system). A reliable system of identity based on acoustic signals might similarly require combinations of relatively discrete units, such as notes.

angry war song to inform the enemy of its strength, quality, and resolve to respond aggressively.

Thus, to advertise territory ownership, indicate group strength, form alliances, and express group-level strategic states, humans needed a signal that closely resembles music: a loud, distinctive, emotionally engaging chorus of highly synchronized sounds performed by group members who had practiced together for weeks, months, or years.

Concluding remarks

Despite evidence that loud calls in primates and other mammals serve more than one function, we have emphasized territorial advertisement for several reasons, chiefly its ability to easily explain features of music that are poorly explained by sexual selection. Furthermore, there is consistent evidence in favor of it across different studies and different species. This contrasts with the more variable results for other functions like mate attraction, especially in primates. Finally, there is a didactic advantage to focusing on a single, intensively researched function like territoriality.

An alternative approach would be to investigate the information coded, *by design*, into a signal like a loud call, and then explore the possibly multiple pathways by which the reactions of various receivers of this information could increase the sender's fitness; each pathway would constitute a 'function' of the signal. To give a simple example, a loud call given by a (non-human) male territorial owner could increase his fitness by two independent paths, thus serving two functions at one and the same time. By reliably indicating the presence of the owner, it would, first, warn off male intruders, avoiding costly fights, and second, it would inform females in the vicinity that the male owns a territory, and thus has resources to offer.

If music is an adaptation, it probably increased fitness by multiple paths. Future work should focus on the information (if any) that is coded, *by design*, into music. We have argued this includes information on the quality of coalitions, though information on individual quality is almost certainly present too; implicitly, a group musical performance could also indicate ownership of a territory, and thus access to substantial resources. Similar to loudspeaker playback studies of animals, the reactions of strategically salient categories of individuals, such as friends, enemies, strangers, and members of the opposite sex, to musical performances should then be explored. According to the hypothesis presented here, proficient group performances of music ought attract allies and, via indications of territory ownership, mates, and it ought to deter enemy intruders.

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