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Musicae Scientiae 2009 13: 291

DOI: 10.1177/1029864909013002131

The online version of this article can be found at:

http://msx.sagepub.com/content/13/2_suppl/291

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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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• ABSTRACT

Group defence of territories is found in many gregarious mammalian carnivores, including lions, canids, and hyenas. In these taxa, group members often mark territory boundaries and direct aggressive behaviour towards alien conspecifics found within the territory (Boydston *et al.*, 2001). Middle Pleistocene hominids such as Neanderthals occupied an ecological niche similar to such large carnivores (Stiner, 2002), and so could be expected to share with them a suite of behavioural traits. Complex, coordinated vocalizations that function, at least in part, to advertise the group defence of a territory is one behavioural 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. Human proto-music, in essence, might have been functionally analogous to the howling of wolves.

Keywords: biomusicology, territorial signaling, coalitions, alliances, feasting.

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?

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). Miller (2000) has recently taken up Darwin’s astute suggestion that this might also explain the evolutionary origins of human music (Darwin, 1871).

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 (as well as infants and children), whereas mating signals should almost always be directed towards adolescent and adult members of the opposite sex; it exhibits rhythm, presumably to synchronize group performances (Merker, 2000; Bispham, 2006); 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). Merker (2000), who postulated that synchronized chorusing of male hominids would have increased signal amplitude to better attract females, also recognized territorial functions of coalitional vocal displays.

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 — alliances between groups — 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.

The importance of cooperative alliances between groups suggests, more generally, that human groups acquired key properties of strategic agents. In our conclusion, we briefly expand on the implied analogy with multicellular organisms and its ramifications for language evolution.

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: defence 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 (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 defensible territories* — organisms should tend to evolve territoriality (Adams, 2001). The crux, of course, is to understand 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 behaviour. 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 forth. 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 PRIOR RESIDENCE EFFECT

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 *et al.*, 2006). One of the first applications of evolutionary game theory aimed to explain the effect using a simple model with two behaviours, 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 evolutionarily 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 when in the intruder

role (but keeping it 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 (neighbours) who have conflicts over territory boundaries but might have a common interest in allying against intruders (Getty, 1987; Pereira *et al.*, 2003; Leiser, 2003), so-called “dear enemies.”

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, faeces, 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 *et al.*, 2003). Like many signals, scent-marks appear to have multiple functions. In addition to territorial advertisement, these include attracting mates, signalling 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

(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.

among them. The bannertail kangaroo rat, for example, spends most of its time on, or inside, a large dirt mound where it has stored as much as 100 litres of seeds. It advertises its presence on the mound by foot drumming spontaneously during the night, as well as in response to the foot drumming of neighbours and during mound challenges (Randall, 1984).

Vocalizations, found in an enormous range of taxa, are probably the most prevalent form of acoustic territorial advertisement. We will focus here on a subclass of vocalizations which exhibit such a clear and recognizable patterning of notes that they are often referred to as songs.²

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 birds are 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

(2) Although Fitch (2006) has argued that that term "song" be restricted to learned vocalizations, we adopt the same definition of song as Geissmann (2002), p. 60: A note is a "single continuous sound of any distinct frequency or frequency modulation, which may be produced during either inhalation or exhalation"; a song, following Thorpe (1961), p. 15, is "a series of notes, generally of more than one type, uttered in succession and so related as to form a recognisable sequence or pattern in time."

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). These experiments found that 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 signalling group strength.

Group living is expected when benefits such as cooperative hunting, parenting, or defence 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 *et al.*, 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 defence, 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 *et al.*, 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 signalling 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 behaviour 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 neighbours, and in response to intrusion and playback; spatial proximity of duetters increases the threat perceived by intruders; and duetters distinguish the duets of neighbours 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.³

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 that they, too, 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

(3) Long-tailed manakins appear to be an exception to our claim that mate choice alone is unlikely to explain cooperative displays of complex, coordinated music and dance. An unrelated alpha and beta pair of males attracts females to leks with highly coordinated duets and dances (Trainer *et al.*, 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.

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 behaviourally 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 travelled in one day), and A is the area of the home range (the denominator thus approximates the diameter 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 primate 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 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 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 defence 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 that 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 our 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 that male chimpanzees actively and aggressively patrol and defend their territory in groups (Herbinger *et al.*, 2001). A detailed study of communities in the Taï chimpanzee population (Herbinger *et al.*, 2001, and references therein) found that males in one community invested time and energy to defend territory at least twice a month by patrolling borders or locating neighbours. 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, which can be heard over distances of 1-2 km. Between-communities, it is produced during border patrols and encounters with neighbours. Within-communities, it is produced when travelling, approaching or meeting members of other parties, arriving at feeding sites, nesting, and during conflicts (Crockford *et al.*, 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 *et al.*, 2004).

In Taï, when auditory contact with a neighbouring 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 signalling of group strength. Wilson *et al.* (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 centre 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 counter-called in 1 trial, presumably because they lacked "military strength." When in parties of three or more, however, males counter-called 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 drum too (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 (Raaum *et al.*, 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 defence, 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 centre 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 behaviour.

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 that 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 *et al.*, 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 artefacts, 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 *et al.*, 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 behaviours 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 behavioural 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.

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*).⁴ 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 group defence of territory and coordinated vocal advertisements by group members.

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 *et al.*, 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 behaviour 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, often in choruses, and the number of distinct roars is used to gauge (and presumably to signal) the strength of a pride (Grinnell & McComb, 1996). 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

(4) The African guild included wild dogs, *Lycaon pictus*, but not grey wolves.

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 *et al.*, 1995).

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 kilometres, 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, 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).

Spotted hyenas. Contrary to popular conception, spotted hyenas are primarily hunters, not scavengers. Like lions and wolves, 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 behaviour of modern spotted hyenas may well reflect the behaviour 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 neighbouring 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 neighbouring 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 neighbours, when rallying group 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). Playback studies show that clan members respond more aggressively to whoops from non-clan members than clan members (Mills, 1990). Unlike most social carnivores, spotted hyenas usually call individually, rather than communally. But, East and Hofer (1991) describe a vocal exchange between neighbouring clans that lasted 58 minutes, comprising 32 whooping bouts by seven females and one male in the study clan. The neighbouring clan was highly vocal in response. This suggests that communal calls play some role in spotted hyena territorial advertisements.

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 have marked territory and signaled 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, howls, and (perhaps) whoops.

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.⁵

TOWARDS A THEORY OF THE EVOLUTION OF MUSIC

Our proposed human proto-music lacked several features of modern human music. There is little reason, for example, for it to have required much learning, or to have exhibited extensive variation, rhythm, or synchronization. To explain these features of music, additional selective forces must be identified. We examine three, with the caveat that this portion of our argument is necessarily much more speculative.

OWNER IDENTITY, VARIATION, AND VOCAL LEARNING

The first selective force derives from the distinction between multiple owners (neighbours, or “dear enemies”) and intruders (also termed “floaters”). It is often observed that owners respond less aggressively to the intrusions or advertisements of neighbours than to those of strangers (Getty, 1987; Leiser, 2003, and references therein). In territorial disputes, neighbours 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 neighbour from the neighbour’s own territory. Floaters, on the other hand, pose a greater 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 neighbours from strangers. Otherwise owners risk over-responding to a neighbour, or failing to respond to a strange floater attempting to assert ownership. (The reverse pattern, where owners respond more aggressively to neighbours than strangers, also occurs, *e.g.*, Müller & Manser, 2007, but the need to distinguish the two categories of intruders remains.)

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. Apes and humans, however, apparently do not scent-mark (Geissmann & Hultegger, 1994).

(5) 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. Space precludes a more detailed comparison of his hypothesis with ours.

Whatever the reason for the lack of scent-marking in apes and 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, and these patterns would have had to have been acquired by all group members. Vocal learning mechanisms relying heavily on imitation are the most obvious means to generate and acquire the necessary variations (on song generation and vocal learning, see, *e.g.*, Lerdahl & Jackendoff, 1983; Merker, 2005, 2006; Fitch, 2006). Interestingly, chimps in closely neighbouring communities actively modify their pant hoots to create community-specific calls (Crockford *et al.*, 2004). The need to signal identity adds two of the missing features of music — learning and variation — to proto-music.⁶

COALITION QUALITY AND SYNCHRONY

In agonistic encounters between groups, relative group size is probably second in importance only to prior residence in determining outcomes. But what about encounters between similar or same-sized groups (such as mated pairs) when there is no convention such as prior residence to determine outcomes?

One major problem in relationships between groups is distinguishing a mere spatial aggregation of individuals from a group of individuals willing and able to cooperate on complex tasks. We refer to the latter as a *coalition*. Unlike mere spatial aggregations of individuals, coalitions have properties of *agents*, entities capable of engaging in strategic interactions such as coordinated aggression or, as we discuss in the next section, cooperation.

Determining, upon first encounter, if a group of individuals is a coalition, and hence a more dangerous enemy, is not trivial. Although group members would know whether they were willing and able to work together, outsiders would not. Moreover, because there is an incentive to be perceived as a coalition, *i.e.*, as a more dangerous enemy, there is also an incentive to give deceptive signals of coalition status.

It could take days, weeks, or months of observations to assess whether a group was, indeed, a coalition, and, if so, how effective it was. 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 human example, despite assembling the top players in the league, “All-Star” sports

(6) The identity afforded by individually-specific proteins is 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. This might explain the evolution of vocalizations with a recognizable pitch (*i.e.*, notes) from hoots, screeches, howls, *etc.*

teams, which come together to play one game with almost no practice time, rarely play as effectively as regular teams. Coalition status is what game theorists refer to as *private information*.

Among singing primates, rhythm is unique to humans (Geissmann, 2000; Merker, 2000). This signature feature of music presumably functions to synchronize the vocalizations of large groups. Hagen and Bryant (2003) argued that highly synchronized vocal and visual displays were a means to quickly and credibly signal coalition quality because these could only be produced with considerable practice (taking days, weeks, months or perhaps even years), reliably indicating the group must have been willing and able to work together for at least that amount of time. Yet such displays, which in humans would correspond to war songs and dances, could be performed for, and assessed by, potential enemies in minutes or hours. The greater the degree of complexity and synchronization of the performance, the greater the quality of the coalition (to prevent cheating, songs would have to be group-specific, another argument for the evolution of musical variation; Hagen & Bryant, 2003).

In support of this hypothesis, Hall and Magrath (2007) found the fraction of highly synchronized duets in magpie-larks increased with the duration of the partnership. Experimental manipulation of duet synchrony during simulated intrusions of territory showed highly synchronized displays were significantly more threatening to the male territory holders than poorly synchronized displays. Hall and Magrath conclude synchrony in this species signals coalition quality above and beyond group strength (which, in this case, is two).

ALLIANCES AND THE EVOLUTION OF MUSIC

Although war songs and dances are ubiquitous in human societies, music and dance displays by foreign groups often attract, not repel, audiences, engendering positive emotions, not fear. If synchronized vocal and visual displays are evolved signals of coalition quality, then such signals probably served functions besides deterring enemies.

Within-group cooperation and between-group competition are found in numerous mammalian species, including primate species. Humans are nearly unique, however, in that to defend territory, groups often form *cooperative* alliances with other groups (Rodseth *et al.*, 1991).

Cooperation between groups 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 *et al.*, 2006; Kummer, 1968).

Humans are apparently unique among primates 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 defence, as groups often call on allies to help deter or respond to enemy intrusions and attacks (*e.g.*, Chagnon, 1968).

Because alliances are so valuable, there is an incentive for individuals to deceptively portray themselves as viable alliance partners (*i.e.*, as a coalition). Only genuine coalitions, however, could successfully perform highly synchronized displays of complex songs and dances.

Hagen and Bryant present some of the ethnographic evidence that, in humans, music and dance are key features of alliance formation. This includes the central role of music and dance in the feasts of traditional societies where alliances are usually forged, the tremendous amount of time spent practicing prior to feasts (often months, even in small-scale societies), and the heavy emphasis placed on achieving high levels of synchrony. Sociopolitical dimensions of feasting, including alliance formation, have experienced a resurgence of interest from anthropologists; for overviews, see Bird and Smith (2005), Hayden (1995), Potter (2000), Wiessner and Schiefenovel (1996). In an experiment, Hagen and Bryant also showed higher levels of synchrony in a song caused perceptions of music quality to increase, which, in turn, predicted perceptions of higher coalition quality (*e.g.*, perceptions of the performers’ willingness and ability to work together).

Choosing allies based on the quality of music and dance performances (as well as the quality of other forms of cultural production prominently displayed at feasts, such as food, clothing, artefacts, *etc.*) 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 signalling system we call music.

Sexual selection redux. The coalition quality hypothesis also neatly integrates aspects of the sexual selection hypothesis. First, high-quality group displays would implicitly indicate ownership of a territory, and thus access to resources by group members, information of considerable interest to potential mates (*c.f.*, Merker, 2000). Second, alliances between human groups are typically formed by the marriage of men from one group with the women of another (Rodseth *et al.*, 1991). During feasts, coalitions are evaluating potential allies and potential mates at one and the same time.

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 the chimpanzee lineage, c. 6-7 MYA (see Mithen, 2005, for discussion of the physiological and archaeological clues of the emergence of music over human evolution).

SYNCHRONY AND ALLIANCES IN MALE BOTTLENOSE DOLPHINS

Synchronized displays also appear to play an important role in alliances in one of the few other mammalian species known to form them: bottlenose dolphins. Male dolphins in stable dyads and triads cooperate to guard and herd females. Like humans, at least one population of bottlenose dolphins also forms alliances between groups: alliances of two or more such coalitions, comprising 4-14 individuals, cooperate in conflicts with other groups over females. There is even evidence for a third level of cooperation, between alliances (Connor *et al.*, 1992; Connor *et al.*, 2006; Connor, 2007).⁷

Connor and colleagues describe elaborate displays by male coalitions in the wild. These include aerial leaps, multiple underwater turns, and surfacing, all often tightly synchronized among coalition members. A study of synchronized surfacing and alliances (Connor *et al.*, 2006) found that in the majority of synchronized surfacing events, males were within 1 meter of one another, and surfaced within 120-130 ms of each other. Such displays are performed in the presence of female consorts, but probably also serve a signalling function within and between coalitions. When multiple coalitions were travelling together, synchronized surfacing was strongly correlated with coalition membership across all four coalitions in the study (*i.e.*, much more synchronized surfacing within, rather than between, coalitions). Although other hypotheses for such synchronized displays cannot yet be ruled out, these researchers conclude that humans and dolphins may have converged on the use of synchrony as a signal among allies.

MUSIC AND EMOTIONS

If coalitions are the group-analogue of agents, then music might also serve as the group-analogue of emotional signalling 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

(7) Connor and colleagues use a slightly different terminology for coalitions and alliances, but, for clarity, we continue to use our terminology.

analogues 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 angry war song to inform the enemy of its strength, quality, and resolve to respond aggressively. As Burrows (1945), p. 78 wrote of music among the islanders of Uvea and Futuna, "Where an emotion may be either individual or collective, it is the collective aspect that finds expression in song."

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

CONCLUDING REMARKS

Does our "human group as strategic agent" perspective on music evolution shed any light on the evolution of that other uniquely rich human signalling system, language? Perhaps. Music and language might have played complimentary roles in the emergence of the sophisticated agent-like properties of human groups. Let us make an analogy: Multicellular organisms, to coordinate their various parts, evolved numerous intercellular signalling systems based on, *e.g.*, cytokines, hormones, and neurotransmitters. Because coalitions, much like multicellular organisms, have properties of strategic agents, they need analogues of molecular signals for coordination. In a recent review, Számadó and Szathmáry (2006) conclude that facilitating group coordination during hunts is one of the most likely scenarios for the evolution of language. Yet they note that other species hunt cooperatively, and have evolved signalling systems to facilitate group coordination, but none of these systems is as sophisticated as language. Among primates (and probably among social carnivores), strategic interactions between geographically dispersed coalitions, especially cooperative interactions, are unique to humans, however, and therefore may have required an inter-individual signalling system with capabilities beyond those found in the signalling systems of most, and perhaps all, other social organisms (Fox 1980; Rodseth *et al.* 1991). Music, we have argued, might have evolved to credibly signal coalition quality (and perhaps also identity), enabling the formation of such cooperative multi-group alliances. Language, in turn, might have evolved to play a complimentary role in these human "super organisms," one analogous to intercellular molecular signals: facilitating coordination both within coalitions as well as among allies.

Music might not be an adaptation (*e.g.*, Pinker, 1997). This remains an important null hypothesis. If music is an adaptation, however, 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. 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 to attract allies and, via indications of territory ownership, mates, and it ought to deter enemy intruders.

ACKNOWLEDGEMENTS

Many thanks to Björn Merker, W. Tecumseh Fitch, Nicole Hess, Sven Krackow, and members of the Institute for Theoretical Biology for numerous helpful comments and suggestions. Support provided by Deutsche Forschungsgemeinschaft SFB 618 and ECAGents Contract No. 001940.1.

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- **¿Cantaban los hombres de Neandertal y otros hombres primitivos?
A la búsqueda de las raíces biológicas de la música en la marcación
de territorio en los primates, los leones, las hienas y los lobos**

La defensa en grupo del territorio se encuentra en muchos mamíferos carnívoros gregarios, incluidos los leones, los perros y las hienas. En este conjunto taxonómico, los miembros del grupo marcan a menudo los límites de su territorio, y fijan un comportamiento agresivo hacia todo congénere extraño encontrado en el interior de este territorio (Boydston, Morelli & Holekamp, 2001). Los homínidos del Pleistoceno medio, como los Neandertales, ocupaban un nicho ecológico similar al de tales grandes carnívoros (Stiner, 2002): eran, por tanto, susceptibles de compartir con ellos todo un conjunto de rasgos de comportamiento. Uno de esos rasgos, presente en numerosos carnívoros sociales, así como en muchos otros animales gregarios, incluidos los primates, son las vocalizaciones complejas, coordinadas, emitidas para advertir que el grupo defiende su territorio. Hagen y Bryant (2003) han propuesto que la evolución de la música y la danza en el ser humano puede tener sus raíces en estas señales territoriales coordinadas en los niveles auditivo y visual: es esta hipótesis la que explotamos y desarrollamos aquí. En esencia, la protomúsica humana podría haber sido funcionalmente similar a los aullidos de los lobos.

- **L'uomo di Neanderthal e gli altri uomini primitivi sapevano cantare?
La ricerca delle radici della musica nei segnali territoriali
di primati, leoni, iene e lupi**

La difesa di gruppo del territorio è riscontrabile in diversi mammiferi carnivori gregari, tra i quali i leoni, i canidi e le iene. In queste unità tassonomiche i membri del gruppo spesso marcano i confini del territorio e dirigono comportamenti aggressivi contro individui della stessa specie ma sconosciuti al gruppo, che si trovino all'interno del territorio (Boydston, Morelli, & Holekamp, 2001). Durante la metà del Pleistocene, l'uomo di Neanderthal occupava una nicchia ecologica simile a quella dei grandi carnivori (Stiner, 2002), perciò è possibile pensare che dividesse con essi una serie di tratti comportamentali. Le vocalizzazioni complesse e coordinate che svolgono la funzione, almeno in parte, di segnalare la difesa del territorio da parte del gruppo sono un tratto comportamentale comune a diversi carnivori sociali, come anche ad altri animali gregari tra cui i primati. Hagen e Bryant (2003) hanno proposto che l'evoluzione della musica umana e della danza pongano le proprie radici in questi avvertimenti territoriali uditivi e visivi, un'ipotesi che svilupperemo ed espanderemo in questa sede. In sintesi, la proto-musica umana potrebbe essere funzionalmente analoga all'ululato dei lupi.

- **Est-ce que les hommes de Neandertal et autres premiers hommes chantaient ? A la recherche des racines biologiques de la musique dans le marquage du territoire chez les primates, les lions, les hyènes et les loups**

La défense en groupe du territoire se rencontre chez beaucoup de mammifères carnivores grégaires, y compris les lions, les chiens et les hyènes. Dans cet ensemble taxonomique, les membres du groupe marquent souvent les limites de leur territoire, et affichent un comportement agressif envers tout congénère étranger rencontré à l'intérieur de ce territoire (Boydston, Morelli, & Holekamp, 2001). Les hominidés du Pléistocène moyen, tels les Néandertalien, occupaient une niche écologique similaire à celle de ces grands carnivores (Stiner, 2002) : ils étaient dès lors susceptibles de partager avec eux tout un ensemble de traits comportementaux. L'un de ces traits comportementaux, présent chez de nombreux carnivores sociaux, aussi bien que chez beaucoup d'autres animaux grégaires, y compris les primates, sont ces vocalisations complexes, coordonnées, émises pour avertir que le groupe défend son territoire. Hagen et Bryant (2003) ont proposé que l'évolution de la musique et de la danse chez l'être humain puisse prendre ses racines dans ces signaux territoriaux coordonnés aux niveaux auditif et visuel : c'est cette hypothèse que nous exploitons et développons ici. Par essence, la protomusique humaine pourrait avoir été fonctionnellement semblable aux hurlements des loups.

- **Sangen Neanderthaler und andere Frühmenschen? Auf der Suche nach den biologischen Wurzeln der Musik im Anzeigen von Reviergrenzen bei Primaten, Löwen, Hyänen und Wölfen**

Gruppenverteidigungen von Territorien finden sich bei vielen geselligen, fleischfressenden Säugetieren, so auch bei Löwen, Hundartigen und Hyänen. In diesen Sippen markieren Gruppenmitglieder oft die Reviergrenzen; aggressives Verhalten wird gegen fremde Artverwandte gerichtet, die innerhalb des Territoriums angetroffen werden (Boydston *et al.*, 2001). Hominiden des mittleren Pleistozäns wie Neanderthaler besetzten eine ökologische Nische, die derjenigen dieser großen Fleischfresser ähnelte (Stiner, 2002). Daher kann erwartet werden, dass sie mit diesen einige Verhaltensgrundzüge teilten. Komplexe koordinierte Lautäußerungen, die zumindest teilweise als Anzeichen der Gruppenverteidigung eines Territoriums fungieren, sind Verhaltensgrundzüge, die bei verschiedenen sozialen Fleischfressern ebenso wie bei vielen anderen in Rudeln lebenden Tieren einschließlich der Primaten auftreten. Hagen und Bryant (2003) schlugen vor, dass die Evolution von menschlicher Musik und Tanz in solchen koordinierten auditiven und visuellen Territorialmarkierungen wurzelt, eine Hypothese, die wir hier weiter entwickeln und ausbauen. Im Grunde könnte menschliche Protomusik eine funktionelle Analogie zum Heulen von Wölfen darstellen.