

Trophic level, arboreal position, and size of both predators and primates gave rise to a diverse and multi-functional musicality

David M. Schruth, Ph.D.

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Abstract

The predator-prey relationship is a fundamental directional dyad underlying trophic dynamics that emerge within food-chain networks. Numerous anti-predational behaviors are possible to help animals mitigate the risk of becoming prey, including crypsis, warding, avoidance, evasion, and confrontation. Most primates leverage both vigilance and alarm calling within groups as well as infant carrying amongst protected trees to avoid being targeted and pursued by predators. Other vocalizations of primates vary greatly and many of them contain myriad manifestations of musical complexity including spectral and temporal patterning as well as diverse contouring. Smaller primates, who may inhabit attenuated terminal branches, use more subtly short melodic sequences to maintain within-group contact, but also to circumvent eavesdropping by predators. Larger primates, who may brave open ground, use calls that are more salient, rhythmic, and syllabically diverse to assert dominance outside the group and possibly towards other species. Body size also tends to scale allometrically with other (usually morphological) traits within an individual—steeply with sexual traits and more shallowly for weaponized traits. The stronger positive correlations of body size with syllable than with rhythm suggests an attractive function of melodic elements and a mildly repulsive function for rhythm. This finding is further backed by affiliative contexts for other spectral aspects (e.g. transposition) and more threat-based contexts for temporal ones (e.g. repetition). Complex rhythms appear more often in larger terrestrial species (e.g. hominid apes and some lemurs), bolstering a possibly analogous purpose, of warding-off predators, by newly terrestrialized hominins. This combination of familial arboreality and larger-group terrestriality may have spawned our uniquely dualistic musicality—as composed of both amiable melodies and imposing rhythms.

Prey behavior, trophic security, life history, and acoustic strategies

Within their respective food webs, animals leverage a vast array of evolved and acquired tactics to avoid falling prey to predators (Fig 1). These can range from blending-in with surroundings, thereby largely avoiding sensory detection, to *aposematically* overwhelming predator senses with a barrage of unpalatability—in the form of odorous, soniferous, or colorfully honest signals (Cooper and Blumstein, 2015). Animals can also evolve *deimatic* ways of deceiving predators as part of an avoidance strategy—via exaggeration, distraction, startling, or just playing dead (Edmunds, 1974). Structural features of phenotype or niche can also be employed to make consumption or pursuit difficult. More active forms of protection may include evasion (e.g. running or flying away) or confrontation (e.g. fighting with claws, teeth, or horns). More socially inclined species (e.g. anthropoid primates) can team-up to post lookouts, warn each other, carry smaller group members away, or even collectively mob their predators.

Species of higher trophic standing may also produce more offspring [r] or increase gestation lengths and lengthen lifespans [k]—by leveraging larger body size, more group members, or higher vertical positioning—as mitigated by both population density and predictability of resources (Wilbur, Tinkle and Collins, 1974). Burrowing, island-dwelling, and arboreal species—such as wild dogs, marsupials, song birds, and primates—are slow to wean their altricial young, thereby also slowing growth rates (Case, 1978) and extending individual offspring security through more concentrated nurture. Such (k -selected) species, particularly primates, have lower parity and longer lifespans (Jones, 2011), perhaps as a result of leveraging trees to mitigate predation. Since many terrestrial predators can climb trees to pursue and corner arboreal residents at these dead-ends, many primates have alternatively evolved means of positional avoidance that employ discontinuous, inter-substrate, and inter-tree locomotion.

Another way [typically larger] animals, and indeed many primates, can deter predators is by producing calls of high amplitude (Wich and Nunn, 2002). These ‘loud calls’ have long-distance transmission properties that evolved as a remote way to demarcate home range and maintain spatial boundaries (Mitani and Stuht, 1998). But it is uncertain to what extent these calls are directed within species, such as towards rivals or the opposite sex (Delgado, 2006), or between species, such as towards predators (Zuberbühler, Jenny and Bshary, 1999). In any case, repulsive territorial calls of primates are typically produced from a position of elevated trophic standing, analogous to the loud-calling of non-primate apex predators—including large carnivores, such as lions, hyenas, and wolves (Hagen and Hammerstein, 2009).

This chapter starts where others have left off, by exploring the idea of acoustics as frequently serving to defend territories by deterring the encroachment of predators and competitors (Hagen and Hammerstein, 2009; Jordania, 2011; Hagen, 2022). This work begins by delineating forms of defense against predators ranging from aposematic repulsion (e.g. chorusing) to inconspicuous silence and camouflage (see chapters by Jordania, Podlipniak, and Alonso, this volume). Here I propose that in primates, more salient acoustic output originated as generically repulsive threats directed more generally towards a multitude of predators. I further argue that such threats, in many cases, likely atrophied towards a less actively repulsive (e.g. aposematic) and possibly even more attractive (e.g. mating) intentionality when those primates (esp. in our lineage) became more secure with regard to predation.

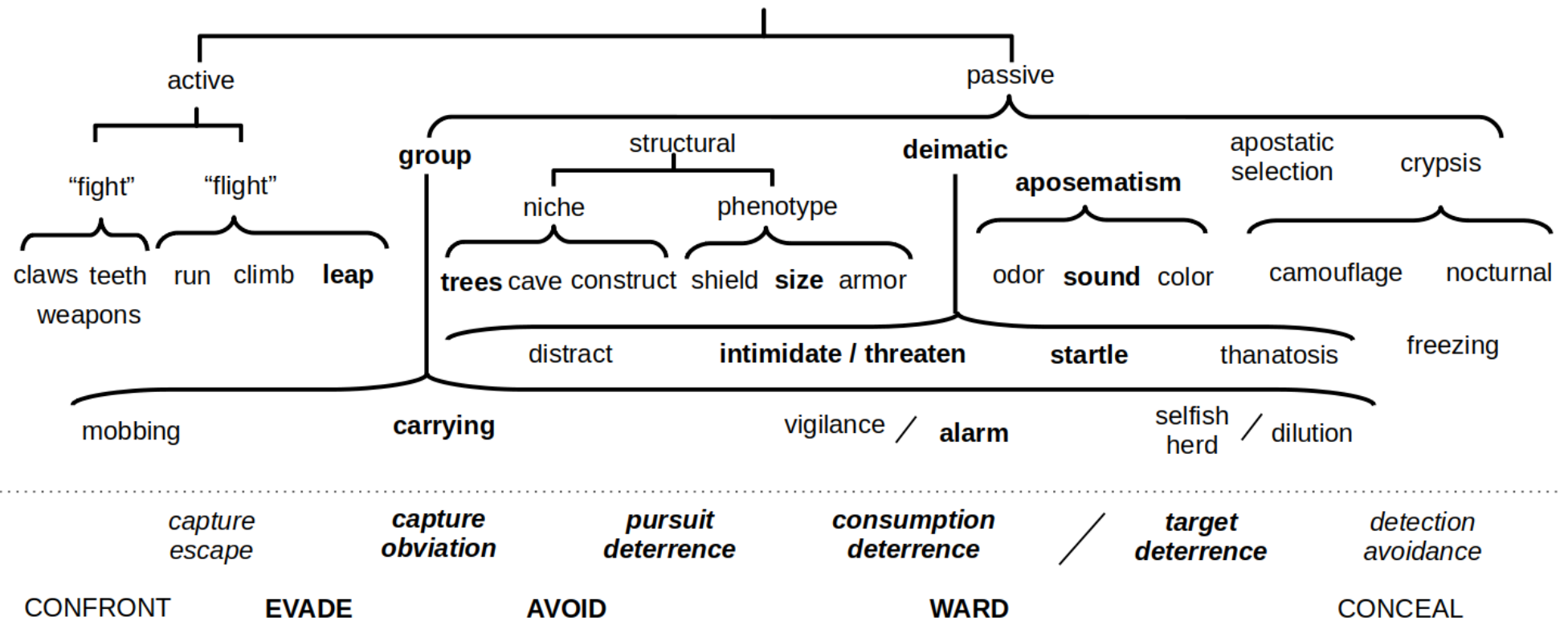


Figure 1. The many forms of anti-predational behavior can be organized into the above diagram according to related strategies—broadly partitioned into a dichotomy of passive (right) or active (left). These more exigent behaviors can be further split into fight or flight (far left) whereby prey actively counter predators by fighting back or fleeing evasively. On the far opposite extreme (far right), potential prey will conceal themselves and avert detection entirely via a variety of means, including crypsis, masquerade, mimicry, or freezing. Aposematism, covered in a previous chapter (by Jordania), appears alongside less hidden defenses such as toxicity and deimatic strategies. This chapter focuses on the intermediate categories, such as ‘warding-off’ and avoidance, that lie between active and passive defenses. These prominently include group strategies, which range from active fighting in the form of mobbing or more passive herd-dependent strategies, as well as the use of motor faculties (e.g. climbing) and structure (e.g. trees) to avoid consumption by terrestrial predators. Carrying, in particular, is a socially facilitated capture-avoidance behavior that often leverages structure—both passively, via intrinsic morphology, and through movement, via extrinsic vehicles. A central point advanced here is that most primates employ these intermediate strategies—favoring evasion, avoidance, and warding of predators rather than either extremes of confrontation or concealment. This manner of capture obviation may have persisted, via phylogenetic inertia, into our hominin line—emboldening and diversifying both intra- and inter- group (as well as anti-predator) acoustics to serve in both attractive and repulsive capacities.

Crypsis, avoidance, masquerade, and alarm

Many smaller primates, including pottos, lorises, tarsiers, and many lemurs, are nocturnal and augment predation avoidance via crypsis (Gursky and Nekaris, 2007). However, primates primarily obviate consumption by occupying trees (see the next section on arboreal positioning). Larger, especially anthropoid, primates evolved socially-facilitated means of protecting themselves from predators, such as nest construction (e.g. apes) as well as vigilance and mobbing (e.g. monkeys). A continuum of warding behaviors—from deimatic (bluff) to (honest) aposematic signal—may stave off imminent confrontations, to varying degrees of success. Alarm acoustics, including both tonal and atonal calls, which are directed both towards the group or the predators themselves, can play a central part of these strategies (Zuberbühler, Jenny and Bshary, 1999). Thus, the danger of many forms of impending predation can induce an array of possible vocal responses in primates.

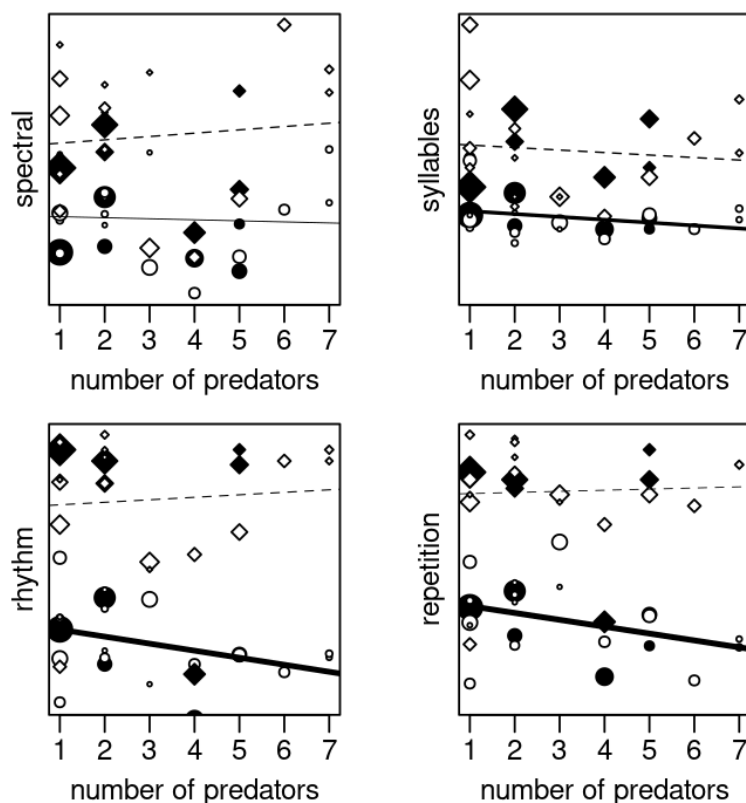
The acoustic features of such alarm-like calls have similarities with many other calls. And some group conflict related calls, may be more syllabic. But those explicitly related to predator presence tend to be more repetitive if not also more rhythmic—an observation also applicable to bird alarm calls (Templeton, Greene and Davis, 2005). Analysis using predator counts at the genus level (Miller and Treves, 2011), compared with various musical features, suggests primates become less vocal when sharing habitats with a greater diversity of predators (Fig 2). Conversely, as certain genera became more adept at inter-arboreal avoidance via specialized locomotion through trees, they may have also been emboldened to vocalize more saliently (Schruth and Jordania, 2020). This inversely associating trend is especially strong for repetition and rhythm (bold lines at bottom of Fig 2). Thus, for species who are threatened by numerous predators—and face a higher risk of being eaten—producing only a few generic anti-predator calls should not necessarily qualify them as being aposematically capable of inducing instinctive retreat (but see Jordania and also Alonso, this volume).

Arboreal apes likely co-evolved above large terrestrial felines, using the canopy to deftly move between trees (Isbell, 1994). And modestly vocal orangutans serve as possible exception to the general emboldening effect of arboreality, outlined above. Unlike gibbons who routinely employ more acrobatic locomotion to avoid consumption by tree climbing felines, more deliberate and often cryptic orangutans have developed capacities for nest building and a correspondingly mystifying “kiss-squeak” atonal alarm call (Lameira *et al.*, 2013). Vocally, such brevity and degraded tonality characterize the calls of orangutans, despite their larger size and composed seclusion. Gibbons, on the other hand, are highly vocal—creating long call sequences with high levels of rhythm and repetition (Geissmann, 2000). But even these lesser apes, whose near crepuscular songs can preempt and possibly even masquerade their [often] sympatric hornbill—which has calls similar in amplitude, frequency and accelerating tempo—subside in singing occurrence throughout the day. Thus even highly soniferous animals can exhibit a diversity of anti-predation behaviors daily. But with lesser apes, such masquerade arguably morphed into a partial feigning of flight capability.

Many other primates also employ such a vocally active role in deterring group-outsiders via generalized deimatic threats—those ambitiously directed towards competitors, predators, or both. The analysis reported here suggests that threatening contexts most often involves repetition and rhythm, and further, that mobbing confrontations are often preceded by such temporal patterning, especially if containing intervallic units. This association between repetition [of barks] and mobbing has not gone unnoticed in other animals (Lord, Feinstein and Coppinger, 2009). Thus, both mild deimatic threats and more active aggressions may be associated with temporal patterning of calls. But primarily only in the former case do (temporal) acoustic features appear to be directed at predators who contend for apically-adjacent trophic positions. Admittedly, disentangling the directionality of causal relations between predation threats and prey acoustics continues to be quite challenging.

An evolutionary progression, from small and quiet to the large and loud, should logically entail crypsis and silence from the very smallest primates. But we might also predict that more vocal, mid-sized primates, who auditorially expose themselves to a greater number of possible predators, would produce vigorous yet generalized deimatic alarm and threat calls. Likewise, we would expect the largest and least easily consumed species, who face the fewest predators, to produce more passive aposematic signals. It is important to note that the difference between deimatic and aposematic largely lies in whether the targeted prey is eventually eaten (Bates and Fenton, 1990). More evolved aposematic signals may require higher specificity—matching certain call types directly and individually to each specific predator. In turn, it is likely also, that most predator directed calls (e.g. of mid-sized primates) initially evolved as generic cues (e.g. of exaggerated size) designed to startle or intimidate a wider array of predator classes. This latter case allows for only a generalized approach to acoustic defenses against predators, and it would occasionally fail to work in all cases. In sum, generalists with many different types of predators (e.g. monkeys) likely evolved a small set of more generalized deimatic calls, whereas species with fewer predators (e.g. apes) might be more efficiently aposematic with an even smaller set of extra-species calls, corresponding to their smaller pool of predators.

Figure 2. Duetting tarsiers and gibbons, who are primarily preyed upon by very few predators (e.g. pythons and leopards), appear in the upper left of most of these plots. Terrestrial (filled points) monkeys, such as vervets and even highly arboreal (open points) but smaller New World monkeys, use exceptional calls (max: dashed lines) to voice alarm for many sources of predation. Although terrestrial taxa face a nearly two-fold higher predation risk and greater “silencing” [less vocally obvious upon grounding] (Schruth & Jordania 2020), exceptions persist for larger-bodied and collectively-acting primates such as hominids and many Old World monkeys. The two strongest trends (thicker lines) are decidedly downward for mean (circles) temporal patterning, but maximum (diamonds) may have positive associations, though not significant (thinner lines) here.



Arboreal positioning and intra-group calling

Primates have specialized as an order to avoid predation by climbing and leaping—moving throughout and between arboreal topological vantage points (Le Gros Clark, 1959). Their clawless and flexible embrace, enabled by use of an opposable thumb, allows not only more comfortable orthograde carrying but also the ability to grip a wide range of branch shapes and orientations. Large primates are capable of impressive inter-arboreal leaping (Druelle *et al.*, 2020) and can also produce salient loud-calls (Wich and Nunn, 2002), although those of leaf monkeys tend to be less elaborately exhibitional than the highly syllabic calls of similarly-sized (yet more acrobatic) gibbons. The difference could result from the many-fold greater number of predators that typically prey upon these leaf-monkeys than exist as threats to gibbons.

Acoustically, strictly arboreal primates prefer to use shorter more subtly-melodic transpositional calls to communicate between group members (Schruth, Templeton and Holman, 2021), without attracting unwanted attention by external threats. In the avian acoustics literature, this phenomenon of predators detecting conspecific-directed calls of their prey, is termed “eavesdropping.” Eavesdropping typically focuses on the coevolutionary arms race between prey sounds and predator hearing (Zuk and Kolluru, 1998). Risk of predation may reduce amplitude of calls (Reichard and Anderson, 2015), shape spectral aspects of acoustic structure of such soft signals (Akçay *et al.*, 2015; Vargas-Castro, Sandoval and Searcy, 2017), drive them to ultrasonic ranges (Arch, 2008), or entirely silence the songs of species (Zuk, Rotenberry and Tinghitella, 2006). An arboreal-descent version of such exposure-based muting has been termed “terrestrial silencing,” and may act to reduce both call length and complexity across primates and possibly also other taxonomic clades (Schruth and Jordania, 2020).

Acoustics signals have helped to compensate for the loss of scent-based communication (Rogers and Kaplan, 1998), all while avoiding unwanted attention discussed above. In many animals, including primates, spectral display features may have co-evolved with locomotion by way of signaling aptitudes for motive emplacement (Schruth, 2021). Precise re-creation of song syllables likely served as intra-specific signals of cognition for pattern matching that could have, in branch landing species, also been useful in rapid visual gauging of distances for high impact grasping (Schruth *et al.*, 2020). As mentioned above, a pronounced contrast between gibbons and orangutans, who face similar predation threats, highlights the feasibility of this selection mechanism. Despite their larger size, orangutans are much less vocal than gibbons. Salient daily singing, by the latter, may not only reflect greater confidence in expedient inter-arboreal avoidance (e.g. to predators), but such vigorous recitation of diversely reappearing syllables may be an essential part of securing both range and mates, as signals amongst gibbons themselves.

Arboreal descent and terrestrial musicality in anthropoids

At some point, in our evolution from apes to humans, we can certainly surmise that our musicality became more complex and multi-faceted. While the most musical primates (e.g. gibbons, tarsiers, and indri) all frequently locomote using agile limb-landing in trees, humans are paradoxically not arboreal. Previous work on this subject speculated that this is because humans repurposed the motor-planning, homologous to the forelimb-dominant branch landing of other apes, for landing of ballistic devices in the hunting of terrestrial game (Schruth, 2005). More recent evidence, for possible connections with hominid hammering of stone, supports this hypothesis (Schruth *et al.*, 2020) through the positive associations of terrestrial hunting with both rhythmic and melodic aspects of the music of traditional human societies (Fig 3). Thus, it may not have been merely the shift to terrestriality that made *Homo* unique, but the associated freeing up of our forelimbs, to craft and deploy tools, which facilitated our trophic dominance over other terrestrial species. And such capacities for crafting and deploying remote weaponry vastly hastened our genus' selection towards a human-like transcendence of nearly all predation threats.

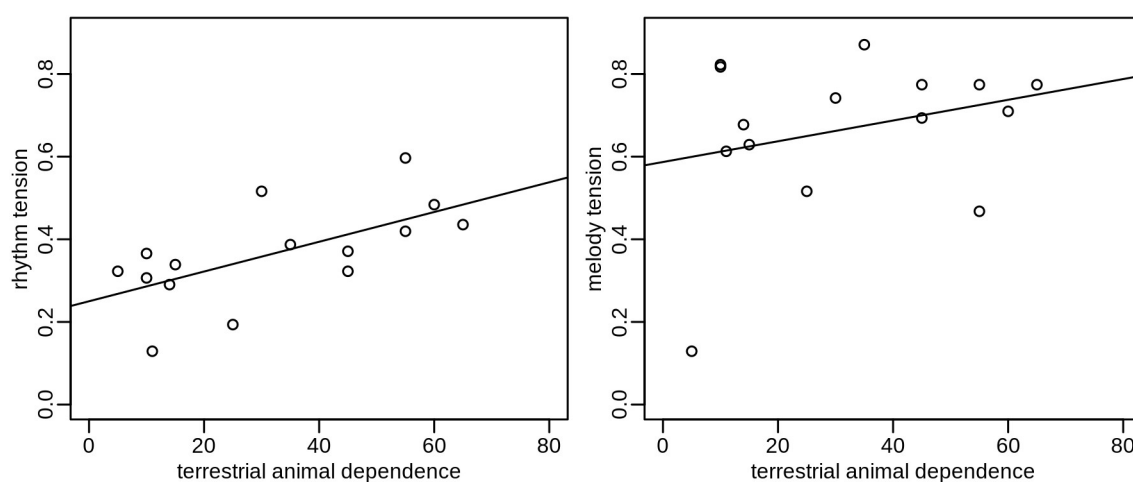


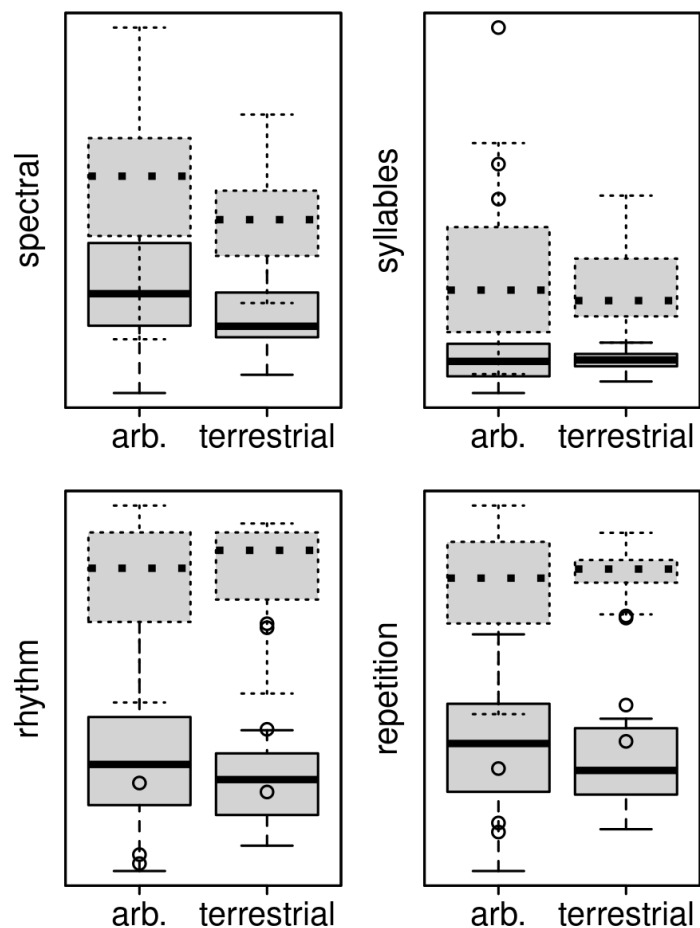
Figure 3. The significant positive associations between a *rhythmic* and *melodic* indexes (from the *Natural History of Song Database*) and degree of terrestrial hunting (from the *Binford Hunter-Gatherer Database*). Rhythmic display may signal collective action abilities useful, for example, in coordinated group hunting. Melodic display could signal precision spatial abilities required for crafting (and deploying) sharp weaponry (e.g. arrow heads) for use in ballistic attacks.

This shift towards increasing terrestriality also likely accompanied diminished forelimb use in hand-eye driven coordination, such as during climbing. Cognition for landing semi-vestigial limbs (those formerly used in more routine rhythmic climbing locomotion) could have been atavistically co-opted as part of an ornamental display signal. That is, as selection pressures on accuracy in forelimb climbing were reduced for increasingly terrestrial and occasionally bipedal primates, the lingering functionality of these limbs were reallocated towards other, perhaps reproductively focused, goals. Large terrestrial gorillas still deploy rapid chest-beating as possibly honest signals, perhaps of motor control for the occasional bout of arboreal clambering. Free arms, as merely accessory appendages (especially in the most visually imposing species), could have enabled other hind limb decoupled display—perhaps even “dancing”—in lemurs, birds, and humans (Schruth, 2022). Acoustic display in these species could also operate to signal motor skill also useful for climbing, carrying, or crafting.

As primates became larger and more capable of coordinating as a group, thus emboldening increasing levels of terrestriality (e.g. in many anthropoids), they also trended towards declining spectral patterning in their calls (Schruth, 2022). This is strongly evidenced by the degradation of spectral definition in the calls of many cercopithecoids (Schruth, 2020). A shift to terrestriality likely also required larger individual or group sizes, or both (Willems and Van Schaik, 2017). Likewise, arboreal species tend to have more spectral features for within-group alarm and contact calling whereas terrestrial species tend to have more complex rhythms, possibly for extra-group threats (Fig 4). A combination of arboreal sleeping and terrestrial ballistics, protective against most predation by large terrestrial carnivora, likely elevated higher trophic standing by further reducing risks of attack from the rear or oblique angles (see also Fig 2). The calls of species with elevated trophic standing in complex and disconnected (e.g. arboreal) habitats reflect this difference in priority for anterior targeting over peripheral vigilance.

This shift towards terrestriality has been characterized previously as a tree-to-ground [sleep or nest] transition (Coolidge and Wynn, 2006; Samson and Nunn, 2015) and likely occurred gradually over millions of years in the late Pliocene (also see Wah, this volume). A handful of key ecological factors associated with hominin life on the ground likely molded ancestral hominid behavior into a fully human form—including low temperature and light conditions as well as evening fatigue, anonymity, predation risks (Varella, 2023) and group cooking (Wrangham, 2009). These more recent (mid-Pleistocene) pressures, associated with nightfall over more open habitats, were alleviated by new forms of evening sociality empowered by the invention of fire—such as eating, singing, dancing, storytelling, and associated rituals (Varella, 2023). The central focus of this chapter explores a preexisting duality of *habitat*—both arboreal and terrestrial—of early hominins that existed several millions of years ago. Any related ideas on *finalizing* our human terrestriality through the controlled use of fire (<1MYA) only serve to complement those proposed here on *initializing* such a transition. And both certainly had profound effects on the structure and dynamics of groups.

Figure 4. Spectral, but not rhythmic, musicality tends to decrease upon transition to terrestrial habitats. Only maximum (dashed) temporal aesthetics (e.g. *repetition* and *rhythm*) appear to increase in terrestrial species. The slight increase in *rhythm* is further accentuated after considering both body mass and climbing frequency. Four macaques, three great apes, and *Lemur catta* (top-most diamonds in Fig 5) primarily drive higher maximum *rhythm* scores here.

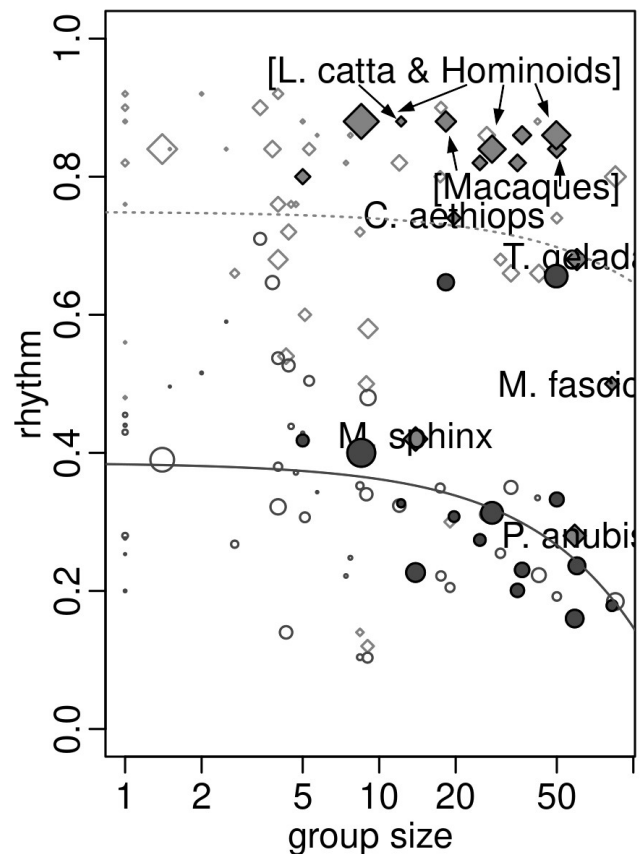


Group functionality of acoustic musicality

Music has been observed to elicit attractive as well as repulsive emotions (Nielzen and Cesarec, 1982) and could have evolved to facilitate group dynamics (Hagen and Bryant, 2003). This dichotomy is also observable across the animal kingdom with calls that can range from affiliative to threatening (Orwen and Rendall, 2001). Intra-group calls can help members localize conspecifics, orient and reunite with one-another, and help warn of impending danger (Arnold, Pohlner and Zuberbühler, 2008). Extra-group calls may help to advertise size, muscular agility (Schruth *et al.*, 2020), as well as to let predators know they have been detected (Zuberbühler, Jenny and Bshary, 1999). A class of calls that span both of these categories includes mobbing calls—that simultaneously serve as alarm, threat, and battle cry—to facilitate rounding up group members to collectively stave off an attack from predators or other groups.

Hominins likely experienced profound social and musical changes that coincided with walking. Bipedal pressures on modern hips selected for more compact brains and also more altricial offspring but therefore also improved social [mother-infant] bonding (Dissanayake, 1992). In humans, rhythm has been hypothesized to serve as a possible catalytic vehicle for inviting in new members into the group and perhaps to facilitate making music collectively (Savage *et al.*, 2021). Accommodation for additional group-display participants (in very small groups) seems to be slightly higher for rhythm than any other forms of musical patterning (Schruth, 2022), but may also serve in a less welcoming extra-group directed capacity (Hagen and Bryant, 2003). Humans are unusual in our extreme use of rhythmic musicality, perhaps due to our unique bipedality (Mithen, 2006) or groupishness (Brown, 2000). Evidence from the vocalizations of a larger swath of primate species suggests that larger group sizes tend to be less rhythmic overall (Schruth, 2022), hampering the plausibility of its use in coordinating large groups. However, the fact that larger bodied species from more sizable [and usually terrestrial] groups also tend to exhibit at least one highly rhythmic call (top of Fig 5), supports rhythm as serving in a more directly threatening capacity across primates (also see Fitch, this volume).

Figure 5. Group size correlates inversely with rhythmicity across primate species. Scores of the most (diamonds) and average of (circles) rhythmic calls highlight a negative correlation across the order—excepting larger bodied terrestrial forms (top) which have higher $\max(\text{rhythm})$. Circles are scaled by *body mass* and filled according to *terrestriality*. The exceptional *Papio anubis* (lowest diamond) climbs the least (<3%) of any primate here except the Japanese [island protected] *M. fuscata* (near top).



Size and extra-group signaling allometry

Recent work using allometric analysis, or the study of changes in the sizes of isolated traits in relation to [usually] overall body sizes across species, has delved into interpretation of the differences between these associations—assessed through their regression slopes. For example many exaggerated traits lie along an ornament vs weapon continuum (Kodric-Brown, Sibly and Brown, 2006) whereby steeper slopes correspond to sexually selected ornaments and shallower ones correspond to weaponry. The former corresponds to within species signals and the latter may further extend to signals out of the group, perhaps including predators. If we extrapolate this reasoning to non-morphological traits (e.g. life history, <1:1 allometry), we might expect even shallower slopes (e.g. syllable and rhythm in Fig 6). Since such acoustic features (e.g. of human musicality) are not typically compared outside our order, we may only speculate here that the down-shift in allometric steepness between syllabic and rhythmic patterning might parallel the down-shift from ornamental to weaponized functionality for morphological traits (Fig 6). This only mildly positively associated trend of rhythm with body size passably supports the deimatic hypothesis introduced above. But the decisively positive slope of syllable could also admittedly be interpreted as validating both hypotheses involving sexual choice for ornamental intelligence (Miller, 2000) and those for musicality as a linguistic precursor (Brown, 2000; Bryant, 2014).

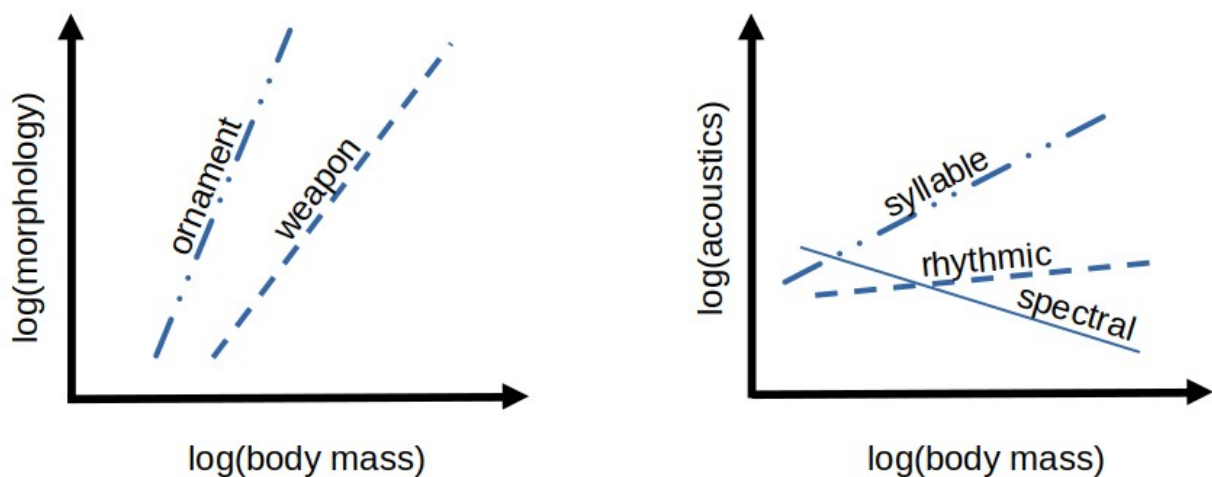


Figure 6. Allometric slopes are steeper for ornaments (dashes+dots) compared with shallower ones for weaponry (dashes) for most morphologies (Kodric-Brown, 2006). By behavioral analogy we might surmise a parallel functionality for the different slopes of primate acoustic data (right). Here syllable may approximate ornament whereas rhythm may be more weapon like. The extremely shallow slope of rhythm implies that there is only very little (size-based) honesty backing the increasing levels of rhythm, though it could proxy associated group-coordination effects. Spectral features (thin, downward-sloping line) have negative allometry with body size, suggesting an intra-group communication functionality in the face of numerous predators. An extension of the deimatic hypothesis suggests that actively functional [anti-predator] threats may act as weaponry—while more passive, exaggerated, or seemingly vestigial traits could act as aposematic signals.

Postitional and musical diversity in transitional hominins

The transition from [fully] arboreal to [partially] terrestrial life likely spanned millions of years leading up to the Pleistocene (Reed, 1997). The continued use of daily climbing is evidenced by Pliocene fossil remains of the semi-arboreal genera of *Ardipithecus* and *Australopithecus* (Kozma *et al.*, 2018). And hunting of terrestrial prey could have co-opted the limb landing abilities of our common ape ancestors who were not incapable of suspensory swinging (Schruth and Jordania, 2020). But increasing temperatures and the reduction of body fur likely complicated the handling of increasingly large-brained and altricial (but instinctively clinging) infants (Stanley, 1992). Further extension into obligate terrestriality may have fully freed up the forelimbs of hunters to allow for specialized dispatching of remote ballistics, perhaps as a primary means of subsistence. As human infants remained altricial and human walking expanded into more rapid and precarious forms of bipedality, spatial aptitudes for groundward-directed single-limb emplacement on unpredictable terrain (e.g. mangrove roots) necessarily proliferated. In sum, the spectral acoustic displays of apes likely perpetuated in modern humans as signals of limb landing ability. Such selection for landing adjustments in hominins likely manifested as both fore and hind limb accuracy—in both crafting and deployment of ballistic hunting tools as well as for onerous carrying of fragile payloads in bipedal locomotion generally.

A newfound stability in terrestrial life by hominins coincided with a reversal of the predator-prey relationship—between these primates and the terrestrial threats that had originally motivated arboreality in previous epochs. These audacious acts against ground predators must have eventually morphed into proactively hunting them for food. And by usurping the dominance of large cats, hominins consequently inherited an apical position over their terrestrial food chains. But long before they worked collectively in groups for terrestrial *offense*, team hunting may have been preceded by millions of years of coordinated *defense*, for example in warding terrestrial predators (e.g. hyenas) away from arboreal kills and sleeping trees. Large African felines appear to have since developed aversions to any resemblance of bipedal hominins, especially when they stand tall (see Blake, this volume). Thus, any such coordination for targeting outsider threats in increasingly bipedal groups—initially used defensively, by semi-arboreal hominins, for scaring-off predators—may have eventually evolved into a more coordinated and ritualistic (therefore human like) acoustic orchestration.

But, as evidenced from other primates, a rising rhythmicity and possibly declining intervallic virtuosity could have also foreshadowed the decline of singing in terrestrial humans towards only a more episodic and ornamental occurrence. These temporal bookends, from known fossils to modern human societies, also suggest an intermediate evolution through hominins who were terrestrially social but also retained a lingering arboreality. For example, even many modern human societies are known to still climb trees regularly to obtain high energy food items, such as honey (Kraft, 2014). A daily circadian cycle of security, both in trees at night and in groups by day, may have been echoed by an equally great diversity of moods and forms of musicality. In short, our unrivaled panoply of musical complexity, composed of both affiliative melodies and warding rhythms, were likely selected by the numerous daily contrasts in positional, predational, social, spatial, and sensory proximity.

Conclusion

Primates can respond to predation pressure in five categorical ways: concealment, evasion, avoidance, confrontation, and warding. Concealment, of both visual and auditory cues, is a strategy typically employed by smaller and nocturnal primates who face numerous predation threats. Evasion can be a regular option for more solitary living primates who may also be diurnal and therefore more easily spotted by predators. Primates primarily leverage trees to evade most predators—climbing them to avoid terrestrial ones and vaulting between them to avoid the climbing ones. Both of these forms of anti-predation strategy are not typically compatible with highly salient vocal output. Instead these species, ranging from mouse lemurs to sifakas, may only produce close calls that are short and atonal or more patterned tonal calls that are hidden from predators in ultra-sonic frequency ranges.

Primates primarily leverage arboreality to not only assist with evasion, but to also avoid becoming prey over the long-term. For this strategy to work, primates must habitually avoid eavesdropping by potential predators. This may require frequently deploying shorter, more subtly melodic phrases to attract group members, with only the occasional (and typically temporally patterned) loud calls to signal alarm in emergencies. A greater diversity of alarm calling, perhaps with higher specificity to individual forms of predation, tends to occur in mid-sized primates. Calls with more intervallic content, especially those produced by arboreal forms living in larger groups, can even serve to exacerbate confrontation in the form of mobbing. Rhythmicity, on the other hand, has a strongly inverse association with group size and predational diversity, despite the fact that larger individuals produce more rhythmic (than other forms of) musicality.

In our more recent ancestry, highly salient extra-group directed (especially rhythmic) sounds could have also been used in preventative repulsion—to ward-off external threats (Fig 1, center-right) with potentially sacrificially intimidating mechanisms (see Wade, this volume). In hominins, such sounding was likely enhanced artificially with percussive instruments to impart a sense of larger, more rapid, more numerous, and perhaps more formidable targets (see Brown, this volume). But, like the salient acoustics of primates generally, the calls with the greatest diversity of spectral contouring are assertable by those possessing high levels of trophic security—notably in (other) species who have so few natural predators, such as tarsiers, gibbons, and indri. In such rare cases, increasingly vestigial alarm calling could have instead been repurposed as salient displays.

This alternative morphing into only mildly confrontational threats may have acted to passively ward off any lingering predators that still competed for top positions in local food webs. Thus, the more active and vociferous alarm calls of apical species conceivably morphed into increasingly passive and ritualistic usage as these species, such as hominins, began to approach trophic invulnerability, in spite of potentially smaller individual body masses. This subtle shift in acoustic warding, from deimatic alarm to aposematic signal, may have honestly reflected more subtle cognition-facilitated abilities of (inter-substrate and inter-personal) coordination with trees and groups rather than more obvious physiological attributes of individuals.

Lastly, a lingering diversity in positional security—manifesting daily as both protected arboreality and vulnerable terrestriality—may have given rise to our uniquely diverse musicality, which evolved over the multi-million year transition from the trees to the ground. That is, primates' exhibition of a variety of different vocal behaviors, ranging from silence to loud calls, corresponds to various anti-predational strategies, ranging from crypsis to confrontation. And likewise, transitional hominins, who likely exhibited a wide range of vulnerably related to extreme daily positional flux, may have spawned an even broader range of musical expression that was integrally melodic and rhythmic alike.

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