

The role of trophic security and arboreal descent in the evolution of complex acoustic display

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ABSTRACT

Animals create salient acoustic displays as a conflict avoidant way to secure mates or territory. Non-scentmarking anthropoids, for example, can use spectrally-rich signals to efficiently relay location, identity, condition, emotion, and intentions across distances separating callers. Arboreal primates, who are not usually the largest animals in a given geographic area, will signal from protected vantage points so as to not also attract terrestrial predators. Such a trophic security strategy can also involve natively protected increases in size or inter-substrate locomotion as added means of predator deterrence and avoidance. Recent work highlights acoustical associations with certain discontinuous forms of locomotion (e.g. leaping) in arboreal strategies that successfully avoid scent-stalking. I investigated sensory, habitat, morphological, ecological, and locomotor factors of primate life as driving complex acoustic display. While melodic display did associate with arboreal acrobatics, complex rhythmic display surprisingly appears more often in bipedally-capable terrestrial lineages (e.g. gorillas and some lemurs). This suggests that rhythmic complexity may emerge in exceptionally trophic-secure species with semi-vestigial limbs formerly used in more routine rhythmic locomotion. Thus, hindlimb-decoupled forelimb displays such as chest-beating in gorillas or dancing in humans could derive from a freeing-up of these accessory appendages, which support only occasional climbing, carrying, or tool use. In humans, the threat of weaponized forelimb tools may have further allowed for canine atrophy and extended terrestriality. Such stable grounding undoubtedly emboldened more aggressive hunting and audacious dancing practices in tandem with an evolution towards acoustic displays in larger groups with specialized singers and instrumental musicians.

INTRODUCTION

Communication: Animals leverage a variety of media to communicate both within and between species. Some combination of auditory, visual, and olfactory modalities are used to facilitate the fundamental functions of such communication. Scent-marking is a primary way mammals relay chemical odorants—by deliberately rubbing parts of their body against (e.g. inanimate or vegetative) objects in their environment—to communicate between individuals and species. Non-anthropoid primates (and many monkeys) are known to use ano-genital rubbing, not only for self-cleaning but also for scent-marking as communication, in order to assert dominance or advertise estrus (Scordato and Drea, 2007). Pheromones (aromatic hormone molecules) can be detected at close distances by other sympatric organisms to determine the identity and condition of neighbors, establish territories, and avoid costly conflicts. But in primates, an arboreality-driven reduction in olfaction may have alternatively given rise to more complex calling (Schruth, 2021).

Acoustic Signaling: Most mammals also produce vocalizations by forcing air through constricted respiratory tracts (e.g. vocal folds) to create wave patterns through compression and rarefaction of gas molecules. These modifications of ambient air can vary in frequency [molecular vibration rate], amplitude [degree of pressure fluctuation], spectral patterning (e.g. transposition, interval), temporal patterning (e.g. repetition, rhythm), and occurrence [rate of calling over time] (Fischer, Noser and Hammerschmidt, 2013). Most often, these vocalizations are utilized by conspecifics to determine location and identity of callers (Rogers and Kaplan, 2002). Additional information such as condition, emotion, and intentions of callers can also be extracted from more complex calls (Seyfarth and Cheney, 2006). Such elaborate display calls, like long or loud calls of many male primates, can be used to attract mates or establish and defend foraging territory (Wich and Nunn, 2002). Interestingly, most musical calls of vertebrates are not typically produced by carnivores and instead tend to be deployed by species that are largely able to avoid such predation, given their size (Schruth and Jordania, 2020). These calls may even advertise perception to stalking predators (Zuberbühler, Jenny and Bshary, 1999).

Trophic Security: Ecosystems consist of complex networks of interconnected food chains composed of species sharing overlapping geographic ranges. Organismal dominance can theoretically be assessed merely via abundance of certain species in a particular community of many species, but can be much more difficult to measure in practice. Species with larger body size, group numbers, or vertical positioning can gain leverage, in the form of trophic security, over other organisms in order to produce more offspring [r] or increase gestation lengths and lengthen lifespans [k]. In primates, who typically use trees as protection to augment trophic standing, possess the latter two but not the former manifestations of such security. Instead, (k -selected) primates have lower parity and associated slower weaning durations (Jones, 2011), as a result of using trees to mitigate predation. Such forms of ‘naturally security’ entail protections for offspring through some combination of defense, scouting, and provisioning (Schruth, 2022). Since many terrestrial predators can climb trees to pursue and corner arboreal residents at these dead-ends, many arboreal primates have alternatively evolved means of positional avoidance that employ discontinuous, inter-substrate, and inter-tree locomotion.

Hypotheses: I proposed that species (of primates) use sophisticated patterning in their vocal displays as a part of signaling high levels of security in their trophic position. Thus many security enabling means of avoiding or deterring predation (including including size, stature, agility, and ballistics) should correlate with measures of musicality.

METHODS

I collected data on 58 extant primate species including spectrograms starting with over 300 different leads in the primary literature on vocal behavior. Five student scorers were first trained using examples of human music universals—*tone*, *interval*, *syllable*, *rhythm*, *repetition*, and *transposition* (Nettl, 1983; Brown and Jordania, 2013)—that were observable in a panel of bird call examples. A total of 829 primate vocalizations (from 1297 spectrograms) were scored blindly for presence of each of the above six acoustic features. I used principal components analysis on these to inform construction of a measure of manifest musicality—as ARDI, the acoustic reappearance diversity index—which was used along with *syllable count*, *song count*, and “*tension*” to assess (quality of) musical output. Information on each of these primate species was also collected including body mass, group size, arboreality, infant carrying, as well as leaping and swinging frequency. I also incorporated data from the Binford hunter-gatherer dataset (Binford, 1962) and the Natural History of Song database (Mehr, 2018). Data on birds were collated from Cornell’s ornithology website (‘All About Birds’, 2015). All of these forms of musical output were compared with security and habitat relevant variables (e.g. size, range, arboreality, carrying, locomotor agility).

RESULTS

Several forms of trophic security correlated positively with measures of acoustic patterning: including body mass (*rhythmic* & *tonal* ARDI variants), arboreality (spectral features), acrobatic locomotion (all ARDI variants), and ventral infant carrying (*intervalic* ARDI). Melodic display did associate with agile locomotion, but more complex temporal display tends to primarily appear more frequently only in terrestrial species (e.g. gorilla and some lemurs)—those capable of bipedal locomotion. Nearly all musical feature scores dropped for terrestrial species, with the exception of temporal ones, such as *rhythm* which has a slight increase (Fig. 1). A correlation between group size and rhythmicity, however, associated significantly negatively across primates (Fig. 2). But species exhibiting a display call, at least one, with highly rhythmic quality, appears to be the ancestral state for all primates (Fig. 3). Gibbons, while exhibiting higher *rhythm* on average, have a lower maximum score for rhythmicity than other apes. A disproportionate five of the top fifteen most rhythmic [display] callers, including *Lemur catta*, gorillas, chimps, and two macaque species, are also habitually terrestrial (Schruth, 2022). Also exceptionally, slightly more numerous groups (4 to 7 individuals), appear to exhibit slightly higher than expected rhythmicity across typical calls (highest blue circles in Fig. 2). Expanding to observations on human musicality, both *melodic* and *rhythmic tension* had significantly positive correlations with terrestrial hunting (Fig. 4).

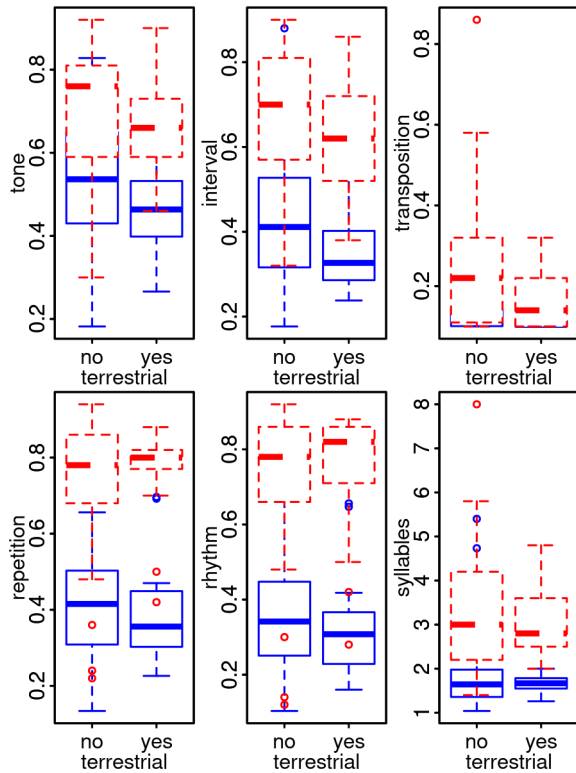


Figure 1. Spectral, but not rhythmic, musicality tends to decrease upon transition to terrestrial habitats. Only maximum (red dashed) temporal aesthetics (e.g. *repetition* and *rhythm*) appear to increase in terrestrial species. The slight increase in *rhythm* is further accentuated after considering both body mass and climbing frequency. Four macaques, three great apes, and *Lemur catta* (top-most red diamonds in Fig. 2) primarily drive higher maximum *rhythm* scores here.

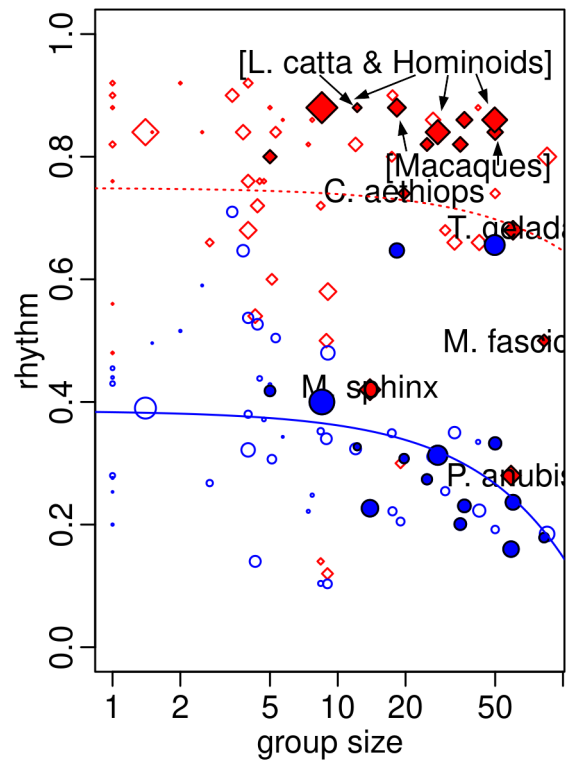


Figure 2. Group size correlates inversely with rhythmicity across primate species. Scores of the most (red diamonds) and average of (blue circles) rhythmic calls highlight a negative correlation across the order—excepting larger bodied terrestrial forms (top) which have higher max(*rhythm*). Circles are scaled by *body mass* and filled according to *terrestriality*. The exceptional *Papio anubis* (lowest red point) climbs the least (<3%) of any primate here except the Japanese [island protected] *M. fuscata* (near top).

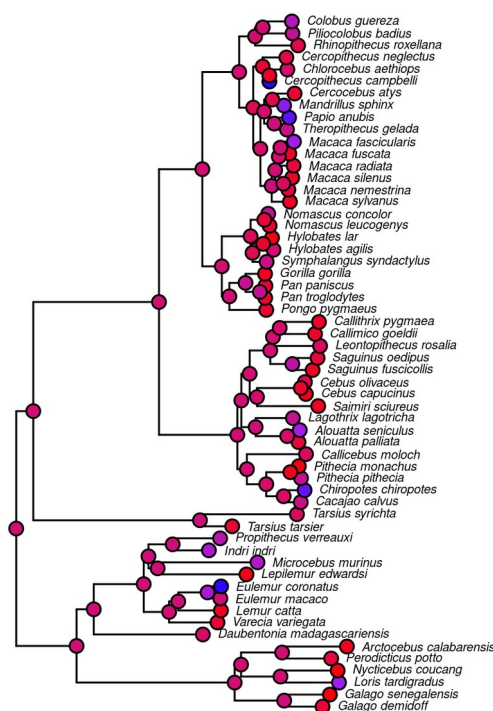


Figure 3 (left). Phylogenetic tree of maximum rhythmic call. Tips (extant species), and internal (ancestral) nodes are colored by actual and predicted values (respectively), with hotter colors indicating higher scores. Ancestral *rhythm* for apes was 0.5, as per ACE-REML in R's 'ape.'

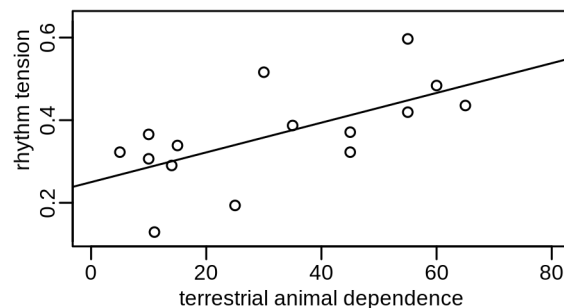


Figure 4. The significant positive association between this *rhythm* metric (from the *Natural History of Song Database*) and degree of terrestrial hunting (from the *Binford Hunter-Gatherer Database*). Rhythmic display may signal collective action abilities useful, for example, in coordinated group hunting or tactical ballistics.

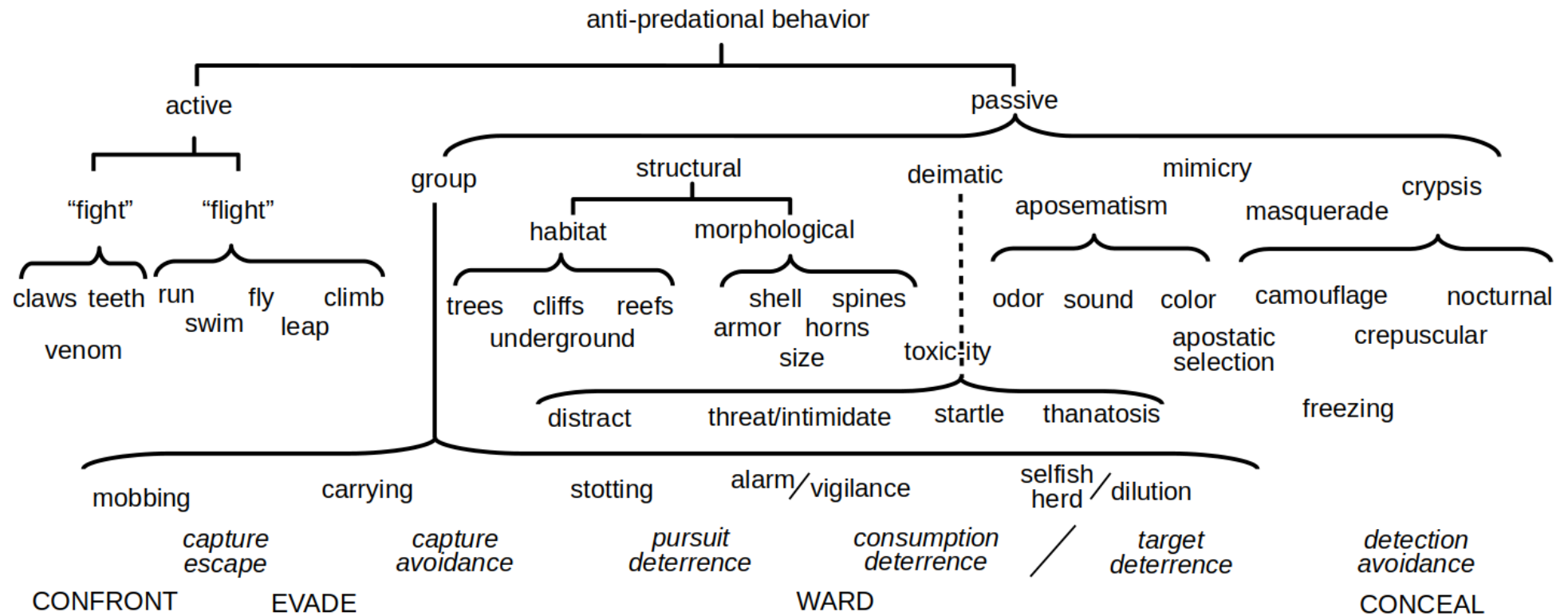


Figure 5. A number of anti-predational behaviors that animals may employ can be organized into the above taxonomy of related phenomena broadly partitioned into the artificial dichotomy of active (left) vs passive (right). Active, or emergency, behaviors can further be partitioned into fight or flight (far left) whereby prey actively confront predators by fighting back or evasive fleeing. On the far opposite extreme potential prey may opt to conceal themselves by avoiding detection entirely via a variety of means, including crypsis, masquerade, mimicry, apostatic selection, or freezing. Aposematism, covered in previous chapters (by Jordania) appears alongside less hidden defenses such as toxicity and deimatic strategies. This chapter covers the middle-zone of warding-off that lies between active and passive defenses. These prominently includes 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 [small] group capture inter-generational avoidance behavior that often uses structural rather than also employs morphological passive defenses. The central point of this chapter is that primates typically employ a unique (non-confrontational and yet also non-concealment) combination through evasion, avoidance, and warding of predators—providing deep phylogenetic inertia persisting to hominins—influencing both a emboldenment and diversity of both intra- and inter- group (as well as also anti-predator) acoustics for attractive and repulsive functions respectively.

DISCUSSION

Primates: Spectral display features, as detected by ARDI, seem to have coevolved with locomotion by way of signaling aptitudes for gap-spanning maneuvers. Primarily, these signals help compensate for the loss of scent-based communication, while louder (and more rhythmic) outbursts are typically only possible due to predation-avoidance endowed movements. High fidelity regeneration of well-defined spectral features (e.g. syllables) may serve as intra-specific signals of cognition for pattern matching (e.g. during learning and performance) that could also be useful in visual depth perception for high speed arboreally landed locomotion (Schruth *et al.*, 2020). As primates became larger and more capable of coordinating as a group, thus emboldening increasing levels of terrestriality (especially in anthropoids), they also trended towards a decline of spectrally patterned features in their calls. Diminished forelimb use in hand-eye driven coordination while climbing likely accompanied a shift towards increasing terrestriality. It is possible that cognition for landing such semi-vestigial limbs, formerly used in more routine rhythmic climbing locomotion, was instead atavistically co-opted for use in acoustic display. Fully terrestrial gorillas, largely secure in their size, may still employ a rapid staccato of chest-beating as an honest signal of motor control used in (rare instances of) a clambering-based escape. Liberation of the arms as accessory appendages also enabled other hindlimb-decoupled exhibitions—in the form of “dancing”—in some lemurs, many birds, and most humans. Acoustic display in these species may operate as signals in indicating motoric proficiency for climbing, tool use, or onerous carrying.

Humans: Extensive infant carrying over the half a dozen epochs of primate evolution likely reduced sharp claws into blunt nails (Schruth, 2014). Similarly, as hominins began adapting to the more open habitats of the late Pliocene, some combination of reduced intra-group aggression and expanded deployment of pointed or bladed weapons for self-defense may have atrophied dependence on canine teeth for fighting (Mamak, 1972). Further extension into obligate terrestriality may have fully freed up the forelimbs to become specialized dispatchers of remote ballistics 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 could have proliferated. Thus, exceptional spectral complexity of acoustic displays could have been retained as signals—not only for ballistic hunting roles but also for complex hind-limb targeting in infant-laden duties as well. Such stable ground-dwelling by hominins undoubtedly coincided with more audacious hunting and dancing in groups capable of sophisticated musical performance—characterized by spectrally specialized singers and rhythmic-instrumental accompaniment. But a rising rhythmicity and possibly declining intervalic virtuosity may have foreshadowed the decline of singing in terrestrial humans towards only a more episodic and ornamental occurrence. These habitual endpoints also imply an evolution through intermediate forms as semi-arboreal but pro-social hominins, thriving both through collective group action by day and familial security in the trees at night. This daily cycle and diversity of positional contexts, both in relation to individual locomotion and the larger group, may have spawned an equally great diversity of moods and forms of musicality corresponding to the many possible gradations of predational, social, spatial, and sensory proximity.

Across primates, I have provided strong evidence of a general decline in rhythmicity as a function of increasing group size, body size is still has considerable association with tonal and rhythmic musicality. While more melodic forms of acoustic musicality may have had more intimate and attractive “aesthetic charms” (see Fitch) perhaps signaling secure inter-arboreality—advertising an ability to avoid capture entirely (Figure 5 center-left). More salient, extra-group directed acoustics, in humans, could have been used repulsively—to ward-off external threats (Fig 5 center-right) with potentially sacrificially (see Brown) intimidating sounds, perhaps with artificially deep percussive-instrumental tones to deceptively impart a sense of larger, rapid, and more numerous targets.

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