Chapter 14
Function of Loud Calls in Howler Monkeys

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Abstract Beyond the unique sound of howler monkey vocalizations, their vigorous loud calling displays are perplexing given the otherwise sedentary lifestyle of these primates. Here we provide potential explanations for this energetic investment by reviewing all available functional studies conducted to date. We highlight the variation among and even within species when we explore whether male loud calls are used in group cohesion, predator avoidance, attraction of females, or competition with other males or other groups over resources. In the competition scenario, we examine strategies of avoidance versus direct competition and whether contests are focused on defense of space, food, mates, or infants. We suggest that much of the debate surrounding the function of loud calls stems from methodological differences among researchers and from the varied levels of analyses used, although we also demonstrate that studies of form and function can be intertwined. We emphasize the need to examine different call types separately and discuss the role of howling in intragroup male relationships. Finally, we address the understudied role of female loud calling and the potential use of hybrid populations to examine the evolution of species-typical loud calls. We conclude with some practical hints for designing field tests to uncover functional significance.

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Resumen Más allá del sonido único de las vocalizaciones de los monos aulladores, estos vigorosos despliegues nos dejan perplejos, dado el sedentario estilo de vida de estos primates. En este capítulo damos explicaciones potenciales a esta inversión de energía, a través de una revisión de los estudios funcionales llevados a cabo hasta la fecha. Remarcamos la variación entre y dentro de las especies cuando exploramos si los aullidos de los machos son utilizados en la cohesión de grupo, evasión de predadores, atracción de hembras o competencia. Sobre este último escenario, examinamos las estrategias de evasión versus la competencia directa y exploramos si la competencia se focaliza en la defensa del espacio, la comida, las parejas o los infantes. Sugerimos que gran parte del debate sobre la función de las vocalizaciones de larga distancia radica en diferencias metodológicas entre investigadores, así como en la variedad de niveles de análisis utilizados, aunque también demostramos que los estudios de forma y función pueden estar entrelazados. Enfatizamos la necesidad de examinar diferentes tipos de llamados separadamente y discutimos el papel de los aullidos en las relaciones intragrupales entre machos. Finalmente, abarcamos el escasamente estudiado papel de las vocalizaciones de larga distancia emitidas por las hembras y la potencial utilización de poblaciones de híbridos para examinar la evolución de las vocalizaciones de larga distancia, típicos de cada especie. Concluimos con consejos prácticos para el diseño de estudios en el campo que permitan descubrir significados funcionales.

Keywords Bark • Mate defense • Infanticide • Resource defense • Resource holding potential • Roar

Abbreviations

%	Percent
>	Greater than
A.	Alouatta
e.g.	For example
i.e.	In other words
kHz	Kilohertz
MA	Massachusetts
Min	Minutes
NY	New York
P.	Pan
pers. obs.	Personal observation
RHP	Resource holding potential
TFT	Tit-for-Tat
UK	United Kingdom
unpubl. data	Unpublished data

14.1 Introduction: Why Howl?

Howler monkeys are unique among the platyrrhines in their complex, loud, long, low-frequency calls (Moynihan 1967; Snowdon 1989). In da Cunha et al. (2015, this volume), we reviewed studies that highlight the acoustic and morphological features that make howler monkeys and their calls unique and the environmental influences on propagation of their sounds. But, a question remains: why should an animal that allots most of its activity budget to inactivity (likely due to the lack of ready energy available from its largely folivorous diet: Milton 1980) invest so much time and effort into loud calling?

Loud calls are ubiquitous in the animal kingdom—occurring in species as distinct as frogs (e.g., Gerhardt 1974; Bee et al. 2000) and whales (e.g., Širović et al. 2007)—and they have always generated an amount of interest proportional to their volume. For all species studied to date, the list of functions can be narrowed down to a few broad categories: (a) maintaining group cohesion (e.g., Cheney et al. 1996), (b) reducing predation risk (e.g., reviewed in Cäsar and Zuberbühler 2012), (c) attracting and bonding with mates (e.g., Blair 1958), and (d) competing with other individuals/groups to protect food/space (reviewed by Fashing 2001), mates (e.g., Steenbeek and Assink 1998; but see Wich and Nunn 2002), or vulnerable offspring (e.g., Steenbeek et al. 1999; Wich et al. 2002). These categories are not mutually exclusive, and howler monkey loud calls may have evolved under a variety of selective pressures.

Here, we critically review all studies conducted so far that have focused on the biological meaning of these peculiar calls, including analyses at different explanatory levels. Because of different fitness limitations on the sexes (Trivers 1972; Emlen and Oring 1977), we discuss the possible functions of male and female loud calls separately. We also discuss the opportunity for evolutionary insights from studies in sympatric zones, particularly those with hybridizing animals. Throughout, we continue to stress the variation among the different howler monkey populations that we highlighted in da Cunha et al. (2015). In our conclusion, we address various methodological issues and provide directions for future research.

14.2 Loud Calls and Group Cohesion

No studies have directly tested whether or not male howler monkey loud calls function in group cohesion (i.e., contact calls during travel or when separated). However, Whitehead (1989) reported that male loud calling (both roars and barks) in *A. palliata* preceded 33 % of all major group travel events, Steinmetz (2005) reported that 14 of 37 (38 %) male *A. guariba* howling bouts were produced during separation of the group (see also Oliveira 2002), and Sekulic (1982b) described cases of males roaring on reunion in *A. arctoidea* (formerly *A. seniculus*). The relatively quieter calls in the repertoire are also good candidates for contact calls (da Cunha et al. 2015).

14.3 Loud Calls and Predators

Several authors describe barks and, less often, roars emitted during encounters with potential predators (including dogs and humans) and following nonthreatening disturbances such as vultures, planes, vehicles, and thunder (e.g., *A. palliata*: Carpenter 1934; Baldwin and Baldwin 1976; Whitehead 1989; *A. arctoidea*: Sekulic 1982c, 1983; *A. pigra*: Horwich and Lyon 1990; *A. guariba*: Oliveira 2002). Although uncommon, human observers sometimes witness predator attacks on howler monkeys. For example, McKinney (2009) observed a male *A. palliata* howling briefly during an attack on the group by northern crested caracaras (*Caracara cheriway*), and Julliot (1994) reported that *A. macconnelli* (formerly *A. seniculus*) gathered together and roared in proximity of crested eagles (*Morphnus guianensis*).

However, most examples in the literature fail to provide specific information on the use of loud calls (e.g., harpy eagle, *Harpia harpyja*, attacks: Eason 1989; Peres 1990). For example, during a playback study, *A. palliata* that had only 1-year experience with introduced harpy eagles responded appropriately to the threat of attack, but no details were given on the call type used or duration of alarm calls produced by the monkeys (Gil-da-Costa et al. 2003). Although Camargo and Ferrari (2007) report that an adult male *A. belzebul* gave “typical” ru-ru-ru alarm calls during an attack on an infant by two tayras (*Eira barbara*), no spectrograms were included. Individuals in a captive group of *A. guariba* responded with barks to the presentation of two taxidermized mammals: an ocelot (*Leopardus pardalis*) and a capybara (*Hydrochoerus hydrochaeris*) (Oliveira et al. unpubl. data). Interestingly, the naive monkeys showed no ability to distinguish predator from non-predator. Finally, it seems that predator presence does not always elicit loud vocal responses; for example, da Cunha and Byrne (2006) reported that four natural encounters with ocelots did not produce any loud vocal response from a group of *A. caraya* nor did a pilot playback study of various predator vocalizations (da Cunha RGT unpubl. data). It is unclear if silence is part of an escape response for howler monkeys (see also silence following black hawk-eagle, *Spizaetus tyrannus*, encounter: Miranda et al. 2006). Given the rarity of predator encounters observed by humans, we suggest future studies increase the use experimental techniques such as acoustic and visual predator models in order to identify differences between loud calls produced in various contexts.

14.4 Loud Calls as Sexually Selected Signals

The exaggerated nature of loud calling displays suggests a role for sexual selection (e.g., Zahavi 1977; but see FitzGibbon and Fanshawe 1988 for exaggerated signaling in predator deterrence). Snowdon (2004) proposed that to be sexually selected, signals must be (1) sexually dimorphic, (2) variable among males, (3) discriminated among individuals, (4) preferred or avoided in context of reproductive access, and (5) related to increased reproductive fitness. Although the first two have been clearly demonstrated in howler monkeys (da Cunha et al. 2015), and criteria 3 and 4 have been established during intrasexual competition (e.g., Kitchen 2000, 2004), the last criterion is difficult to measure in any primate. Indirect measures such as "winning" an encounter or relative access to cycling females are often used to approximate fitness.

Assuming howler monkey loud calls do function in sexual selection, the potential intersexual component has been largely ignored. This is not unique to howler monkeys—female choice is a challenging topic to test on any wild animal, especially when it has to be disentangled from strong male-male competition and male-female sexual coercion (including infanticide). In most howler monkey species with bisexual dispersal patterns, females can join established groups (reviewed in Crockett and Eisenberg 1987; Di Fiore and Campbell 2007) and immigrating females may target groups based on the qualities of a male expressed through his loud calls. Females might choose males based on direct benefits if, for example, aspects of his loud call correlate with his ability to defend a resource or an infant (see Wiley and Poston 1996) or on indirect benefits if call features correlate with "good genes" (Zahavi 1977).

There is evidence that females have preferences among males. In multi-male groups, for example, females frequently keep close proximity to one male (the "central male" following Van Belle et al. 2008) over another during howling bouts or intergroup encounters (e.g., *A. pigra*: Kitchen 2000; Van Belle et al. 2008, 2009a; *A. palliata*: Zucker and Clarke 1986; *A. guariba*: Oliveira et al. unpubl. data). Although not causal evidence for female choice, there also appears to be a relationship between male calling and female reproduction; captive male *A. caraya* with higher calling rates had higher reproductive rates than quieter males, and females in this population were more likely to conceive if they heard male conspecifics calling (Farmer et al. 2011). However, whether females base their preferences on specific acoustic features has not been tested in howler monkeys or, with a few notable exceptions (humans, *Homo sapiens*, red deer, *Cervus elaphus*, and koalas, *Phascolarctos cinereus*: reviewed in Charlton et al. 2012), in any mammalian species.

Taken together, these studies suggest that female choice might be an important influence on the production of loud calls by males (e.g., *A. arctoidea*: Sekulic 1982b). How to construct a female choice study in howler monkeys in light of the relatively low rate of sociosexual behaviors, the lack of external signs of estrus, the potentially confounding effects of male competition, and the threat of infanticide remains problematic. One option is to monitor female dispersal patterns. Although anecdotal evidence exists (e.g., a solitary female moving preferentially toward a calling male in *A. palliata*: Whitehead 1989), only long-term studies would be able to adequately address this question. Additionally, as da Cunha and Jalles-Filho (2007) point out, howling happens daily at some sites, yet female immigration events are rare. It is possible that long-term memory of male howling bouts—either within a multi-male group or over an entire area—eventually affects female mating or dispersal decisions. However, even if females do base their choices on male quality as expressed through loud calls, intersexual selection may not be the sole pressure shaping the evolution of these vocalizations.

14.5 The Competitive Nature of Howler Monkeys

Ever since Carpenter's pioneering work in 1934, pioneering work, most studies on howler monkeys have proposed, in some way or another, a function related to regulating space use between groups (reviewed in da Cunha and Jalles-Filho 2007). Explanations for how and why this spacing is maintained have nevertheless differed widely. Some explanations are based on real population differences, but some, we suspect, are due to the varying perceptions or approaches of different authors. On one end of the spectrum, some researchers have advocated for a "territorial" function of howling displays (e.g., Collias and Southwick 1952; Altmann 1959; Bernstein 1964; Horwich and Gebhard 1983). But, according to Mitani and Rodman (1979), howler monkeys are not territorial because group home ranges overlap too substantially, at least in some species or in high-density populations (e.g., 32–63 % in *A. arctoidea*: Sekulic 1982a; 14–63 % in *A. palliata*: Whitehead 1989; but see Agostini et al. 2010b), and they typically have daily path lengths that are too short to theoretically patrol boundaries (reviewed in Crockett and Eisenberg 1987). In fact, as our knowledge of different *Alouatta* species expands, Milton's (1980) original description seems to hold true: likely due to energetic constraints, howler monkeys appear to be "travel minimizers." Still, although howler monkeys do not patrol the borders of their home range, there is ample indication that at least some populations aggressively defend their group or their space (see below).

At the other extreme, some have described howler monkey spacing in fairly cooperative terms, with individuals apparently calling to indicate where in their range they are so that other groups do not approach. For example, several studies of *A. palliata* have described evidence for "mutual avoidance" between groups (e.g., Carpenter 1934; Southwick 1962; Baldwin and Baldwin 1976). Chivers (1969) found that when two *A. palliata* groups slept close together (<220 m on average), they generally moved away from each other following the dawn chorus, and Whitehead (1987) found that groups of *A. palliata* met each other less frequently than would be expected by chance based on a model of random movement.

Of course, it would be unlikely for such avoidance to evolve as a purely cooperative strategy (defined in West et al. 2007). In a world of cooperators, individuals who opted to cheat and thereby exploit this information would have an advantage (e.g., Maynard Smith and Price 1973). For example, if *group X* announces that it is in *location Y*, then *group A* can exploit *X*'s unguarded fig tree at *location Z*. As Sekulic (1982a) pointed out, although "informing neighbors may reduce energy expended in interaction one day, it could also reduce the resources available at the other side of the home range for the following day." A similar conclusion was drawn by da Cunha and Byrne (2006), who found that the calls of an *A. caraya* group were disproportionately distributed in the exclusive core area and not along the borders. Although they suggested that this regular advertisement of occupancy allows regulation of the space use in this species, they suggested that this was because it is a competitive strategy of assessment for settling disputes without chases and fights.

Instead of some cooperative social contract, avoidance is probably most often explained as a by-product mutualism, where the group's collective behavior (insofar as individual interests overlap) "maximizes its own immediate fitness and any positive effects on the fitness of other individuals are coincidental" (Clutton-Brock 2002). Avoidance between groups is, in fact, one of the outcomes predicted by evolutionary game theory (e.g., Maynard Smith 1974; Maynard Smith and Parker 1976). If groups are avoiding the potential costs, to both winners and losers, of escalating a contest, then only when two individuals (or two groups) are similarly matched should rivals approach one another and compete for some resource. It is then possible that the "mutual avoidance" scenarios proposed in *A. palliata* occur because animals avoid escalating contests they would likely lose. Howler monkeys may use aspects of loud calling as a means to monitor their opponents' relative resource holding potential (RHP: Parker 1974) and avoid one another if the outcome is clear (see RHP discussion below). Other asymmetries could also exist that might be assessed through motivational cues. For example, one group/individual might be less willing to back down if they have more at stake (e.g., an investment in females, vulnerable offspring, or a rich food source), a territory holder may have more to lose than an intruder (i.e., ownership games: Maynard Smith and Parker 1976), or losing a fight to a stranger might be more costly than losing to a familiar neighbor (i.e., "dear enemies": Ydenberg et al. 1988).

Rather than a by-product mutualism, Whitehead (1987) suggested that the mechanism producing "mutual avoidance" was in fact a reciprocation of movements, which took the shape of a Tit-for-Tat (TFT) or reciprocity strategy. TFT is theoretically a stable solution to a problem that mimics a Prisoner's Dilemma (see Axelrod and Hamilton 1981)—where avoiding one another has benefits for both contestants, yet being exploited by a cheating rival has high costs. If interactions are iterated indefinitely, a TFT strategy, unlike a purely cooperative strategy, is successful because it mirrors the response of a rival and thereby avoids exploitation while still being readily "forgiving," so to speak. Whitehead (1987) played calls that mimicked both retreating and approaching neighbors to *A. palliata* individuals, with subjects retreating from rivals in the first case and approaching them in the latter. These are exciting results because few empirical studies have found support for the existence of natural reciprocity strategies (Stevens and Hauser 2004). However, although a few other cases have been documented, (e.g., Seyfarth and Cheney 1984), the psychological and cognitive constraints might make TFT strategies beyond the abilities of animals like howler monkeys (Stevens et al. 2011).

Whether intergroup avoidance in howler monkeys is termed cooperative, competitive, reciprocal, or mutually beneficial in the literature may purely be a semantic issue when researchers use different terms to describe the same type of event (see West et al. 2007 for description of term usage in the literature). Alternatively, it is possible that the difference between these terms has real biological significance if there are tangible differences in the strategies used by animals in different populations. For example, as we described above, overt aggression seems to be a rare phenomenon among groups of *A. palliata*. In contrast, intergroup encounters—rather than avoidance between groups—are common in other species. For example, in Chiarello's (1995) study of *A. guariba*, 93 % of calling bouts were directed at nearby groups and 35 % escalated to chases. Such a striking difference between reports of *A. palliata* compared to other species is a dichotomy that seems to be a theme in this volume (e.g., da Cunha et al. 2015).

However, a third possibility is that species and populations are not actually that different but simply need to be studied under similar population densities and time periods to see similarities. For example, although Chivers (1969) found evidence for mutual avoidance in *A. palliata*, he also contemplated a role for intergroup dominance (based on variability in the amount that some groups roared compared to others), and he noticed that 15 % of the males in his study had fresh wounds or scars on their face. Chivers assumed these wounds were the result of intragroup conflict, but they could easily be the result of intergroup conflict. For example, DeGusta and Milton (1998) analyzed *A. palliata* skeletons from Barro Colorado Island (BCI) and reported: "We attribute the trauma primarily to fighting, and its frequency (16.4 % of adult males) contradicts previous assertions that BCI howlers are nonaggressive." Similarly, in another population of *A. palliata*, 38 % of all males were wounded and the majority of injuries were attributed to takeover attempts (Cristóbal-Azkarate et al. 2004). Thus, although *A. palliata* might be less aggressive than other species, they may actively compete when necessary, particularly at high densities.

If so, rather than uncovering real differences in the aggressive nature of different species, it is possible that sites differ in important ways (e.g., population density, habitat quality, and extent of home range overlap). Such differences could affect the costs and benefits of contest escalation, pointing to an interesting possibility of facultative use of loud calls in this genus (e.g., Lichtenberg et al. 2012). Therefore, populations—rather than species—could fall on a continuum from mutual avoidance to advertisement of occupancy to active defense of space without needing to invoke an explanation that focuses on the cooperative nature of a species. Innovative playbacks, such as those used by Whitehead (1987), and comparative studies are promising ways to test such hypotheses.

At the intraspecific level, Sekulic (1982b) further speculated that there might be a difference among types of calling bouts. She suggested that dawn choruses could function in intergroup spacing/avoidance, whereas bouts produced during the day might serve more directly competitive functions (but see Waser 1977). For example, in *A. palliata*, Chivers (1969) found evidence that the dawn chorus functioned to allow animals to assess their location relative to other groups (described above). Conversely, Chivers noted that when daytime encounters occurred, they were likely to escalate to approaches and vocal battles, with one or both groups eventually retreating (i.e., resulting in a win vs. a draw). Alternatively, we suggest that it might not be necessary to invoke wholly different functional explanations. If howler monkey intergroup encounters follow game theoretical predictions, then dawn versus daytime calling might simply represent different levels of sequential or cumulative assessment (e.g., Payne 1998). Given the variation in calling across the genus (e.g., some populations only call at dawn and others have no dawn chorus: see da Cunha et al. 2015), a comparative study of cost-benefit factors might be particularly fruitful.

14.6 What Is Defended?

Beyond potential differences in the competitive nature of males, it is also likely that species (and even populations) vary in the currency defended—females, vulnerable offspring, or food and other resources in a home range. Once again, answering these questions has proved logistically difficult, a problem compounded by variation within and between species.

14.6.1 Space/Food/Resource Defense

Despite their largely folivorous diet, there is indication that food can be a limiting factor for *Alouatta* (Jones 1980). Howler monkeys are more selective feeders than we once thought (Glander 1978), in part because they have few adaptations to deal with the secondary compounds in leaves (Milton 1980) and there appears to be food competition that limits the optimal group size in at least *A. arctoidea* (Crockett 1984) and *A. pigra* (van Belle et al. 2008).

If howling bouts are related to defense of these resources, we expect a spatial and/or temporal pattern to emerge. Temporally, animals might be expected to refrain from calling if costs become too high such as during food-limited times of the year or when climactic conditions impose a physiological burden. Alternatively, calling might increase at food-limited times, when losing access to valuable resources would be most costly. The empirical findings in howler monkeys are inconclusive. Although some howler monkey populations have demonstrated no seasonal variation in howling patterns, others have shown an increase in calling during the dry season, when fruits and new leaves are least abundant (e.g., *A. macconnelli*: Drubbel and Gautier 1993; *A. arctoidea*: Sekulic 1982b; *A. pigra*: Horwich and Gebhard 1983; *A. guariba*: Chiarello 1995, but see Holzmann et al. 2012).

Many studies have uncovered spatial patterns to calling, though scales range from sites to quadrants to entire areas. For example, Sekulic (1982b) found that during the dry season, most (>70 %) *A. arctoidea* intergroup interactions occurred near patchy distributions of fig trees (*Ficus* spp.). Similarly, Chiarello (1995) found that a disproportionate number of *A. guariba* intergroup encounters (19 of 42) occurred in just two of the 67 delineated home range quadrants and always near large emergent guapinol trees (*Hymenaea courbaril*), which provide important feeding and sleeping sites in this population. Whitehead (1989) also found that simulated *A. palliata* intruders heard from high use areas typically prompted howling and approaches toward the speakers, whereas similar calls heard from low use areas did not and, in fact, typically resulted in movement away from the speakers. Whitehead suggests that aggressive defense is therefore site dependent in *A. palliata*.

Differential behavior in the border versus center of a home range can also be indicative of space or resource defense. As such, da Cunha and Byrne (2006) found evidence that *A. caraya* both used and called more frequently from the center of their home range; whereas the border area overlapped with other groups, the study group had almost exclusive use of the center. Furthermore, these authors found that the group was more likely to call at and approach playbacks simulating intruders in the center of the range than from the border area.

In contrast to the *A. caraya* finding, other populations of howler monkeys tend to concentrate their calls along the boundary of their home range (e.g., *A. pigra*: Horwich and Gebhard 1983; Kitchen DM unpubl. data). For example, in both a dry season (Bernstein 1964) and a wet season (Altmann 1959) study of *A. palliata* on Barro Colorado Island, all non-dawn chorus vocal bouts were directed at another group and occurred at the edge/border of the callers home range. Similarly, Drubbel and Gautier (1993) advocate that *A. macconnelli* acoustically mark their home range borders with their loud calls. Likewise, da Cunha and Jalles-Filho (2007) found that *A. guariba* calls occurred disproportionately on the borders of their range, despite no indication that they used the border more intensely. It appears that calling in this population served to reinforce borders, particularly in areas susceptible to invasion by other groups. Because males defending females or vulnerable offspring should not have a site-specific pattern in their calling, da Cunha and Jalles-Filho instead suggest that the group was defending their entire home range. In another study of *A. guariba*, Oliveira (2002) also argued that defense of space or specific food sources was the cause of most intergroup conflicts, although he did not discard the mating defense hypothesis in some circumstances or at other sites. However, in a third population of *A. guariba* where they live in contact with *A. caraya*, Holzmann et al. (2012) found no relationship between howling frequency and location (exclusive areas, boundary areas, or important feeding sites) or seasonality (despite food availability changing markedly over the study period), although some groups tended to howl in areas of their home range that were closest or overlapped with conspecific groups (but not heterospecific groups: see below). However, as the authors point out, there was a lower roaring than rate other study sites of this species, likely due to a lower population density. Thus, perhaps food competition is not as strong as at other sites.

In sum, many studies have found evidence that males defend aspects of their group's home range, be it an important site, a well-used quadrant, an area, or a boundary. Any variation in how/where space is defended is probably dependent on factors such as population density, habitat quality, and the extent of home range overlap among groups. Whether this defense protects food resources, sleeping sites, or merely space is not clear and may also vary among populations.

14.6.2 Female Defense

Few studies have found evidence for mate defense in *Alouatta* (see also Wich and Nunn 2002), a hypothesis originally proposed by Sekulic (Sekulic 1982b; Sekulic and Chivers 1986). The strongest argument so far for mate defense comes out of a contact zone between *A. guariba* and *A. caraya*. In this population, there is ample heterospecific but almost no conspecific home range overlap (Agostini et al. 2010b), and

Holzmann et al. (2012) reported that subjects called more at conspecifics than heterospecifics (see below). Given both species have nearly perfect overlap in their feeding niche (Agostini et al. 2010a), the howling patterns seen are not consistent with defense of food/space. Instead, these findings are suggestive that howling is, at least in part, used in defense of females from potentially transferring male conspecifics.

14.6.3 Infant Defense

Given infanticide has an obviously strong impact on reproductive fitness and has been documented in at least eight populations of five howler monkey species (reviewed in Van Belle et al. 2010), it seems reasonable that calling could be used to defend vulnerable offspring. Kitchen (2004) conducted a playback study on *A. pigra* where she presented 12 central males with the recordings (both barks and roars) of unfamiliar, and therefore potentially infanticidal, males. Central males had an overall stronger howling response to playbacks if they had offspring in their group that were younger than 9 months old (the age at which they remain vulnerable to infanticide: see Crockett and Sekulic 1984). In fact, the only time males called in trials when the simulated group outnumbered their own was when there was a small offspring in the group. Still, 94 natural interactions between neighboring, and thus familiar, groups in this population revealed no effect of small offspring presence on contest outcome (Kitchen 2000). Although male transfers and takeover events are relatively common at this site (e.g., Horwich et al. 2000) and infanticide has been observed (Brockett et al. 1999), these events are relatively uncommon between neighboring groups. Assuming howler monkeys can discriminate among individuals based on their calls, then the playback study (Kitchen 2004) was more likely than the observational study to simulate an actual infanticidal threat.

Holzmann et al. (2012) observed 79 natural howling bouts produced by four different male *A. caraya* and *A. guariba* and found no pattern related to the presence of small offspring (see also *A. guariba*: da Cunha and Jalles-Filho 2007). However, neighbors were unlikely to pose an infanticidal threat at this site; in fact, to date, no immigration events or infanticide has been observed at this site (Holzmann pers. obs.). More studies employing experimental playback studies (as in Wich et al. 2002) will be necessary to rule out infant defense and to disentangle it from mate and food defense.

14.7 Loud Calls and Within-Group Male Cooperation and Competition

Loud calling bouts may also function in male-male competition within groups. For example, Fialho and Setz (2007) report howling during an event where one resident male permanently ousted another in *A. guariba*. During a year-long study, Sekulic (1982b) reported 20 intragroup aggressive interactions among males in one of her four study groups, six (30 %) of which resulted in short roaring bouts of less than 1 min.

When one group is in a contest with another, the group males might have similar interests and should therefore join each other in a vocal display directed at extra-group competitors; yet, multi-male social groups do not always call together. For example, in a group of *A. guariba*, the central male initiated almost all loud calling bouts, whereas the subordinate male, a newcomer in the group, participated in less than 50 % of episodes (Oliveira et al. unpubl. data). Similarly, the central male initiated all howling bouts in a group of *A. caraya*, and although the subordinate adult male joined him during 87 % of these bouts, the two subadult males only joined during an average of 28 % of bouts (da Cunha 2004). Dias et al. (2010) reported that in two three-male groups of *A. palliata*, one or more noncentral males joined the central males only 65–70 % of the time. Similarly, in *A. pigra*, Kitchen (2000) found that noncentral males in nine groups joined the central male in howling during only 59 % of 112 natural intergroup encounters.

If howling helps defend some aspect of the group (space, food, females, infants), an interesting question is what might lead noncentral males in multi-male groups to participate with the central male as opposed to "free-riding" (see reviews in Nunn 2000; Nunn and Lewis 2001; Kitchen and Beehner 2007). For example, in *A. arctoidea*, Sekulic (1982b, 1983) suggested that males in strong alliances had longer roaring bouts than males in weak or antagonistic male-male relationships. Similarly, Dias et al. (2010) found that a coalitionary dyad of *A. palliata* howled together more often than either male called with the usurped male (who remained a resident in the group following the takeover). Additionally, these three males howled together only half as often as another three-male group that had been in a stable relationship for many years. Likewise, in Belizean *A. pigra*, five noncentral males in long-term relationships with the central male in their group had much stronger responses (i.e., called for longer, were quicker to approach and got closer to the speaker) to playbacks simulating intruders than five noncentral males in short-term relationships with their central male (Kitchen et al. 2004). On the other hand, in an observational study of two multi-male groups of Mexican *A. pigra* (van Belle et al. 2008), coalitionary males and long-term residents were not more likely to have more affiliative or fewer aggressive interactions than other dyads; in other words, males in this population howled together regardless of relationship duration. However, the authors point out that this group was studied during a socially unstable time period with frequent male membership changes.

Future studies should attempt to include measures of relationship status (preferably genetic evidence of relatedness) and of reproductive skew among males. Playback experiments are useful to increase sample size of intergroup encounters and also to simulate unfamiliar and thus potentially more threatening rivals (e.g., Ydenberg et al. 1988; Kitchen 2000).

14.8 Different Types of Loud Calls

Although loud call types are distinctive (see description and spectrograms in da Cunha et al. 2015), Whitehead (1985) is one of only a few contemporary authors who has actually tested for functional variation among call types. He found that *A. palliata* had site-dependent responses to roaring but not to barking.

Responses to barks were instead dependent on acoustic features that mimicked approach or retreat. In an observational study of *A. palliata*, Baldwin and Baldwin (1976) found that whether loud calling bouts included roars depended on the intensity of the eliciting stimulus. Likewise, in *A. pigra*, loud call bouts are more likely to include roars during close than distant interactions, although there may be some individual variation among males in this tendency (Kitchen 2000 pers. obs.). This contextual difference may be even clearer in South American species because they are less likely to combine barking and roaring in the same bout. In *A. guariba*, for example, Chiarello (1995) found that 39 of 43 close encounters elicited loud calling bouts made up of only roars, whereas only four of these encounters elicited barks only or barks plus roars.

There may be even more subtle differences in the graded calls within a call type. For example, Drubbel and Gautier (1993) categorized two types of roars in *A. macconnelli* and found that "long roars" (>1 min) were typically produced during nighttime choruses (58/62 cases), whereas "short roars" were frequently produced during short-range interactions (36/62). Whitehead (1987) also found a difference among roar types in *A. palliata*—he reported that "roar variants" (see da Cunha et al. 2015) were typically produced in dawn choruses or during mild/distant interactions, whereas "full roars" were more likely to be associated with close encounters.

However, a cross-species comparison is premature because it hinges on resolving nomenclature issues that exist in the literature (see da Cunha et al. 2015). The problem is compounded by the different nature of loud calling in the two taxonomic clades of *Alouatta* (Cortés-Ortiz et al. 2003); for example, the howling bouts of Central American species typically include both roars and barks, whereas the two call types are usually produced in separate bouts in South American species. Virtually all studies on South American species have focused on roars; thus, barks remain a largely unexplored vocalization.

14.9 Mechanisms of Competition: Form Meets Function

Since authors do not always state at which level they are working, the bioacoustics literature is full of seemingly different "functions" for the same call; however, we suggest that many researchers are simply approaching the same phenomenon from different angles. Here we consider another level of analysis that we have not considered in detail so far—a more proximate approach. Although there is of course an ultimate function of competition, we focus here on the mechanisms by which males announce "intent," convey individual or group-level RHP, or signal deceptively.

14.9.1 Motivational State

Calls such as those produced by howler monkeys have been interpreted as aggressive signals, part of the motivational-structural rules proposed by (Morton 1977; Owings and Morton 1998). In this theoretical model, aggressive calls are harsh, low-frequency sounds that mimic the larger body size of a more dominant and dangerous animal, because larger individuals have larger vocal folds that vibrate at lower frequencies and in a more unstable pattern than smaller individuals, generating lower-pitched, atonal sounds (e.g., August and Anderson 1987; Hauser 1993). Morton (1977) claimed that a dominant frequency around 1,500 kHz would be effective in long-distance propagation in forests, yet howler monkeys have roars with much lower frequencies (<1,000 kHz, da Cunha et al. 2015); therefore, Morton viewed the unnecessarily low-frequency roars as an aggressive long-range signal that originally evolved from a short-range signal. Aggressive signals are also predicted to be intense (Bradbury and Vehrencamp 1998), and the amplitude of howler monkey loud calls, usually interpreted as necessary for long-range signaling, is also intense in close range confrontations between groups.

In support for Morton's theory, Oliveira (2002) observed that, relative to spontaneous choruses, intergroup encounters in *A. guariba* were associated with longer and louder loud calling bouts, perhaps relating to a greater aggressive motivation in such contexts, and we have noticed this phenomenon in other species as well (*A. caraya*: da Cunha pers. obs.; *A. pigra* and *A. palliata*: Kitchen pers. obs.). Similarly, Whitehead (1994) observed that the first formant in roars of *A. palliata* uttered in response to playbacks of roars from unfamiliar males had lower frequencies than those emitted naturally. He also found that males produced even lower frequency calls when playbacks elicited an approach than when they elicited a retreat, a possible effect of the motivational state of the caller in the production of these sounds, which would parallel the trends predicted by Morton. Although vocal frequency can be correlated with a male's fighting ability or condition, when the same male flexibly changes frequencies during different contexts, it may possibly reflect some sort of affect, motivation, or deception.

Game theoretical predictions suggest that when signaling intentions is low in cost, then individuals should always "lie" about intentions, and these cues will become meaningless to rivals. However, if there is a threat of retaliation, then high cost signals (e.g., Poole 1989) could be used as honest indicators of intention (Zahavi 1977). This is an interesting avenue for further research in howler monkeys.

14.9.2 Resource Holding Potential: RHP

Because they are so salient and so clearly tied to male-male competition, many researchers (e.g., Sekulic 1982b; Chiarello 1995; Kitchen 2000; Oliveira 2002) have suggested that howler monkeys assess one another's RHP using reliable features of the loud calling bouts. The source-filter approach (Owren and Linker 1995; Fitch and Hauser 1995; Frey and Gebler 2010) proposes that the vocal tract can provide cues to the body size of a vocalizing animal: the resonances present in a vocal tract are dependent on its extension, which has a direct relationship with the size of the caller. Harsh sounds or those with a low fundamental frequency and several harmonics should accurately reflect these resonances and could therefore be honest signals of body size. Because howler monkey loud calls have wide frequency bands, they should clearly show these resonances, or formants, in their structure. As we discuss in elsewhere (da Cunha et al. 2015), marked and usually stable frequency peaks are found in the roars of most *Alouatta* species indicating the presence of such formants. Kitchen (2000) found a relationship between the number of formants per roar, some formant frequencies, and the width of some bands with age and size in male *A. pigra*. In a set of playback experiments on this same population, subject responses were strongly correlated with some of these same acoustic features.

However, Fitch and Hauser (1995) also remarked that other cues, like call duration and emission rate, may be more reliable signals of RHP than static body size ones because they provide better indication of the present energetic condition of the caller (e.g., baboons, *Papio* spp.: Kitchen et al. 2003; Fischer et al. 2004; red deer: Clutton-Brock and Albon 1979). If aspects of a loud call are energetically costly to produce, a more fit animal should be able to vocalize louder, longer, and more frequently than a weaker opponent, leading to dynamic processes of evaluation between opponents (e.g., Zahavi 1977; Payne 1998; Frey and Gebler 2010).

In *A. pigra*, Kitchen (2000) reports that higher roaring rates per bout, longer periods of continuous loud calling per bout (including roars, barks, and pauses of less than 1 s), and lower proportion of silent periods per bout were correlated not only to age and body size but also to which group won a natural contest. When she experimentally manipulated the proportion of loud calling per bout, subjects had the strongest howl and move response to males who were most similar to them and had the weakest response to males whose acoustic features suggested that they had either a higher or lower RHP.

Finally, group-level fighting ability is another aspect that can be reliably indicated in howler monkey choruses in that, at least in *A. pigra*, multiple calling males offset their roars and barks so that at least a minimum estimation of males in the group can be determined. Using playbacks to simulate invasion by strangers, Kitchen (2004) found that the relative number of males in two groups (i.e., the "numeric odds": McComb et al. 1994) influenced the responses of central males (although not the noncentral males: Kitchen et al. 2004) during playback experiments. Central males had a stronger response (defined above) the more their group outnumbered the simulated group (see also lions, *Panthera leo*: McComb et al. 1994; chimpanzees, *Pan troglodytes*: Wilson et al. 2001). Conversely, Kitchen (2000) found that numeric odds did not influence contest outcome among familiar opponents. Interestingly, only when the odds were even and thus the outcome was least clear based on group-level fighting were responses during playbacks highly correlated with specific acoustic features (as above) of individual callers. This suggests that howler monkeys might employ a system of either sequential or cumulative assessment (e.g., Payne 1998).

In a general perspective, it is likely that the structure of loud calls in howler monkeys reflect several selective forces acting upon their design. Perhaps a species like

A. guariba, which are unique among *Alouatta* in that dawn choruses are absent (reviewed in da Cunha et al. 2015) and whose roars are used almost solely during direct confrontations between groups, can shed more light on the contributions of honest signaling and long-range communication in shaping the form of howler monkey loud calls.

In this sense, perhaps the brief forms of roaring in *A. palliata* are indicative that a lower selective pressure acted in the elaboration of the roars of this species when compared to other members of the genus that evolved longer continuous roars. Sekulic and Chivers (1986) proposed that *A. palliata* living in larger, multi-male groups faced greater intragroup competition compared to *A. arctoidea*, who, they suggested, had longer calls due to the pressures of intergroup competition. However, the overall bouts (including pauses between loud calls) of *A. palliata* are very long, so this hypothesis requires more testing.

14.9.3 Deception

One last form and function nuance was pointed out by Fitch and Hauser (1995), who observed that vocal resonances could also be manipulated and therefore provide opportunities for deceptive signaling. They suggested that lip protrusion could be used as a maneuver that would lower the dominant frequency in a vocalization, simulating a longer vocal tract and, as a consequence, a larger body size (see also baboons: Fischer et al. 2004). Lip protrusion is clearly visible in roaring howler monkeys (Schön Ybarra 1986), and perhaps the wider opening of their mouths in the inhaling phase can be related to the rising modulation observed in this period (see also da Cunha et al. 2015).

Fitch and Hauser (1995) further suggested that laryngeal air sacs, which howler monkeys have, could mimic a larger body size. Additionally, the hyoid bulla in *Alouatta* is a kind of rigid laryngeal air sac (Schön Ybarra 1988, 1995), and this organ plays an important role in first formant production (see modeling studies by Riede et al. 2008; de Boer 2009), and dynamic articulations are probably responsible for the modulation of howler monkeys formants, perhaps resulting in manipulation of body size cues. This possibility is reinforced by Whitehead's (1994) study showing a lower pitch in the roars of *A. palliata* males when responding to the roars of strangers during playbacks: they could be simulating a larger body size through such a maneuver rather than a greater aggressive motivation as has been proposed. Such hypotheses are not in fact mutually exclusive given an aggressive animal could also mimic the lower dominant frequencies found in the calls of larger animals (see above), and a clear distinction between motivation versus body size simulation explanations is difficult to make. Interestingly, Schön Ybarra (1995) found that *Alouatta* was the single exception to the correlation between body size and vocal tract length among primate species, with the extension of the vocal organ in howler monkeys being close to that found in the much larger *gorillas*.

Game theory suggests that, unless it is done relatively infrequently (reviewed and tested by Hughes 2000), bluffing will not be a stable strategy because animals should periodically test and retaliate against dishonest signals. Thus, although the maneuvers of howler monkeys described here may alter the features of a call, if they are done regularly, it is possible that they would no longer be a part of the suite of features assessed by rivals. However, if some animals can exaggerate more than others based on some underlying characteristics, the signal might remain honest (but see Bee et al. 2000).

14.10 Girl Power

Although females also produce loud calls, relatively little has been published in this area, particularly with respect to the acoustic structure of these calls. In both acoustic features (da Cunha et al. 2015) and functional strategies of these vocalizations, we predict that females will have differences that are not necessarily correlated with those of conspecific males and we also anticipate strong interspecific differences.

As in males, the loud calls of females likely serve multiple functions including alarm calls and group cohesion. For example, Steinmetz (2005) suggested that female *A. guariba* produced loud calls when isolated or "lost" (a common occurrence in her study); females called alone in three such situations, during 92 days of fieldwork (see also Oliveira 2002).

Perhaps the most interesting question is why females should participate in choruses with males. In most species, it appears that females are only occasional participants. For example, Chiarello (1995) reported that *A. guariba* females participated in 31 % of howling bouts, Holzmann et al. (2012) found *A. caraya* and *A. guariba* females participated in 29 %, Whitehead (1989) reported *A. palliata* females joining in 18 %, and Kitchen (2006) reported that one or more *A. pigra* females joined in 47 % of bouts.

Because the dominant male is usually responsible for the onset of roar emissions by a group, the participation of other males and females can be seen as a form of cooperation with the alpha male (e.g., Kitchen et al. 2004; Kitchen 2006). However, the final decision about participation should be contingent on the costs and benefits of the individual in that particular situation (reviewed in Kitchen and Beehner 2007). For example, females in several species seem to be more likely to invest by joining howling bouts during close interactions with other groups rather than during interactions with distant groups or during spontaneous choruses (e.g., *A. palliata*: Baldwin and Baldwin 1976; *A. guariba*: Chiarello 1995; *A. pigra*: Kitchen 2000; *A. caraya*: da Cunha and Byrne 2006; *A. guariba* and *A. caraya*: Holzmann et al. 2012).

In multi-female groups, females may differ among themselves in their decisions to join. For example, Kitchen (2006) found that on occasions that females joined a chorus, only 60 % of the females present participated. Similar findings have been found in a group of *A. guariba*, with one of the two females in the group showing a greater degree of participation in loud calling bouts than the other (Oliveira et al.

unpubl. data). Thus, the focus should be on the conditions that vary among females that may be related to their participation in the sessions.

In the first thorough approach to the subject, Sekulic (1982b, 1983) presented a series of hypotheses that we examine here. First, she hypothesized that the roars of female *A. seniculus* incite male competition. However, this predicts that females should call first, which rarely happens in howler monkeys; in fact, it is more likely that the male's incipient roars, usually uttered at the onset of roar bouts (da Cunha et al. 2015), can act as a recruitment call, prompting other group members to join in the roar chorus (Oliveira 2002). Moreover, Sekulic's hypothesis suggests that males are in a state of constant intragroup competition, another unlikely assumption. It is also unclear why males should need female loud calls as incentive to compete.

Second, Sekulic (1982b, 1983) hypothesized that females roar to intimidate and thereby deny access of extra-group females, as a way to limit competition for food or mates. In her study, *A. arctoidea* males and females frequently roared at solitary females. In fact, Sekulic (1983) also described female-only sessions in *A. arctoidea*, apparently directed at other females. Oliveira (2002) also reported three episodes of loud calling by *A. guariba* females alone, when the central male of the group was injured and not always with the group. Additionally, Miranda et al. (2004) describe a case where an *A. guariba* female became the dominant member of a group, the most frequent caller and sometimes the only caller. However, none of the *A. guariba* incidents were apparently directed solely at females, and female-only sessions have not been recounted in other study populations. In *A. caraya*, da Cunha and Byrne (2006) reported an encounter between a group and a lone female that did not result in any howling. Thus, it remains possible that there are differences among *Alouatta* species in their tolerance to female immigration.

Future studies designed to evaluate whether female loud calls affect female emigration/immigration need to consider the following: target of the call (neighbors vs. strangers), proximity to target, sex of target, influence of calling on migration decisions, and age of the calling female (e.g., older and established females should be more resistant to migration, and, thus likely to participate in loud calling more often, particularly given hierarchy is inversely related to age in some howler monkey species: Jones 1980).

Related to the above hypothesis, Sekulic (1983) also hypothesized that, through calling, females may attempt to control access to the group's central male. In *A. arctoidea*, Sekulic documented cases of intragroup female-female competition over proximity to certain males during a howling bout. Among females within the same group, cooperation with the male could be just one more aspect of a suite of behaviors connected to status and hierarchy maintenance. If so, participation should be directly proportional to a female rank, and females may even attempt to interfere with one another, with high-ranking females preventing close access to the central male or directly interfering with the call production of lower-ranking females. The biggest obstacle to testing these predictions is determining female rank hierarchies in most *Alouatta* species.

In a third hypothesis, Sekulic (1982b, 1983) proposed that females loud calling alongside a central male could provide pair bond reinforcement and thereby encourage him to protect infants against infanticide. Under this hypothesis, female participation could reflect the risks associated with a takeover—the main source of infanticide risk. Playback experiments are an excellent way to simulate infanticidal threat because callers can be unfamiliar to subjects. To analyze female decisions to participate, aspects that could be manipulated via playback studies include the numeric odds (assuming more males in a group means better protection from invasion by potentially infanticidal males), the presence of small offspring at an age where they are still vulnerable to infanticide (see formula in Crockett and Sekulic 1984), and the number of females (maybe more females can better defend against potentially infanticidal males, even if the takeover is successful).

To test this, Kitchen (2006) measured the responses of females with and without vulnerable offspring to the sounds of unfamiliar, and therefore potentially infanticidal, males. Curiously, the presence of small, vulnerable offspring did not predict participation in a chorus (which is in contrast to the strong response of the central males in that population: see Section 14.6.3). More recently, Holzmann et al. (2012) studied the natural behavior of both *A. guariba* and *A. caraya*. The presence of infants also did not influence female decisions to join a session or not (see also da Cunha and Byrne 2006). However, Sekulic (1982d, 1983) provides several reports that, following a takeover, one cycling female *A. arctoidea* howled with the new dominant male, whereas females who were pregnant or who had a vulnerable offspring in the group continued to call with the former dominant male (the likely sire of their offspring). This strategy of choosing the usurped over the new and potentially infanticidal male leaves opens the suggestion that females may bond with males through howling as a counterstrategy to infanticide.

Finally, in a related and not mutually exclusive possibility, da Cunha and Byrne (2006) hypothesized that females could cooperate with males in the coordination of space use (be it border/resource defense, announcement of occupation, or mutual avoidance). Female decisions to participate should also be contingent on the situation, but reflecting the benefits and risks associated with guaranteeing an exclusive area and/or resources. Other aspects that could be tested in future studies of this hypothesis include numeric odds based on the entire group size, irrespective of sex, presence of relatives in the group (not just vulnerable offspring), and female status (with older, established females expected to invest more in defense than young and potentially migratory females).

Supporting a defense scenario, Whitehead (1989) found that groups of *A. palliata* were much more likely to move away from playback recordings that included the sounds of females roaring than to those with only males roaring. Using another angle to examine group-defense (although it is unclear what is being defended—space, resources, mates, or offspring), Kitchen (2006) found that females were most likely to join a howling bout if the numeric odds (resident vs. intruder males) were even. This result suggests that females join when their assistance would best improve the group's odds of winning a contest. Their responses were also different from males, who tended to join when odds were most in their favor (Kitchen 2004) or when they had a long-term relationship with other intragroup males (Kitchen et al. 2004). This provides further evidence that males and females differ in their strategies.

Future research should remain sensitive to potential sex differences in usage and function of loud calls. After all, males and females have different ecological needs (Trivers 1972) and usually differ in the strategy they use to solve problems. For example, if in a given species males migrate and females stay in the natal group, males could be more concerned with takeover attempts (especially in non-infanticidal populations), while females might be more interested in securing an area on a longer-term basis (Emlen and Oring 1977). The important message here is not to neglect the issue by considering females as merely supporting actors. Female decisions to call might reflect different pressures and reveal different functions to their calling behavior than males (e.g., Hill 1994), providing rich insights for socio-ecological theory.

14.11 Sympatric Zones and Hybrid Voices

Understanding the evolution of howler monkey loud calls would require an extensive comparative study within the *Alouatta* genus and between howler monkeys and their sister taxon, the Atelinae (Eisenberg 1976; Oliveira and Ades 2004). However, areas of sympatry and hybrid zones also represent novel scenarios for evolutionary studies (Hewitt 1988), addressing aspects of both behavioral ecology and vocal behavior.

Most of the studies of vocal behavior carried out on two (or more) sympatric primate species (none of them in howler monkeys) are related to alarm calls and mutual benefits from heterospecific associations (e.g., Fichtel 2004) or to diurnal distribution of vocal patterns (Geissman and Mutschler 2006). Another aspect of vocal behavior in sympatric primates, virtually unstudied, is related to the mutual influence from closely related species living in sympatry that could result in divergence of some vocalizations (especially long-distance calls) due to character displacement (Brown and Wilson 1956; Marler 1973) or convergence of vocal signals due to vocal learning. While character displacement (e.g., Kirschel et al. 2009) and convergence (e.g., Baker 2008) have been demonstrated in the calls of amphibians and birds, we do not know if it plays a role in the diversification of primate communication. Primates, in contrast to birds and cetaceans, have long been considered inflexible in their vocal behavior (e.g., cross-fostering between two *Macaca* spp. resulted in little vocal change: Owren et al. 1993). Although studies have demonstrated that there is learning involved in call usage (e.g., reviewed in: Seyfarth and Cheney 2010), primate repertoires and the structure of their vocalizations have been considered largely innate. However, recent studies have begun to question this assumption, demonstrating acoustic variation at different levels—regional dialects (e.g., *M. sylvanus*: Fisher et al 1998; *Pan troglodytes*: Clark Arcadi 1996; but see Mitani et al. 1999), call convergence within groups in the same population (e.g., *Cebuella pygmaea*: Elowson and Snowdon 1994; *P. troglodytes*: Crockford et al. 2004), and changes within individuals of the same population (e.g., *Nomascus concolor*: Sun et al. 2011).

Researchers (Kitchen DM, Bergman TJ, Cortes-Ortiz L, unpubl. data) are investigating the impact of sympatric species on one another in howler monkeys in a zone of contact between two species (*A. pigra* and *A. palliata*) in Tabasco, Mexico. They found that roars are at least partially genetically determined, since roars from both species living in sympatry have similar acoustic features to their allopatric conspecifics. However, these researchers also found enough notable difference between allopatric and sympatric conspecifics—with sympatric animals from the contact zone converging slightly in a few acoustic features (see Fig. 14.1)—to question whether this is the result of simple variation within a species, learned behavior, and/or extensive backcrossing of hybrids (the latter has been confirmed in this population: Kelaita and Cortés-Ortiz 2013).

Beyond acoustic features, there is also the question of how heterospecifics respond to each other within contact zones. Holzmann et al. (2012) conducted a year-long study of two groups of *A. guariba* that overlap with two groups of *A. caraya* at a site in northeastern Argentina. Both species were more likely to howl at conspecifics

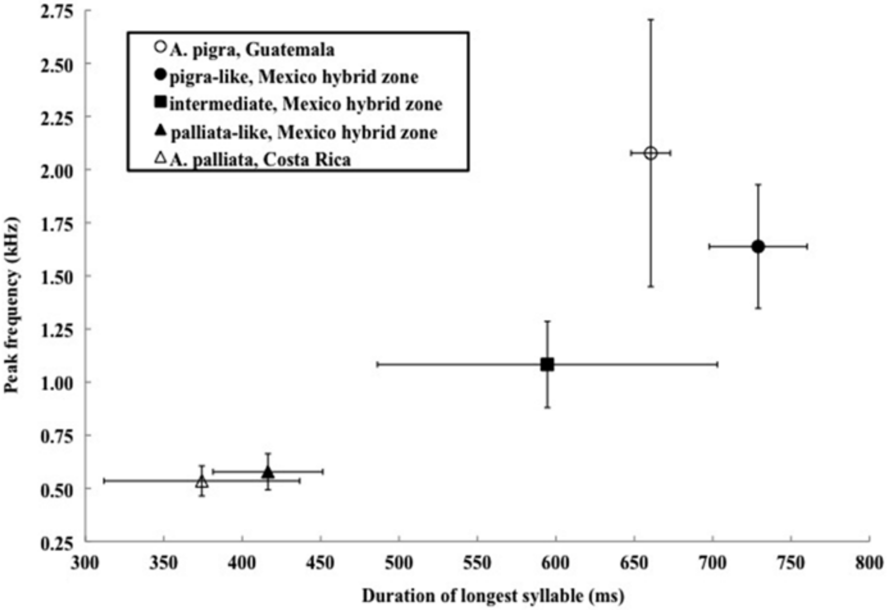

Fig. 14.1 Mean ± SD of longest sustained syllable and peak frequency of roars (see Fig. 14.2) from males recorded within and outside a hybrid zone. Legend indicates species and provenance of calls with 4–8 roars from 2–4 individuals used per point (measurements made with PRAAT 5.1.02). Data from a pilot study by Kitchen, Bergman, and Cortés-Ortiz (unpubl. data). The genetic makeup of most individuals in the hybrid zone in Tabasco, Mexico, is the result of multigenerational backcrossing, with an admixture that ranges from nearly purebred of each parental type to intermediates (Kelaita and Cortés-Ortiz 2013). Individuals were categorized as *pigra*-like, intermediates, and *palliata*-like based on morphological features (but see Kelaita and Cortés-Ortiz 2013 for problems using only morphology)

(83 % of 18 encounters) than at heterospecifics (21 % of 29 encounters) during close range intergroup encounters and never howled at distant interactions with heterospecifics (yet howled at 57 % of distant conspecifics roars). Similar findings were reported by Aguiar (2010), who studied hybrid groups (*A. caraya*×*A. guariba*) in a population where *A. guariba* predominates and found greater agonistic responses (e.g., piloerection, roaring) during intergroup encounters of conspecifics, followed by encounters with groups composed of purebreds and hybrids, and the weakest responses during interspecific encounters. Playback experiments in the contact zone in Mexico suggest similar trends in *A. pigra* and *A. palliata* (Kitchen et al. in prep).

Even more information on the evolution of vocalizations can be ascertained when species living in sympatry actually hybridize individuals is a subject relatively well studied in birds and anurans, information is almost absent for mammals and especially for primates, despite natural primate hybridization observed in many taxa (Gabow 1975; Bynum et al. 1997; Alberts and Altmann 2001; Detwiler et al. 2005) including those of howler monkeys: (Cortés-Ortiz et al. 2007). Studies carried out so far on non-primates describe three different patterns in hybrid vocalizations: (1) the hybrid can inherit one of the two parental songs; (2) the hybrid can have an intermediate song, formed by the mixture of elements from the two parental songs; and (3) the hybrid can have a unique song, different from both parental songs (anurans: Blair 1958; Gerhardt 1974; Scroggie and Littlejohn 2005; birds: Ficken and Ficken 1967; Lemaire 1977; de Kort et al. 2002). Relatively little is known about how hybridization would impact nonhuman primate communication. A study on vocalizations in *H. muelleri* and *H. lar* in captivity revealed that hybrids show both types of songs—a female hybrid produced a unique song, whereas a male hybrid produced an intermediate song (Tenaza 1985; see also *Saimiri sciureus* hybrids: Newman and Symmes 1982). Because of their distinctive calls, the few contact zones between different howler monkey species in this otherwise parapatric genus might reveal additional insights into the function and evolution of vocalizations. In some of these sympatric zones, mixed groups and hybrids have been observed (Cortés-Ortiz et al. 2007; Aguiar et al. 2007, 2008; Agostini et al 2008; Bicca-Marques et al. 2008). To the best of our knowledge, however, there is currently only one ongoing study focused on the vocal behavior of hybrids (*A. palliata*×*A. pigra* in southern Mexico: Kitchen et al. in prep). Preliminary results from this site suggest that genetically intermediate hybrids produce a roaring behavior intermediate between both parental roars (Figs. 14.1 and 14.2), further evidence for strong genetic influence on howler monkey vocal behavior.

14.12 Summary and Future Directions in Vocal Research

Both here and in da Cunha et al. (2015), variation has been our theme. It seems that howling (including roars and, in the case of Central American species, barks) has different functions within a population as well as between populations. Although calls produced at any time might “regulate space use,” there is a possibility that the

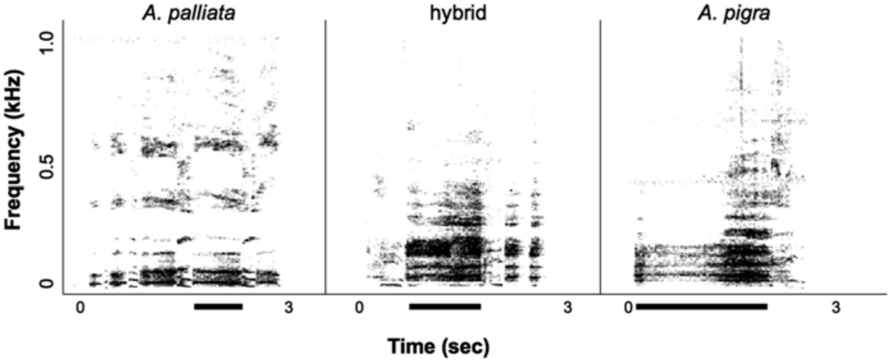

Fig. 14.2 Example spectrograms of roars from a male purebred *A. palliata* (*left*), *A. palliata*×*A. pigra* hybrid (*middle*), and purebred *A. pigra* (*right*). Dark bars under the *x*-axis indicate the duration of the longest sustained frequency in each roar (From a pilot study by Kitchen, Bergman and Cortés-Ortiz (unpubl. data))

more ritualized, spontaneous dawn choruses may function more in avoidance between groups than daytime calls. Alternatively, we argue that both dawn and daytime calls might function in sequential assessment of rivals. Playback experiments along with simultaneous documentation of movement patterns in neighboring groups (using GPS tracking technology) will be useful to test between these hypotheses.

Among species and populations, the rate and patterns of vocal battles and intergroup encounters varies, as does the likelihood that groups will escalate to physical aggression. Much of the variability probably has to do with the cost-benefit ratio of avoiding confrontations based on population density (e.g., Lichtenberg et al. 2012), the extent of home range overlap, availability of mates, habitat quality, level of feeding competition, and the threat of infanticide. However, some of this variation might have to do with the varying competitive nature among species. For example, perhaps *A. palliata* differs from other species in the likelihood that encounters will escalate because their social system is driven more by intra- rather than intergroup competition.

Although there is strong support that howling evolved at least in part under male intrasexual selective pressures, the focus of the competition is less clear. In at least one population of every species highlighted in this chapter, there is some evidence that males defend resources (either important sites, quadrants, areas, or home range boundaries). It remains unclear if such space/resource defense is driven by the mutual goals of males and females, by male defense of food/space to attract females, or if it is merely coincidental, with males acting as "hired guns" while they defend mates or infants (Wrangham and Rubenstein 1986). Despite infanticide being confirmed at several sites, only one study in *A. pigra* (Kitchen 2004, 2006) found support that howling is used to defend vulnerable infants. However, we suggest that more studies need to incorporate playback tests that include the sounds of unfamiliar, and therefore potentially infanticidal, intruders. In terms of mate defense, only a few studies have so far provided evidence (Sekulic 1982b; Holzmann et al. 2012). Endocrine research has demonstrated that central males are sensitive to threats to their reproductive success, suggesting that males compete for females (Cristóbal-Azkarate et al. 2006; Van Belle et al. 2009b; Rangel-Negrín et al. 2011), but future research should search for causal connections between reproductive access, hormone levels, and loud calling. Whereas legitimate arguments against the mate defense hypothesis have been proposed (e.g., howling happens more often than females cycle, howling should not be site specific, etc, see also Wich and Nunn 2002), most researchers seem reluctant to reject this hypothesis outright. However, the logistics of designing a mate defense study remain problematic given there are no reliable external indicators of reproductive state and both sociosexual behaviors and immigration events are observed only rarely.

After decades of speculation that males use howling bouts to assess their rivals, there is finally some evidence that howler monkey loud calling bouts may be honest indicators of RHP (e.g., Frey and Gebler 2010). Such studies are at the intersection of form and function in vocal research. However, confusion has been created in the bioacoustics literature because authors fail to define the level at which they are working (e.g., Tinbergen 1963). For example, uncovering proximate mechanisms such as evidence for a reliable relationship between acoustic features of calls and an individual's RHP (be it male age, size, condition, stamina, fighting ability, numeric odds) is not an ultimate explanation for the call. Only experimental playback tests can determine if receivers actually attend to these particular acoustic features (e.g., Kitchen 2004) and thus whether it affects contest outcome and fitness. Likewise, if studies continue to confirm that calls function in intergroup spacing in some population and thus impact fitness, this does not explain the particular strategy employed that resulted in this spatial distribution.

Because their functional significance remains unsettled, the ideal approach to future howler monkey vocal research is to simultaneously address as many alternative hypotheses within each explanatory level as possible, using a combination of systematic observational studies with carefully planned field experiments. Given questions of intergroup relationships are so central in the function of howling, the ideal observational methodology would include multiple researchers observing multiple groups simultaneously (reviewed in Kitchen and Beehner 2007). Because sites and subjects can vary in ways that are only obvious when you have visited them, the same researchers should preferably visit different populations of their species and even different species (we found this to be very enlightening!). Of course, we are aware that these approaches are not always logistically feasible or economically possible. When not cost-effective, we believe researchers would benefit from the kind of collaborative effort we have used to create this review.

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