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Howler Monkeys and Harpy Eagles: A Communication Arms Race

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Introduction

Predation is considered by many researchers to be a selective pressure and strong evolutionary driving force in natural ecosystems. Predation phenomena are dynamic interactions that by definition need more than one agent: at least one predator and one prey. The interaction gets exponentially more complicated when we consider multiple agents and different strategies. These predator-prey interactions can be viewed as evolutionary arms races. There have been numerous studies on prey adaptations (Blumstein et al., 2000; Hauser & Caffrey, 1994; Marler et al., 1992; Endler, 1991; Cheney & Seyfarth, 1990; Hauser & Wrangham, 1990; Ryan et al., 1982), but few report both detailed adaptive responses to predation and ways predators can improve their killing efficiency (Berger et al., 2001). This lack of knowledge is even more striking for predation upon primates (Shultz et al., 2004; Gil-da-Costa et al., 2003; Zuberbühler, 2000a; Zuberbühler et al., 1999).

The adaptation of each agent can take many forms, such as anatomical, physiological, and/or behavioral modifications. In this report I will focus on behavioral modifications that seem to be elicited by communication. More specifically, I will describe a case study of harpy eagles (*Harpia harpyja*) and howler monkeys (*Alouatta palliata*) in the Barro Colorado Island, Panama. Here, the behavioral adaptations of both predator and prey will be reviewed, followed by a brief discussion on data that might provide insights into the neural basis of these adaptations. This chapter will conclude with final considerations and potential applications.

Many field studies have expanded our knowledge on primate communication. Amongst them are the African vervet monkey studies. Vervets possess a specific alarm call system, one that discriminates between leopards, snakes, and eagles. This system includes both call production, with acoustically distinct alarm calls, and perception, with appropriate behavioral escape strategies (Cheney & Seyfarth, 1990; Seyfarth et al., 1980; Struhsaker, 1967). Also, more recently Zuberbühler's (1999) work on Diana monkeys showed again the use of species-specific alarm calls, but now functionally expanding it to *predator-deterrent* calls. In this case call production by the prey contributes to a decrease of the attack rate of stealth predators, since these predators become aware of being spotted. All these findings have strengthened the case for non-human primates as being capable of creating acoustic labels for mental representations and using them as part of their surviving strategies (Zuberbühler, 2000b). Although the core of these studies is commonly associated with conspecific (i.e., intraspecies) communication, several cases have been reported on the use of heterospecific (i.e., inter-species) communication, including communication between different primate species (Zuberbühler, 2000b), primates and birds (Hauser & Wrangham, 1990), and primates and mammal stealth predators (Zuberbühler et al., 1999). In these cases one species seems to be exploiting the other species' acoustic signals.

Seyfarth & Cheney (2003) argued: "In animal communication natural selection favors callers who vocalize to affect the behavior of listeners, and listeners who acquire information from vocalizations, using this information to represent their environment" (p. 250–291). I will argue that this is precisely what happens in the reported interaction between harpy eagles and howler monkeys, and therefore I approach it as a *communication arms race*. It should be noted that, unlike what is offered in previous reports, here I discuss the vocal signals produced by the predator, not by the prey.

My colleagues and I took advantage of a unique situation where two radio-collared harpy eagles were introduced to Barro Colorado Island (BCI), Panama. BCI is home to several primate species, including the howler monkey and has been a biological reserve since 1923, continuously monitored by resident biologists. Harpies have not existed in this region of Panama for at least the last 50 to 100 years (Willis & Eisenmann, 1979).

Methods

Predator: Harpy Eagles (Harpia harpyja)

Harpy eagles are powerful raptor predators. Their name comes from the Greek word *harpe*, referred by Aristotle and others as probably mythological, winged creatures with a vulture's body, strong claws, and a woman's face. This eagle, although in some areas close to extinction, can be found in Neotropical lowland forests of Central and South America. It is the largest raptor species in America, and certainly one of the largest worldwide (Brown & Amadon, 1968). This species is sexual dimorphic with females reaching twice the size of males. A female can grow to an impressive 35 to 41 inches in body length with a 6-foot wingspan and weight between 10 to 20 pounds (The Peregrine Fund, unpublished data). As part of their amazing hunting traits, they have thick tarsus with large hind talons and sharp claws, which together can exert tremendous pressure upon a selected prey. Although they are specialized in hunting arboreal mammals, their diet includes monkeys, sloths, iguanas, large birds, and even the occasional terrestrial prey as big as a deer. The harpy predation strategy can vary depending on prey and environment type (Gil-da-Costa et al., 2003; Palleroni, 2003; Touchton et al., 2002; Rettig, 1978; Fowler & Cope, 1964). Harpy eagles have exceptional aerobatic skills that allow rapid attacks through the trees within the forest canopy.

In this study two adult harpies (one male, one female) were used. The Peregrine Fund, an international organization for the conservation of birds of prey in nature, had previously bred the two eagles and ran radio-tracked releases on the Panamanian mainland. Both eagles, the male (J) and female (MV), had experienced over 9 months of freedom in a natural habitat, including active primate killing, before they were released in BCI during 1999 at 19 and 20 months of age, respectively. At the time of their release into the BCI ecosystem, the eagles were already radio-tagged so that, as in the mainland, it was possible to locate and follow them at all times. This provided us detailed records of locations, general behavior, hunting strategies, predation attempts, and kill rates for both eagles. During a period of over 15 months harpy eagles were present in BCI. The pair flew over almost the entire island (1564 ha). However, they preferred hunting grounds on the west side of BCI, spending about 75% of their time within 100-ha home ranges on the western extreme of the island. Altogether, this allowed for a period of almost continuous observation of their natural behavior in the wild for 450 days—240 days in the mainland and 210 days in BCI.

Prey: Howler Monkeys (Alouatta palliata)

The mantled howler monkeys (*Alouatta palliata*) present in Barro Colorado Island are anthropoid primates from the Family: Cebidae. Adult males are estimated to weigh from 16 to 20 pounds with an average length of 45 inches and adult females from 12 to 18 pounds with an average length of 43 inches (Carpenter, 1965). The mantled howler diet consists mostly of leaves, fruits, and flowers from canopy trees. According to a census of the BCI population done in 1977, 65 troops exist in the island, with an average of 19 individuals *per* troop (Wong & Ventocilla, 1995).

Previous studies made on the BCI howler population focused on foraging, physiology, population density, population growth and social behavior (Froehlich et al., 1981; Gaulin et al., 1980; Milton, 1980). Although extensive research has gone into these issues, only a few studies address this genus' vocal repertoire, where their vocalizations were functionally associated with inter-troop spacing, conspecific competition, and sexual selection (Sekulic & Chivers, 1986; Baldwin & Baldwin, 1976; Chivers, 1969). The harpy eagles seemed to use the loud howler roars, a characteristic vocalization from this species, as their localizer of the monkey troops (Palleroni, Touchton & Gil-da-Costa, unpublished data). Before the harpies' introduction the primate populations in BCI (Geoffrey's marmosets, capuchins, spider, and howler monkeys) had no significant mammal, bird, or snake predation (Carpenter, 1965). With the lack of relevant predators, pathogens seem to have been the controlling factor of the howler monkeys population in the island (Milton, 1996). Howlers are parasitized by larvae of the cuterebrid (*Alouattamyia baeri*), resulting in relevant host mortality. Until 1999 the lack of growth of the howler population on BCI was probably mostly a consequence of the primary and secondary effects of this parasitism.

Behavioral Observations

Barro Colorado Island has great logistic conditions offered by the Smithsonian Tropical Research Institute. It houses several laboratory and dormitory amenities while an organized network of trails enables access and orientation. Starting in July 2000, two extra observers joined the Peregrine Fund team and divided their daily time (approximately six hours of observation) between following the harpy eagles and recording both their behavior as well as the encountered howler troops; and scouted, localized, and recorded the behavior of howler troops without the eagles' presence. The observers positioned themselves between approximately 10 to 30 m of the howler groups and at varied distances from the eagle. Data collection from this part of the study was mostly done in a qualitative manner. Observed descriptions of harpy and howler behaviors, both when the animals were on their own and when they interacted, were recorded. Observation time and duration for each event were varied and determined opportunistically in the field.

Playback Experiments

Using howler troops previously localized during the observational part, the playback study included two groups—the "exposed group" and the "control group." The exposed group consisted of 10 troops of howler monkeys dispersed within BCI (3 troops off Stanley trail, 3 troops off Armour trail, 2 troops off Zetek trail, 1 troop off Snyder Molino trail, and 1 troop off Pena Blanca trail). The control group consisted of 5 troops in the Gigante Peninsula. Each group of howlers was only tested a single time.

The following protocol was used: First we located both the male and female harpy eagles using radio telemetry, and then we moved a minimum of 1000 m away from the eagles, but within their home range (only in BCI); next, we located a group of howler monkeys and established a position within visual and auditory proximity to the group; two experimenters remained between 5 and 15 m from the group while a third one, carrying a speaker, moved to an occluded position approximately 30 m away from the howler group. We waited between 15 to 30 min to allow the animals to habituate to our presence. Once the animals were calm, a sample started as soon as an appropriate subject was selected. Throughout the trial one experimenter recorded a 60-sec focal sample on an adult male approximately every 2 min. During a sample, the recorded information included foliage density, spatial position, vigilance rate (percentage of time spent scanning per 60-sec sample), direction of scanning and "other behavioral activities" ("resting," "moving," "foraging," and "socializing"). The resting, moving, foraging, and socializing activities were scored as either "present" or "absent" in each 60-sec sample.

We never conducted focal samples on animals that were in a position scored over 1 on Cords (1990) scale for foliage density, which classifies foliage as "sparse" (0), "medium" (1), or "dense" (2). We used Treves' (1997) definition of "vigilance" as scanning beyond arm's reach. Resting was scored when the focal animal had its eyes closed; socializing included social and allogrooming, as well as play. Since videotaping was not possible due to the density of the forest, one experimenter recorded behavioral data onto a handheld computer, while a second experimenter scored the spatial position (absolute and relative) of each visible animal within the group, once every 6min, meaning one sample at the beginning and two after playback for a total of 3 samples. Behavioral data were collected for 5 min prior to playback, during playback and 10 min post-playback, although sometimes the pre-playback recording period was extended to 6 or 7 min due to factors unrelated to our experiment objective (e.g., subjects moved briefly out of view, equipment problems, etc.). This sampling was based on the established times for assessing baseline behaviour and stimulus effect and decay from previous reported studies, as well as pilot data collected prior to the playback study.

The third experimenter, who occluded the speaker, controlled the stimuli playback. In the 2000 season, the playbacks consisted of different exemplars of the call produced by the female harpy during prey pursuit; a playback presentation included two bouts of calls separated by a 120-sec silence interval. During the 2001 study period, the BCI howlers' response to 8 different calls (4 from harpy eagles, including the male and female introduced on BCI, plus another 4 from a male and female unfamiliar to the howler population) was tested. Different exemplars were used to avoid problems of pseudoreplication and test for discrimination of harpy calls by individual, sex, and familiarity. Other colleagues and I also broadcast other acoustic stimuli as an acoustic control condition. The control stimuli were tinamou (*Tinamus major*) and bald eagle (*Haliaeetus leucocephalus*) calls. The tinamou is native to BCI, and thus, its calls are likely to be familiar to howlers, but non-threatening. Like harpies, the bald eagle is a raptor, but is non-native to Panama; its calls are therefore unfamiliar to the study population of howlers. During the 2000 study season we broadcast the harpy calls using a Sony DAT TCD-D8 recorder and a portable Sony SRS speaker (frequency response = 70 Hz to 20 kHz; mean amplitude: 67.2 dB SPL; range: 58.3 to 79.8 dB SPL at 10 m from the speaker); during the 2001 study season, we used a Sony D-191 CD player and a portable Cambridge Soundworks customized speaker (frequency response = 60 Hz to 18 kHz with broadcast values at 10 m as follows: harpy—mean amplitude: 66.66 dB SPL; range: 58.3 to 78.4 dB SPL; tinamou—mean amplitude: 67.8 dB SPL; range: 57.65 to 79.2 dB SPL; bald eagle—mean amplitude: 67.2 dB SPL; range: 57.98 to 78.8 dB SPL. The speaker was occluded at a mean distance of 30(+/–5) m from the closest animal within the howler group. The mean duration of playback stimuli was 159 sec (range: 148–168 sec). We did not initiate playbacks in groups that remained agitated after 30 min of our arrival and aborted every trial in which the focal animal was out of the observer's visual range for more than 2 min. Following these aborted attempts, we searched for another group of howlers, and moved to a distance of approximately 1000 m if the playback stimulus had been broadcast. Approximately 35% of the trials were aborted.

Results

The Predator's Perspective: Harpy Eagle Assessment Calls

Attacks with successful kills covered a period of 294 days, during which the female captured prey every 4.39 days and the male every 3.71 days. Taking a closer look at the type of prey captured, it was verified that 34.78% of female and 12% of the male prey were primates (Palleroni & Hauser, 2003; Touchton et al., 2002).

The surprising finding, however, was the strategy these eagles seemed to use to hunt their primate prey. Instead of rapid stealth attacks, the eagle would perch in a tree nearby, in plain view of the monkey troop, observe the animals and then utter a series of calls (Gil-da-Costa et al., 2003) (Figure 14.1). These calls always presented the same acoustic structure, being composed by two different elements. A first element uttered only once at the beginning, followed by multiple repetitions of the second element. Observations on and off BCI indicated that this hunting behavior occurred before prey pursuit and only when engaging primate prey (Palleroni & Gil-da-Costa, unpublished data). In the 35 observed cases where the howler monkeys displayed a coordinated defensive response (i.e., increased vigilance, group repositioning, etc.) after the harpy calls, the eagles either moved to a different troop or delayed the attack, hunting later by stealth. When the howlers' response was minimal or chaotic the eagles' approached and in most cases performed the attack. Therefore, the question of whether the eagle delayed the attack, moved to search for another troop, or struck seemed to be contingent on the preys'

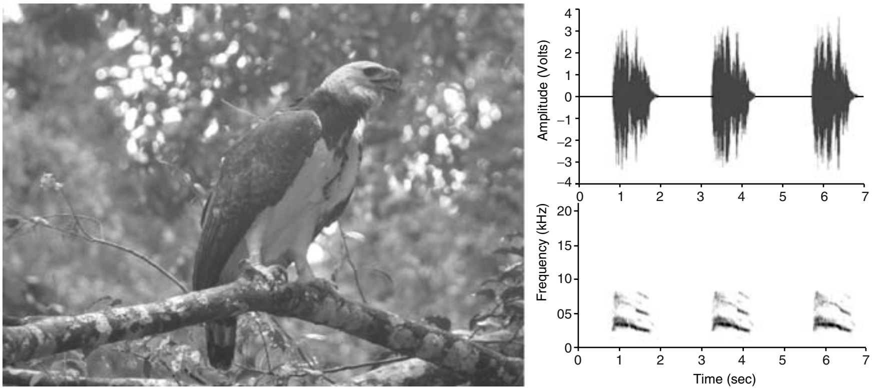


FIGURE 14.1. Female adult harpy eagle (MV) uttering a call during the study. The tagging and the radio antenna used for tracking are noticeable in this photograph of the eagle. Waveform and spectrogram of harpy eagle vocalizations used in the study

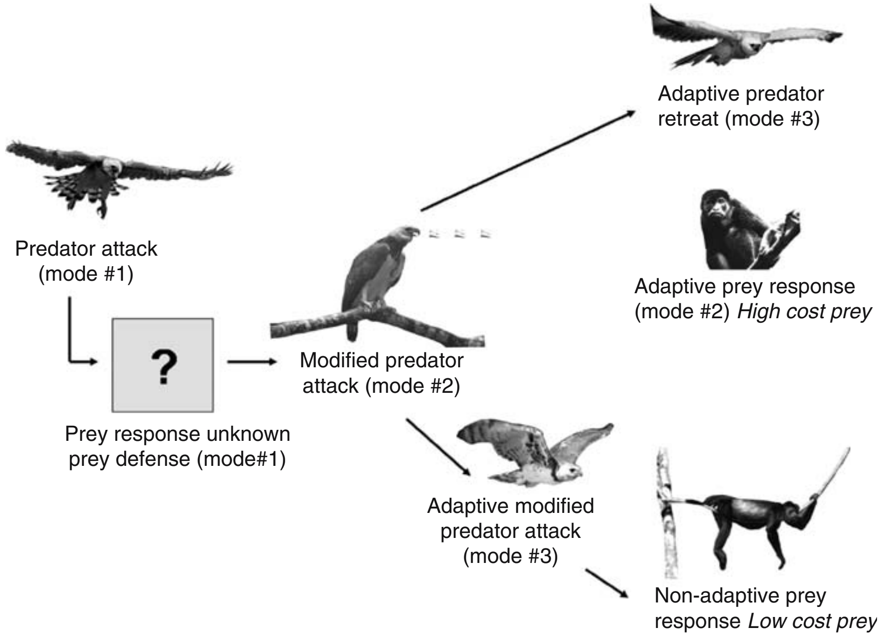


FIGURE 14.2. Communication arms race. In "Predator attack (mode #1)" the eagle spots its prey from the distance and attacks by surprise; In "Prey response unknown—Prey defense (mode #1)" the predator does not know a priori the prey's defense strategy, which makes it vulnerable to rapid prey protective responses. The prey is unaware of the predator's potential attack, therefore it is only possible to produce a *last minute* response; in "Modified predator attack (mode #2)—Predator-assessment call" The predator's attack is modified to a probing strategy, vocalizing in full view and observing the prey's response *before* attacking; when the prey's response is non-adaptive, either disregarding the eagle or displaying a panic chaotic response, then "Adaptive modified predator attack (mode #3)" is elicited and the eagle moves to a rapid striking attack.; in contrast, when howlers show an anti-predator response "Adaptive prey response (mode #2)", including increased vigilance, upward scanning, and coordinated group protective measures (mothers and infants move closer to trunk, males to more distal positions in branches), then "Adaptive predator retreat (mode #3)" occurs, with the eagle flying away in search of another troop

behavioral response (Figure 14.2). While this behavior was observed with both howler and capuchin monkeys, we focus here on the howler monkey predation since it accounted for 81% of the female and 100% of the male primate captures (Palleroni, in prep.; Touchton et al., 2002).

The Prey's Perspective: Howler Monkeys "Live and Learn"

Based on the data collected in the first part of our study in which we documented naturally occurring encounters between the harpy eagles and howler troops, we believe that the reintroduction of these raptors may have triggered an adaptive

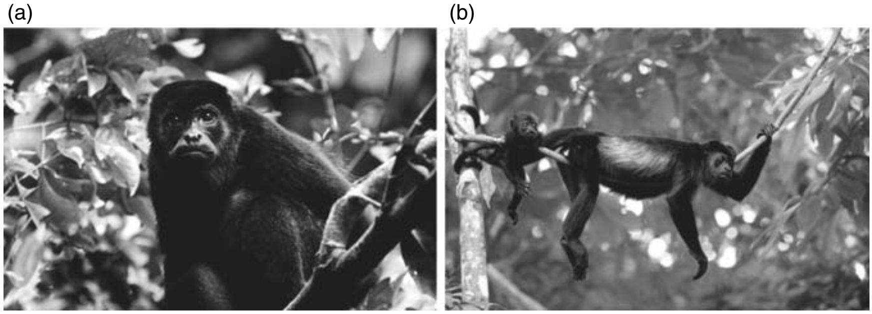


FIGURE 14.3. a. Vigilant howler monkey. b. Adult and young howler monkeys at rest

anti-predator response by the primate populations. When the monkey troop seemed to react with a vigilance increase (Figure 14.3a) and group protective measures (such as the adult males moving to distal branch positions, placing themselves between the eagle and rest of the troop, and females carrying their infants to more occluded positions near the trunk, where it is harder for the eagle to maneuver) the eagle would typically leave and search for another group to prey, or return later to the first troop but then hunt by stealth. In the cases where monkeys either remained calm (Figure 14.3b) or reacted with random panic agitation, the eagle initiated pursuit in a rapid flight, through the trees, directed at its chosen animal target (Figure 14.4), in most events making a kill. Considering the strong association between this harpy call and the predatory attacks, one would expect that an adaptive learning mechanism could arise from it. Since these calls are given in a hunting context and the prey's response to it influences the predator's attack strategy, we gave the call a probe function, naming it a "predator-assessment" call. Also, to further explore this possibility we ran a playback study using the howlers as our primate subjects.

Experimental Playback

Using the harpies' hunting strategy of calling prior to attack to our advantage, we broadcasted their species-specific call to various howler troops. The assumption was that this call would not only be associated with the eagles' presence but also with the recognition of the eagle as a predator. Building from previous playback studies where it was shown that both primate and non-primate animals were able to recognize and react to predators based on acoustic cues alone (Zuberbühler et al., 1999; Hauser & Caffrey, 1994; Cheney & Seyfarth, 1990; Hauser & Wrangham, 1990), here, myself and colleagues explored how fast this adaptive behavior emerges in howler monkeys and the specificity of their responses.

The program of localization and observation of howler monkey troops in BCI was extended to Gigante, an adjacent peninsula. The population in Gigante is estimated to be smaller than in BCI, but in both cases there have not been any

FIGURE 14.4. Harpy eagle (MV) in rapid flight through the canopy

significant predators for the last 50 to 100 years. Therefore, the Gigante peninsula, out of reach of the newly introduced harpy eagles, presented the ideal "control" population for our study.

The observational data collection started approximately one year after the raptors' introduction to the island. Once the necessary number of monkey troops was located and their natural occurring interactions with the eagles (in BCI) and their baseline behavior (in both BCI and Gigante) were recorded, it was possible to initiate the experimental playback part of the study.

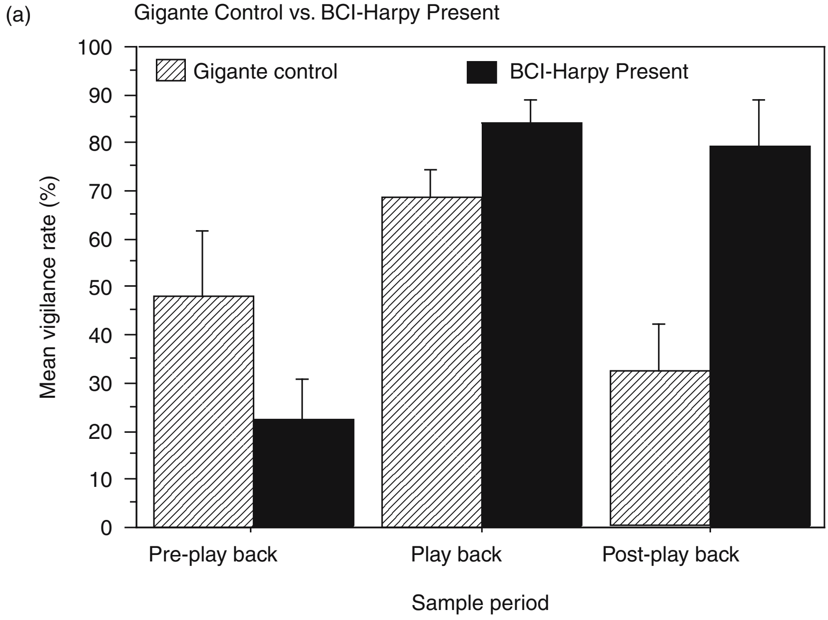
Throughout two research seasons, 2000 and 2001, harpy eagle calls (from both familiar and unfamiliar harpies) were broadcasted from a hidden speaker to the exposed troops in BCI and to the control groups in Gigante. I refer to these as "BCI harpy present" and "Gigante control," respectively. During the 2001 season two acoustic controls, tinamou (*Tinamus major*) and bald eagle (*Haliaeetus leucocephalus*) calls were broadcasted to the BCI howlers. The former, a common bird in BCI that, although known to the monkeys, does not represent a threat, and the latter a raptor, like the harpy eagle, but one that does not exist in Panama, therefore unfamiliar to the monkeys. These playbacks were labeled "BCI control." Finally, also during the 2001 research season, approximately seven months after the eagles were withdrawn from the island, the howler troops in BCI were tested again with harpy eagle calls, assessed for potential maintenance or extinction of their specific anti-predator response. For analysis purposes these data were labeled "BCI harpy absent." As stated in the methods section, several parameters were tested and recorded during each playback condition. The behavioral parameters studied included vigilance rate, direction of scanning, display of other behavioral activities (resting, moving, foraging and socializing), and utterance of alarm calls.

Vigilance Rate

Focal behavioral samples were recorded during three different periods: pre-playback, playback, and post-playback. Within BCI it was possible to observe some variation in the level of predation exposure for the several tested groups. Nevertheless, there were no statistically significant differences within the studied troops in BCI, or in Gigante, regarding vigilance rate (BCI: $n = 60$, $H = 9.0$, $p = 0.4373$; Gigante: $n = 30$, $H = 4.0$, $p = 0.4060$) (Gil-da-Costa et al., 2003). However, when we compare vigilance rates between the exposed BCI howlers (BCI harpy present) and the Gigante troops (Gigante control) (Figure 14.5a), we find there is a highly significant difference across the two conditions ($n = 90$, $F = 16.553$, $p < 0.0001$) (Gil-da-Costa et al., 2003). This finding indicates a learned adaptive vigilance response in the BCI howlers that can be elicited by the harpy call alone. Moreover, this result was replicated one year later, seven months after harpy absence. There was no significant difference in vigilance rate between the conditions "BCI harpy present" and "BCI harpy absent" ($n = 96$, $F = 0.108$, $p = 0.8977$) (Gil-da-Costa et al., 2003). The vigilance rate was also shown to be specialized for the harpy eagle call, since it was not elicited by the other playback stimuli tested during the condition "BCI control" (Figure 14.5b). The vigilance rates for "BCI control" significantly differed from those during "BCI harpy absent" ($n = 60$, $F = 16.591$, $p = 0.0001$) and did not differ from "Gigante control" ($n = 54$, $F = 0.501$, $p = 0.0823$) (Gil-da-Costa et al., 2003).

Harpy calls from different individuals were used, namely from MV, J, and other unfamiliar harpies. There were no significant differences in the howlers' vigilance response when we compared responses to harpy calls from the different individuals (male vs. female harpies: $n = 36$, $F = 0.925$, $p = 0.6325$; MV vs. other harpies: $n = 36$, $F = 0.841$, $p = 0.4661$) (Gil-da-Costa et al., 2003). There was also no differential response between the two control stimuli (tinamou vs. bald eagle: $n = 24$, $F = 3.002$, $p = 0.4676$) (Gil-da-Costa et al., 2003). This indicates a recognition and behavioral response selective for the harpy eagle species call, independent of individual familiarity.

Further analysis of the temporal patterning of playback responses revealed significant differences between tested conditions. In the BCI howlers, both with harpy presence and absence, the vigilance increase seen during playback was maintained during the post-playback period, as one would expect, considering the danger level that this predator imposes. In the Gigante populations, however, the response significantly decreased between playback and post-playback periods, leading to the conclusion that the initial increased vigilance was novelty response rather than predator recognition (Figure 14.6). As stated before, the acoustic control stimuli never elicited a protective response.



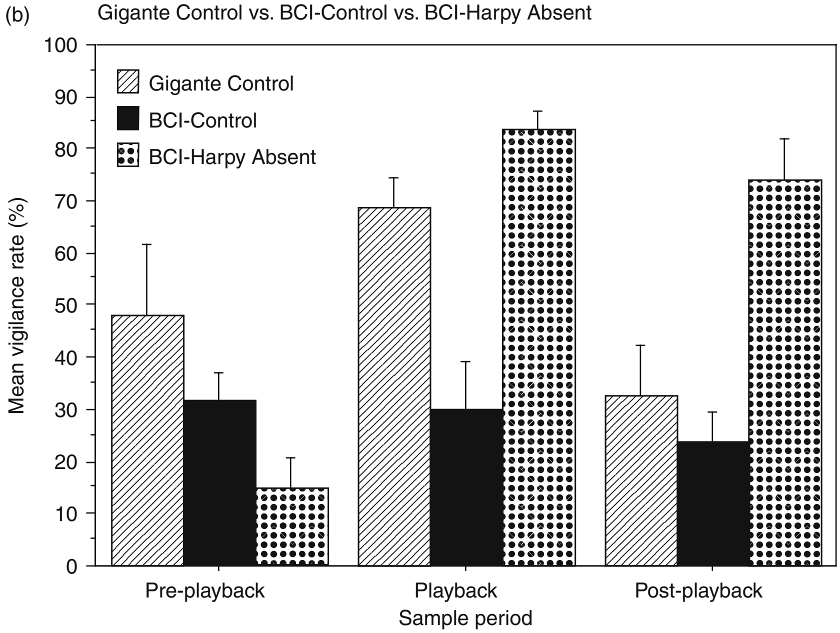


FIGURE 14.5. a. Mean vigilance rates of the howler monkey groups on BCI and in Gigante, during the period of harpy presence. b. Vigilance rates of the howler groups for the various experimental conditions. (Adapted from Gil-da-Costa et al., 2003)

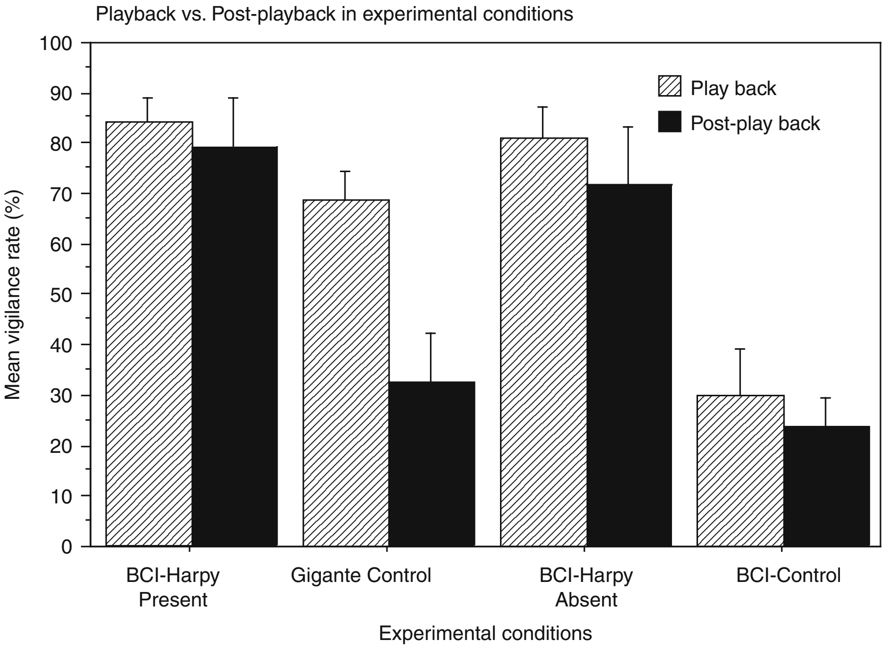


FIGURE 14.6. Mean vigilance rates of the howler groups during the playback and post-playback periods in the various experimental conditions. (Adapted from Gil-da-Costa et al., 2003)

Direction of Scanning

Further behavioral responses contributed to complement the picture of complex anti-predator behavior elicited by the harpy call playback. The BCI howler monkeys scanned upward significantly more than the other groups (BCI harpy present vs. Gigante control: $n = 60$, $\chi^2 = 13.33$, $p = 0.0025$; BCI harpy absent vs. Gigante control: $n = 44$, $\chi^2 = 9.6$, $p = 0.0165$; BCI harpy absent vs. BCI control: $n = 40$, $\chi^2 = 10.91$, $p = 0.0086$) (Gil-da-Costa et al., 2003). Even though the speaker was hidden far away and beneath the monkeys' position in the trees, in BCI the animals scanned upward to areas above them where typically a harpy eagle would perch. The Gigante howlers would orient toward the real sound source location, i.e., the speaker.

Display of Other Behavioral Activities

Quantitative study of the display level of other behavioral activities was carried out using a comparison of the percentage of time the animals would spend resting, moving, foraging, and/or socializing, as described in the methods section. When we compared the display level of these behaviors between the four experimental conditions, we found only one significant difference, namely, howler monkeys in BCI display resting behavior significantly less frequently than the troops in Gigante ($n = 128$, $\chi^2 = 6.196$, $p < 0.05$).

Also, descriptive reports show sex differences as part of a complex protective behavior. After hearing the eagle's call, adult males would often move to more distal positions in the branches, sometimes clustering in the direction of the potential eagle presence and assuming mobbing positions, but the females would pick up the younger infants and move closer to the trunk, as though trying to occlude themselves in harder to maneuver, more dense areas of the canopy. In some cases, different members of the troop would produce alarm calls, but this did not occur during every playback trial.

Altogether, these results show that howler monkeys acquired a selective anti-predator response in a period of one year or less of exposure to harpy eagles. This adaptive response suggests recognition and association of an acoustic cue to a mental representation of a specific predator threat. Also, it was shown that the howlers' sensitivity to the harpy call and appropriate protective behavior was maintained for at least seven months after the predators were removed. How long this protective behavior will be maintained remains an interesting open question.

Discussion

Another Piece of the Story

The study reported here refers to behavioral adaptations within the harpy eagle–howler monkey predator-prey interaction. However, another interesting piece of this dynamic puzzle is the neurophysiological adaptations underlying the behavioral changes. Previous work has presented convincing cases of prey adaptation to predators' acoustic signals at both the behavioral and neurophysiological levels. The bat-moth interaction is a well-studied and quite illustrative case. Noctuoid moths are under severe predation from bats as the moths conduct their night flights (Hoy et al., 1989). During a night time scenario sound is the main communication and cueing channel between predator and prey. The auditory system of noctuoid moths has been intensively studied as a model for anti-predator adaptations (Fullard, 2003; Roeder, 1975). Bats perform prey location by using a biosonar system, and moths have adapted hearing to be sensitive to the range of ultrasonic frequencies present in the bats' biosonar signals (Hoy et al., 1989; Roeder, 1975). When flying, moths can react to detection of the bats' ultrasounds by rapidly altering their behavioral output, in this case their flight pattern. Amongst different groups moths have evolved anti-predator abilities that range from ultrasonic hearing detection, to evasion strategies and bat sonar jamming techniques (by producing loud clicks) (Fullard, 2003; Rydell, 1998; Hoy et al., 1989; Roeder, 1975). Similar cases can be found in other phylogenetic groups and different ecosystems. In the ocean, for example, the American shad (*Alosa sapidissima*), a bony fish, developed ultrasonic hearing to match the frequencies of the echolocation system of one of its stronger predators, the dolphin (*Tursiops truncatus*) (Mann et al., 1998, 1997). This fish species seem to have developed behavioral and neurophysiological adaptations to counteract selective pressures from echolocating odontocete cetaceans. These systems demonstrate clear cases of an evolutionary arms race based on coupled behavioral and neurophysiological adaptations. The understanding of the underlying mechanisms of brain physiology relating to these rapid adaptations brings a valuable insight. Although there are no studies exploring the neural basis of acoustic perception in the howler monkey, there are interesting, and, I believe, relevant, findings in the harpy eagle.

The same head-orienting technique utilized to explore perceptual asymmetries during auditory processing in primates (Hauser & Andersson, 1994) and sea lions (Boye, 2005) was used to test harpy eagles. The technique consists of the playback of sounds from an occluded speaker centered behind the subject's back. The subjects' response is video-recorded and later blindly scored as the percentage of head-turns to each side for every stimulus category. Because an orienting bias increases the strength of the signal entering the leading ear, it is likely to create a processing bias with respect to the contralateral hemisphere. Therefore, a systematic head-turning to the right, for instance, would imply a left hemispheric bias.

Two groups of harpy eagles were tested. One group experienced in hunting howlers and another naïve to hunting this primate. Both groups were tested with sets of harpy eagle calls (conspecifics) and howler vocalizations. Results showed that both naïve and hunting expert eagles presented a left hemispheric bias for their own vocalizations. However, for the howler monkey calls the naïve harpies show a right hemisphere bias and the experienced harpies show a left hemisphere bias (Palleroni & Hauser, 2003). This finding provides evidence of an orienting response and, by implication, a brain hemispheric bias that can be altered by explicit hunting experience. This supports the idea of adaptive plasticity for the processing of acoustic cues, which can be molded within the animals' life by predation experience. It provides a rapid physiological adaptation that can accompany, and probably support, the adaptive behavioral strategy. Building from previous work in other primate species (Gifford et al., 2005; Gil-da-Costa et al., 2004; Poremba et al., 2004; Ghazanfar, 2003), it would be very valuable to explore the neural basis, and perhaps plasticity, of auditory processing in the howler monkey, expanding the understanding of auditory-driven interactions. Only with further knowledge regarding the occurrence of this type of brain adaptation across different taxonomic groups and in which contexts the adaptation appears, can we better understand the implications and functionality of this finding.

Conclusions

The findings reported here, besides providing additional support for previous general findings (Berger et al., 2001; Bshary, 2001; Caro, 1995; Woodland et al., 1980), go further by demonstrating: (i) how rapid primate prey adaptation can be within one generation; (ii) the maintenance of the response following predator absence; and (iii) the importance and use of a predators' call in prey assessment.

To minimize risk and increase efficiency a predator needs specific critical information about its target prey. Namely, the level of prey alertness and relative escape ability, its defense mechanisms, and its nutritional value (Hasson, 1991). My colleagues and I argue that by using this *predator-assessment* call, harpy eagles extract more accurate and extensive information regarding the first three items than they would by using mere visual observation alone, prior to an attack. By probing the potential defense strategies of the prey before engaging in confrontation, the predator can assess the attack risk and make an a priori decision, minimizing risks from surprise defenses during attack. The prey can also benefit from this advanced warning by developing defense/escape strategies and gaining more time to prepare to counteract the attack. One may then ask, if the predator is seemingly back at step one, what is the point of it all? Indeed, the predator loses the ambush/surprise advantage but gains a better control of the situation by learning about the preys' abilities and therefore choosing more vulnerable prey. This risk avoidance may provide an altogether better fitness. From the preys' perspective there is a clear advantage in developing specific anti-predator behaviors that can be elicited by this auditory cue prior to attack. We can speculate that this trend will gradually occur in all exposed prey, developing in them anti-predator behaviors and increasing their fitness. If this happens in the whole population it will ultimately cancel any advantage for the predator to call. At which point in time the predator would have to create another modified behavior, exploring alternative strategies.

And so the arms race continues. It is important to keep in mind, at all times, that predator-prey interactions are dynamic, and more than finding definitive solutions each agent tries to have at least a temporary advantage.

In an attempt to model predator-prey adaptive behaviors Jim & Giles (2000) used a genetic algorithm to evolve multi-agent communication systems for the predators in an artificial version of the predator-prey interaction. Their simulations show that predators' performance in prey pursuit increases with the evolution of a communication system. There are numerous studies reporting cooperative hunting between predators, from wolves to lions to chimpanzees, some of them presenting cases where communication plays a crucial role (McGregor, 2005; Stanford, 1998; Heinsohn, 1995; Boesch & Boesch, 1989; Schaller, 1972). However, these studies refer to communication between conspecifics. That is, multiple individuals from the same species communicate amongst themselves in order to perform elaborate group hunting strategies resulting in coordinated attacks. This is different from the harpy eagle–howler monkey case, where communication seems to occur between the different species, between predator and prey. One can hypothesize that, in a case like this, communication can ultimately lead to temporary beneficial adaptations in both species if the two of them can explore the use of the acoustic signal in a way that increases each one's fitness.

The inexistence of a protective response in the Gigante howlers that were only exposed to harpy predation over 75 years ago leads to the conclusion that those monkey populations lost their ability to recognize this predator's call and elicit an anti-predator response. The call of a predator that has long been extinct in an area will not re-elicit response in a prey who first hears it; hence, this prey is highly vulnerable to first encounters with such a predator. The situation in Gigante contrasts with the situation of the newly re-exposed population in BCI, which in a short period of time (less than one generation) developed recognition and specific anti-predator mechanisms.

As a final note I would like to stress the applicable conservation implications beyond the theoretical study of predator-prey interactions and animal communication. The extinction of large predators worldwide has provoked tremendous ecological imbalances, leaving mammal (including primate) prey without predation pressures. This loss of anti-predator response makes them extremely vulnerable to new predators and, as such, re-population attempts of extinct predators can have catastrophic consequences over prey populations (Gittleman & Gompper, 2001). The use of potential predator-assessment calls, as well as other relevant training cues in prey population assessments, prior to a full scale predator re-introduction, should help prepare populations for an adequate and balanced interaction. This kind of methodology could prevent, or at least significantly reduce, some of the negative impact of predator re-population over prey species.

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