

# Rapid acquisition of an alarm response by a neotropical primate to a newly introduced avian predator

Ricardo Gil-da-Costa<sup>1,2\*</sup>, Alberto Palleroni<sup>1</sup>, Marc D. Hauser<sup>1</sup>, Janeene Touchton<sup>3</sup> and J. Patrick Kelley<sup>1</sup>

<sup>1</sup>Primate Cognitive Neuroscience Laboratory, Department of Psychology, Harvard University, Cambridge, MA 02138, USA

<sup>2</sup>Program in Biology and Medicine, Gulbenkian Science Institute, Lisbon, Portugal

<sup>3</sup>Neotropical Raptor Center, The Peregrine Fund, Panama City, Panama

Predation is an important selective pressure in natural ecosystems. Among non-human primates, relatively little is known about how predators hunt primate prey and how primates acquire adaptive responses to counteract predation. In this study we took advantage of the recent reintroduction of radio-tagged harpy eagles (*Harpia harpyja*) to Barro Colorado Island (BCI), Panama to explore how mantled howler monkeys (*Alouatta palliata*), one of their primary prey, acquire anti-predator defences. Based on the observation that harpies follow their prey prior to attack, and often call during this pursuit period, we broadcast harpy eagle calls to howlers on BCI as well as to a nearby control population with no harpy predation. Although harpies have been extinct from this area for 50–100 years, results indicate that BCI howlers rapidly acquired an adaptive anti-predator response to harpy calls, while showing no response to other avian vocalizations; howlers maintained this response several months after the removal of the eagles. These results not only show that non-human primates can rapidly acquire an alarm response to a newly introduced predator, but that they can detect and identify predators on the basis of acoustic cues alone. These findings have significant implications both for the role of learning mechanisms in the evolution of prey defence and for conservation strategies, suggesting that the use of ‘probing’ approaches, such as auditory playbacks, may highly enhance an *a priori* assessment of the impact of species reintroduction.

**Keywords:** predator–prey arms races; playbacks; predator-assessment calls; evolutionary mechanisms; conservation biology

## 1. INTRODUCTION

Predator–prey interactions are commonly viewed as evolutionary arm races. Although there have been many studies documenting how animals respond to predators (Ryan *et al.* 1982; Cheney & Seyfarth 1990; Endler 1991; Marler *et al.* 1992; Hauser 1996; Blumstein *et al.* 2000), relatively few studies reveal both how predators hunt prey and how prey acquire an alarm response to a novel or newly introduced predator (Berger *et al.* 2001). This gap in our knowledge is particularly striking for primates (Zuberbühler *et al.* 1999).

To fill this gap, we took advantage of the recent reintroduction of two radio-tagged harpy eagles to Barro Colorado Island (BCI), Panama. Harpies have not been observed in the BCI region of Panama for 50–100 years (Willis & Eisenmann 1979). With the exception of rare accidental sightings, harpy eagles have been absent from forests bordering the Panama Canal since the commencement of activity in the Panama Canal. BCI has been a biological reserve since 1923, continuously monitored by resident biologists for the last 79 years and, with the

exception of the introduced pair, no harpy eagles have resided there during this period.

The harpy eagle, typically found in neotropical forest, is the largest raptor in America and one of the largest in the world (Brown & Amadon 1968). It is uniquely specialized for foraging in the canopy, hunting mostly arboreal mammals. Although few detailed field studies have been conducted, observations suggest that harpies prey on monkeys, sloths, iguanas, large birds and, occasionally, terrestrial prey such as deer. Predation strategies vary depending on prey and environment type (Fowler & Cope 1964; Rettig 1978; Touchton *et al.* 2002; Palleroni 2003). Moreover, with the exception of occasional visits from boas and large cats, the non-human primate population on BCI (howlers, capuchins, spider monkeys, Geoffrey’s marmosets) has had no other relevant predators.

The reintroduction of these eagles may have led to the triggering of an adaptive anti-predator response by the howler and capuchin populations. The last census of mantled howler monkeys on BCI was conducted in 1977 and indicated the presence of 65 troops, each with an average of 19 individuals (Wong & Ventocilla 1995). Extensive studies have been made on the BCI howler population regarding foraging, physiology (Milton 1980), population density, population growth and group behaviour (Gaulin *et al.* 1980; Froehlich *et al.* 1981). Relatively fewer studies have been conducted on the howler mon-

\* Author and address for correspondence: National Institutes of Health, 10 Center Drive, MSC 1366 Building 10, Room 4C103, Bethesda, MD 20892-1366, USA (rcosta@helix.nih.gov).

keys' vocal repertoire (Baldwin & Baldwin 1976; Sekulic & Chivers 1986), especially their use of anti-predator alarm calls. It is important to note that until the reintroduction of the harpies, the howler population had not been exposed to predation from mammals, birds or snakes (Carpenter 1965; Milton 1996); pathogens are likely to have been the most important regulators of the howler population on BCI.

We explore whether howler monkeys acquired an adaptive anti-predator response to harpy eagles even though the period of exposure was less than one year. Instead of documenting naturally occurring encounters with harpies, we used playback experiments to simulate harpy presence. In particular, we took advantage of the fact that harpies often call prior to attacking their prey to broadcast a species-typical call, clearly associated not only with their presence, but their potential threat as a predator. The logic of our study therefore follows other playback studies where both primate and non-primate species demonstrated the capacity to recognize predators on the basis of acoustic cues alone (Cheney & Seyfarth 1990; Hauser & Wrangham 1990; Hauser & Caffrey 1994; Zuberbühler *et al.* 1999). We explore this further by investigating the specificity of this response, and the extent to which it depends on explicit experience with harpies.

## 2. MATERIAL AND METHODS

The adult male harpy (J) was released on BCI in June 1999 at 19 months of age, having previously experienced 10 months of freedom (or since fledging) and 5 months of active killing (he had captured only a few howler preys). The adult female (MV) was released in October 1999 at 20 months of age, with a history of 14 months of freedom (or since fledging) and 8 months of active killing (with many howler captures on her prey list). The initial phase of our study, involving observational data on the howler monkeys and playbacks of 'BCI harpy present' and 'Gigante control', started in July 2000, approximately 12 and 8 months after the male and female introductions to the island, respectively.

Both birds were radio-tagged making it possible to locate, follow and keep a detailed record of their daily behaviour, including their location, predation attempts, kill rates and hunting strategies. Both eagles were present on BCI for a period of approximately 15 months, and at least one of them was present for a period of 18 months. The eagles flew over almost the entire island (1564 ha). Based on our tracking data however, they favoured hunting grounds on the west side of BCI. Both eagles hunted the entire island but spent most of their time (75%) within 100 ha home ranges on the western extreme of the island.

Each group of howlers was only tested once. During the year 2000 study, 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 120 s. In the 2001 study period, we tested the response of howlers on BCI to eight different calls from four harpy eagles, including the male and female introduced on BCI and another male and female that were unfamiliar to both howler populations. We used different exemplars to both avoid problems of pseudoreplication and to test for discrimination of harpy calls by individual, sex and familiarity. The control stimuli were tinamou (*Tinamus major*) and bald eagle (*Haliaeetus leucocephalus*) calls. The tinamou is native to BCI, and its calls are therefore 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.

We used the following protocol for each trial with the howler groups. First, we located both the male and female harpy eagles using radio telemetry, and then moved a minimum distance 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 observers were stationed between 5 and 15 m from the group while the third observer, carrying a speaker, moved to an occluded position *ca.* 30 m from the group. We waited for 15–30 min to allow the animals to habituate to our presence. During this time we determined age–sex classes of the individuals in the group. Throughout the trial, one observer recorded a 60 s focal sample on an adult male, approximately every 2 min. A sample started as soon as an appropriate subject was selected. During the sample, we recorded information on foliage density, spatial position, vigilance rate (percentage of time spent scanning per 60 s sample), direction of scanning and 'other behavioural activities' (resting, moving, foraging and socializing). The 'resting', 'moving', 'foraging' and 'socializing' activities were scored as either present or absent in each 60 s sample.

We never conducted focal samples on animals that were in a position that scored over 1 on the Cords (1990) scale for foliage density, which classifies foliage as sparse (0), medium (1) or dense (2). We used Treves's (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 allo-grooming, as well as play.

Videotaping was not possible owing to the density of the forest. Therefore, one observer recorded behavioural data on a handheld computer, while a second observer scored the spatial position (absolute and relative) of each visible animal within the group once every 6 min, resulting in one sample at the beginning and two after playback for a total of three samples. Behavioural 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 owing to factors unrelated to our experiment (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 studies, as well as pilot data collected prior to our study.

During the year 2000 study, we broadcast the harpy calls using a Sony DAT TCD-D8 recorder and a portable Sony SRS speaker (frequency response: 70 Hz–20 kHz; mean amplitude: 67.2 dB SPL; range: 58.3–79.8 dB SPL at 10 m from the speaker); during the year 2001 study, we used a Sony D-191 CD player and a portable Cambridge Soundworks customized speaker (frequency response: 60 Hz–18 kHz with broadcast values at 10 m as follows. Harpy: mean amplitude of 66.66 dB SPL and range of 58.3–78.4 dB SPL; tinamou: mean amplitude of 67.8 dB SPL and range of 57.65–79.2 dB SPL; bald eagle: mean amplitude of 67.2 dB and range of 57.98–78.8 dB. The speaker was occluded at a mean distance of  $30 \pm 5$  m from the closest animal within the howler group. The mean duration of playback stimuli was 159 s (range: 148–168 s). We did not initiate playbacks in groups that remained agitated 30 min after 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 *ca.* 1000 m if the playback

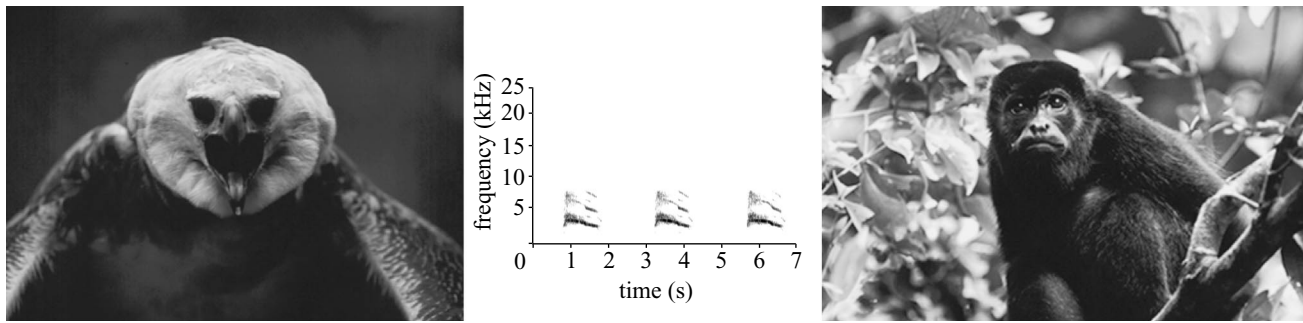


Figure 1. Photographs of a harpy eagle and a howler monkey separated by a spectrogram of one of the harpy eagle calls used for the playbacks.

Table 1. Statistical analysis of ‘vigilance rate’ and ‘scan upwards’ in the four experimental conditions.

	d.f.	test statistic	<i>p</i>
vigilance rate (by group) <sup>a</sup>			
BCI harpy present versus Gigante control ( <i>n</i> = 90) <sup>b,c</sup>	2	<i>F</i> = 16.553	< 0.0001
BCI harpy absent versus BCI control ( <i>n</i> = 60) <sup>c</sup>	2	<i>F</i> = 16.591	0.0001
BCI harpy absent versus BCI harpy present ( <i>n</i> = 96) <sup>c</sup>	2	<i>F</i> = 0.108	0.8977
BCI harpy absent versus Gigante control ( <i>n</i> = 66) <sup>c</sup>	2	<i>F</i> = 18.87	< 0.0001
Gigante control versus BCI control ( <i>n</i> = 54) <sup>c</sup>	2	<i>F</i> = 0.501	0.0823
BCI harpy absent (male versus female harpy) ( <i>n</i> = 36) <sup>c</sup>	2	<i>F</i> = 0.925	0.6325
BCI harpy absent (tinamou versus bald eagle) ( <i>n</i> = 24) <sup>c</sup>	2	<i>F</i> = 3.002	0.4676
BCI harpy absent (MV versus other harpy) ( <i>n</i> = 36) <sup>c</sup>	2	<i>F</i> = 0.841	0.4661
vigilance rate (within condition) <sup>a</sup>			
BCI harpy present ( <i>n</i> = 60) <sup>d</sup>	9	<i>H</i> = 9.0	0.4373
Gigante control ( <i>n</i> = 30) <sup>d</sup>	4	<i>H</i> = 4.0	0.4060
BCI harpy absent ( <i>n</i> = 36) <sup>d</sup>	5	<i>H</i> = 4.304	0.5065
BCI control ( <i>n</i> = 24) <sup>d</sup>	3	<i>H</i> = 2.744	0.4329
scan direction upwards (by group) <sup>a</sup>			
BCI harpy present versus Gigante control ( <i>n</i> = 60) <sup>c</sup>	2	$\chi^2 = 13.33$	0.0025
BCI harpy absent versus Gigante control ( <i>n</i> = 44) <sup>c</sup>	2	$\chi^2 = 9.6$	0.0165
BCI harpy absent versus BCI control ( <i>n</i> = 40) <sup>c</sup>	2	$\chi^2 = 10.91$	0.0086

<sup>a</sup> For the ‘vigilance rate’ tests (applied by group and within condition), Bonferroni correction lowers the alpha to 0.004. For the ‘scan direction upwards’ tests, Bonferroni correction lowers the alpha to 0.02.

<sup>b</sup> *n*: number of focal samples.

<sup>c</sup> ANOVA test.

<sup>d</sup> Kruskal–Wallis test.

<sup>e</sup> Kolmogorov–Smirnov test.

stimulus had been broadcast. Approximately 35% of the trials were aborted.

We examined the howlers’ responses in four experimental conditions: (i) BCI howlers presented with harpy calls during a period of harpy presence on BCI (‘BCI harpy present’); (ii) Gigante howlers, who have never been exposed to harpies in the last 50–100 years, presented with harpy calls (‘Gigante control’); this peninsula is located *ca.* 250 m away from BCI and, like BCI, has not been subjected to predation during the last 50–100 years. The current population in Gigante is estimated to be smaller than the one on BCI. The animals belong to the same species (*Alouatta palliata*), the surrounding neotropical forest environment is the same in Gigante and BCI, and there are no apparent significant differences in the baseline behaviour of the two populations; (iii) BCI howlers presented with harpy calls during a later period when the harpies were absent from BCI (‘BCI harpy absent’); for reasons that were independent of our studies, the eagles were removed approximately 7 months before

these playbacks started; (iv) BCI howlers presented with the calls of other avian species (‘BCI control’). During each playback, we scored vigilance rates, scan directions, utterance of alarm calls, display of other behavioural activities and group movement and dispersion.

### 3. RESULTS

#### (a) *Predatory behaviour by harpy eagles*

Based on an almost continuous period of observation since their introduction in 1999 (450 focal days consisting of 240 days on the mainland before resettlement and an additional 210 days on BCI), results indicated that the harpies were hunting capuchins and howler monkeys with great success. During a period of 294 days, when virtually all kills were observed, the female harpy captured prey every 4.39 days and the male every 3.71 days. Primates were taken 34.78% of the time by the female and 12% of

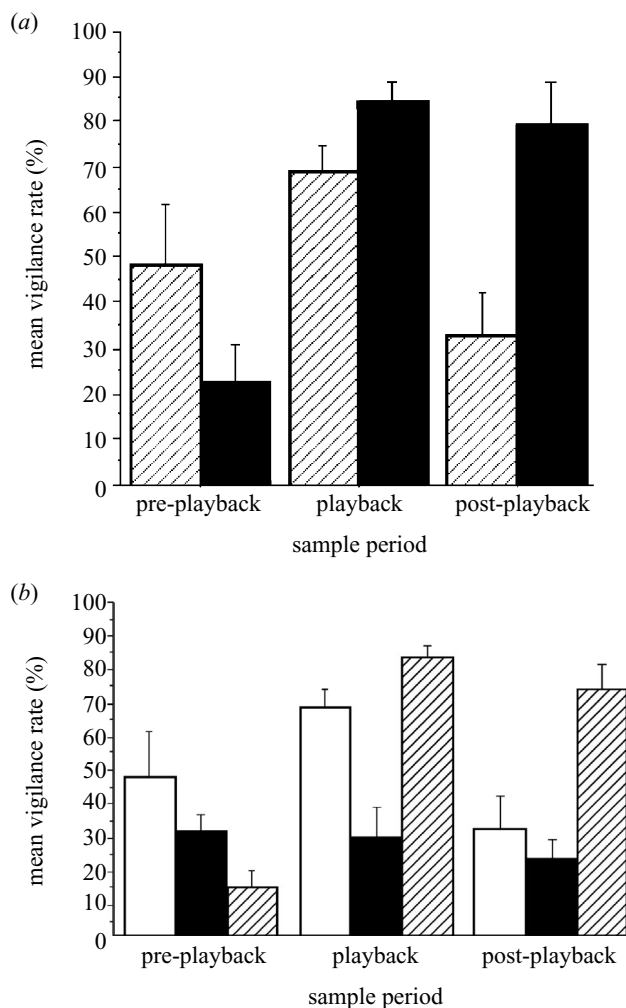


Figure 2. (a) Vigilance rate of howler groups on Gigante and on BCI (during a period of harpy presence), before, during and after broadcast of harpy eagle calls. Hatched bars, Gigante control; filled bars, BCI harpy present. (b) Vigilance rate of howler groups for various experimental conditions: Gigante control (open bars); BCI control (filled bars; playback of other avian species) and BCI harpies absent (hatched bars; playback of harpy calls).

the time by the male. Howler monkeys comprised most of the primate captures for the female (81%) and all of the male's (100%) primate kills (Touchton *et al.* 2002; Palleroni 2003). Although we cannot determine how often each of our howler groups was attacked, successfully or unsuccessfully by harpies, their distribution on the island suggests that all groups were exposed to the harpies many times. Critically for our analyses, we focused on the contrast between BCI howlers responding to harpy calls versus other stimuli, as well as the contrast between BCI and Gigante howlers. If some experience with harpy predation is necessary to develop an alarm response, then BCI howlers should show such a response to harpy calls, but not to other stimuli, and Gigante howlers should not show an alarm response to harpy calls. If a certain level of exposure to harpy predation is necessary to develop an anti-predator response, then one might expect to see significant variation in the level or kind of response to harpy calls by different groups of BCI howlers.

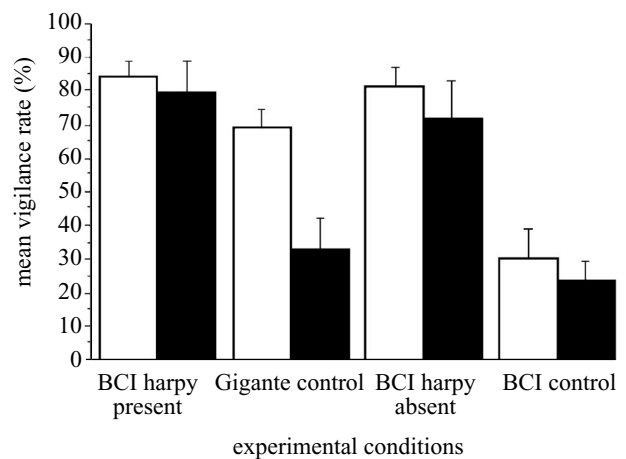


Figure 3. Vigilance rate of howler groups during the sample periods playback (open bars) and post-playback (filled bars) in the various experimental conditions.

During radio tracking, we observed that harpies pursued their primate prey by perching on a tree nearby, watching, and often uttering a series of calls. The structure of the call in this context was always the same and consisted of a sequence of two structurally different elements. The first was uttered once at the beginning of the call, followed by multiple repetitions of the second element (figure 1). A. Palleroni and R. Gil-da-Costa's observations (unpublished data) of harpies both on and off BCI indicated that this vocalization was commonly associated with prey pursuit, and is therefore called a 'predator-assessment' call. Whether a harpy attacks, delays or moves on to a new target may be contingent upon the prey's response to these calls. Given the association between predatory attack and the harpy's call, therefore, an adaptive learning mechanism would clearly pick up on this association. We therefore explore this problem in the next section.

#### (b) *Anti-predator responses by howler monkey prey*

To examine the extent of variance between groups within experimental conditions, we first analysed the effects of harpy playbacks on vigilance rates. For the analysis of vigilance rate, we used the data from the two samples that included the playback period (playback period), the two samples immediately prior to these (pre-playback period) and the two immediately following (post-playback period). There was no significant difference (table 1). By contrast, we observed highly significant differences in vigilance rates across conditions, especially between BCI harpy present and Gigante control (figure 2a; table 1). This result was replicated one year later even though the harpies on BCI were no longer present (BCI harpy absent versus Gigante control). Furthermore, howlers showed little to no change in vigilance to the control stimuli, nor did they show any differences in response to different exemplars of the harpy calls (figure 2b; table 1).

These results show that in a period of one year or less, howlers on BCI acquired a selective anti-predator response to a new predator, the harpy eagle. Further, the response to harpy calls was maintained even in the absence of harpies, for at least 7 months, as evidenced by the lack of signifi-

Table 2. Statistical analysis of the different behaviour rates in the four experimental conditions.

experimental condition	<i>n</i> <sup>a</sup>	behaviour			
		rest (%)	move (%)	forage (%)	social (%)
BCI harpy absent	60	61.7	15.0	18.3	50.0
BCI control	45	97.8	17.8	0.0	51.1
BCI harpy present	86	59.3	26.7	2.3	45.3
Gigante control	42	71.4	31.0	4.8	35.7
BCI harpy present versus Gigante control		$\chi^2 = 6.196$ $p < 0.05$	$\chi^2 = 0.713$ $p > 0.05$	$\chi^2 = 1.126$ $p > 0.05$	$\chi^2 = 3.477$ $p > 0.05$

<sup>a</sup> *n*: number of focal samples.

cant difference in vigilance rates between BCI harpy present and BCI harpy absent (table 1).

Further analyses of the temporal patterning of responses to the playback also revealed group differences. Specifically, subjects in the BCI harpy present and BCI harpy absent conditions showed no significant differences in vigilance rates during the playback and post-playback sample periods, while subjects in the Gigante control showed a significant decrease in vigilance between these two periods (figure 3; table 1). Consequently, the initial vigilance rates among the Gigante howlers represent a response to novelty, rather than a specific anti-predator response.

To determine whether exposed and control groups differed with respect to their recognition of the source of the playback, or the kind of threat imposed, we examined the direction of their scanning responses. BCI harpy present and BCI harpy absent groups scanned at a significantly higher frequency following playbacks of harpy calls than did Gigante control groups (table 1); the latter typically responded to the playbacks by orienting towards the speaker.

Analyses of other behavioural activities (i.e. rest, move, forage, socialize) revealed only one significant difference: howlers on Gigante rested more often than howlers on BCI (table 2). Less systematic observations also revealed sex differences in response to harpy calls among BCI howlers, but not among Gigante howlers. For example, upon hearing the harpy call, adult females on BCI would pick up their infants and move towards the more dense areas of the canopy, while adult males would move to more distal locations of the canopy and often give alarm calls. Such responses were never observed among BCI howlers in response to control stimuli.

#### 4. DISCUSSION

Although several studies have explored the kinds of cues used by prey to escape from predators (Woodland *et al.* 1980; Caro 1995; Bshary 2001), relatively few studies have examined how prey acquire their anti-predator responses, and the extent to which acoustic cues are sufficient to elicit such responses. Our results show that howlers on BCI rapidly learned to recognize the harpy's call, and to use this acoustic signal to initiate an escape response. By contrast, the howlers on Gigante have apparently lost their anti-predator response to harpy calls; moreover, simply hearing the call is insufficient to elicit an anti-predator response. These results parallel those recently

reported by Berger *et al.* (2001) for moose populations and wolf predation. Specifically, prey that were unfamiliar with a predator for 50–100 years lost their ability to recognize the predator calls, becoming highly vulnerable to first encounters, but the populations exposed in this study developed behavioural adjustments to counteract predation in a remarkably short period, displaying a capacity for rapidly processing predator-related information in less than one generation. Our results provide additional support for the general findings of Berger *et al.* (2001), but go further by showing the specificity of the prey's response, the maintenance of the response following a period of predator absence and the importance of the predator's call in prey assessment.

Overall, the results presented here suggest that harpies may be using their calls to enable them to extract critical information about prey behaviour. In 35 observed cases, both on BCI and previously on the mainland, where the prey's response was coordinated, with individuals maintaining vigilance, the harpy either delayed its attack or moved on to a different prey target; when the response was chaotic or vigilance was minimal with some animals showing no response, the harpy typically attacked or moved closer. We are currently following up these observations to test whether the harpy's predator-assessment call is functionally similar to 'prey-deterrent signals' (Hasson 1991; Caro 1995).

Finally, the increasing worldwide extinction of large carnivores has left various prey, including primates, without recent selective predatory pressure and the display of adequate self-protective behaviours. This phenomenon can result in catastrophic consequences if a species' ability to reactivate anti-predator responses is not explored in reintroductions. The 'first contact' can have grave implications if the dynamics of these relationships is not studied. The potential danger is compounded in island habitats or within medium and small prey populations (Gittleman & Gompper 2001).

Our experimental findings are not only of direct relevance to those interested in the dynamics of predator-prey interactions but, in addition, should have significant implications for those concerned with conservation and the process of reintroducing predators into novel and historical habitats (Gittleman & Gompper 2001). If the patterns presented here generalize to other populations, then playbacks of predator calls could be used as probes designed to assess the presence or absence of evolved prey

adaptations, a finding that would greatly enhance conservation approaches.

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