Age Differences in the Responses to Adult and Juvenile Alarm Calls by Bonnet Macaques (*Macaca radiata*)

Uma Ramakrishnan & Richard G. Coss


Abstract

This study examined the differential responses to alarm calls from juvenile and adult wild bonnet macaques (*Macaca radiata*) in two parks in southern India. Field studies of several mammalian species have reported that the alarm vocalizations of immature individuals are often treated by perceivers as less provocative than those of adults. This study documents such differences in response using field-recorded playbacks of juvenile and adult alarm vocalizations. To validate the use of playback vocalizations as proxies of natural calls, we compared the responses of bonnet macaques to playbacks of alarm vocalizations with responses engendered by natural alarm vocalizations. We found that the frequency of flight, latency to flee, and the frequency of scanning to vocalization playbacks and natural vocalizations were comparable, thus supporting the use of playbacks to compare the effects of adult and juvenile calls. Our results showed that adult alarm calls were more provocative than juvenile alarm calls, inducing greater frequencies of flight with faster reaction times. Conversely, juvenile alarm calls were more likely to engender scanning by adults, a result interpreted as reflecting the lack of reliability of juvenile calls. Finally, we found age differences in flight behavior to juvenile alarm calls and to playbacks of motorcycle engine sounds, with juveniles and subadults more likely to flee than adults after hearing such sounds. These findings might reflect an increased vulnerability to predators or a lack of experience in young bonnet macaques.

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Introduction

In a number of prey species, predation has led to the evolution of specific vocalizations, induced by the presence of a predator. These vocalizations often allow perceivers to escape predation through access to an early warning system,
leading to the subsequent avoidance of the predator. Such alarm vocalizations are prominent in non-human primates; almost every species has been reported to emit at least one type of alarm call (Cheney & Wrangham 1987). Similarly, several ground squirrel species (e.g. *Spermophilus beldingi* and *Spermophilus beecheyi*) rely on an analogous system in which warnings are issued through distinct vocalizations (Leger et al. 1987; Mateo 1985; Hanson & Coss 1997).

Alarm calls are vocalizations elicited by predators and alarm-call responses are behaviors displayed by individuals that have heard the call (Mateo & Holmes 1997). Bonnet macaques (*Macaca radiata*), like most other primates, frequently emit alarm calls after detecting predators. Our observations and recordings of the alarm vocalizations of wild bonnet macaques during encounters with several leopards (*Panthera pardus*), dozens of domestic dogs (*Canis familiaris*), and one python (*Python molurus*) during this study indicated two different types of vocalization. There was an alarm grunt, which was a single, low-frequency unit, and an alarm sequence, which consisted of a string of high-frequency units (also see Hohmann 1989). A call unit is characterized as a continuous tracing along the temporal axis of the spectrogram (Struhsaker 1967). On the basis of our observations, the choice of alarm vocalizations used did not appear to be based on the type of predator, but on the degree of danger. Alarm grunts were observed when a potential predator was sighted at distances beyond 0.99 m, or when the caller appeared uncertain of the danger imposed by the source. We observed vocalizations of alarm sequences when the predator posed a more immediate threat (within a distance of 0.99 m), and the intensity of calling and number of callers increased as the predator approached.

The typical response of bonnet macaques to alarm vocalizations was to run up trees or other structures. Animals already off the ground when they heard alarm vocalizations visually scanned the area and aggregated closer to other troop members. Unlike alarm grunts, vocalizations of alarm sequences were only produced by animals that had reached safety or had detected the predator from a safe position. We observed individuals of both sexes and all ages alarm calling, with the exception of young infants. However, we observed males alarm calling more frequently than females. The alarm vocalizations of adult and juvenile bonnet macaques appeared to be acoustically similar; however, we could distinguish adult and juvenile calls without actually sighting the calling animals. Our ability to differentiate the relative age of calling bonnet macaques argues for the possibility that bonnet macaques exhibit the same ability. The age of the caller might provide information on the caller’s experience and, hence, on its reliability in predicting danger. Although not necessarily related to the caller’s age, the ability of other species to discriminate callers has led to conspecific assessment of the caller’s reliability (e.g. Seyfarth & Cheney 1990; Hare 1998), with animals ignoring the alarm vocalizations made by unreliable callers.

The ontogeny of alarm-call production and response has also been studied in a variety of species. For example, in vervet monkeys (*Cercopithecus aethiops*), the ability to call correctly to a particular class of predators develops gradually via experience (Cheney & Seyfarth 1980; Hauser 1988). Responses after hearing alarm
vocalizations also differ between adults and juveniles: in Belding’s ground squirrels (S. beldingi), juveniles initially responded to both alarm calls and non-alarm calls, with discrimination improving with age (Mateo 1996). In keeping with this developmental perspective, Hanson (1995) reports that young California ground squirrels (S. beecheyi) differ from adults in their treatment of alarm vocalizations. In young vervet monkeys, Hauser (1988) reports a positive association between the frequency of exposure to starling (Spreo superbus) alarm calls and the frequency of appropriate responses. These studies indicate the significance of age and experience in the recognition and use of alarm vocalizations, and suggest the possibility of observing similar age-related differences in bonnet macaques.

Experimental Objectives and Rationale

The purpose of this study was to determine whether bonnet macaques differentiated juvenile and adult alarm vocalizations. Since actual sightings of predatory events are rare (Ali 1981), we used indirect evidence of predation via the analysis of scats from leopards and tigers (Panthera tigris) at our two study sites: Mudumalai Wildlife Sanctuary and Kalakad-Mundanthurai Tiger Reserve, southern India. Details of this scat-analysis study are presented in Ramakrishnan et al. (1999). We found no evidence of bonnet macaques in tiger scat. The scat analysis complemented our field observations that leopards elicited alarm vocalizations and provided a context for using a leopard model to generate the alarm vocalizations used in this study.

We addressed three questions in our experimental design. The first question determined the validity of using playbacks to study reactions to alarm vocalizations by comparing the responses to natural calls and playbacks of these calls. The second question focused on whether bonnet macaques distinguished juvenile and adult alarm calls. We predicted that, if the age of the caller reflected call reliability, bonnet macaques would not react uniformly to the two sets of calls. The third question addressed whether younger and older perceivers differed in their responses to the two sets of calls. In this context, we predicted that differences in response may indicate differences in age-related vulnerability and experience.

Methods

Study Sites

The experiments were carried out between Apr. and Oct. 1997, at two sites in southern India. The Mudumalai Wildlife Sanctuary is located at a latitude of between 11°32’ and 11°43’N and a longitude of between 76°22’ and 76°45’E and covers an area of 321 km². Four troops were selected for the study from this site. The second study site, the Kalakad-Mundanthurai Tiger Reserve, is located at a latitude of between 8°25’ and 8°53’N and a longitude of between 77°10’ and 77°35’E and covers an area of 817 km². Three troops were selected for the study, all situated on the Mundanthurai plateau. The major predators at these two study sites were leopards, tigers, wild dogs (Cuon alpinus), domestic dogs, hyenas (Hyaena hyaena)
and pythons, all of which elicit alarm calling. We did not observe alarm calling to raptors, in keeping with similar observations by Hohmann (1989).

Individuals from the seven study troops were identified and classified into one of six sex and age (demographic) categories based on size: infants (unweaned animals that were aged less than 1 yr); juveniles (weaned animals aged 1–2 yr); subadult females (2–4 yr, smaller than adult females and larger than juveniles); subadult males (same size as adult females, smaller than adult males); adult females (females older than 4 yr with at least one offspring); adult males (older than 5 yr, larger than adult females). All troops lived near human settlements and were thus habituated to humans.

**Experimental Treatments**

Multiple exemplars of three playback sounds were used in this study: 1. adult alarm vocalizations, 2. juvenile alarm vocalizations, and 3. motorcycle engine sounds. The motorcycle engine sounds were included as familiar control sounds because motorcycles are frequently heard at both sites. Juvenile and adult alarm vocalizations were recorded in the same antipredator context, the 10-s presentation of a model leopard. This realistic-looking model of a stalking leopard (Fig. 1),

![Model leopard](image)

*Fig. 1: Model leopard used to elicit alarm vocalizations. The model had a shoulder height of 63 cm and a total length of 1.5 m, including tail*
erected manually by a cord from a distance of 50 m, was presented when perceivers were approximately 25 m from the model. To selectively record juvenile alarm calls, we waited for juveniles to move to the periphery of the troop and then presented the leopard model out of direct view of other troop members. This allowed us sufficient time to record alarm calls given by juveniles before adults detected the model and began to give alarm calls. Calls were recorded using a Sennheiser ME 79 directional microphone and a Sony TC-D5 PROII stereo cassette-recorder. To avoid potential differences in response caused by the sex of the callers, only the calls of males (both adults and juveniles) were used in the playback experiments. A total of 78 adult alarm-calling episodes, and 23 juvenile alarm-calling episodes were recorded from the two sites. For each of the three playback treatments, we employed six exemplars with a 30-s duration, each recorded from different individuals (Fig. 1). To study the effects of natural alarm vocalizations, we presented the leopard model and then examined the video tapes to identify those individuals that did not see the leopard model, but heard either juvenile or adult alarm calls given in response to the model. Individuals included in this data set were not facing the model when it was presented, and did not turn their heads to look at the model before responding.

**Experimental Layout**

To create a standardized context for perceiving playback sounds, feeding stations were set up in a 1-m radius, which caused bonnet macaques to aggregate for video recording. All troops were fed periodically throughout the study period to preclude any reliable association of food with the experimental treatments. A Panasonic AG-185 U VHS camcorder was used for video taping responses from a distance of 20 m to the center of the feeding station. The camera field of view encompassed the entire feeding area. Audio playback was conducted using a Marantz PMD 430 stereo tape recorder with a pre-amplified single-channel output fed into a Coustic MP 380 (125-W/channel) amplifier, powered by a 12-V motorcycle battery. This audio output was fed into a Radio Shack Optimus Pro LX5 loud speaker (85 Hz–25 kHz roll-off) positioned out of view 20 m from the feeding station. Playback volume for all sounds was standardized at 90 dB SPL at the source.

Experiments were conducted between 06.00 and 10.00 h and between 15.00 and 17.00 h, corresponding to the peak foraging periods of this species. Video recording was initiated after animals arrived at the feeding stations. After 2 min of video recording, the animals were presented with one playback treatment for 30 s. For each troop, playback treatments were presented in random order, with a minimum interval of 2 wk between presentations. Since the identity of the caller has been shown to influence responses in some species (Cheney & Seyfarth 1987; Hare 1998), the call used in the playback was from an unfamiliar individual in a different troop. Video recording continued for 5 min after the playback.

**Behavioral Measures**

Video tapes recorded in the field were copied using a Panasonic FA-400 time-base corrector coupled to a FOR.A VTG-22 video field labeler. Such labeling
permitted field-by-field analyses to quantify the latency to flee in 16.67-ms time steps. To measure behavior prior to sound playback, each monkey in camera view was labeled in a silhouette drawing at its initial position at the moment the sound playback started. For each animal, the time period (ms) between the playback sound onset and onset of flight behavior was recorded. Flight behavior is defined as a shift in activity to running off camera view. The frequency of responses was scored for three categories of flight behavior: (1) fast reaction time for flight, (2) slow reaction time for flight, and (3) no flight. It is possible that the flight response of one individual might trigger flight responses of other individuals nearby. Since we were interested in treating the flight response of each individual as an independent event influenced by only the playback treatment, the first category of fast reaction time for flight included only those individuals who fled under a time frame

Fig. 2: Spectrograms of exemplars of one unit of each alarm-call playback treatment. (a) Adult bonnet macaque alarm vocalization. (b) Juvenile bonnet macaque alarm vocalization. Spectrograms of the sound treatments were obtained with a Kay Signal Analysis Workstation Model 5500. Note that the adult call exhibits more energy at low frequencies than the juvenile call.
that encompassed the duration of the first unit of the call (350 ms) added to a 600-
ms time interval. The first unit of the call provides the context for call recognition
while the latter 600-ms time interval is the minimum time that laboratory-trained
macaques react to sound onset (~250 ms; Lamarre & Jacks 1978), initiate goal-
directed eye movements (~100 ms; Boch & Fischer 1986; Ferrera & Lisberger
1995), and react to visual cues (~250 ms; Rogal et al. 1985). The category of slow
reaction time for flight included individuals who fled after the duration defined for
the fast reaction time category. We also recorded the number of individuals who
scanned during a 1-min interval following playback onset. Scanning was char-
acterized as lifting the head from a feeding orientation and/or rotating the head
from side to side.

Statistical Analyses

Each of the study troops was exposed to each sound treatment only once to
ensure that the same playback treatments were not repeated on the same indi-
viduals. Because reaction times are typically skewed to the right because of the
inherent physiological limits on information processing and recognition, the data
are typically not normally distributed. A parametric test of latency distributions
revealed that flight latencies to the adult alarm calls were significantly skewed
(p < 0.01). Therefore, non-parametric tests were applied to the data. To include
data from individuals that did not flee in response to the sound treatments, we
used survival analyses coupled with pairwise comparisons using log-ranked tests.
Responses of individuals were summed across troops to generate behavioral fre-
quencies for multinomial log-linear analyses with maximum likelihood estimations
(Agesti 1990). An alternative analytical approach, albeit reduced in statistical
power, is to treat each troop as the unit of analysis and then apply a Friedman
two-way analysis of variance (ANOVA) by rank (Siegel & Castellan 1988). In these
analyses, the proportions of all individuals fleeing and scanning within each troop
(n = 7 troops) constitute the data sets to compare response differences to the three
sound treatments.

Results

Comparison of Responses to Natural Alarm Calls and Alarm-Call Playbacks

Behavior was recorded from all bonnet macaques in camera view at the onset
of each experimental treatment. Twenty-nine individuals were in camera view for
the juvenile alarm-call playbacks and 35 individuals were in camera view for the
adult alarm-call playbacks. To verify the use of alarm-call playbacks as accurate
simulations of naturally occurring alarm calls, we analysed, as described above,
the video-recorded responses of individual bonnet macaques to natural adult alarm
vocalizations (n = 14) and natural juvenile alarm vocalizations (n = 11).

The median reaction times to flee after hearing the two playback treatments
and the two sets of natural alarm calls appear in Fig. 3. Latencies for the four
treatments differed significantly (Kruskal–Wallis test: $H = 11.33$; $df = 64$;
Fig. 3: A box and whiskers plot of the latencies to flee after the onset of four experimental conditions: juvenile alarm vocalization playbacks, natural juvenile alarm vocalizations, adult alarm vocalization playbacks, and natural adult alarm vocalizations. The dashed line shows the cut-off separating the categories of fast and slow reaction times for flight. This cut-off is based on the duration of one unit of the call plus 600 ms. Natural and playback treatments were not significantly different for adult vocalizations and for juvenile vocalizations.

Flight Responses to Playback Treatments

The responses to juvenile and adult alarm-call playback treatments were compared using survival analysis with right-censored data. As in epidemiological studies of patients who outlive the sampling period (e.g. Gehan 1975; Gail et al. 1980), such censoring permitted the inclusion of animals that failed to flee during the 1-min sampling period. This increased the total number of monkeys in the juvenile alarm-call treatment to 29 (including 11 censored animals). Pairwise com-
parison using the Kaplan and Meier survivorship function (Fig. 4) revealed that reaction times to adult and juvenile alarm-call playbacks differed significantly (log-ranked test $= -3.995; p < 0.0001$). Multinomial log-linear analysis revealed that the proportion of individuals that fled in response to the adult alarm-call playbacks was significantly higher than the proportion of individuals that fled in response to the juvenile alarm-call playbacks (likelihood ratio $\chi^2 = 31.361; \text{df} = 2; p < 0.001$, Fig. 5a). The frequencies of flight to both the adult and juvenile alarm-call playbacks were significantly greater than the frequency of flight recorded in response to the motorcycle engine sound playbacks (motorcycle compared with adult calls: likelihood ratio $\chi^2 = 81.038; \text{df} = 2; p < 0.001$; motorcycle compared with juvenile calls: likelihood ratio $\chi^2 = 20.828; \text{df} = 2; p < 0.001$). The Friedman ANOVA by ranks revealed similar findings, with the frequency of flight differing significantly

![Kaplan & Meier Survivorship Function](image)

**Fig. 4**: Plots of Kaplan and Meier survivorship functions of latencies to flee. Pairwise comparison of the adult and juvenile alarm vocalization playback treatments reveals a significant difference ($p < 0.05$). Note the broad distribution of reaction time latencies engendered by the juvenile alarm-call playbacks.

![Percentage Flight Response](image)

**Fig. 5**: (a) Frequency of flight responses in the fast reaction time category to the three playback treatments. (b) Frequency of scanning responses to the three playback treatments. Number of bonnet macaques recorded for statistical comparison of each sound treatment: adult alarm playbacks = 36, juvenile alarm playbacks = 30, motorcycle engine sound playbacks = 48.
among sound treatments ($F_1 = 13.23; df = 2; p < 0.001$) and for all pairwise comparisons between treatments ($p < 0.05$).

**Scanning Responses to Playback Treatments**

A multinomial log-linear analysis was used to examine the proportion of individuals that scanned the area after hearing the three playback treatments (Fig. 5b). The interaction between treatments and the frequency of scanning individuals was significant (likelihood ratio $\chi^2 = 20.50; df = 2; p < 0.001$). Planned comparisons revealed that a significantly greater number of individuals scanned in response to the juvenile alarm-call playbacks compared with that in response to adult alarm-call playbacks (likelihood ratio $\chi^2 = 18.384; df = 1; p < 0.01$). The frequency of scanning in response to juvenile alarm-call playbacks was also significantly greater than the frequency of scanning in response to motorcycle-engine sound playbacks (likelihood ratio $\chi^2 = 10.59; df = 1; p = 0.01$). However, the frequency of scanning in response to the adult alarm-call playbacks did not differ significantly from the motorcycle-engine sound playbacks (likelihood ratio $\chi^2 = 2.00; df = 1; p = 0.157$). While the motorcycle engine sound was generally ignored, the adult alarm call was more likely to induce flight rather than scanning. The Friedman ANOVA by ranks revealed similar findings, with the frequency of flight differing significantly among sound treatments ($F_1 = 8.538; df = 2; p < 0.01$) and for pairwise comparisons between the juvenile and adult alarm-call playbacks and the juvenile and motorcycle-engine playbacks ($p < 0.05$).

**Age Differences in Response to the Playback Sounds**

Since all individuals fled in response to the adult alarm-call playbacks, comparisons of age differences could only be made to juvenile alarm-call playbacks and motorcycle-engine sound playbacks. We analysed the differences in the proportion of adults, subadults and juveniles for the three flight response categories after hearing the juvenile alarm-call playbacks (Fig. 6a). Analysis of the interaction of age and frequency of flight showed that these age classes differed significantly (likelihood ratio $\chi^2 = 14.508; df = 4; p = 0.006$). Further analyses using planned comparisons revealed that adults were significantly less likely to flee than subadults or juveniles (likelihood ratios for subadults and juveniles, respectively: $\chi^2 = 6.730$ and $8.823; df = 2; p < 0.05$). In contrast, a comparison of flight frequencies for subadults and juveniles showed that these age classes did not differ significantly after hearing juvenile alarm-call playbacks (likelihood ratio $\chi^2 = 4.878; df = 2; p = 0.087$). The motorcycle-engine sounds were less provocative (Fig. 6b), and the interaction of age and flight categories was not statistically significant (likelihood ratio $\chi^2 = 8.549; df = 4; p = 0.073$). However, planned comparisons revealed that adults were significantly less likely to flee than juveniles (likelihood ratio $\chi^2 = 7.050; df = 2; p = 0.029$). The frequencies of flight between subadults and juveniles were not significantly different (likelihood ratio $\chi^2 = 0.956; df = 2; p > 0.5$).
Age Differences in Use of Conspecific Alarm Calls

Discussion

Our study initially examined the validity of using playbacks of conspecific alarm vocalizations to study bonnet macaque antipredator behavior. We found that flight and scanning responses to natural alarm vocalizations and to vocalization playbacks were similar, indicating that playbacks of field-recorded vocalizations were realistic proxies of natural calls. Thus, we chose to study the effects of alarm calls using playbacks in place of natural calls since it provided a controlled experimental context. Our findings showed that adult alarm-call playbacks were more provocative than juvenile alarm-call playbacks, inducing greater frequencies of flight with faster reaction times. Conversely, juvenile alarm-call playbacks were more likely to engender scanning by adults. Finally, we found age differences in flight behavior to juvenile alarm-call playbacks and motorcycle-engine sound playbacks, with juveniles and subadults more likely to flee than adults after hearing such sounds. Adult alarm-call playbacks caused immediate flight in all individuals, precluding analyses of age differences.

One advantage of using playbacks is that they separate an animal’s response to an alarm call from responses that result from the independent detection of a predator (Shriner 1995). However, since we presented a leopard model to elicit natural calls, we found differences in behavior in the longer time domain, extending beyond our 1-min sampling period. These observations provide insight into the function of alarm vocalizations. The primary differences were that individual bonnet macaques never alarm-called after hearing alarm-call playbacks whereas several called to the predator model. Some animals were observed calling after detecting a calling animal without actually sighting the model themselves. Again, in response to the model, they aggregated closer to conspecifics in the tree canopy and moved in the canopy as a group towards where the predator was last seen. These behaviors were not observed in response to the playbacks. Therefore the

Fig. 6: Age differences in the frequency of flight responses in the fast reaction time category to two playback treatments. (a) Juvenile alarm vocalization playbacks. Number of bonnet macaques in each age class for statistical comparisons: adults = 30, subadults = 15, juveniles = 14. (b) Motorcycle engine sound playbacks. Number of bonnet macaques in each age class for statistical comparisons: adults = 24, subadults = 12, juveniles = 18

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inference that naturally occurring alarm vocalizations and playbacks are equivalent in eliciting antipredator behavior is restricted to the initial assessment of these calls, which in our study was confined to the first minute following the onset of sound treatments.

Age-Related Differences in the Reliability of Alarm Vocalizations

The faster reaction times to adult alarm calls compared with those elicited by juvenile alarm calls are congruent with the greater likelihood of fleeing. These results suggest that juvenile alarm calls are perceived as less provocative than adult alarm calls. Seyfarth & Cheney (1986) have reported that infant vervet monkey alarm calls were more unreliable than those of adults, with infants calling to a much wider variety of species than did adults. They presented two possible explanations for this behavior: 1. immature vervet monkeys might be vulnerable to a larger range of species than adults, and 2. immature vervet monkeys have yet to learn which species are dangerous, and thus alarm call to non-predatory species. If generalizable to our study, juveniles frequently alarm-calling to non-predator species might lead other troop members to associate these calls with no change in circumstances; that is, frequently heard juvenile alarm calls might engender habituation (Pearce 1997). Alternatively, frequent exposure to these false indications of danger might produce some inhibitory conditioning to flee (see Cotton et al. 1982), thus accounting for the less provocative nature of juvenile alarm calls.

One of the advantages of distinguishing reliable from unreliable callers is avoiding the energetic cost of time lost from foraging and other activities resulting from engaging in inappropriate antipredator behavior (Hare 1998; Ydenberg & Dill 1986). While it can be argued from the findings of our study that juvenile alarm vocalizations are perceived as more unreliable than adult alarm vocalizations, it appears that adults cannot afford to completely ignore juvenile alarm vocalizations. Although they were less likely to flee to juvenile alarm vocalizations, a significant proportion of adults engaged in scanning activity. Such scanning activity suggests that animals are capable of making behavioral adjustments by focusing their attention on more reliable sources of information predicting the presence of predators (see Markl 1985).

Age-Related Differences in Response to Alarm Vocalizations

Our results did not reveal marked differences between adults and juveniles in the latency to flee or the frequency of flight in response to adult alarm vocalizations. However, we recorded age differences in response to the juvenile alarm vocalizations and to the motorcycle-engine sounds, with juveniles and subadults more likely to flee than adults. Such age differences in flight response might reflect developmental priming prior to weaning in which the clinging infant hears loud sounds paired with the mother’s rapid flight. This process of learning during infancy precludes the necessity for trial-and-error learning later in development, where failure to respond to alarm vocalizations could be fatal (Mateo 1996). Further support for this argument of early learning is evident from our study on
heterospecific alarm-call recognition by bonnet macaques (Ramakrishnan & Coss, in press). In keeping with the current findings, this study also showed that juveniles responded appropriately to heterospecific alarm vocalizations, but, unlike adults, they often treated other loud sounds as threatening. Both studies indicate that young bonnet macaques exhibit a propensity to overestimate risk, with the recognition of appropriate threats improving slowly with age.

An alternative view is that the enhanced responsiveness to juvenile calls by juveniles might result from their greater vulnerability to a broader range of predators than adults. Cheney & Seyfarth (1988) noted that juveniles often alarm-call to species that prey on younger animals but not adults; thus, such calls would be more beneficial to younger animals. However, the playbacks in our study were elicited by the same predatory threat to which all age classes are vulnerable. This use of a standardized predator does not permit us to evaluate this hypothesis.

In summary, our results indicate that the responses of bonnet macaques to conspecific alarm vocalizations are dependent upon age-related experience. A major issue in animal communication is how unreliable signals might be detected by perceivers (Cheney & Seyfarth 1988). The results of the present study suggest that adult bonnet macaques associate call reliability with the age of the caller. Calls produced by mature individuals were treated as significantly more provocative than calls produced by juveniles. The findings of increased excitability by younger individuals might reflect their increased vulnerability to predators or their lack of experience or a combination of enhanced vulnerability and inexperience.

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