Age Differences and Developmental Trends in Alarm Peep Responses by Squirrel Monkeys (*Saimiri sciureus*)

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Alarm calls can code for different classes of predators or different types of predatory threat. Acoustic information can also encode the urgency of threat through variations in acoustic features within specific alarm call types. Squirrel monkeys (*Saimiri sciureus*) produce an alarm call, known as the alarm peep, in highly threatening situations. Infant squirrel monkeys appear to have an innate predisposition to respond to alarm peeps but require experience to associate alarm peeps with the appropriate type of predatory threat [Herzog & Hopf, American Journal of Primatology 7:99–106, 1984]. Little is known about age-related differences in the type or frequency of response to alarm peeps, or the development of alarm peep response in infants. The purpose of this study was to test experimentally the response strategies of different age classes of squirrel monkey to the playback of alarm peeps that were produced by infants, juveniles, or adults. Results suggest that infants, juveniles, and female subadults respond more frequently to alarm peeps than do adult females. Infant squirrel monkeys showed different behavioral strategies in response to alarm peeps as a function of age. Adult females differentiate between infant and adult alarm peeps by responding more frequently to the alarm peeps of adult females. These data demonstrate that squirrel monkeys use acoustic information to discern when to respond to the alarm peeps from conspecifics, and that infants gradually develop an adult-like response to alarm peeps over the first year of development. Am. J. Primatol. 53:19–31, 2001. © 2001 Wiley-Liss, Inc.

Key words: vocal communication; development; adaptive behavior; squirrel monkey; playback experimentation

INTRODUCTION

The study of alarm calling behavior in several species of nonhuman animals [Seyfarth et al., 1980; Owings & Hennessy, 1984; Pereira & Macedonia, 1991; Marler et al., 1992; Macedonia & Evans, 1993; Weary & Kramer, 1995] has documented the specificity of different alarm calls for different predators or types of

predatory threat [Seyfarth et al., 1980; Owings & Hennessy, 1984; Ficken, 1990; Pereira & Macedonia, 1991; Slobodchikoff et al., 1991; Marler et al., 1992; Macedonia & Evans, 1993; Mateo, 1996a, b]. Alarm calls can contain information on the class, type, or urgency of predatory threat either through acoustically different call types or by acoustic variations within a call type.

The effect of age on both the usage of and response to different alarm call types also has been demonstrated in a number of species [Seyfarth & Cheney, 1980; Loughry & McDonough, 1989; Mateo, 1996a, b; Hanson & Coss, 1997]. In vervets, adults tend to respond less vigilantly to the alarm calls of young individuals [Seyfarth & Cheney, 1980] and, under experimental conditions, to those of adult individuals produced repeatedly during inappropriate contexts [Cheney & Seyfarth, 1988]. Young vervets produce alarm calls to a much wider range of species than do adults and show poor discrimination between alarm call types [Cheney & Seyfarth, 1990]. Age-related differences in alarm call responses and in behavioral response to different predatory threats also have been found in ground squirrels [Hersek & Owings, 1994; Mateo, 1996a, b; Hanson & Coss, 1997].

Squirrel monkeys (*Saimiri sciureus*), like many prey species, also produce acoustically different alarm calls in different contexts; however, these different calls, alarm peeps, and yaps likely code for different levels of urgency to threat rather than for different classes of predators [Jürgens, 1982; Newman, 1985]. Squirrel monkey alarm peeps have been described as "aerial" alarm calls [Newman, 1985], but other data suggest that they are also produced to rapidly-moving terrestrial species and objects [Herzog & Hopf, 1984]. The alarm peep appears to function in contexts of high alarm [Jürgens, 1982], inducing a "high-flight" response [Jürgens, 1982]. The yap appears to function in contexts of both fright and aggression [Jürgens, 1982]. Response to alarm peeps and yaps is highly predictable. Adult squirrel monkeys respond to yaps with vigilant gazing and mobbing behavior [Herzog & Hopf, 1984]. They respond to alarm peeps with flight (rapid movement) and/or prolonged immobility (freezing behavior) [Jürgens, 1982; Herzog & Hopf, 1984]. Upon hearing an alarm peep, adult squirrel monkeys generally leap rapidly—usually to a higher location—and then abruptly discontinue all locomotory and vocal activity for several seconds [Herzog & Hopf, 1984; Newman, 1985]. Experimental studies with laboratory-raised squirrel monkeys have revealed that behavioral responses to alarm peeps and yaps are innately predisposed. Infant squirrel monkeys raised in social isolation from birth respond differentially when acoustically exposed to alarm peeps and yaps [Herzog & Hopf, 1984]. Subjects responded to alarm peeps by approaching their surrogate mothers and to yaps by cautiously inspecting the source of threat. However, infant squirrel monkeys appear to learn to associate the type of predatory threat with each alarm call type [Herzog & Hopf, 1984].

Little is known about age-related differences in the type or frequency of response to alarm calls or the development pattern of specific behavioral responses by infants to specific alarm call types in squirrel monkeys. The purpose of this study was to examine the differences in the behavioral responses of four different age classes of squirrel monkeys to alarm peep playback. Infant, juvenile, subadult, and adult squirrel monkeys were tested using an experimental playback design for their response to alarm peeps under two experimental conditions and two control conditions. First, we confirmed that the acoustics of alarm peeps alone were sufficient to elicit an appropriate and differential response with respect to controlled conditions for each age class. Second, we tested for age differences in the type and frequency of response to alarm peeps to determine if squirrel monkeys showed age-related or developmental modification in their response strat-

egies to alarm peeps. Finally, we compared the responses by each age class to alarm peeps produced by infants, juveniles, and adults to determine if squirrel monkeys of different age classes aurally discriminated between signalers of different ages and degrees of reliability.

METHODS

Study Subjects and Living Arrangements

Three social groups of Peruvian squirrel monkeys (*Saimiri sciureus*) from the California Regional Primate Research Center consisting of four to five adult females housed with their offspring of 0–49 months of age were the subjects of this study. Groups were housed indoors in standard living cages (1.2 × 1.2 × 2.1 m H), equipped with four parallel perches arranged in stepwise fashion. Focal subjects included four captive-born infants less than 12 months of age (three males and one female), four captive-born juveniles between 14 and 21 months (two males and two females), four captive-born subadult females between 30 and 49 months, and five adult females (two wild-born and three captive-born) over 96 months from the three different social groups (see Table I). The infant and juvenile age classes were determined by developmental landmarks in squirrel monkey life history and defined by the degree to which young individuals were dependent upon their mothers. Subadults and adults were distinguished by their large differences in age (see Table I) and the fact that all subadults, while near reproductive age, were still nulliparous at the time of the study.

Experimental Housing

A subset of animals from a single group was moved in transport cages to an indoor experimental enclosure in a separate building. Prior to the study, the sub-

TABLE I. Description of Focal Subjects Used in Playback Study

Individual	Group	Sex	Age at start of of six-month experimental period	Wild- or captive-born	Age class
Martha	1	F	>96[a]	Wild	Adult
Bridget	2	F	144	Captive	Adult
Zola	3	F	84	Captive	Adult
Kim	3	F	252	Captive	Adult
Sonia[b]	3	F	>96[a]	Wild	Adult
Shasta	3	F	44	Captive	Subadult
Simone	3	F	41	Captive	Subadult
Leila	2	F	30	Captive	Subadult
Aileen	1	F	28	Captive	Subadult
Silvia	3	F	16	Captive	Juvenile
Lance	2	M	15	Captive	Juvenile
Felix	1	M	15	Captive	Juvenile
Polly	2	F	14	Captive	Juvenile
Stuie	3	M	6	Captive	Infant
Sean	3	M	5	Captive	Infant
Adam	1	M	5	Captive	Infant
Laraine	2	F	4	Captive	Infant

[a]Estimated age based on date of acquisition.
[b]Adult female with a dependent offspring.

jects were habituated to the new enclosure over a 2-month period, during which the subjects were exposed to the enclosure on a nearly daily basis. Habituation to the enclosure was measured by the decline in isolation peep production (calls emitted by squirrel monkeys when separated from other group members) by the subjects over the 2-month period. The experimental enclosure provided a large area (2.31 × 3.84 × 2.09 m) with one perch (measured and marked in 0.3-m intervals) that spanned the entire length of the enclosure. An opaque wall was located in the middle of the enclosure, with a window through which the monkeys could travel using the perch [McCowan & Newman, 2000]. The opaque wall was inserted to provide a visible barrier between the subjects and the playback apparatus to authenticate the playback procedure. Water was available ad libitum to the subjects during each 45-min testing period. Each subject was tested with its mother and one unrelated adult female. This testing protocol was conducted to reduce the group separation response (e.g., continuous isolation peeps) that frequently occurs when individuals are isolated from the rest of their social group [Newman, 1985].

Playback Exemplars

A total of six alarm peeps (one alarm peep each from two infants, two juveniles, and two adults) from each social group was chosen for playback to subjects from the same social group. Alarm peeps were recorded during observations for a study on vocal development in squirrel monkeys using a Sanyo Hi-Fi VHS Tape Recorder (frequency response to 22 kHz) and Audio-Technica directional microphones (frequency response to 22 kHz) (n = 120 hr; McCowan and Newman, unpublished data). Selection of alarm peep playback stimuli from the recordings was based upon a high signal-to-noise ratio and at least a 30-sec period between the last alarm peep emitted and the alarm peep chosen as playback stimuli. The latter criterion was used to ensure that any acoustic differences that might be present in vocally-evoked alarm peeps would not confound our tests. Calls were digitized using Cool Edit Signal Software (Syntrillium Incorporated, Scottsdale, AZ) on the PC at a sampling rate of 44 kHz. Alarm peeps from infants, juveniles, and adults were selected from within each social group for playback to subjects from the same social group to determine if subjects differentially responded to alarm peeps as a function of caller age. Alarm peeps from our infant, juvenile, and adult subjects were not used as playback stimuli during sessions in which the subject was tested. The alarm peeps were filtered for background noise [McCowan & Newman, 2000] and normalized for amplitude (at –20 dB) using Cool Edit Signal Software.

In addition to alarm peeps, two controls were broadcast: "shams" (500 msec of recorded silence) and the chuck calls from individuals within and outside of the social group. The chuck calls were also selected from our library of vocalizations and processed for playback parameters. These controls were randomly interspersed in the procedure. The object of the "sham" control was to evaluate whether the incidence of response to alarm peep playbacks was greater than that which occurs under identical conditions, but with no alarm peep stimulus presented. The purpose of the "chuck call" control was to distinguish the behavioral and vocal responses specific to alarm peeps from those to other vocalization types.

Playback Collection Methods

A 6-month experimental period was conducted using a cross-sectional study design for age class (infants, juveniles, subadults, and adults) and a longitudinal

study design on infant age (4–11 months of age). Each focal subject (infant, juvenile, subadult female, and adult female) was tested twice per month (see Table I). A total of 133 sessions and 2,660 trials were conducted during the experimental period. The order in which groups and subjects were tested was systematically varied. No individual or group of individuals was tested twice in one day.

Playbacks were broadcast using a Micron Pro 200 computer equipped with a SoundBlaster 32-wavetable sound board (sampling rate: 44.1 kHz) and Cool Edit Signal Software through one of two Advent V270 computer speakers (frequency response to 22 kHz), mounted on platforms at opposite ends (termed "left" and "right") of the experimental enclosure. The speakers were sufficiently hidden from the experimental subjects to closely mimic authentic vocal behavior. A playback list consisting of four alarm peeps (two alarm peeps from an infant or juvenile, and two from an adult), four shams, and 12 chuck calls was generated with a pseudorandom ordering of playback stimuli for each session. Thus a total of eight alarm peeps were broadcast to each focal subject during a 1-mo period. A total of four alarm peeps were broadcast during each 40-min session, consistent with the emission rate of alarm peeps under more natural conditions (B. McCowan, personal observation). This small sample of alarm peep playbacks per session was chosen to minimize habituating the animals to alarm peep playback over the course of the 6-mo study.

The ordering of playback stimuli was conducted such that no individual exemplar was repeated within a session, and no two stimuli of the same type (e.g., alarm peeps in sequential trials, and chucks from the same individual) immediately followed another. Trials were conducted every 2 min, and the broadcast speaker (left or right) was determined by the location of the focal infant, juvenile, or subadult in the experimental enclosure (e.g., if the infant was in the right partition of the enclosure then the playback stimuli was broadcast through the left speaker). Each session began with a 5-min pre-session habituation period.

Four experimenters conducted each session. One experimenter ran the recording and playback procedures on the computer. The second experimenter collected focal behavioral data on the infant, juvenile, or subadult. The third and fourth experimenters collected focal behavioral data on the two adult females. Behaviors scored immediately prior to playback included the location of the individuals in the enclosure including proximity to other individuals (within arm's reach of another individual) prior to playback, and the general activity of the individuals (e.g., locomoting vs. stationary). Behavioral responses scored within a 5-sec interval after playback included the adult-like response of rapid movement or freezing behavior (adult-like response), and two infant-like responses: 1) approach mother/other adult to proximity (within arm's reach), and 2) infant retrieval (infant moves to the carrying position on the back of the mother or another adult). In addition, rapid movement and/or freezing behavior were required to occur within 1 sec after playback to be scored. This strict criterion was used to ensure that this response was due to the playback stimulus and not to any other stimulus. Rapid movement and/or freezing responses by squirrel monkeys to alarm peeps under more natural conditions support this criterion (B. McCowan, personal observation). Gaze toward or away from speaker was not used as a behavioral measure because it is an unreliable response variable for squirrel monkeys (B. McCowan, personal observation). Interobserver reliabilities ranged from 92–97% agreement based upon the correspondence between observers of the same focal subjects for 100 trials [also described in McCowan & Newman, 2000].

Analytical Methods

Logistic regression is the statistical method of choice for binary data, because unlike other tests such as chi-square, logistic regression indicates both significance as well as the magnitude of the association in the form of an odds ratio. Furthermore, logistic regression is free of a number of problematic distribution assumptions that affect other types of analyses.

Using mixed effects logistic regression in Egret Statistical Software for the PC [Egret, 1997], infant (infant retrieval behavior, approach mother to proximity) and adult alarm responses (the presence of rapid movement and/or freezing behavior) were each analyzed by playback stimulus type (sham, chuck, and alarm peep), age of alarm peep caller (infant, juvenile, and adult), and age class (infant, juvenile, subadult, and adult). Proximity to mother before playback was also tested as a fourth outcome variable for all age classes. In addition, we included the covariates, captive- vs. wild-born, and sex composition in each model to determine if these variables contributed to the variation in each model. In each model, these terms were insignificant and thus removed from the model. Furthermore, to ensure that trends in alarm peep response over the 6-mo study period were not due to habituation to presented stimuli, we included time in study as an additional covariate in the analysis.

Finally, because three subjects were tested simultaneously in a given session (one young subject and two adult subjects), we also calculated the probability that the responses by infants, juveniles, and female subadults to alarm peep playback were independent from adult female responses by analyzing whether infants, juveniles, and female subadults responded similarly to adult females in each trial of all sessions for each infant, juvenile, and female subadult subject. If a younger subject responded like their mother or the other adult female, the trial was scored as a similar response between the subjects. We then compared these probabilities to chance probabilities. The probability that infants or juveniles or subadults and adults respond similarly due to chance is the product of the probabilities that each class responds with rapid movement and/or freezing behavior added to the product of the probabilities that each does not respond with rapid movement and/or freezing behavior. In each analysis, the random effect or repeated measure was designated as individual or subject [Searle et al., 1992]. The results below show the significance of the regression model including the β coefficient and its significance for each outcome [see McCowan et al., 2000, and McCowan & Newman, 2000, for further descriptions of logistic regression].

In the event that random effects were present (intrasubject correlation of alarm response status), fitting a mixed effects logistic regression model would adjust the Type 1 error to properly reflect this clustering of alarm response status by subject [Searle et al., 1992]. The probabilities generated from the logistic regression model were used to generate the figures shown because the probabilities from the statistical test are more accurate than the raw data, due to the adjustments for intrasubject correlation and significant interactions in each model. Goodness-of-fit tests (using standard deviation parameters in the models) revealed the aptness of the models.

For all statistical tests, significance was evaluated at the 0.05 level, and where appropriate Holm's sequential Bonferroni test was used to adjust alpha levels for multiple comparisons [Rice, 1988]. Goodness-of-fit statistics for each logistic regression model were conducted using a likelihood-ratio chi-square statistic [Agresti, 1990]. All models presented below exhibited appropriate goodness-of-fit.

RESULTS

Response to Alarm Peeps vs. Other Call Types

Responses to the playback of alarm peeps were significantly different from those to sham and chuck call controls for each age class. Response with rapid movement/freezing behavior to alarm peeps over the course of the study was significantly higher than to either chuck calls ($\beta = -1.33$, $P < 0.001$) or sham controls ($\beta = -4.56$, $P < 0.003$).

Dependency of Alarm Peep Responses on Adult Female Responses by Age Classes

To ensure that younger subjects were responding independently of their mothers or another adult female, we analyzed the dependency of infant, juvenile, and female subadult responses on adult female responses (Fig. 1a). Infants responded significantly more often like adult females than did juveniles or female subadults across the entire study period ($\beta = 0.939$, $P < 0.005$). In addition, all age classes showed a significant decline in responding like adult females ($\beta = -0.272$, $P < 0.001$). However, with the exception of infants during the first month of study, no age class showed responses like adult females greater than chance would predict. In fact, infants, juveniles and female subadults showed a response similar to adult females significantly less often than chance would predict (Fig. 1a). This negative correlation was simply due to the fact that adult females responded significantly less often than the younger age groups. Thus infant, juvenile, and female subadult responses were statistically dependent on adult female responses, but they were functionally independent of adult female responses.

Responses to Alarm Peeps by Age Class

The adult-like response of rapid movement or freezing behavior to alarm peeps showed significant differences by age class, and as a function of time in study. Figure 1b presents the logistic regression model on the probability of adult-like response to call playback as a function of time in study by age class. As indicated by this figure, a significant difference was found among the age classes. Juveniles and female subadults showed a more frequent and consistent rapid movement/freezing response to alarm peep playback over the course of the study when compared to adult females (juveniles: $\beta = 1.35$, $P < 0.05$; female subadults: $\beta = 1.27$, $P < 0.05$; Fig. 1b). Adult females showed a slight decline in response to the playback of alarm peeps over the study period while infants showed a marked increase in adult-like response to alarm peep playback ($\beta = 4.23$, $P < 0.005$) when compared to adults, juveniles, and female subadults.

Responses to Alarm Peeps from Callers of Different Ages

When the responses of different age classes to adult, juvenile, and infant alarm peeps were considered, only adult females showed a significant difference in their responses to adult vs. infant alarm peeps. Adults responded significantly more often to adult alarm peeps than to infant alarm peeps ($\beta = 1.29$, $P < 0.004$ using a Holm's sequential Bonferroni adjusted α of 0.017 for multiple comparisons [Rice, 1988]; Fig. 2a. Adult females did not respond significantly more often to juvenile over infant alarm peeps ($\beta = 0.69$, $P > 0.05$; Fig. 2a) nor adult over juvenile alarm peeps ($\beta = -0.57$, $P > 0.05$; Fig. 2a). As a side note, because the covariate of "time in study" significantly contributed to the type and frequency of
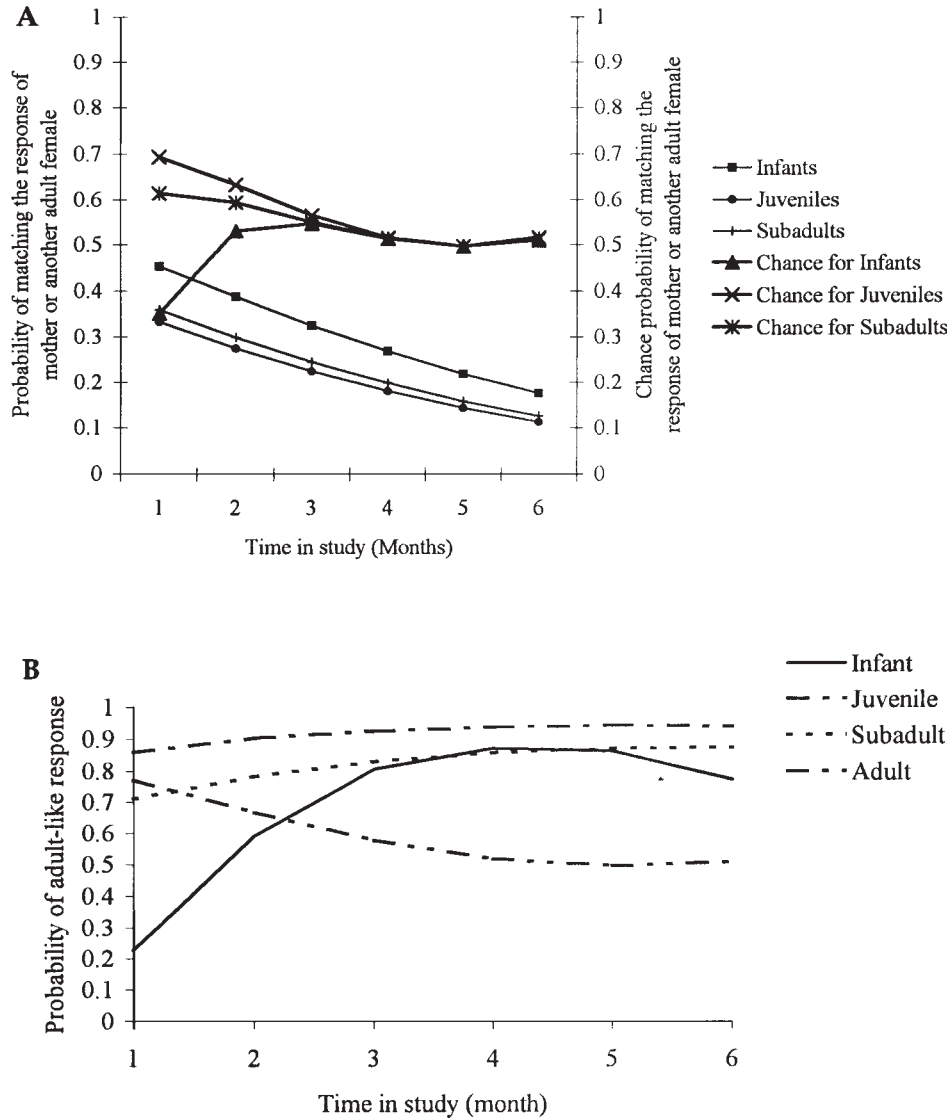
A

B

Fig. 1. Logistic regression model of the probability that (**a**) infants, juveniles, and female subadults responded like adult females as a function of time in study in relationship to chance probabilities and (**b**) adult-like response after alarm peep playback by age class as a function of time in study.

response in two of the four age classes, as indicated in the previous analyses, we included this covariate in the above statistical models. While the covariate and its interaction with age class remained significant, we did not present the covariate of "time in study" in the figures because they were identical to those found in Fig. 1b and did not differ among the categories of alarm peeps (infant, juvenile, and adult) in this particular analysis. Therefore, for ease of comparison we graphed only the overall differences in frequency of response to alarm peeps from different age classes of callers (refer to Fig. 1b for the "time in study" trends for each age class).
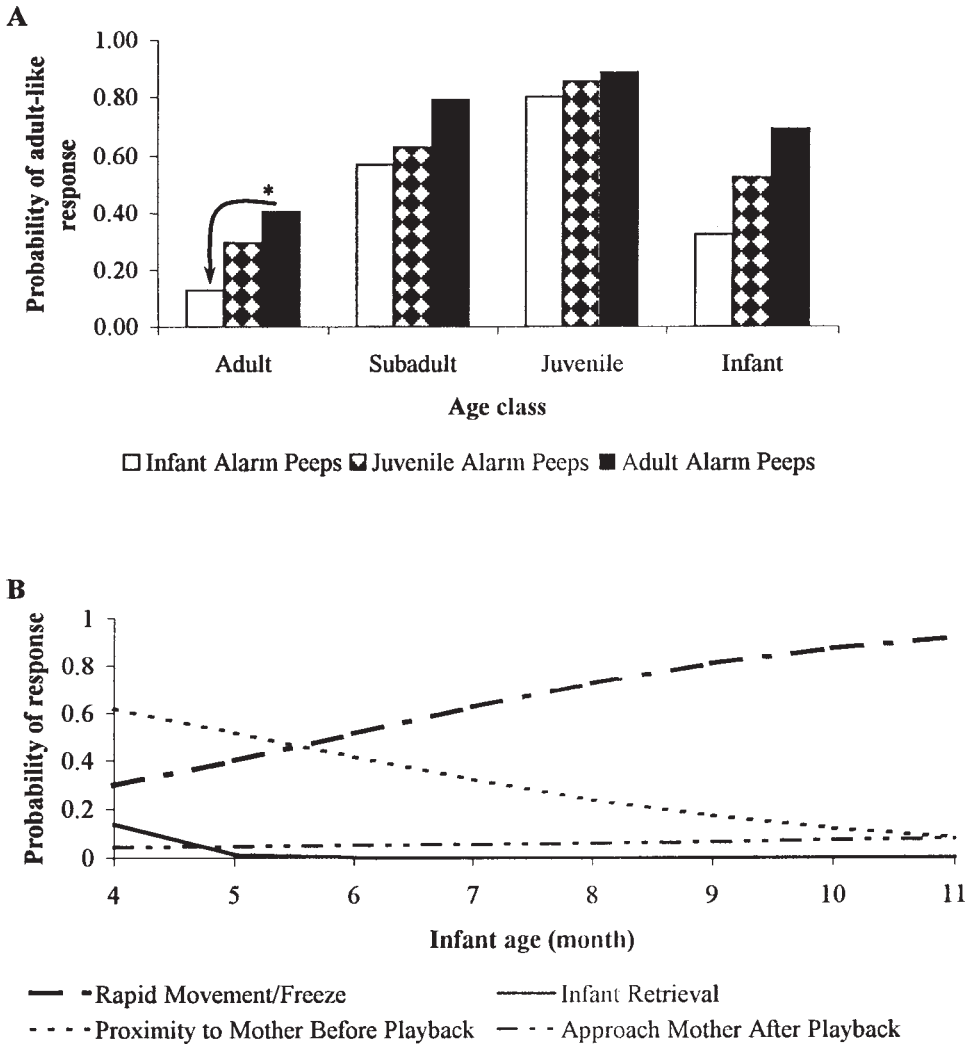
A

B

Fig. 2. **a**: Probability of adult-like response after alarm peep playback to adult, juvenile, and infant alarm peeps by age class. Note that the "time in study" pattern presented in Fig. 2b represents the "time in study" pattern for this model (* indicates significance at 0.05) and **b**: probability of infant-like and adult-like responses by infants to alarm peep playback as a function of infant age.

Developmental Trends in Infant Alarm Peep Response

Because infants showed an increase in adult-like responses to alarm peeps over the course of the study, we examined both infant-like and adult-like responses by infants to adult alarm peeps as a function of infant age (Fig. 2b). Infant squirrel monkeys ranged in age from 4 to 6 months at the beginning of the study, and were collapsed into the infant age class because they met the infant age class criterion of being less than 1 year of age. Thus, including "infant age" as a time covariate (as opposed to "time in study") takes into account age differences within the infant age class and tests a slightly different response trend: that of developmental changes within the first year. When infant age was

used as the time covariate, neither infant retrieval (β = –2.3, P > 0.05) nor approach mother to proximity (β = –0.48, P > 0.05) contributed significantly to infant responses by the fourth month of age (first month of study for infants). Rather, infants showed a significant increase in adult-like rapid movement and freezing behavior (β = 0.46, P < 0.002; Fig. 2b) concomitant with an almost perfectly correlated decrease with proximity to mother prior to playback (β = –0.41, P < 0.002; Fig. 2b). Thus, infants do not begin to respond with adult-like responses until they begin spending considerable time independent from their mothers at approximately 6 months of age. By 11 months of age, infants responded with rapid movement/freezing behavior at the frequency found for juveniles and female subadults (see Fig. 1b).

DISCUSSION
Age-Related Differences in Alarm Peep Response

This study has demonstrated that alarm peep signals alone contain sufficient information for appropriate behavioral response by different age classes of squirrel monkeys [Herzog & Hopf, 1984]. Alarm-like responses to the playback of alarm peeps were significantly different from those to sham and chuck call controls for each age class. These data on squirrel monkeys correspond well to those found in other species [Seyfarth et al., 1980; Owings & Hennessy, 1984; Ficken, 1990; Pereira & Macedonia, 1991; Slobodchikoff et al., 1991; Marler et al., 1992; Macedonia & Evans, 1993] and emphasize the importance of acoustic information in adaptive behavioral responses to predatory threat. In addition, we have shown that the frequency of responses to alarm peep differs among age classes of squirrel monkeys. Infants, juveniles, and female subadults responded significantly more often to alarm peeps than did adult females. Adult females showed a decline in response with "time in study," and we think this apparent habituation was due to overexposure to the playback stimuli. Adult females were exposed more often to the playback stimuli than were infants, juveniles, or subadult females due to the testing protocol. Thus, the first month of study is likely most indicative of adult response frequency and was similar in frequency to that of subadults.

The difference between younger and adult squirrel monkeys in alarm peep response frequency is not unexpected; young squirrel monkeys, as in most prey species [e.g., Mateo 1996a], are likely more vulnerable to predation than are adults, and thus must respond to alarm with greater vigilance. The difference found between infants when compared to juveniles and female subadults early in the study is more difficult to explain. Given that younger individuals are more susceptible to predation than older ones, we might predict age to be negatively correlated with predatory vulnerability and thus readiness to respond to threat. Yet, in many nonhuman primate species, infants remain highly attached to their mothers or other caregivers for several months after birth [Rowe, 1996, for review]. In squirrel monkeys, strong maternal attachment continues through at least 6 months of age [Baldwin, 1969]. In contrast, juveniles and young subadults are often seen playing at the terminal branches of trees, perhaps partially at times unaware of their immediate surroundings. Indeed, data analyzed on proximity measures to adult females for each age class of young squirrel monkeys reveals that infants spent a significantly greater proportion of their time in proximity to adult females than did juveniles or female subadults (β = 12.38, P < 0.002; odds ratio for infants vs. subadult females: 12.43:1; and odds ratio for juveniles vs. subadults: 0.84:1), and that the difference dissipated with increas-

ing infant age (interaction between infant age class and month of study: $\beta = -0.38$, $P < 0.01$). In addition, the fact that infants responded like adult females only during the first month of this study (Fig. 1a) in which infants spent considerable time in proximity to their mothers (Fig. 2b) supports this interpretation. Therefore, juveniles and subadults may respond more frequently to alarm peeps than do infants because they receive less direct or indirect protection from their adult companions.

Age-of-Caller Effect on Alarm Peep Response

As in other primate species [Seyfarth & Cheney, 1980, 1986], the age of caller in squirrel monkeys appears to affect the frequency with which adults respond to alarm peeps. Adult females were found to respond significantly more often to alarm peeps if emitted by an adult than by an infant but not by a juvenile. Adult females showed a gradual increase in response to alarm peeps in relationship to the age of the caller. These data suggest that some acoustic feature(s) of alarm peeps contain sufficient information about the age of the caller. Whether this acoustic feature(s) is related to individual recognition of callers of different age classes or to recognition of age class despite individual identity is not known. Further experimental research is necessary to determine the mechanism by which such recognition is achieved. Nevertheless, these data suggest that adult females assess the reliability of specific callers based upon their age. As Herzog and Hopf [1984] reported, infants must learn to associate their alarm calls with the appropriate predatory threat and thus are likely unreliable alarm callers early in life.

Interestingly, younger squirrel monkeys did not respond differentially to the alarm peeps of adults or juveniles over those of infants. This result could be due to two alternative explanations. First, younger individuals may need to learn to distinguish infant from adult alarm peeps. This explanation does not coincide well, however, with the lack of significant discrimination found for our female subadults. We would expect that subadult squirrel monkeys would have acquired the requisite experience to discriminate between infant and adult callers. Another explanation might be that younger squirrel monkeys do discriminate between infant and adult alarm peeps but do not respond differentially because they are more vulnerable to predation than are adults and therefore take the safest course of responding to all alarm peeps regardless of the identity or reliability of the caller.

Developmental Trends in Infant Alarm Peep Responses

Perhaps our most interesting result was found in the developmental trends of alarm peep response by infant squirrel monkeys. During the course of the study, over which infants aged from 4 to 11 months, infants modified their strategy in responding toward alarm peeps. Infants showed a marked increase in adult-like responses while infant-like responses declined over development, which was linked to their dependency on adult female responses (Fig. 1a). These data suggest that infants gradually develop adult-like responses to alarm peeps over the first year. In contrast, juveniles and female subadults exhibited adult-like responses throughout the entire study period.

Two alternative explanations have been proposed to account for this type of developmental trend observed in our squirrel monkey alarm peep responses. The traditional view suggests that infants must develop adult-like responses to behavioral input, and that the differences between infant and adult responses are

due to infant error or because the developmental process is not yet complete [Smith, 1977; Marler, 1982; Snowdon, 1982; Cheney & Seyfarth, 1990]. An alternative explanation, known as the age-specific interpretation of ontogeny [Galef, 1981; Owings & Loughry, 1985; Hersek & Owings, 1994], suggests that infants behave in ways that are specialized and adaptive for their age group. Similar to ground squirrels [Hersek & Owings, 1994], the differences found between infant and older squirrel monkeys seem to fit the latter explanation. The developmental increase in rapid movement and freezing behavior by infants does not seem to be linked to a developmentally incomplete response strategy. Indeed, infants did respond to alarm peeps early in development. They either moved to carry position (retrieval) or maintained close proximity to their mothers earlier in development. As infants matured, they gradually spent less time in proximity to their mothers and, perhaps as a result, a concurrent increase in adult-like response gradually emerged over development. Proximity to mother and thus proximity to the carrying position may represent a better or more adaptive strategy for younger perhaps less coordinated infants than responding with adult-like behavior during earlier stages of development. However, to conclusively choose between these alternative explanations, further experimental research on the responses by infants from birth through the first year of development, particularly prior to 4 months of age, will be needed. We might test infants, for example, under two separate experimental conditions: 1) with peers, and 2) with mothers, to determine whether infants change their response strategy as a function of group composition, and, specifically, in relationship to the presence or absence of their mothers. If young infants respond with rapid movement/freezing behavior when tested with peers but respond with infant retrieval, approach mother to proximity, or maintain consistent proximity with mothers (as found in this study) when tested with their mothers, it would suggest that infants respond to alarm peep playback with age-appropriate strategies. Conversely, if no difference is found between these two experimental conditions, it would suggest that infants learn to respond with adult-like behavior over development.

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