

Development of alarm-call responses in Belding's ground squirrels: the role of dams

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Abstract. Experiences with adult conspecifics can influence the ontogeny of species-typical behaviours in naive young of many species. Two processes of influence, direct and indirect, are proposed to describe the effect of adult behaviours on juvenile development. In Belding's ground squirrels, *Spermophilus beldingi*, exposure to adults experienced with responding to alarm calls may affect how juveniles respond to calls and/or the rate at which juveniles acquire adult-like responses to calls. Because dams and their juvenile offspring interact extensively during early development, the influence of dams on the ontogeny of juvenile alarm-call responses was investigated by conducting playbacks of alarm calls and non-alarm calls to captive ground squirrels. Juveniles were more likely to respond to auditory stimuli if their dam responded, but the responses of unrelated adult females did not influence juveniles. A dam's presence at the time of a playback had no consistent effect, however, on the type of initial response made by her juvenile, its response duration or the vigilance of its postures. The permanent absence of adult models (dams) after weaning appeared to delay the rate at which juveniles developed a discrimination between alarm calls and non-alarm calls, but had no long-term influence on juveniles' expression of responses. Thus, dams indirectly influenced juvenile response development by acting as models of species-typical responses. The outcome of dams' influence was facilitative rather than inductive, because exposure to dams affected the rate of response development but was not necessary for juveniles to acquire alarm-call responses.

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Interactions with conspecifics can influence the acquisition and expression of many complex behaviours (Galef 1976), yet the processes and outcomes of influence remain largely unknown for most behaviours in most species. An understanding of these influences would clarify some unresolved issues in the study of social learning (e.g. Galef 1988; Cheney & Seyfarth 1990; Caro & Hauser 1992), as well as the roles of parental investment and behavioural plasticity in juvenile development. Here we investigated both the processes and outcomes of a mother's (dam's) influence on the development of alarm-call responses in immature Belding's ground squirrels, *Spermophilus beldingi*.

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Alarm calls are vocalizations typically elicited by predators that can alert other animals of impending danger. Alarm-call responses are the various behaviours displayed by individuals that have detected and discriminated an alarm call from other auditory stimuli. Juvenile *S. beldingi* (weaned young of the year) do not discriminate behaviourally between alarm and non-alarm calls when they first experience these auditory stimuli, but this discrimination quickly develops through additional exposure to the calls. In contrast, the expression of alarm-call responses continues to develop throughout their first summer of life (Mateo 1996). Mateo (1995) proposed that the ontogeny of alarm-call responses in naive young can be facilitated (Gottlieb 1976) if young have opportunities to observe the responses of adults that are experienced with alarm calls and other auditory stimuli. Our observations of free-living and captive juveniles suggested that dams in particular may serve as models of species-typical

behaviour and thus indirectly facilitate the development of alarm-call responses by their offspring (J. Mateo & W. Holmes, personal observations).

For species in which parental investment includes parent-offspring interactions in the presence of predators, a juvenile's anti-predator behavioural patterns (the suite of behaviours that includes avoiding, detecting and/or escaping from predators) may be influenced by and thus resemble its parent's behaviours. The process of parental influence on the development of offspring anti-predator behaviour, or any other behavioural repertoire, can range from direct to indirect. Parents have a direct influence when they orient their behaviour towards their young, such as when they block a predator's approach or lead their young to a refuge (e.g. Rasa 1977; Huntingford & Wright 1993; see also Maestripieri 1995 for direct influences on infant locomotion). For a parent's influence to be direct, its behaviour must change qualitatively or quantitatively as a function of its offspring's presence.

At the other end of the continuum, parents have an indirect influence when their normal behaviour inadvertently affects juvenile behaviour, but is not directed towards their young. Adults are thus incidental models of behaviour and juveniles are inadvertent observers. That is, how a parent behaves is not contingent on whether its offspring are present. Examples of indirect influences include parents' own escape responses and mobbing behaviours when a predator appears (Culley & Ligon 1976; Mineka & Cook 1988; Hersek & Owings 1993). Alarm calls by adults can be an example of a direct or indirect influence, depending on whether the likelihood of calling is contingent on the presence of the adults' young (e.g. Cheney & Seyfarth 1985; references in Hoogland 1995).

Direct and indirect parental influences on juvenile behaviour share at least four characteristics. First, influence may have an immediate effect, for example, when the response of an adult to an alarm call evokes almost simultaneously a response by a juvenile, or it may have a delayed effect, as when an immature monkey observes an adult's response to a call but does not show its own responses until the infant can locomote independently. Second, neither process of influence implies complex mental states or awareness of juveniles' abilities by adults (cf. Cheney & Seyfarth 1990). Third, juveniles may be passive observers or recipients of adult actions; that is,

young do not actively seek out adults and copy their behaviour. Finally, 'direct' and 'indirect' describe processes rather than outcomes of influence; thus a direct influence is not necessarily a more significant process for a particular developmental outcome than an indirect influence.

If exposure to experienced parents influences the ontogeny of juvenile behaviour, then this influence can have two general outcomes. First, adults induce juvenile development if experience with adults is necessary for or determines the expression of species-typical behaviours. In contrast, adults facilitate juvenile behaviour if they influence the rate of development, but all juveniles would eventually show species-typical behaviour even in the absence of specific experience with adults (Gottlieb 1976).

Because *S. beldingi* dams rarely retrieve their young or manoeuvre them towards burrows when an alarm call is given (personal observations; but see Turner 1973; Robinson 1981), dams do not seem to exert a consistent, direct influence on the development of their offspring's alarm-call responses. A dam's own responses may indirectly influence her juveniles' behaviours, however, because young can observe their dam's reactions to calls and adjust their own behaviour accordingly. For example, free-living *S. beldingi* juveniles and their dams remain near their natal burrow during the first few days after offspring come above-ground from their natal burrow. During this time, dams are more responsive to and more vigilant in their reactions to alarm-call playbacks than they are prior to the emergence of their offspring. Juveniles' responses to alarm calls are also more intense when their dam is nearby than when she is not (Mateo 1996). Thus, both anecdotal and systematic evidence suggest that *S. beldingi* dams affect the development of their offspring's alarm-call response behaviours, but the exact nature of this influence is unknown.

In this paper, we report two alarm-call playback experiments designed to examine the role of dams in mediating the development of juvenile *S. beldingi* alarm-call responses. First, we studied the process (direct, indirect) of dams' influence on the responses of captive juveniles. We did this by contrasting how juveniles responded when dams were or were not nearby at the time of the playback. Second, we examined the long-term outcome (induce, facilitate) of adult models' effect on juvenile development. We did this by

contrasting the development and expression of responses of two sets of juveniles: one housed with and one housed without their dams after natal emergence for 2 weeks.

GENERAL METHODS

Natural History

Belding's ground squirrels are group-living diurnal rodents inhabiting alpine and sub-alpine regions of the Sierra Nevada and southern Cascade mountains (Jenkins & Eshelman 1984). Dams rear their young (mean litter size = 4.4 ± 2.1 ; Sherman & Morton 1984) in underground burrows for about 4 weeks, after which their nearly weaned young come above-ground for the first time as juveniles (their 'natal emergence': Sherman 1976). Juveniles continue to reside and interact with their dams during the following 4–6 weeks prior to hibernation. During this post-emergent period, dams are vigilant and may give alarm calls when predators appear, but because they typically are 15–25 m from each of their offspring (Mateo 1995), dams cannot directly influence juvenile behaviour, such as by moving them away from a predator or by herding them into a burrow when an alarm call is heard (personal observations). Predation accounts for up to 60% of juvenile mortality during the first summer of life (Sherman & Morton 1984).

Adult (>1 year old) *S. beldingi* routinely display escape behaviours in response to their species' two auditorily distinct alarm calls (Leger et al. 1984). Multiple-note trills are typically elicited by slow-moving predators and cause adults to post (a bipedal stance, defined below) and scan the area for what evoked the call. Single-note, high-frequency whistle alarm calls are usually given in response to fast-moving predators, and prompt animals to run to the nearest burrow, often entering the refuge (Sherman 1977, 1985; Robinson 1981; Mateo 1996). On the day of their natal emergence, juvenile *S. beldingi* do not differentially respond to alarm and non-alarm calls. This discrimination develops during the 5 days after emergence (Mateo 1996).

Animals and Facilities

We observed captive ground squirrels at the Sierra Nevada Aquatic Research Laboratory

(SNARL), located near Mammoth Lakes, California. We trapped field-mated females from populations at two elevations, both within 100 km of SNARL, and housed them in a nursery building there. We placed each female in a stainless steel cage ($61 \times 45 \times 35$ cm) that included a nest box ($28 \times 20 \times 20$ cm) fitted with a 6-cm diameter entry hole and a removable top. Females gave birth and reared their young in this nest box, which contained wood shavings for bedding. The nursery building was maintained on a 13:11 h light:dark schedule, with temperature regulated by a combination of a heater and automatic fans. We provided Purina mouse chow (#5015) and water ad libitum with occasional supplements of vegetables and sunflower seeds. We sexed pups the day after their birth and inspected and weighed them every 5 days. At the conclusion of the study, we released juveniles with their dam at the site where we originally trapped the dam.

We transferred young and their dams to an outdoor enclosure when pups were 23–24 days of age. Before transfer, we individually marked all pups with a combination of hair dye (Lady Clairol blue-black) and coloured vinyl discs attached to ear tags. Each of four $9.7 \times 9.7 \times 1.6$ -m open-air enclosures included natural vegetation, food and water stations and four partially buried 1.8-m long tunnels of plastic pipe, each of which was attached to a buried nest box (details in Holmes 1994). This semi-natural environment allowed captive ground squirrels to hear naturally elicited alarm calls routinely from adjacent enclosures and from *S. beldingi* living immediately outside the enclosures. The opaque walls of the enclosures limited animals' visual fields to what they could observe inside the enclosure or overhead.

We placed each group of two litters (young born to a common dam; typically four to five/litter) and their dams in an enclosure and observed them for up to 4 weeks. Three categories of refuge were available to captive animals: the plastic tunnels leading to the buried nest boxes, single-entrance 1.8-m long 'duck holes' made of plastic piping, and two-entrance, 1.8-m long plastic pipes (9 cm diameter) that were laid on the ground surface of the enclosure.

Playback Stimuli

We studied alarm-call responses by using auditory playbacks of four categories of stimuli: three

types of *S. beldingi* alarm calls and one house wren, *Troglodytes aedon*, song category, used as a heterospecific control stimulus. The three categories of alarm calls included *S. beldingi* whistle choruses, single whistles and trills (Robinson 1981; Leger et al. 1984). Because aerial predators typically elicit a whistle from a number of individuals, resulting in a chorus of whistles (Sherman 1985; personal observations), we included a 'whistle chorus' category of playbacks in which each exemplar was a recording of single whistles given by numerous adults. House wrens are sympatric with *S. beldingi*, and their songs are not associated with predatory contexts.

To produce playback tapes, we recorded stimuli with a Sony TC-D5M Stereo cassette recorder and AKG condenser microphone (SE 5-10), 6–9 m from the vocalizing animal. Stimuli were naturally elicited (wren songs and some trills) or evoked by flying a Frisbee over a colony or by slowly approaching the ground squirrels (whistles and some trills). We band-pass filtered the recordings between 300 and 16 000 Hz and digitized them at 50 000 points/s using Signal Software (Engineering Design 1992; Table I). We played the recordings through either a Sony TC-D5M or Sony WM-D6C cassette player connected to a Nagra DH amplifier-speaker. All playbacks were presented at peak amplitudes approximating natural intensities (whistles: ~85 dB; trills: ~75 dB; wren songs: ~60 dB), measured with a Realistic sound level meter on 'A' weighting at 9 m from the speaker, the distance at which we measured naturally occurring calls). The whistles in a chorus ranged in intensity during recording (and subsequent playback), depending on the distances of individual callers from the microphone, and thus mimic naturally occurring multiple whistles in amplitude variation. Because we were interested in whether newly emergent juveniles could discriminate between natural calls the first time they were heard in the field, and because a predator may elicit only one alarm call (Sherman 1976; personal observations), stimuli were presented once at their natural durations rather than at equal durations (Gerhardt 1992). We used eight exemplars of each of the four stimuli, selected for their signal clarity and lack of background noise, and each exemplar within a category was recorded from a different individual (or individuals for whistle choruses). We presented all playbacks in a balanced order (Kroodsmas 1986).

Playback Protocol

We conducted playbacks daily between 0700 and 1800 hours, and began playbacks when juveniles were 25 days old (around their age of natal emergence; Sherman 1976) and continued until juveniles were about 50 days old. We usually conducted two playback sessions (morning and afternoon) per day to each group. A playback session typically lasted 2 h, and consisted of one playback of one exemplar of each of the four playback categories. We presented one playback about every 15 min, unless we heard a natural alarm call or saw a potential predator during the preceding interval. For each of the four call types, we played back the recorded stimuli at a lower rate (once per 2 h either once or twice a day) than that naturally heard in the field or at the enclosures (personal observations). Mateo (1995) found that this schedule minimized habituation to the playbacks. Because juvenile responses developed over time, we cannot examine the potential effect of repeated presentations on responses. Dams continued to respond to alarm calls across time, however (range=91.9–96.8% of playbacks elicited adult responses across three age cohorts); responses to wren songs were too infrequent to interpret (0–10% of playbacks).

We observed and videotaped ground squirrels from an elevated platform about 3 m above an enclosure. To videotape the responses of juveniles and adults, we used either a Panasonic AG 450 VHS camera with a $\times 10$ zoom lens or a Sony CCD-F35 8 mm camcorder with a $\times 6$ zoom lens. We randomly selected a focal ground squirrel and began taping when that individual was above ground and at least 1 m from a burrow. Each individual served as a focal animal for each of the four playback categories at least once, and was videotaped at least every other day. We videotaped the focal ground squirrel beginning 15 s prior to the onset of the playback stimulus and continued until the animal resumed a non-alert behaviour, such as feeding or socializing (typically within 2 min of the playback). We fixed a second camcorder on a randomly chosen burrow to tape the responses of non-focal individuals that were near that burrow. This allowed us to tape the entire responses of two or three additional juveniles and thus increase our sample sizes without conducting additional playbacks each day (which could habituate the animals to the playbacks).

Table I. Summary of acoustic characteristics* of auditory stimuli used in playback studies (N=8 exemplars for each playback category)

	Duration (s)	Frequency (kHz)		No. of bands	Frequency of harmonic (kHz)	No. of notes	Mean inter-note interval (ms)	Burst duration (ms)
		Minimum	Maximum					
Whistle chorus	1.26 ± 0.21	3.99 ± 0.13	5.10 ± 0.07	1.11 ± 0.12	9.53 ± 0.29	5.63 ± 1.03	0.21 ± 0.03	0.19 ± 0.09
Single whistle	0.10 ± 0.01	4.13 ± 0.20	4.53 ± 0.50	1.04 ± 0.08	9.47 ± 0.33			
Trill	1.95 ± 0.17	4.23 ± 0.10	4.84 ± 0.14	1.32 ± 0.52	8.37 ± 1.18	11.63 ± 0.80	0.08 ± 0.02	0.40 ± 0.23
Wren song	1.34 ± 0.08	2.68 ± 0.22	3.99 ± 0.23	1.76 ± 0.04		1.13 ± 0.13		0.21 ± 0.01

* Data generated from Canary Acoustic Software v 1.1, on spectrograms imported from SoundEdit Pro, v 1.0.

Duration = from beginning of first note to end of last note; minimum frequency = lowest frequency of fundamental note; maximum frequency = highest frequency of fundamental note; frequency range = maximum minus minimum frequency; number of bands = number of harmonics in first note; frequency of harmonic = frequency of highest harmonic's midpoint; number of notes = total number of discrete notes in signal; mean inter-note interval = mean duration between each pair of notes in signal; burst duration = duration of first note (or burst in wren song).

Response Measures

We quantified playback responses from videotapes 2–4 months after data collection using Ethos22 event-recorder software (G. Gerstner, unpublished computer program). Videotapes were scored by one of us (J.M.M.) to ensure consistency of response times and categorization of behaviours. Although she was not blind to the stimulus presented for each playback, she did not know the ages of responding individuals, whether a juvenile's dam was present or what group the animals belonged to when scoring tapes. The software generated the frequency of vocalizations given by the focal ground squirrel, as well as the frequencies and durations (to the nearest 0.01 s) of six alert behaviours (horizontal, slouch, posting and vertical-stretch postures (defined below), below-ground and running) and four non-alert behaviours (stationary, feeding, grooming, and socializing; Mateo 1995).

During the scoring of each taped playback, we recorded four response measures. (1) 'Responsivity' was the likelihood of some type of behavioural response, that is the proportion of individuals displaying any detectable reaction to a playback. (2) 'Initial response' was an individual's first reaction to the stimulus, categorized as entering a burrow, running to a burrow, posting or freezing (or looking up). (3) 'Response duration' was the total time engaged in any of the six alert behaviours measured from onset of the stimulus until the individual resumed a non-alert behaviour. Response durations were normally distributed and did not require transformation. (4) 'Vigilant posture' was a quantitative measure of the most vigilant posture shown by an individual during any point of its response (see also Harris *et al.* 1983), as follows: 4=Below-ground (full body enters a burrow for ≥ 2 s), 3=Post (standing on hind feet with torso held straight, with or without legs fully extended), 2=Slouch (sitting on hind-quarters, torso not fully extended) and 1=Horizontal (head raised with three or four feet on the ground). For descriptive purposes, we present these ordinal vigilant-posture data as means.

To examine how dams affected juveniles' responses to playbacks, we scored a juvenile's dam as 'dam available' (to influence juvenile responses) during a playback if she was above-ground and within 5 m of her offspring. At this distance, juveniles could view their dam regardless of the

dam's or juvenile's location in the enclosure. Because we could not record every time each juvenile looked towards its dam, we instead quantified the potential for observing dams. As the analyses below suggest, juveniles did often see their dam when she was available. We classified juvenile responses as 'socially facilitated' if the behaviour or presence of one ground squirrel (the 'facilitator') appeared to elicit or prolong another juvenile's behaviour. For example, a juvenile may not have shown a response to the playback, but did react when the facilitator ran past the focal juvenile toward a burrow. Similarly, we considered a response to be socially facilitated if a focal ground squirrel began to engage in a non-alert behaviour after the playback, only to immediately resume vigilance when a facilitator posted nearby. Although we can not be certain that it was the facilitator that stimulated the focal individual's behaviour, such closely associated reactions were infrequent (<20% of all responses), yet were unanimously judged as facilitated by all observers ($N=2-3$). Thus, our categorization of responses as socially facilitated was conservative, limited to instances when a conspecific, but no other auditory or visual stimulus, was available to prompt a ground squirrel's behaviour.

Analyses

Because we often recorded the responses of non-focal as well as focal ground squirrels to a single playback, and sometimes the responses of more than one individual from a litter, the data potentially lacked independence. We therefore conducted two one-way ANOVAs on the data from experiment 1 and from experiment 2, using response duration as the dependent variable. We first used each individual playback as a level of the independent variable, and then we analysed the same data with each litter as a level of the independent variable. For both data sets, we found no significant effect of either variable, failing to demonstrate that the responses of multiple juveniles to one playback, or the responses of siblings to all playbacks, were dependent. Therefore, we used individual responses to each playback as the unit of analysis for each response measure (Leger & Didrichsons 1994). We rarely recorded one individual's response to a given playback category in more than one cohort (defined below), so the across-cohort analyses do

not significantly violate assumptions of independence. Finally, we performed a one-way ANOVA on the response-duration data following each of the eight exemplars for each playback category. For each of the four categories, the F -ratio was not significant ($P > 0.05$), so we pooled all data from the eight exemplars for each playback category. We pooled data from multiple groups only if there were no significant differences ($P > 0.05$) between the groups in responsivity, duration or vigilant postures.

Because we conducted playbacks equally throughout the morning and afternoon, we did not control for time of day in the analyses below. For all chi-square analyses, we used Yates' correction for continuity when $df=1$. For all ANCOVAs, the covariate was juvenile age, because juvenile response duration varies with age (Mateo 1996). Repeated measures analyses were inappropriate, because not all juveniles were recorded responding to each playback category in each cohort. We considered results significant when $P < 0.05$, and present the data as mean \pm SE.

EXPERIMENT 1: THE PROCESS OF DAMS' INFLUENCE

Methods

To examine the influence of *S. beldingi* dams on the development of juvenile behaviour, we analysed juvenile responses as a function of their dam's presence. These results summarize the influence of a dam's availability (to act as a model of species-typical responses, defined as within 5 m of her focal offspring at the time of a playback) on the responses of captive juveniles to playbacks of alarm and non-alarm calls (similar data from free-living ground squirrels are reported in Mateo 1996). Because dams do not directly influence juvenile responses by running towards them when an alarm call is heard or by manoeuvring them into a burrow (Mateo 1996), these data largely address whether dams have an indirect influence. In 1993, we observed six groups of juveniles ($N=60$) and their dams ($N=12$) from the juveniles' natal emergence (day 1) until they were approximately 50 days old (day 25). We divided the data into three cohorts, which are based on recognizable behavioural changes displayed by free-living juveniles (Mateo 1996): days 1–5 post-

emergence when juveniles spend most of their time within 5 m of the natal burrow; days 6–15, when juveniles begin to explore the surrounding meadow but the natal burrow remains the centre of activity; days 16–25, before natal dispersal activity begins. Because cohort sample sizes were fairly equal and variances were homogeneous, we did not weight the analyses to control for differences in cohort lengths (5 versus 10 days). We also did not find different results when we analysed the 10-day cohorts in 5-day subsets.

We do not report rates of alarm calling by dams, which may influence juvenile alarm-call responses, because enclosure-housed animals do not call frequently. Although the alarm-call responses (responsivity, response duration and vigilant postures) of captive dams do not differ significantly from free-living dams' responses (Mateo 1995), a free-living dam's behaviour may undergo more subtle changes in captivity. For example, dams initially have little experience with the ecology of the enclosure, including their vulnerability to predation and the locations of refuges, and this may influence their vigilance or their above-ground movements.

Results

Influence of a dam's availability

Captive dams were available during playbacks more often during days 1–5 than days 6–15 or days 16–25 (present during 64.7, 44.1 and 37.1% of juveniles' responses, respectively; $\chi^2_2=11.42$, $P=0.003$). A dam's availability, compared with her absence, had no significant influence on juvenile response likelihood during days 1–5 or 6–15 ($\chi^2_1=0.09$, $P=0.76$ and $\chi^2_1=0.90$, $P=0.34$, respectively). During days 16–25, juveniles were less responsive to playbacks when their dam was available than when she was not ($\chi^2_1=4.55$, $P=0.03$; Fig. 1). A dam's availability also had no significant influence on juveniles' initial responses, response durations or vigilant postures ($\chi^2_3=5.14$, $P=0.16$; ANCOVA: $F_{1,206}=0.29$, $P=0.59$; Mann-Whitney U -test: $U=5456$, $P=0.85$, respectively).

Relative influence of dams and unrelated adult females

We conducted additional analyses to determine whether a juvenile's response to a playback was specifically associated with its mother's responses

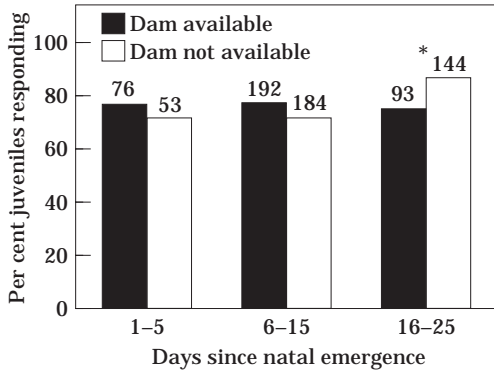


Figure 1. Percentage of available juveniles showing any type of observable behavioural response to an alarm-call playback in each cohort when their dam was available (within 5 m) at the time of the playback. Day 1 refers to juveniles' first day above-ground in the enclosure. See text for number of juveniles observed. Numbers above bars represent the total number of respondents and non-respondents. Asterisk denotes significant difference in responsivity when a dam was present compared with when she was absent ($P < 0.05$).

versus another adult's responses. The data set consisted of 346 dam-offspring pairs of responses and 276 juvenile responses randomly paired with unrelated adult-females' responses (to the same playback category; all juveniles were 1-25 days post-emergence). No juvenile-adult pair was observed more than once for each playback category. Adults and juveniles were within 5 m of each other at the time of the playback. These analyses do not control for juvenile-adult proximity, because there was no significant difference in the distance between captive juveniles and either their own dam or an alien dam at the time of a playback ($\bar{X} = 1.50 \pm 0.2$ m and $\bar{X} = 2.03 \pm 0.6$ m, respectively; Mateo 1995). Juveniles typically responded to a playback to which their dam also responded, and did not respond when their

dam did not respond (Table II). For example, a juvenile responded on only 28.6% of 42 occasions when its dam did not respond, compared with 64.1% of 39 occasions when an alien dam did not respond. The frequencies with which dams responded and juveniles did not, and vice versa, did not differ significantly (McNemar change test = 2.00, $P = 0.16$), indicating a close association between dam and juvenile responsivity. The agreement between the responsivity of a dam and her juvenile offspring was stronger during days 1-5 (McNemar change test, one-tailed binomial: $P = 0.69$) than days 6-15 or days 16-25 ($P = 0.03$ and $P = 0.04$, respectively). The responses of unrelated adult females were not associated with juvenile responses in any cohort (McNemar change test = 13.33, $P < 0.001$; all cohorts combined).

When both a juvenile and its dam responded to a playback, their response durations were positively correlated (when outlying juvenile durations over 200 s are omitted: $r = 0.500$, $N = 213$, $P < 0.001$; Fig. 2a). Vigilant postures were also correlated between juveniles and their dams ($r_s = 0.341$, $N = 231$, $P < 0.001$). Dams' and offsprings' response durations did not differ significantly ($\bar{X} = 40.98 \pm 2.99$ s and 29.53 ± 3.87 s, respectively; paired $t_{220} = 0.16$, $P = 0.87$), nor did the vigilance of their postures ($\bar{X} = 2.62$ and 2.72 , respectively; Wilcoxon signed-ranks test: $z = 0.67$, $P = 0.50$). Conversely, the response durations and vigilant postures of unrelated dams and juveniles were not significantly correlated (Fig. 2b, and $r_s = 0.108$, $N = 184$, $P = 0.07$, respectively). Vigilant postures, but not response durations, differed between juveniles and unrelated dams (postures: $\bar{X} = 3.70$ and 2.49 , respectively; $z = 2.30$, $P = 0.02$; duration: $\bar{X} = 57.36 \pm 4.45$ s and 31.22 ± 2.49 s, respectively; paired $t_{148} = 1.13$, $P = 0.26$). These results therefore demonstrate that juveniles' response likelihood and response patterns (duration, vigilant postures) were more contingent on

Table II. Responsivity of juveniles compared with responsivity of dams to same playback and with responsivity of unrelated (to juveniles) adult females to same playback category

	Dam		Unrelated female	
	Respond	Not respond	Respond	Not respond
Juvenile				
Respond	261	12	178	25
Not respond	20	30	5	14

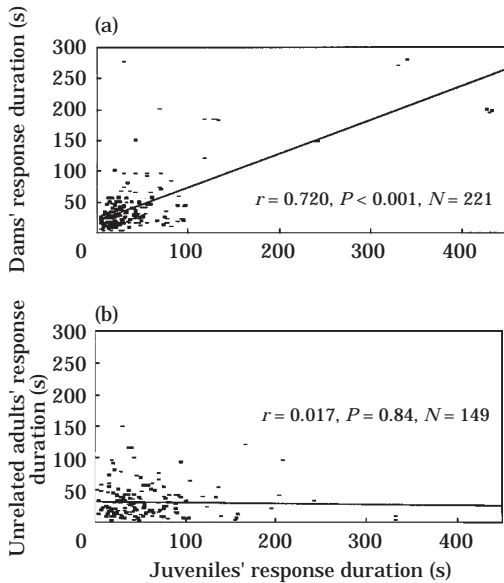


Figure 2. (a) Paired response durations (\bar{X} s) of juveniles and their dam to the same playback. (b) Paired response durations (\bar{X} s) of juveniles and unrelated adult females to the same playback category. The linear regression lines are shown. See text for the numbers of juveniles and adults observed.

their dam's behaviour than on the behaviour of unrelated adult females, despite juveniles' equal proximity to both types of adults during playbacks.

Dam's vocalizations

Juveniles are more responsive to their own dam's behaviour than to an alien dam's behaviour (see above), and if juveniles have more exposure to their own dam's vocalizations, then a dam's trills may be more salient than trills of alien dams in eliciting alarm-call responses. Male *S. beldingi* post-copulatory trills are statistically distinct among individuals (Leger et al. 1984), so the calls of adult females may be individually identifiable as well. We recorded the vocalizations of six captive dams during the pre-emergent period in the nursery building. We recorded both trills and single chirps (see Leger et al. 1984) and later arbitrarily played them to each dam's offspring in the enclosure during regular playback sessions.

Juveniles were as likely to respond to playbacks of their own dam's trill (92.3% of 13 playbacks responded to) as another dam's trill (94.3% of 122;

$\chi^2_1 = 0.09$, $P > 0.90$). There was no significant difference in response durations following trills of related and unrelated dams (ANCOVA: $F_{1,35} = 0.01$, $P = 0.93$). Juveniles were more likely to respond to their dam's trills (12 of 13 playbacks) than chirps (13 of 20), yet this difference was not significant (Fisher's exact test: $P = 0.11$).

Litter effects

If individual differences exist in adult anti-predator behaviour, and if dams influence the responses of their offspring, then the responses of litter-mates may be more similar than the responses of non-litter-mates, due to shared genes and/or shared experiences with their dam. If between-litter response variation exceeded within-litter variation, then one could infer a heritable component to alarm-call responses (e.g. Herzog & Burghardt 1988), or that exposure to a dam's own pattern of responding influences the responses of her offspring (e.g. Caro 1980; Martin & Bateson 1985). All juveniles had similar pre-emergent rearing histories (in the nursery building with similar foods and environmental conditions), so between-litter differences are likely to be due to post-emergent experiences with a dam or to heritable differences among dams' alarm-call responses. Because *S. beldingi* litters are multiply sired (Hanken & Sherman 1981), differences among litters are unlikely to be attributed to sires. We found no significant between-litter ($N = 8$ litters) variation in response durations (ANCOVA: $F_{7,337} = 1.31$, $P = 0.25$) or in vigilant postures, which we analysed by cohort and litter (Kruskal-Wallis ANOVA: $H_7 = 3.73$, $P = 0.81$ for all cohorts combined). Thus, we found no evidence that individual variation in alarm-call responses among captive juveniles resulted from differences among dam phenotypes.

Discussion

Taken together, our results (Figs 1, 2, Table II) indicate that a dam's presence has a modest but detectable influence on the alarm-call responses of her juvenile offspring, and that this effect is indirect. Juvenile response likelihood matched dam responsiveness, but was not associated with responses of other nearby adult females. Although these results indicate an association between dam and juvenile responses, they do not demonstrate a

causal relationship between the two. The presence of its familiar dam may decrease a juvenile's arousal, allowing it to better attend to and process auditory and visual stimulation (Clayton 1978). During days 1–5, when juveniles develop a behavioural discrimination between alarm and non-alarm calls (Mateo 1996), the responses of a juvenile and its dam were similar, yet a dam's presence or absence had no differential effect on a juvenile's response likelihood. The data imply that juveniles are more responsive to auditory stimuli than to their dam, and, although juveniles are sensitive to their dam's behaviour when she is present, young do not rely on her behaviour to indicate which stimuli they should respond to and which to ignore. We also never observed juveniles seeking out dams to learn from their dam's responses, nor did we observe dams actively directing juvenile behaviour, indicating that juveniles passively acquire information from dams' responses. There was no evidence that juveniles were more influenced by their own dam's alarm calls than an alien dam's calls. This could mean that, unlike male post-copulatory calls, dams' calls are not individually distinct or that juveniles respond to an alarm call regardless of who gives it. Lastly, there were no between-litter differences in juvenile responses.

EXPERIMENT 2: THE OUTCOME OF DAMS' INFLUENCE ON JUVENILE RESPONSES

Methods

It is not clear whether adult models are necessary for the development of species-typical alarm-call responses. Does experience with dams also have a delayed effect on juvenile development, such that exposure to a dam's alarm-call response influences subsequent juvenile responses in the absence of the dam? To determine whether experience with dams induces or facilitates (Gottlieb 1976) juvenile behavioural development, we observed juveniles housed in enclosures either with or without their dams beginning at natal emergence. If dams have a delayed influence on response development in addition to an immediate influence, then juveniles that continually experience alarm calls without adults present may fail to develop age-appropriate responses (if experience

is inductive) or may develop responses at a different rate (if experience is facilitative), compared with juveniles living with their dams. If a dam's influence is only immediate (restricted to the period of time immediately following an alarm call), then the development of juvenile responses should not differ between the groups.

We studied two types of juveniles in 1994 that were born in the nursery building and reared by their dam until they were transferred to an enclosure at 24 days of age (about the age of natal emergence). We transferred one type to an enclosure with their dams (Dam-present juveniles: four groups of two litters each; $N=40$ juveniles) and placed the other type in a separate enclosure without their dams (Dam-absent juveniles: two groups of one or two litters; $N=12$ juveniles) so that they could not observe adult responses to alarm calls. We had previously studied juveniles housed without their dams during the post-emergent period and did not detect abnormal behaviours, based on physical development, social interactions and the general expression of anti-predator behaviours (W. Holmes & J. Mateo, unpublished data). Because juveniles continue to nurse for a few days after natal emergence (J. Mateo & W. Holmes, unpublished data), we placed Dam-absent mothers in their offsprings' nest box at about 2000 hours each evening for 6 nights and removed dams at about 0700 hours the following morning. Thus, dams could nurse their young during the night, but juveniles could not observe their dam's responses to alarm calls, since alarm calls are rarely produced at night (personal observations) and dams were absent from the enclosure during the day. Playbacks began 1–3 h after dams were removed from the enclosure each morning, giving juveniles time to move about the enclosure without their dams present.

Although the number of juveniles in the Dam-present group was greater than in the Dam-absent group, the two groups had a similar number of opportunities to respond to playbacks (532 and 694 opportunities, respectively). We analysed data by 5-day cohorts for differences in rates of development between Dam-present and Dam-absent juveniles (days 1–5, 6–10 and 11–15). First we present the results of analyses on the four response measures; then we present data on the rate of development of alarm-call discrimination. Although the presence of a knowledgeable individual can inhibit the acquisition of a new

Table III. Number of available Dam-present and Dam-absent juveniles responding (%) to alarm-call and non-alarm-call playbacks

	Dam present	Dam absent	χ^2_1	<i>P</i>
Alarm calls				
Days 1–5	91/98 (92.9)	92/112 (82.1)	4.44	0.04
Days 6–10	70/72 (97.2)	151/154 (98.1)	0.09	0.99
Days 11–15	29/32 (90.6)	162/167 (97.0)	1.42	0.23
Non-alarm calls				
Days 1–5	17/43 (39.5)	10/35 (28.6)	0.59	0.44
Days 6–10	7/61 (11.5)	7/60 (11.7)	0.06	0.99
Days 11–15	9/26 (34.6)	10/63 (15.9)	2.82	0.09

behaviour (e.g. Giraldeau & Lefebvre 1987; Beauchamp & Kacelnik 1991), we predicted that if a dam's influence is facilitative, her presence would accelerate rather than decelerate the rate of response development (based on prior observations; see experiment 1 and Mateo 1995); therefore all tests were one-tailed.

Results

The permanent presence or absence of a dam after natal emergence had no consistent effect on juveniles' likelihood of response to alarm calls and non-alarm calls. Overall, Dam-absent juveniles were less likely to respond to non-alarm calls (17.1% of 158 possible respondents) than Dam-present juveniles (26.0% of 146), but not significantly so ($\chi^2_1=3.10$, $P=0.08$). We found no difference in responsivity to alarm calls when all cohorts were combined (93.5% of 433 and 94.6% of 223, respectively; $\chi^2_1=0.14$, $P=0.71$). When examined by cohort, Dam-absent juveniles were more responsive to all playbacks during days 6–10 than Dam-present juveniles (78.3% of 258 and 66.5% of 179, respectively; $\chi^2_1=6.97$, $P=0.01$). We found no significant difference in responsivity to all playback categories combined during days 1–5 (73.8% of 172 and 79.7% of 172, respectively; $\chi^2_1=1.32$, $P=0.25$) or days 11–15 (77.7% of 260 and 75.3% of 85, respectively; $\chi^2_1=0.10$, $P=0.76$). When analysed by call type (alarm versus non-alarm), however, the Dam-absent young were less responsive to alarm calls during days 1–5 than were Dam-present juveniles ($P=0.04$; Table III). When analysed by playback category, there were no significant differences in responsivity between the two groups. Thus the continuous absence of an adult model did not

promote or attenuate the long-term likelihood of responding to playbacks of alarm calls or non-alarm calls.

The response durations of the two groups did not differ significantly following playbacks of alarm calls (ANCOVA: $F_{1,578}=0.82$, $P=0.37$). After non-alarm call playbacks, however, Dam-absent juveniles resumed non-alert behaviour sooner (14.22 ± 6.0 s) than Dam-present juveniles (45.60 ± 9.5 s; ANCOVA: $F_{1,57}=8.50$, $P=0.01$; Fig. 3). When analysed by playback category, Dam-present juveniles remained alert longer than Dam-absent young following single whistles (38.74 ± 3.3 s and 27.09 ± 2.0 s, respectively; ANCOVA: $F_{1,187}=10.06$, $P=0.002$) and wren songs (51.69 ± 11.2 s and 16.51 ± 6.7 s, respectively; ANCOVA: $F_{1,48}=8.13$, $P=0.01$).

The permanent presence or absence of dams had no significant effect on initial responses (frequency of four initial responses by the two groups: $\chi^2_3=7.26$, $P=0.06$) or vigilant postures in any cohort (overall, alarm calls: $U=40771$, $P=0.84$; non-alarm calls: $U=608$, $P=0.17$). Dam-absent juveniles were more likely to display socially facilitated responses (see Methods) following non-alarm calls (16.7% of 18 responses) than Dam-present juveniles (0 of 36; Fisher's exact test: $P=0.03$).

Dams did influence the rate of development of discrimination between alarm call and non-alarm call playbacks (Table IV). Neither group of juveniles showed differential responsivity to the two call types on day 1, which is when they were first exposed to the stimuli (Fisher's exact test: $P=0.10$ and $P=0.34$ for Dam-present and Dam-absent juveniles, respectively). Dam-present juveniles discriminated alarm-call from non-alarm call playbacks on day 2 (Fisher's exact test: $P=0.002$), yet

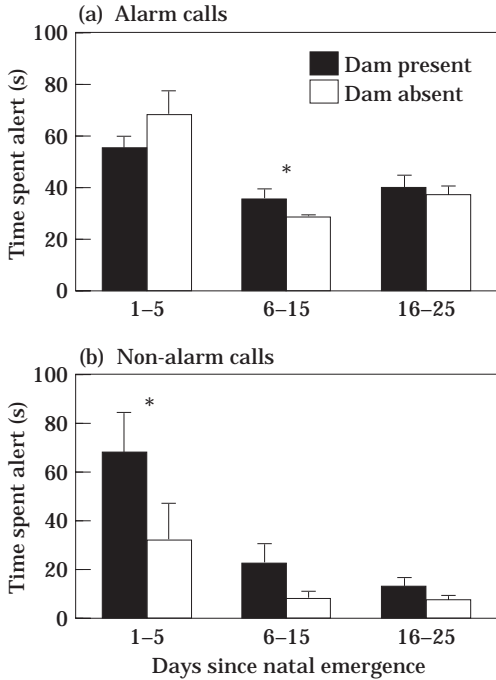


Figure 3. Mean \pm SE response durations (s) of Dam-present and Dam-absent juveniles in each cohort to (a) alarm-call and (b) non-alarm-call playbacks. Day 1 refers to juveniles' first day above-ground in the enclosure. See text for number of juveniles observed. Asterisks represent significant differences in response duration between Dam-present and Dam-absent juveniles (ANCOVA: $P < 0.05$).

Dam-absent individuals did not achieve this discrimination until day 3 ($P = 0.001$). In contrast to juveniles, on day 1, dams responded to all

whistle choruses (2 of 2 playbacks) and trills (2 of 2) but did not respond to wren-song playbacks (0 of 2).

Discussion

The permanent absence of adult models (dams) affected the rate of acquisition of behavioural discrimination between auditory stimuli by juvenile *S. beldingi*, but had no prolonged effect on their expression of alarm-call responses. For example, a dam's absence had an inconsistent effect on juvenile responsiveness, since newly emergent (days 1–5) Dam-absent juveniles tended to be less likely to respond to alarm calls than Dam-present young, but were more responsive to all playbacks during days 6–10. Moreover, Dam-absent juveniles tended to resume non-alert behaviour sooner than Dam-present young following non-alarm call playbacks, but the two groups showed similar vigilant postures. Dam-absent juveniles made more socially facilitated responses to non-alarm calls than Dam-present young, suggesting that without the opportunity to view how and when adults responded, Dam-absent juveniles attended to the responses of nearby litter-mates. In summary, the data from experiment 2 suggest that dams facilitate rather than induce the development of alarm-call responses by their juvenile offspring, since both groups eventually developed normal responses, albeit at different rates, but that dam behaviour does not have a delayed effect on when and how juveniles respond to auditory signals.

Table IV. Number of Dam-present and Dam-absent juveniles that displayed a response (of the total number of juveniles available to respond, %) in each of the four playback categories during each of the first five days after natal emergence

	Day 1	Day 2	Day 3	Day 4	Day 5
Dam present					
Whistle chorus	1/1 (100)	3/3 (100)	1/1 (100)	3/3 (100)	1/1 (100)
Single whistle	3/5 (60.0)	8/9 (88.9)	9/10 (90.0)	13/13 (100)	2/2 (100)
Trill	6/7 (85.7)	2/2 (100)	15/16 (93.8)	17/18 (94.4)	7/7 (100)
Wren song	4/11 (36.4)	1/6 (16.7)	3/9 (33.3)	8/12 (66.7)	1/5 (20.0)
Dam absent					
Whistle chorus	5/5 (100)	7/7 (100)	11/12 (91.7)	3/4 (75.0)	8/8 (100)
Single whistle	2/5 (40.0)	4/10 (40.0)	9/11 (81.8)	6/6 (100)	5/5 (100)
Trill	9/15 (60.0)	6/7 (85.7)	9/9 (100)	3/3 (100)	5/6 (83.3)
Wren song	2/5 (40.0)	2/5 (40.0)	3/11 (27.3)	4/7 (57.1)	1/7 (14.3)

GENERAL DISCUSSION

Spermophilus beldingi dams indirectly facilitated the development of species-typical responses to alarm calls in their juvenile offspring. Juveniles living with their dam after natal emergence appeared to develop discriminative responses to auditory stimuli faster than juveniles living without their dams. Individuals responded selectively to alarm calls and not to non-alarm calls at least 1 day earlier if they were exposed to adults (Table IV). It is difficult to know whether this 1-day acceleration in behavioural development is biologically significant. On their natal-emergence day, however, free-living juveniles do not discriminate between alarm calls and non-alarm calls, but they do so by their fifth day above-ground (Mateo 1996). In this light, a 1-day acceleration translates into a 20% increase in the rate at which relatively predator-inexperienced juveniles acquire a skill critical to survival. Newly emergent juveniles are highly vulnerable to predation (Sherman & Morton 1984; Mateo 1995), and free-living juveniles are more likely to disappear as a result of predation during their first 2 weeks above-ground (Mateo 1996). Thus, although observing dams is not necessary for the development of response discrimination, juveniles that acquire the discrimination sooner by watching their dam may be more likely to escape from an otherwise fatal encounter with a predator.

Because our non-alarm control calls were wren songs and not *S. beldingi* vocalizations, we cannot exclude the possibility that dams may influence differential responsivity to conspecific and heterospecific calls, and not affect juveniles' responses to classes of conspecific calls. Our choice of a control stimulus was limited by the vocal repertoire of our study species. The only other *S. beldingi* vocalization that is acoustically distinct from whistles, trills and chirps but is not associated with predators is the juvenile squeal. Squeals are given by juveniles during rough play or during agonistic encounters with adults. We did not present squeals during playbacks because dams are acutely responsive to these calls, often posting, running towards the squealing animal and/or giving trill vocalizations (Sherman 1977; personal observations). The acute responsiveness of dams to squeals may be explained by newly emergent juveniles' continued vulnerability to infanticide (Sherman 1981), and the tendency of juveniles to

squeal when attacked by adults (personal observations). Because dams respond to squeals much as they do to alarm calls the first few days after natal emergence (Mateo 1996), juveniles may learn to respond to squeals as alarm calls if they are influenced by their dam's responses to squeals. Consequently, it was not appropriate to use them as a control stimulus in this study. Nevertheless, our results indicate that juveniles acquire a discriminative response to threatening and non-threatening stimuli faster by observing adult responses to the calls.

Adult models facilitated the development of response discrimination, but did not consistently affect response patterns (initial response, duration, posture). If juveniles can learn more quickly when to respond, and with fewer errors, by incorporating the responses of conspecifics into their own repertoire (Galef 1976), then why do not dams also influence how juveniles respond? The development of discriminative responses must precede the development of response patterns (Mateo 1995). Juveniles that first learn when to respond to alarm calls are more likely to survive than those that first learn how to respond. Moreover, when juveniles initially emerge above-ground, their motor systems are not fully developed and they have a limited response repertoire (e.g. freezing, entering a burrow). Thus, attention to conspecifics may affect the development of juveniles' response discrimination more than the early development of their response patterns.

Considerable variation exists across taxa in how parents protect their young from predators (e.g. Moehlman 1983; O'Connor 1984; Huntingford & Wright 1993; Le Boeuf & Campagna 1994). This variation is, in part, correlated with the time young are dependent on their parents. With extended parental care, young may have many opportunities to observe and learn from their parents' anti-predator behaviours (e.g. Cheney & Seyfarth 1990; Poran & Coss 1990). Conversely, species with little parental care usually acquire these behaviours independently of adults (e.g. Herzog et al. 1992). Thus, the length of dependence on parents will influence the development of offspring's response repertoires, and extended parental care may result in variable pathways of behavioural development, including social facilitation of responses (e.g. Culley & Ligon 1976; Seyfarth & Cheney 1986; Huntingford & Wright 1993).

Belding's ground squirrel mothers can protect their young from predators in many ways. During the pre-emergent period, dams construct well-concealed natal burrows (personal observations), vigorously defend burrows from potentially infanticidal conspecifics (Sherman 1981) and may move their litters if predators disturb the natal burrow (McLean 1983; Trulio et al. 1986; personal observations).

The predator-protection behaviour of *S. beldingi* dams differs during the post-emergent period (see also Poran & Coss 1990 on *S. beecheyi*), taking the form of warning their offspring of potential predators. Alarm-calling behaviour by dams increases in frequency after the natal emergence of young in some ground-dwelling squirrel species (Sherman 1977; McLean 1983; Davis 1984; Owings et al. 1986; Hoogland 1995; not all reports, however, control for the frequency of predator appearances). After their young emerge, *S. beldingi* mothers are also more likely to respond to alarm calls and display heightened vigilant postures (Mateo 1996). The increase in dam vocal and non-vocal anti-predator behaviour peaks at the time that newly emergent young are learning to discriminate behaviourally between auditory stimuli and may create a context that facilitates this developmental process.

Dams do not typically stay near their offspring when above-ground, however (Mateo 1996), and dams are not always present when their young first encounter predators or alarm calls (Owings & Coss 1977; personal observations). Nor do dams run to their natal burrow after hearing an alarm call, as though to retrieve or defend their offspring (e.g. McCarley 1966; Rasa 1977; cf. Poran & Coss 1990) or to coach juvenile responses (Caro & Hauser 1992). Dams may return to their natal-burrow area when a predator appears somewhere in the colony, and their behaviour in this context may give juveniles an additional opportunity to form associations between predators, alarm calls and species-typical escape responses. Thus, *S. beldingi* dams engage in time-dependent forms of predator-protection behaviour: they actively guard pre-emergent pups from predators and infanticidal conspecifics and later warn their post-emergent juveniles (among others) of potential danger by giving alarm calls. As a consequence of their own alarm-call response behaviour, dams can also inadvertently aid their juveniles

by indicating which auditory stimuli to attend to and how to respond (e.g. Seyfarth & Cheney 1986).

It probably is not critical that a juvenile's own dam serve as a model, although a juvenile's dam may be the only adult that her newly emergent offspring can observe, since most other adults avoid that dam's home area (Sherman 1976; personal observations). Because the behaviour of reproductive and non-reproductive ground squirrels differs (reproductive females spend more time vigilant and less time foraging, and are more likely to give an alarm call or to chase a predator; Sherman 1977; Leger & Owings 1978; Davis 1984; MacWhirter 1991; Hoogland 1995; see Burger & Gochfeld 1994 for a review of ungulate mothers), selection may have favoured juveniles that attend to their dams in particular. Most adult *S. beldingi* females bear litters each season, however (Sherman & Morton 1984; Mateo 1995); therefore juveniles are likely to have been selected to observe the alarm-call responses of any adult female, regardless of relatedness. Whether juveniles could gain information by also observing the responses of experienced adult males is unclear. Although we do not expect sex differences in responses to alarm calls (e.g. Sherman 1985), females, but not males, alter their vigilance after the emergence of their litters, and adult males tend to be spatially and socially peripheralized after the mating season (Morton & Parmer 1975; W. Holmes & J. Mateo, unpublished data).

In summary, the influence of *S. beldingi* dams on the development of alarm-call responses in juveniles is indirect, yet a mother's presence when an alarm call is heard affects her offspring's responses to the call. Exposure to the responses of adult conspecifics also appears to facilitate the development of alarm-call discrimination by newly emergent juveniles. Juveniles that had opportunities to observe the reactions of their dam to alarm calls showed differential responses to threatening and non-threatening auditory stimuli sooner than juveniles without adult models. Experience with dams is not necessary for response discrimination to develop, but juveniles that incorporate the responses of experienced conspecifics into their repertoire, and thus learn what stimuli to respond to earlier, may be more likely to survive attacks during a period of high susceptibility to predation.

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