Anim. Behav., 1996, **52**, 489–505

The development of alarm-call response behaviour in free-living juvenile Belding's ground squirrels

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*(Received 28 July 1995; initial acceptance 17 October 1995;
final acceptance 7 December 1995; MS. number: A7372)*

Abstract. The production of and responses to alarm calls by adult ground-dwelling squirrels has been widely documented, yet the development of alarm-call behaviours has not been systematically addressed. The responses of free-living Belding's ground squirrels, *Spermophilus beldingi*, to playbacks of conspecific (three alarm calls and juvenile squeals) and heterospecific (wren song) vocalizations were observed from natal emergence until the age of dispersal. Discrimination of the five auditory stimuli was not present at emergence but developed within the next 5 days, with responsivity to whistle alarm calls, indicative of fast-moving predators, developing earlier than to trill alarm calls, associated with slow-moving predators. Response patterns (response duration, vigilant postures and initial responses) changed throughout the following 4 weeks, and approximated adult responses before juveniles dispersed. Juvenile responses were indirectly influenced by conspecifics, particularly the dam, as well as by the physical environment, including distance from the natal burrow and location within the meadow. Alarm-call responses appeared to be adapted to the juvenile's current stage of development, with younger juveniles making a trade-off between information gathering and escape responses. The development of appropriate responses to each alarm call is hypothesized to be facilitated by observations of experienced ground-squirrels' responses. Despite their vulnerability, juveniles may not emerge with fully formed associations between alarm calls and responses if the local predator context changes over time, thus favouring plasticity in the response repertoire.

In many species of birds and mammals, predators elicit vocal responses from potential prey labelled alarm calls, which can alert other animals to impending danger (Klump & Shalter 1984). I use 'alarm call' descriptively to refer to a vocalization elicited by a predator, and do not imply a function or motivation on the part of the caller (Hennessy et al. 1981). For alarm calls to have communicative value (recipient perceives and interprets the information in the sender's signal: Dawkins & Krebs 1978; Owings & Hennessy 1984), or adaptive significance (Sherman 1977), recipients must know how to respond appropriately to the calls, such as with approach or withdrawal behaviours. Responding appropriately involves a cumulative four-stage process (Fig. 1): recipients must hear the alarm call, discriminate it from other stimuli, decide whether to respond and, finally, decide how to respond (I do not imply complex mental processes here). The ontogeny of alarm-call response behaviour occurs at all four stages, with each stage contributing to the next (Galef 1981) as sensory, perceptual and motor systems independently develop and integrate (Hogan 1988). How and when alarm-call responses develop varies between species; some young birds and primates can recognize and respond to conspecific calls upon first exposure (Miller 1983; Herzog & Hopf 1984), but other naïve young display poor initial discrimination between alarm calls (Rydén 1982; Cheney & Seyfarth 1990). I have studied the alarm-call responses of young Belding's ground squirrels, *Spermophilus beldingi*, at the developmental level of analysis (Sherman 1988; Hill 1995) and also interpret their responses within a functional framework.

Ground-dwelling squirrels (*Cynomys*, *Marmota* and *Spermophilus* genera) provide an excellent opportunity to examine the conditions that affect

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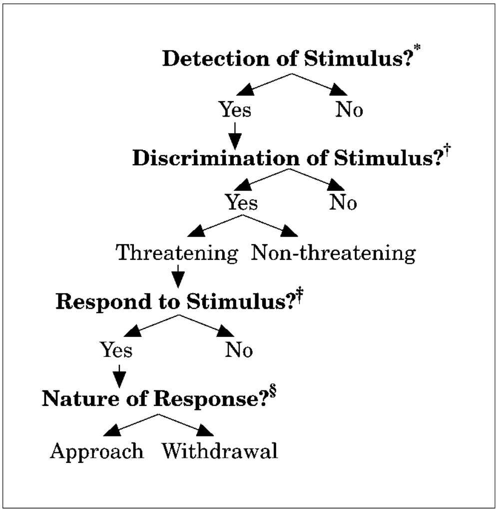

Figure 1. Four stages of the development of alarm-call response behaviour. Stages also broadly apply to the expression of anti-predator behaviour by experienced individuals of any species. *Rydén 1982; Cheney & Seyfarth 1990; Buitron & Nuechterlein 1993; Mateo 1996. †Rydén 1982; Miller 1983; Berntson & Boysen 1989. ‡Schwagmeyer & Brown 1981; Cheney & Seyfarth 1990; Macedonia 1990; Buitron & Nuechterlein 1993. §Herzog & Hopf 1984; Cheney & Seyfarth 1990; Macedonia 1990.

alarm-call response development. First, the ecological and social contexts in which adults produce and respond to alarm calls have been well documented. Second, several terrestrial and aerial species prey on sciurids. Finally, ground-dwelling squirrels face challenges from environmental factors that change markedly during early development, particularly as young move from the safety of an underground burrow to an independent life above ground.

Belding's ground squirrels are one of several species of ground-dwelling squirrels that give alarm calls when they detect predators, although much variation exists between species in the production of and responses to alarm calls (Hoogland 1995). Adult *S. beldingi* produce two acoustically distinct alarm calls, trills and whistles, which elicit different behavioural responses and serve different functions (Robinson 1980; Leger et al. 1984; Owings & Hennessy 1984; Sherman 1985). Trills, which are composed of a series of five or more short notes, are elicited by slow-moving predators, primarily terrestrial animals such as coyotes and badgers, or other predators that pose no immediate threat (e.g. perched raptor). Adults typically respond to trills by posting (a bipedal stance accompanied by visual scanning), with or without changing location. Whistles, which are single, non-repetitive high-frequency notes, are elicited by fast-moving, typically aerial, predators or other predators that do pose an immediate threat (e.g. very close terrestrial predators). Whistles usually result in evasive behaviours, such as crouching, running to or entering a burrow and scanning the area only after reaching safety (Sherman 1977, 1985; Robinson 1980, 1981). The development of juvenile alarm-call responses has not been documented in detail for any ground-dwelling squirrel, especially with respect to developmental changes after emergence from the natal burrow (but see Schwagmeyer & Brown 1981; Davis 1984; MacWhirter 1992 for short descriptions of juvenile alarm-call production and responses).

Like all members of the genus, *S. beldingi* young develop for the first few weeks of life in relatively dark and quiet underground, natal burrows and do not routinely hear alarm calls until they first come above ground. When young emerge as nearly weaned juveniles (around 25 days of age, the 'natal emergence': Sherman 1976), they enter a very different environment that includes intense auditory and visual stimulation, predators and conspecifics. Because trial-and-error learning can be fatal, one might expect juveniles to respond appropriately to alarm calls upon first exposure to them (Galef 1976). Newly emergent juveniles can discriminate between trills and whistles (Mateo 1996), yet their behavioural responses to both call types are not fully developed despite their susceptibility to predation (Sherman & Morton 1984).

Here I describe the development of alarm-call responses in free-living *S. beldingi*, based on responses to auditory playbacks from natal emergence through dispersal. I addressed stages 2 to 4 of alarm-call response development (Fig. 1) to determine when and how juveniles begin to respond selectively to alarm calls and give age-appropriate patterns of responses. Using an epigenetic framework, I studied the behaviour of juveniles as they interacted with their social and ecological environments across time, to determine what stimuli young were exposed to and how these stimuli influenced the ontogeny of their response behaviour (Lehrman 1970; Johnston 1987; West & King 1987).

Table I. Description of study animals

Year	1993	1994
No. of litters	13	4
No. of juveniles	65	17
Emergence dates	3–13 July	24–28 July
Litter size	$\bar{X}$=5 (4–7)	$\bar{X}$=4 (2–6)
Sex ration (M:F)	1:0.67	1:0.89
Emergence weight (g)*	50.17 ± 0.83, *N*=64	59.11 ± 2.94, *N*=17
'Dispersal' weight (g)*†	138.33 ± 4.08, *N*=30	

*$\bar{X}$ ± SE.

†1993 and 1994 data combined due to small samples for each year; $\bar{X}$=48.47 days of age.

METHODS

Study Site and Animals

I studied juvenile *S. beldingi* between June and August in 1993 and 1994 within the 4-ha Lower Horse Corral in Rock Creek Canyon, Mono County, California (2900 m elevation). The main site (30 × 91 m) was typical of Eastern Sierra sub-alpine meadow habitat, and was bounded by a stream, dry streambeds, scattered willow bushes (*Salix* spp.) and pine trees (*Pinus* spp.). The meadow's vegetation ranged from 3 to 10 cm high, allowing for good visibility of marked animals.

I conducted playbacks to 13 litters in 1993 and four litters in 1994. In 1994, I marked 12 females that had prominent nipples (indicative of nursing), but eight of their litters never emerged. I observed 65 juveniles during 1993 and 17 during 1994 (Table I). I sexed, weighed and marked juveniles individually (with hair dye and coloured vinyl discs attached to ear tags) within 1 to 2 days of their natal emergence. Disappearance of juveniles during their first two weeks above ground ranged from 12.5% in 1993 to 26.7% in 1994. I witnessed one juvenile's death each year, caused by an adult male *S. beldingi* and a sharp-shinned hawk, *Accipiter striatus*, respectively. The remaining disappearances were presumably a result of predation, because juveniles appeared to be healthy individuals but were too young to disperse from the area.

Playback Stimuli

I used five categories of auditory playbacks: three types of *S. beldingi* alarm calls, one *S. beldingi* squeal (conspecific control stimulus) and one house wren, *Troglodytes aeodon*, song (heterospecific control stimulus). The alarm calls included *S. beldingi* whistle choruses, single whistles and trills (Robinson 1981; Leger et al. 1984). Because fast-moving predators commonly elicit a chorus of whistles from a number of individuals (Leger & Owings 1978; Leger et al. 1979; Sherman 1985; personal observation), I included a 'whistle-chorus' category of playbacks in 1994 in which each exemplar was a recording of numerous adults producing single whistles. Unlike previous playback studies that used artificial sounds or silence as control playbacks (Harris et al. 1983; Evans et al. 1993; Weary & Kramer 1995), I used two naturally occurring vocalizations, squeals and wren songs, as control stimuli to enhance interpretation and generalization of the juveniles' responses to them. Juveniles often squeal during rough play, during agonistic encounters with adults or when held by a human (Sherman 1977; personal observation). Although squeals may be associated with aversive situations, they are also elicited in non-predatory contexts and are not produced upon visual detection of the eliciting stimulus alone; therefore I do not consider squeals anti-predator alarm calls. House wrens are oscines sympatric with *S. beldingi*, and their songs are not associated with predatory contexts. These five playback categories enabled me to determine when *S. beldingi* begin to respond differentially to alarm call and non-alarm call (squeal and bird song) playbacks. I also included an 'aerial-object' category to record responses to single-whistle alarm calls paired with a visual stimulus (a frisbee flown 2–4 m over the head of the focal individual 1–2 s after presentation of an alarm call playback: Davis 1984; MacWhirter 1992).

Stimuli were recorded with a Sony TC-D5M Pro Stereo cassette recorder and Realistic Omnidirectional microphone. Recordings were bandpass filtered (300–16 000 Hz) and digitized (sampling rate=50 000 points/s) using Signal software (Engineering Design 1992). I played back the recordings through either a Sony TC-D5M or Sony WM-D6C cassette recorder–player connected to a Nagra DH amplifier–speaker. All playbacks were presented at peak amplitudes approximating natural intensities (whistle= ~85 dB, trill= ~75 dB, squeal= ~50 dB, and wren song= ~60 dB, measured with a Realistic sound level meter on 'A' weighting 9 m from the speaker). I used eight exemplars of each stimulus, selected for their signal amplitude and lack of background noise, and each exemplar within a category was recorded from a different individual (or individuals, for the whistle choruses). I presented all exemplars in a balanced order (Kroodsma 1986).

Playback Protocol

My assistants and I conducted playbacks daily between 0700 and 1200 hours; playbacks began on the day of natal emergence and continued until juveniles were approximately 50 days of age. Observers sat on 3-m high viewing stands approximately 20 m from a natal burrow, and positioned the speaker about 4 m from the viewing stand. The speaker was typically not visible to the focal juvenile due to meadow topography, and its location was changed for each playback session. Each session consisted of one playback of each of the six playback categories (five auditory and one audio-visual), presented at about 15-min intervals unless I heard a natural alarm call or saw a potential predator during the preceding interval. This schedule minimized the effects of habituation to playbacks, and all animals continued to respond to natural and recorded alarm calls.

I videotaped the responses of juveniles and adults with either a Panasonic AG 450 VHS camera with a 10 × zoom lens or a Sony CCD-F35 8 mm camcorder with a 6 × zoom lens. I randomly selected a focal ground squirrel and began filming when that individual was ≥ 3 m from a burrow. Each individual was the focal ground squirrel for each of the six playback categories at least once, and was videotaped at least every other day. I filmed the focal ground squirrel from 15 s prior to stimulus onset until it resumed a non-alert behaviour, such as feeding or socializing. After filming ended, I noted the location and initial response (see below) of all non-focal individuals within the camera's field of view. The spatial location of all visible *S. beldingi*, including the dams, was also recorded every 20 minutes.

A juvenile's dam was scored as 'dam present' during a playback if she was above ground and within 5 m of the juvenile. At this distance, most quadrupedal juveniles could view their dams regardless of the topography surrounding them. When no conspecific of any age class was within 10 m of the focal ground squirrel during a playback, I considered it 'visually isolated'. Adults and juveniles outside of this range were well out of the field of view of focal juveniles, whether they were in a bipedal or quadrupedal posture. I classified responses as 'socially facilitated' if the behaviour or presence of one ground squirrel (the 'facilitator') prompted or prolonged the focal juvenile's behaviour. For example, the focal juvenile may not have given any immediate response to the playback, but did react a few seconds later as the facilitator ran past it toward a burrow. Similarly, I considered a response to be socially facilitated if the focal ground squirrel began to engage in a non-vigilant behaviour after the playback, only to resume posting when another individual posted. Responses were not scored as facilitated if there was a possibility that the focal juvenile reacted to some cue other than the facilitator. I use the term 'facilitate' descriptively rather than functionally, and prefer it over 'reinforcement' to avoid implying intention or active guidance on the part of the facilitator (Clayton 1978).

Analyses

Playback responses were quantified from videotapes using Ethos22 event-recorder software (G. Gerstner, unpublished computer program). This program generated the frequency of vocalizations made by the focal ground squirrel as well as the frequencies and durations (to the nearest 0.01 s) of 10 mutually exclusive behaviour patterns, grouped into alert and non-alert types of behaviour (alert: horizontal, slouch, posting and vertical-stretch (legs extended) postures (see below; Betts 1976), below ground, and locomoting; non-alert: stationary/resting, feeding, grooming, and socializing: Mateo 1995).

Response measures

Spermophilus beldingi alarm-call responses were multi-dimensional and required at least four qualitatively different measures to quantify them. 'Responsivity' was the likelihood of an individual giving a detectable response to a playback, such as posting, freezing or entering a burrow. If an individual's behaviour did not change following the playback, it was scored as not responding. 'Initial response' was the respondent's first behavioural reaction to the stimulus, categorized as enter a burrow, run to a burrow, post or freeze/look up. 'Response duration' was the total time spent alert (running to a burrow, entering a burrow or above ground in horizontal, slouching, posting or vertical-stretch postures; see 'vigilant posture', below), measured from onset of the stimulus until the individual resumed a non-alert behaviour. Response durations were normally distributed and did not require transformation. 'Vigilant posture' quantified the maximum alert posture given by an individual during any point of its response (see also Leger & Owings 1978; Harris et al. 1983) as follows: 4=below ground (full body enters a burrow for a minimum of 2 s), 3=post (standing on hind feet with torso held straight, with or without legs fully extended), 2=slouch (sitting on hindquarters, torso not fully extended), and 1=horizontal (head raised with three or four feet on the ground). For descriptive purposes, these ordinal data are presented as means.

I recorded 1671 individual responses by 82 juveniles and 17 dams to 1065 separate playbacks (471 in 1993 and 594 in 1994). Because I often recorded the responses of non-focal as well as focal ground squirrels to a single playback, or the response of more than one individual from the same litter, the data potentially lacked independence. I therefore conducted two one-way ANOVAs on each data set, using response duration as the dependent variable. I first used each separate playback as a level of the independent variable, and I then analysed the same data with each litter as a level of the independent variable. For all data sets, I found no significant effect of either independent variable, and thus did not find that the responses of multiple juveniles to one playback, or the responses of litter-mates (young born to a common dam) to all playbacks, were dependent. Therefore, the unit of analysis for each response measure was the individual's response to each playback (see Leger & Didrichsons 1994 for a discussion of data pooling). Finally, I performed a one-way ANOVA on the response duration following each playback category, using the eight exemplars of that category as levels of the independent variable. For each of the six playback categories, the F-ratio was insignificant ($P>0.05$), so I pooled all data from the eight exemplars for each playback category.

I based the longitudinal description of the development of juvenile alarm-call responses on data from 1993, when all responses were videotaped until juveniles were approximately 50 days of age (data on whistle choruses in 1994 were added to these analyses). I conducted the remaining analyses on data pooled from both seasons, because I found no significant differences in adult or juvenile behaviour between the years. In 1994, responses were videotaped only during a juvenile's first five days above ground, to allow observers to collect other data on older juveniles. Therefore, data on response duration are not available for free-living juveniles' responses to whistle choruses, which were only presented in 1994. To determine whether a dam's responses change as a function of her offspring's post-emergence vulnerability, dams were also filmed for up to 12 days prior to the emergence of their litters. Because I conducted playbacks equally throughout the morning, time of day was not controlled in analyses. For all chi-squared analyses, I used Yates' correction for continuity when $df=1$. I considered results significant when $P<0.05$, and present the data as mean ± SE.

I grouped juvenile responses into three age cohorts based on the ecological relevance of the ages. 'Days 1–5' included the first five days after natal emergence. This is a period of frequent interactions between kin, as juveniles, and to a certain extent the dam, remain near the natal burrow (personal observation). 'Days 6–15' encompassed the period when a juvenile's natal area (Holekamp 1984) was its centre of activity, particularly at night, and 'days 16–25' included the remaining days post-emergence (dispersal activity begins about 20 days post-emergence: Holekamp 1984). Smaller cohorts during days

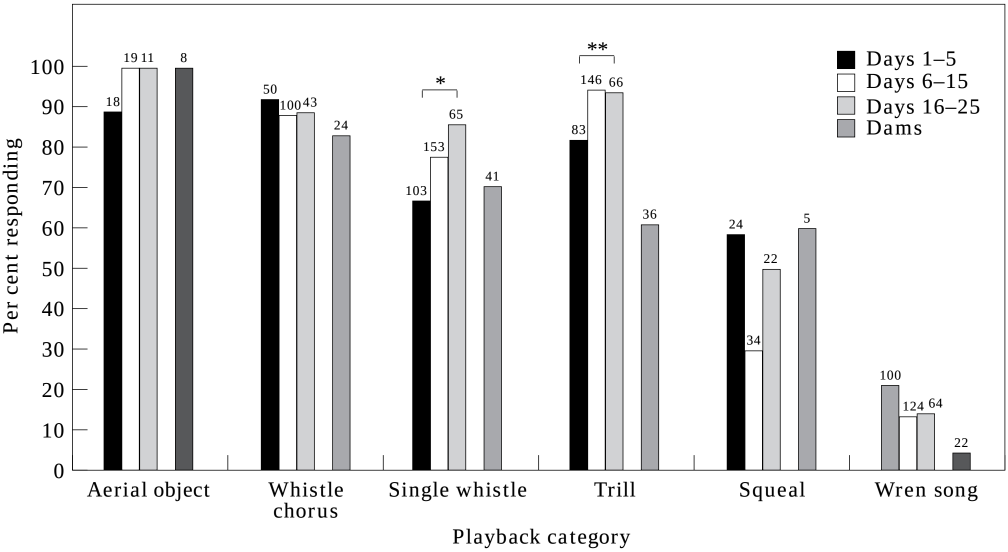

Figure 2. Percentage of juveniles in each age cohort responding to playbacks. Day 1 refers to juveniles' first day above ground. Data are grouped by playback category, and include responsivity of dams for comparative purposes. Numbers above bars represent the total number of responders and non-responders to each playback–age cohort category. Numbers of juveniles and dams observed are in Table 1. Asterisks represent a significant difference between age cohorts (*$P<0.05$, **$P<0.001$).

6–25 did not yield results that were significantly different from those reported here. I rarely recorded one individual's response to a given playback category in more than one age cohort, so the across-cohort analyses do not violate assumptions of independence. I included data from 16 dams (responding during the 25 days after their litter's natal emergence) for a general comparison between juvenile and adult responses. I do not know how representative dams' responses are of all adult *S. beldingi* responses (including males and the few non-reproductive females); in contrast to alarm-call production (Sherman 1977), however, I did not expect alarm-call responses to vary with sex (Sherman 1985; but see Leger & Owings 1978).

RESULTS

Longitudinal Development of Alarm Call Responses

Responsivity

In each of the three age cohorts, juveniles were significantly more likely to respond to the three alarm calls than the two non-alarm calls (each of three chi-squared tests, $df=1$, $P<0.001$). The proportion of juveniles responding to the whistle, trill and aerial-object playbacks increased as juveniles aged, significantly so for trills and single whistles ($\chi^2=11.07$, $df=2$, $P=0.004$ and $\chi^2=8.53$, $df=2$, $P=0.01$, respectively; Fig. 2). By days 16–25, at least 90% of juveniles gave a response to alarm-call playbacks. In contrast, juveniles became less responsive to squeals and wren songs as they aged, with the decline in responsivity to the former approaching significance ($\chi^2=5.26$, $df=2$, $P=0.07$). Juveniles were more likely to respond to squeals during days 1–5 than days 6–15, which may be explained by their continued vulnerability to infanticide at the younger age (Sherman 1981b), and the tendency of juveniles to squeal when attacked by adult conspecifics (personal observation). Dams only responded to squeals (3 of 5 playbacks) during the first five days following their litter's natal emergence. The oldest juveniles (days 16–25 above ground), approaching the age of natal dispersal, were more likely to respond to trill alarm-call playbacks than dams ($\chi^2=15.09$, $df=1$, $P<0.001$), yet I found no difference for responsivity to other categories ($\chi^2=0.44$, $df=1$, $P=0.51$).

Table II. Initial responses of juveniles (by age cohort) and dams to each playback category

Playback category	Enter burrow	Run to burrow	Post	Freeze	*N*	χ^2
Aerial object						11.26, $P=0.08$
Days 1–5	87.5	6.3	0.0	6.3	16	
Days 6–15	50.0	33.3	5.6	11.1	18	
Days 16–25	25.0	50.0	25.0	0.0	4	
Dams	25.0	25.0	50.0	0.0	8	
Whistle chorus						30.65, $P<0.001$
Days 1–5	32.6	30.4	17.4	19.6	46	
Days 6–15	8.1	35.6	49.4	6.9	87	
Days 16–25	7.9	36.8	52.6	2.6	38	
Dams	15.0	35.0	35.0	15.0	20	
Single whistle						28.73, $P<0.001$
Days 1–5	34.2	18.4	21.1	26.3	39	
Days 6–15	5.0	35.0	45.0	15.0	40	
Days 16–25	0.0	63.2	31.6	5.3	19	
Dams	0.0	17.2	55.2	27.6	29	
Trill						19.85, $P=0.003$
Days 1–5	32.4	16.1	29.0	22.6	31	
Days 6–15	3.1	40.6	37.5	18.8	32	
Days 16–25	0.0	52.6	36.8	10.5	19	
Dams	0.0	27.3	40.9	31.8	22	
Squeal						21.82, $P=0.001$
Days 1–5	35.7	14.3	7.1	42.9	14	
Days 6–15	0.0	10.0	70.0	20.0	8	
Days 16–25	0.0	54.6	27.3	18.2	11	
Dams	0.0	0.0	100.0	0.0	3	
Wren song						N/A*
Days 1–5	35.3	23.5	11.8	29.4	17	
Days 6–15	0.0	12.5	37.5	50.0	8	
Days 16–25	0.0	0.0	0.0	100.0	1	
Dams	0.0	0.0	100.0	0.0	1	

*Insufficient data to conduct a χ^2 analysis.
Numbers represent the percentage of respondents giving each initial-response type within each age cohort. Chi-squared analysis examine changes in juveniles' four initial responses across three age cohorts to each playback category (*df*=6). Data on dams' initial responses are included for comparative purposes.

Initial responses

The initial responses given by juveniles also changed over time (Table II). Partitioning of the tables revealed that during the first five days above ground, the most frequent initial response to all playbacks (except whistle choruses) was to freeze or enter a burrow. Older juveniles (days 16–25) were more apt to post or run to a burrow following aerial-object, single whistle, trill and squeal playbacks. In contrast, the few individuals responding to wren songs typically only froze or looked. Initial responses to whistle choruses changed from running to or entering a burrow to posting. The oldest juveniles (days 16–25) and dams differed significantly in their initial responses. Juveniles typically ran to burrows, but dams were more likely to freeze (or look up) or post in response to alarm calls ($\chi^2=16.92$, $df=3$, $P<0.001$).

Response duration

Juveniles spent less time alert in response to all playbacks as they aged, $r=-0.331$, $N=63$, $P<0.01$ (Fig. 3). With age controlled, however, juveniles remained alert more than twice as long following alarm calls (38.01 ± 3.05 s) than non-alarm calls (18.77 ± 2.56 s; ANCOVA: $F_{1,237}=14.11$, $P<0.001$). The response durations following aerial-object ($F_{2,34}=3.10$, $P=0.05$), single-whistle

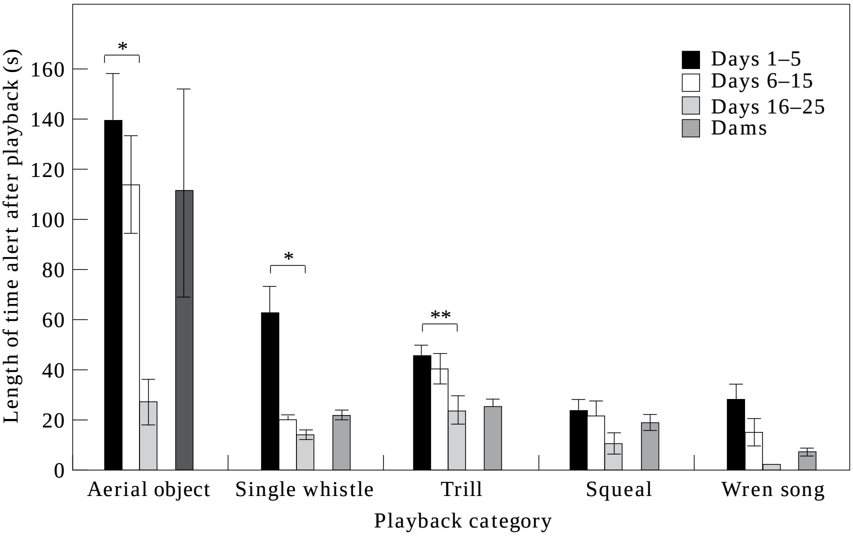

Figure 3. $\bar{X} \pm$ SE response durations (s) of juveniles during each age cohort, measured from presentation of playback until non-alert behaviour was resumed. Data are grouped by playback category. Asterisks represent a significant difference between age cohorts (*$P<0.05$, **$P<0.001$).

($F_{2,90}=11.73$, $P<0.001$) and trill ($F_{2,76}=4.88$, $P=0.01$) playbacks decreased significantly over time. Juveniles that had been above ground for only five days remained alert longer after these playbacks than in days 16–25, with responses to single whistles in days 1–5 also longer than in days 6–15. As juveniles aged, they spent less time alert following squeal and wren-song playbacks, yet these declines were not significant ($F_{2,32}=1.98$, $P=0.15$ and $F_{2,23}=1.29$, $P=0.29$, respectively). The aerial-object data for days 16–25 include only four responses to four playbacks, and a larger sample of same-aged captive juveniles indicates that their response durations are comparable to those of the free-living dams (Mateo 1995).

Dams' response durations were negatively correlated with their offspring's age ($r=-0.294$, $N=50$, $P=0.04$). A one-way ANOVA with playback categories as levels of the independent variable (aerial object, trill, single whistle and squeal) revealed significantly longer response times to the aerial object than to the three auditory playbacks alone ($F_{3,19}=6.03$, $P=0.01$).

Vigilant posture

I found a significant decrease in vigilant postures across age cohorts (Kruskal–Wallis ANOVA: $H=26.36$, $df=2$, $P<0.001$; all playbacks combined, $\bar{X}=3.36$, 2.98 and 3.03 for days 1–5, 6–15 and 16–25, respectively), with postures significantly higher during the first cohort than the next two cohorts. I conducted similar ANOVAs for each playback category to further analyse the effect of age on vigilant postures. As juveniles aged, their postures became significantly lower following aerial-object playbacks ($H=10.30$, $df=2$, $P=0.01$; $\bar{X}=3.94$, 3.33 and 3.00), but I found no other significant changes in posture following the other playback categories.

I opportunistically recorded responses of individuals to naturally occurring trills, whistles and squeals. These analyses did not control for juvenile age, and I was probably biased towards noting responses rather than lack of responses to naturally occurring signals. Juveniles were more likely to respond to naturally produced single whistles (98% of 43 calls) than to recorded single whistles (76% of 322; $\chi^2=9.28$, $df=1$, $P=0.002$). There were no differences in responsivity to natural and recorded whistle choruses (92% of 13 calls and 89% of 193, respectively; $\chi^2=0.01$, $df=1$, $P>0.95$) or trills (89% of 192 calls and 91% of 295, respectively; $\chi^2=0.24$, $df=1$, $P=0.62$). I also compared the time spent alert following natural and played-back calls with independent t-tests;

response durations did not significantly differ for trills or single whistles ($t=0.88$, $df=139$, $P=0.38$ and $t=0.84$, $df=102$, $P=0.40$, respectively; data were insufficient for a whistle-chorus analysis). I found a significant effect of time of the day on juvenile and dam responses, but no consistent sex differences in the development of responses (Mateo 1995).

Responses of Newly Emergent Juveniles to Alarm Calls

The alarm-call responses of juveniles changed markedly during their first summer above ground (see above), suggesting either that their response repertoire is not fully formed at emergence, or, more appropriately, that responses are adapted to each stage of development (Burghardt 1978; Galef 1981; Owings & Loughry 1985; Alberts 1987). During their first morning above ground, juveniles often hear alarm calls, and because natal emergence tends to draw predators (Luttich et al. 1970; Sherman 1976; Coss et al. 1993), the likelihood is high that juveniles will see, if not encounter, a predator on this day. One of the most striking aspects of ground squirrels during their first few days above ground is that, besides being uncoordinated, they do not appear to distinguish between threatening and non-threatening stimuli (*S. beldingi*: personal observation; *S. beecheyi*: R. Coss, *S. armatus*: J. Rieger, *S. parryii*: E. Lacey, personal communications). For example, I watched one litter fail to respond on their first day above ground to their dam's repeated alarm calls elicited by a weasel, yet later they all went below ground when a butterfly flew by. Given these observations, I examined the alarm-call responses of juveniles on the first to the fifth days above ground.

Figure 4 depicts the proportion of newly emergent young responding to playbacks on the first day above ground (and first time experiencing the various playbacks) compared with responsivity on the fifth day. Because of small sample sizes, I pooled the data into alarm calls (whistle choruses, single whistles and trills) and non-alarm calls (squeals and wren songs) for analyses. Juveniles were as likely to respond to alarm calls as non-alarm calls on their first day above ground ($\chi^2=1.37$, $df=1$, $P=0.25$). Four days later, a significant difference emerged: juveniles selectively responded to the alarm-call playbacks, but not to the squeal and wren songs ($\chi^2=19.93$, $df=1$, $P<0.001$). Thus, within just five days, a marked difference in responsivity appeared. Responsivity to trills increased from 52.2% of 23 trills on day 1 to 100% of 12 on day 5 ($\chi^2=11.49$, $df=4$, $P=0.02$); likewise, single-whistle responsivity increased from 50% of 12 calls to 76.5% of 17 ($\chi^2=10.66$, $df=4$, $P=0.03$). Responsivity to squeals remained fairly constant (60–75% of squeal playbacks; $\chi^2=1.67$, $df=3$, $P=0.64$), but fewer juveniles responded to wren songs on day 5 (11.8% of 17 playbacks) than on day 2 (33.3% of 30; $\chi^2=3.12$, $df=3$, $P=0.37$). Whistle choruses, indicative of fast-moving predators, elicited high levels of responding (85.7–100% of choruses responded to) on all five days ($\chi^2=2.28$, $df=4$, $P=0.69$). Similarly, the aerial-object playbacks reliably elicited responses from juveniles, even on the first exposure: 85.7–100% of juveniles responded ($\chi^2=1.66$, $df=3$, $P=0.65$), and 18 of 20 responders immediately ran below ground. These data indicate that fast-moving visual objects, and to a lesser extent whistle choruses, were very salient when first encountered, and juveniles did not require direct experience with them to give a discriminative response.

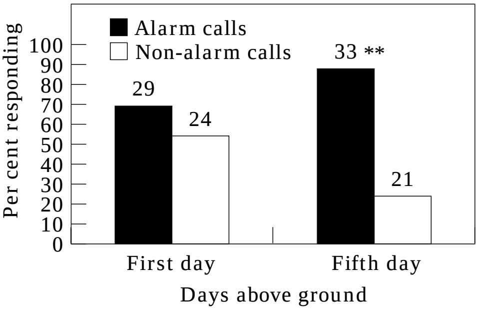

Figure 4. Percentage of newly emergent juveniles giving a response to alarm call and non-alarm call playbacks on their first and fifth day above ground. Numbers above bars represent the total number of responders and non-responders to each playback–age category. Asterisks represent a significant difference between alarm and non-alarm calls ($P<0.001$).

Most juveniles either froze or went down a burrow following both alarm calls and non-alarm calls on their first day above ground, accounting for 63 and 68% of their initial responses, respectively (Fig. 5a). The call types (alarm versus non-alarm call) did not influence the frequency

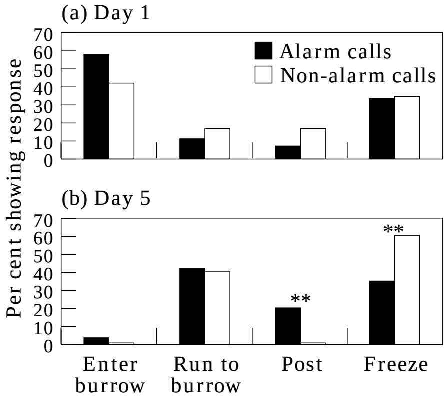

Figure 5. Percentage of newly emergent juveniles on their first and fifth day above ground responding to alarm call and non-alarm call playbacks with each of four initial-response types. Asterisks represent significant differences between alarm and non-alarm calls ($P<0.001$).

of the four initial-response categories on day 1 ($\chi^2=7.00$, $df=3$, $P=0.06$). By day 5 (Fig. 5b), however, juveniles' reactions did depend on call type ($\chi^2=31.06$, $df=3$, $P<0.001$). Partitioning of the frequency tables revealed that juveniles posted to alarm calls and froze to non-alarm calls ($\chi^2=14.81$ and $\chi^2=13.04$, respectively; both $df=1$, $P<0.001$).

Response durations following alarm calls did not significantly decrease over the 5 days (42.09 ± 7.17 s on day 1 to 27.47 ± 4.71 s on day 5; $F_{4,176}=2.19$, $P=0.07$). Postures became significantly less vigilant from the first ($\bar{X}=2.93$) to the fifth ($\bar{X}=2.00$) day ($U=734$, $P=0.001$). I found no significant differences in response durations or vigilant postures between alarm- and non-alarm calls on day 1 or on day 5.

Social factors strongly affected the responses of juveniles shortly after emergence. Juveniles were significantly more likely to respond on day 1 if their dam was present ($\chi^2=5.44$, $df=1$, $P=0.04$, Table III), but a dam's presence no longer influenced her juveniles' responsivity on day 5 ($\chi^2=0.63$, $df=1$, $P=0.43$). Visually isolated ground squirrels, that is, with no conspecific of any age class within sight, did not respond on the first day (compared with non-isolated juveniles: $\chi^2=24.42$, $df=1$, $P<0.001$), but were likely to respond on the fifth day ($\chi^2=0.01$, $df=1$, $P=0.93$, Table III). Finally, 18% of 161 juvenile responses were socially facilitated on days 1–5, compared with only 4.7% of 43 responses by dams.

Table III. Proportion of juveniles responding to playbacks on the first and fifth day after natal emergence

	Day 1	Day 5
Dam present	25/38	27/37
Dam absent	5/16	15/25
Visually isolated	0/17	9/16
Not isolated	20/24	6/9

Dam's Effect on Juvenile Responses

Ordinarily, after morning emergence, dams immediately moved away from the natal burrow (personal observation), and their mean distance from the natal burrow increased as juveniles aged ($F_{2,71}=9.45$, $P<0.001$; distance from the burrow was significantly shorter during days 1–5 than the later cohorts: Table IV). Dams were present more often during playbacks to the youngest than the two older cohorts ($\chi^2=63.84$, $df=2$, $P<0.001$). Dams were not significantly more likely to respond to playbacks themselves (all categories combined) after their litter's natal emergence compared with a 12-day period prior to emergence ($\chi^2=3.14$, $df=3$, $P=0.37$; Table IV). Their vigilant postures did increase significantly from the pre-emergent period to days 1–5 ($U=136$, $P=0.04$; $\bar{X}=2.2$ and 2.9, respectively).

A dam's presence significantly affected the responsivity of her offspring during days 1–5 ($\chi^2=5.84$, $df=1$, $P=0.02$), with juveniles more apt to respond to all playbacks when the dam was absent than present (Table IV). Most socially facilitated juvenile responses were in the presence, rather than the absence, of the dam (74.4% of 43 facilitated responses observed during the summer). It was not often possible to identify the individual that influenced the response by the focal ground squirrel, yet these data suggest that the dam may have been the facilitator.

The dam's presence also affected the amount of time her offspring (1–25 days post-emergent) remained alert after all playbacks combined (ANCOVA, covariate=juvenile age, $F_{1,397}=4.11$, $P=0.04$), with juvenile response duration longer when the dam was present (44.34 ± 3.66 s) than when she was absent (34.73 ± 3.08 s). Juvenile

Table IV. Proportion of individuals giving a response (%) and $\bar{X}$ ± SE spatial behaviour (m) of dams and juveniles as a function of days since juvenile natal emergence

	Days above ground			
	− 12–0*	1–5	6–15	16–25
Dam responsivity	10/19 (52.6)	34/51 (66.7)	23/30 (76.7)	14/20 (70.0)
Dam present at playback to juvenile		238/381 (62.5)	267/695 (38.4)	206/376 (54.8)
Juvenile responsivity when dam was:				
Present		132/238 (55.5)	188/267 (70.4)	159/206 (77.2)
Absent		98/143 (68.5)	318/428 (74.3)	126/170 (74.1)
Dam distance from natal burrow	8.38 ± 1.8	4.49 ± 1.3	14.34 ± 2.4	14.08 ± 1.9
Juvenile distance from natal burrow when:				
Dam present		2.43 ± 0.3	13.15 ± 1.0	15.22 ± 1.4
Dam absent		2.19 ± 0.5	20.33 ± 1.7	34.47 ± 2.8

Figures in parentheses are percentages.
*Dams were observed for up to 12 days prior to the natal emergence of their litters.

postures similarly varied as a function of the dam's presence (U=11 432, P=0.03), with higher vigilant postures (e.g. posting versus horizontal) when the dam was present than when she was not ($\bar{X}$=3.21 and 3.05, respectively). Mothers also influenced the initial responses of their juveniles (χ^2=36.78, *df*=3, P<0.001), with more juveniles entering a burrow when the dam was in proximity (15.8% of 480 respondents) compared with when she was absent (5.2% of 541; partitioned χ^2=6.03, *df*=1, P=0.01).

Social Environment

Unless significant differences were found across cohorts, the following analyses were conducted on responses from all age cohorts combined (1–25 days after natal emergence).

Surrounding conspecifics

Juvenile response duration was correlated with the number of visible conspecifics (range 0–5) also responding to that particular playback (r=0.436, N=75, P<0.001). The duration of responses to alarm calls was more strongly associated with the number of other respondents (r=0.514, N=51, P<0.001) than the duration of responses to non-alarm calls (r= − 0.194, N=14, P=0.51). Juvenile response duration was negatively correlated with number of litter-mates in their litter (range 1–6) during days 1–5, when litter-mates were still close to the natal burrow (r_S= − 0.131, N=238, P=0.02), but response duration of dams was positively associated with the size of their litter (r_S=0.607, N=63, P<0.001).

Social facilitation

Juveniles did not display significantly more socially facilitated responses (14.2% of 339 responses) than dams (4.7% of 43; χ^2=2.25, *df*=1, P=0.13). However, juveniles in the youngest cohort gave most of the socially facilitated responses (days 1–5: 29 of 161 responses, days 6–15: 16 of 113; days 16–25: 3 of 65; χ^2=6.84, *df*=2, P=0.01), and these responses were significantly longer than non-facilitated responses (93.48 ± 10.9 s and 37.06 ± 2.56 s, respectively; one-way ANCOVA, covariate=age; $F_{1,316}$=53.06, P<0.001). Dam response durations were similarly affected, t=8.01, *df*=95, P<0.001 (202.28 ± 72.28 s for facilitated responses and 38.00 ± 3.25 s for non-facilitated responses). Most socially facilitated responses followed aerial-object (14 of 35) and trill (9 of 35) playbacks (χ^2=29.78, *df*=5, P<0.001).

Visual isolation

Visual isolation, when no conspecifics were within 10 m of a focal ground squirrel, significantly affected the responsivity of newly emergent juveniles, with fewer juveniles responding to alarm calls (57.7% of 52 visually isolated juveniles responding) and non-alarm calls (4.4% of 46) when isolated than when another *S. beldingi* was within sight (alarm calls: 84.1% of 138 non-isolated juveniles, $\chi^2=13.31$, $df=1$, $P<0.001$; non-alarm calls: 47.8% of 69, $\chi^2=22.63$, $df=1$, $P<0.001$). Visual isolation also affected the responses of juveniles to non-alarm calls on days 6–15 ($\chi^2=7.14$, $df=1$, $P=0.01$; 4.6% of 44 isolates responding versus 26.1% of 69 non-isolates). These analyses do not control for the response, if any, of non-focal conspecifics. Across all ages, the most common initial response of a visually isolated juvenile was to post (63.6% of all responses), but non-isolated individuals displayed all initial-response types ($\chi^2=38.44$, $df=3$, $P<0.001$). Dam responsivity was not affected by visual isolation ($\chi^2=1.34$, $df=1$, $P=0.25$).

Vocalizations

I also noted whether *S. beldingi* of any age class chirped (repetitive single-note calls; Leger et al. 1984) or trilled for more than 1 min after a playback. When one or more ground squirrels vocalized after a playback (typically chirps following aerial-object or whistle-chorus playbacks), it prolonged the focal juvenile's response (one-way ANCOVA, covariate=age, $F_{1,181}=25.58$, $P<0.001$), from 50.13 ± 4.52 s without vocalizations to 136.25 ± 23.37 s with vocalizations. Dams also remained alert longer when vocalizations were heard after a playback than when they were not ($\bar{X}=84.72 \pm 24.55$ s and 32.30 ± 4.23 s, respectively; ANCOVA, covariate=juvenile age, $F_{1,70}=4.36$, $P=0.04$).

Spatial Location

I calculated the distance to a ground squirrel's natal burrow at the time of a playback, rather than the distance to the nearest burrow, because I could not be sure that all burrows in the meadow would be potentially used by *S. beldingi*. For all playback categories, there was no significant difference in the distance from the natal burrow between responders and non-responders. With all alarm call playbacks combined, however, the response durations of juveniles during days 1–5 and days 16–25 were significantly correlated with distance ($r=-0.202$, $N=120$, $P=0.03$ and $r=0.389$, $N=37$, $P=0.02$, respectively). Durations decreased with increasing distance from the natal burrow for the youngest juveniles but increased for the older juveniles. Vigilant postures were also associated with the distance (>0 m) a juvenile ran during its response ($r_S=-0.159$, $P=0.01$, $N=232$). Juveniles remained alert longer (all playbacks combined) and expressed heightened vigilance after running to their natal burrow than to a non-natal burrow (ANCOVA, covariate=age, $F_{1,301}=34.23$, $P<0.001$ and $U=15\,532$, $P<0.001$, respectively; Fig. 6).

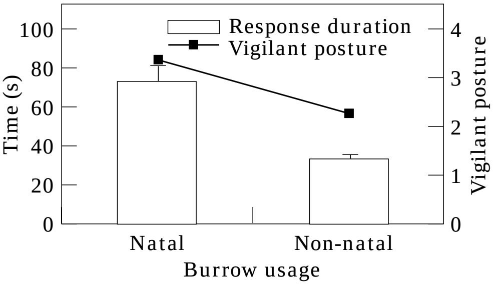

Figure 6. $\bar{X} \pm$ SE response durations (s) and vigilant-posture scores ($\bar{X}$) of juveniles running to natal or non-natal burrows. Vigilant-posture scores, which are ordinal data, are presented as means for illustrative purposes.

I also analysed alarm-call response behaviour as a function of the location of a respondent's natal burrow in the meadow, because individuals on the edge of the meadow may display heightened responses compared with those in the centre (Elgar 1989). These analyses do not control for an individual's exact location in the meadow at the time of the playback. Juveniles whose natal burrows were near the edge of the meadow ($N=8$ litters) were more likely to respond to all playbacks (72.5% of 1190 playbacks) than those from the centre of the meadow ($N=6$ litters; 61.6% of 310 playbacks; $\chi^2=13.49$, $df=1$, $P<0.001$). Dams from the edge tended to respond more often to non-alarm calls (4 of 13 playbacks) than those from the centre (0 of 11 playbacks responded to; Fisher's exact test, $P=0.09$). Juveniles from the meadow's edge were more vigilant following alarm calls than those from the centre ($\bar{X}=3.2$ and 2.91, respectively, $U=4490.5$, $P=0.002$); dam vigilance was not similarly affected ($\bar{X}=3.04$ and 3.00, respectively; $U=66$, $P=0.84$).

DISCUSSION

Development of Alarm-call Response Repertoire

Each of the four alarm-call response measures revealed a change in the behaviour of juvenile

S. beldingi from when they first emerged above ground until shortly before natal dispersal began (Figs 2, 3; Table II). In general, juveniles became more selective in their responses, reacting more often to playbacks of alarm calls, particularly single whistles and trills, and less often to the control playbacks. Newly emergent young tended either to freeze or to enter a burrow in response to all playbacks, but later selectively ran to a burrow or posted in response to alarm calls, and froze or posted the few times they did respond to non-alarm calls. The duration of responses decreased with age, but as a rule, young remained alert longer following playbacks of alarm calls than other vocalizations. Finally, postures were most vigilant in the youngest juveniles, and became significantly less vigilant with age. These response measures illustrate a significant change in the anti-predator strategies of juvenile *S. beldingi* as they age.

Juveniles readily responded to whistle-chorus and aerial-object playbacks at emergence, and their initial responses to these stimuli changed little over the summer. In contrast, young did not distinguish between single whistles, trills, squeals and wren songs until their fifth day above ground, and response patterns to these playbacks were modified over the next 25 days (Figs 2, 3; Table II). Selection may have favoured early responses by newly emergent young to aerial objects and whistle choruses, because responding quickly to a fast-moving predator is critical to survival. In contrast, adaptive responses to slow-moving predators, which elicit trills, are contingent upon the particular predator (e.g. remain above ground if confronted with a weasel, but run to a multiple-entrance burrow in response to a badger), and thus responses to trills may develop more slowly. Responses to single whistles also developed over time, perhaps because these calls do not convey as much information to the perceiver as whistle choruses.

Juveniles in the oldest age cohort (days 16–25) were more likely to respond to playbacks and gave different initial responses than dams, suggesting that prior to dispersal, juvenile responses are not yet fully adult-like. Whether this reflects an increased vulnerability to predators relative to adults is unclear. The alarm-call responses of dispersing juveniles (and yearlings) are difficult to distinguish from adults in the field (personal observation), however, and can be considered functionally, if not statistically, adult-like (see also Loughry 1992).

Epigenesis of Adaptive Alarm-call Responses

If an anti-predator system that required each juvenile to learn how to recognize and respond to alarm calls was prone to fatal errors in learning (Bolles 1970; Galef 1976; Johnston 1982), then why do juveniles not give discriminating responses to all auditory stimuli, especially alarm calls, when they first emerge above ground (Fig. 1, stages 2 and 3)? I propose two proximate and two ultimate explanations (Hill 1995). First, developmentally, the transition from a quiet, dark natal burrow to the intense post-emergent stimulation may increase arousal but decrease the attention needed to give discriminating responses (Ruff 1971). Also, because ontogeny occurs in stages (Galef 1981), juveniles may need time to form the necessary associations between each alarm call and its eliciting stimulus before they can respond differently to the calls. Second, functionally, juveniles may not emerge with these associations already formed if selection has favoured plasticity in alarm-call responses (Johnston 1982). Temporal or spatial changes in predator contexts (Robinson 1980; Towers & Coss 1990; personal observation) would favour different response repertoires in adults as well as naïve juveniles, based on experience with the local environment. Moreover, the likelihood of a naïve juvenile surviving a predation attempt is extremely small; during *S. beldingi* phylogeny, 'successful' escape responses were probably uncommon, and not strongly selected (but see Coss 1991). Consequently extant Belding's ground squirrels do not emerge with associations between alarm calls and their specific escape responses already formed, and thus do not respond differentially to all of the stimuli.

During their first days above ground, juvenile *S. beldingi* typically either move below ground in response to all playbacks, which can attract a predator's attention, or freeze, leaving them vulnerable above ground (Fig. 1, stage 4). The preponderance of these responses may be explained when they are interpreted in an age-appropriate framework. Proximately, the discrimination of stimuli may be contingent upon freezing and observing what follows, as juveniles learn through habituation that harmless stimuli are not associated with danger or take cues from adults that the stimuli are unimportant (Cheney & Seyfarth 1990; Caro 1994). Furthermore, juvenile development is constrained by their short active season (about 8 weeks from natal emergence to autumnal immergence) and their need to gain adequate body fat prior to hibernation (Maxwell & Morton 1975; Murie & Boag 1984; more than 60% of juveniles do not survive their first winter: Sherman & Morton 1984). As a result, juveniles do not emerge with completed physical development, and their response repertoire is initially limited to freezing and entering a burrow, without the motor competence to post or to run to a burrow (personal observation). Ultimately, the responses of naïve juveniles may actually increase their chances of survival. A below-ground juvenile is safe from visual detection by a predator, yet a juvenile that remains above ground may learn to discriminate between stimuli faster. For newly emergent juveniles then, there is a trade-off between escape behaviour and information gathering. Furthermore, if the likelihood of an individual encountering a predator is small (see Introduction), then the benefits of remaining above ground and observant can outweigh the costs of prolonged exposure. Juveniles may have the capacity to independently acquire alarm-call responses, but they may develop these responses faster, and with less chance of fatal errors, if they incorporate the responses of conspecifics into their own repertoire (Galef 1976).

Responses of Newly Emergent Juveniles

During juveniles' first 5 days above ground, their alarm-call responses changed markedly. Discrimination, defined here as the ability to exhibit differential behavioural responses to alarm calls and non-alarm calls, developed rapidly (Fig. 4). This process may reflect perceptual sharpening, and is probably facilitated by the pre-emergent discrimination of *S. beldingi* alarm calls by pups (as evidenced by differential heart-rate responses; Mateo 1996).

The lack of discrimination on day 1 is especially compelling, given that young hear numerous alarm calls and are likely to see, if not encounter, predators. Whether these juveniles are able to discriminate predators from non-dangerous visual stimuli after they emerge is unclear (see also Ivins & Smith 1983; Poran & Coss 1990; Coss 1991). Juveniles did respond reliably to aerial-object playbacks without having experienced similar objects, indicating that adaptive escape responses to overhead visual stimuli may have been selected in newly emergent juveniles (Johnston 1982). The ability of juveniles to respond immediately is equivocal, however, as witnessed by some responses delayed until after the frisbee had landed and my ability to catch juveniles by hand at the burrow entrance.

Social Environment

Adult ground squirrels, particularly dams, probably serve as indirect models of appropriate responses, helping juveniles to form associations between predators, alarm calls and alarm-call responses (Galef 1976; Cheney & Seyfarth 1990). Vigilant postures, response durations, and to a lesser extent, responsivity, were influenced by the presence of the dam, even though she was typically 20 m away from her young (Mateo 1995). Juveniles do not look to their dam before responding as reliably as infant vervet monkeys do (Cheney & Seyfarth 1990), however, nor do dams run to the natal burrow following an alarm call (personal observation), as if to 'teach' their juveniles how to respond (Robinson 1981; Caro & Hauser 1992).

The presence and behaviour of other ground squirrels, including litter-mates, also affected juvenile alarm-call responses, as early as the day they first emerged. Most socially facilitated responses given by juveniles occurred within the first 15 days after natal emergence, and these responses were significantly longer than non-facilitated responses. Attention to the reactions of other ground squirrels would be important for individuals that do not see the predator and would otherwise respond on the basis of auditory cues alone. Visually isolated juveniles (days 1–5 and 6–15) were less likely to respond to playbacks. Isolated juveniles may experience increased fear or arousal (Ruff 1971; Clayton 1978), which in turn could inhibit their responses to playbacks. Because the context for each alarm call is different, the decision to respond may depend on the reactions of conspecifics, and when this cue is unavailable, the safest strategy may be to give no response. The most common initial response when visually isolated was to post, which enables individuals to gather more auditory and visual information about what elicited the vocalization (Owings & Virginia 1978; Brown & Schwagmeyer 1984). Finally, vocalizations produced after playback presentations dramatically increased the amount of time juveniles and dams remained alert, and may serve as a form of tonic communication between ground squirrels (maintaining conspecifics' vigilance when a predator may still be in the area; Owings et al. 1986).

That juveniles reacted to the behaviour of others, and at times adjusted their own behaviour accordingly, suggests a mechanism for social facilitation of anti-predator behaviour. First, inexperienced juveniles may learn the association between alarm calls, eliciting stimuli and appropriate responses faster by observing the responses of nearby ground squirrels than by not attending to them. Second, animals that live in groups, whether for increased predator detection, 'dilution' effects or 'selfish herd' benefits (Alexander 1974), would be expected to monitor the behaviour of surrounding individuals (but see Lima 1995). There were age differences in the effect of the social environment on responsivity and response patterns (young juveniles> older juveniles>adults, see above), which may reflect age differences in both vulnerability and the rate of monitoring of conspecifics (Alberts 1994).

Spatial Behaviour

Overall, distance from the natal burrow did not influence juvenile responsivity, but did correlate with response duration and vigilant postures (Fig. 6; see also Holekamp 1983), suggesting a compromised vigilance for predators when outside of the home area. Because the non-natal burrows to which juveniles ran were often in another female's home range, it might be unsafe to remain in that area for an extended period of time and risk attack from that female (Sherman 1981a; Holekamp 1983).

The location of a ground squirrel's natal burrow within the meadow influenced its responses to playbacks. These differences are even more intriguing because they are without regard to the respondent's location at the time of the playback, which could be anywhere within the meadow. Individuals from the edge of the meadow may encounter greater predation risks if they cannot detect approaching predators rapidly, if they are more easily ambushed by predators hiding in the adjacent features or if their escape routes are limited (Elgar 1989; Hoogland 1995). The centre–edge effect further suggests a plasticity in the expression of alarm-call responses by both dams and juveniles according to temporally changing contexts (individuals may use burrows in different locations in consecutive years; Sherman 1976). Juveniles may develop location-dependent responses on their own, assessing their vulnerability as a function of location in the meadow. Alternatively, they may monitor their dam's behaviour and use it as a model for their own. Dams' responses, in turn, may reflect their own vulnerability, or may be a form of maternal care, becoming more vigilant if they locate their natal burrow, and thus their offspring, in a dangerous area (edge) and less vigilant if in a safer region (centre).

Epigenesis, viewed as a series of interactions between an organism and its environment (Lehrman 1970; Johnston 1987), suggests that juvenile *S. beldingi* alarm-call responses are not impoverished versions of adult responses, but instead are ontogenetic adaptations, functional in their current stage of development (Galef 1981; Owings & Loughry 1985; Alberts 1987). A juvenile's alarm-call response repertoire develops during its entire first summer of life, in part due to interacting factors such as experience with the calls, facilitation from conspecifics and increasing motor abilities.

ACKNOWLEDGMENTS

This article is based on research conducted in partial fulfilment of the requirements for the Ph.D. degree in Psychology at the University of Michigan. The research was supported by a National Science Foundation Dissertation Improvement Grant as well as funding from Sigma Xi, American Society of Mammalogists and Rackham School of Graduate Studies. I thank A. Bell, M. Clancy, W. Holmes, J. Osborn and L. Starr for their tireless assistance in collecting the data discussed herein. I particularly thank W. Holmes for facilitating and encouraging my ongoing research, and J. Mitani and B. Smuts for use of their audio and visual equipment. Finally, this manuscript benefited greatly from comments by W. Holmes, P. Loesche, D. Owings, N. Peters, P. Sherman and an anonymous referee.

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