Calling and Vigilance in California Ground Squirrels: Age, Sex and Seasonal Differences in Responses to Calls

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ABSTRACT.—Vigilance by California ground squirrels (Spermophilus beecheyi) following two kinds of naturally occurring "alarm" calls was examined. Chatters were usually singly emitted calls while repetitive calls were initiated by one or more chatters and continued with a variable, but long, series of "chats." During noncalling periods adults tended to be more vigilant than were pups (young of the year); adult male and female levels were similar, but males altered the time they spent in various forms of vigilance seasonally (before vs. after pup emergence). There was little evidence of age differences in vigilance elicited by either call type. However, prior to pup emergence, adult females had higher levels of bipedal vigilance to chatters than did males, but males had higher levels of vigilance to repetitive calls than did females. These differences disappeared after pup emergence. Repetitive calling has been shown to increase vigilance over that elicited by chatters alone. This effect was found to hold when adult males were examined separately and pups also tended to show the same result, but adult females did not. This may have been because females responded with high levels of vigilance to both types of calls.

INTRODUCTION

The amount of time individuals allocate to vigilance, i.e., scanning their surroundings, may be influenced by a number of variables. For example, it is well-known that the time an individual spends vigilant decreases with increasing group size (e.g., Pulliam, 1973; Caraco, 1979; Hoogland, 1979; Bertram, 1980; Pulliam and Caraco, 1984; Sullivan, 1984; Brown and Brown, 1987) and may also be influenced by the individual's microhabitat location (Leger et al., 1983; Holmes, 1984; Carey, 1985; Devenport, 1986). Classes of individuals may also differ in the amount of time they spend vigilant. Some studies have reported that young animals are more vigilant than adults while others have shown the reverse (Barash, 1973; Carey and Moore, 1986; Devenport, 1986; Ferguson, 1987; Heinsohn, 1987; Sullivan, 1988). However, most of these studies have examined vigilance only during uninterrupted foraging bouts and it remains to be seen whether such differences persist in other circumstances. One objective of the present study was to determine whether differences in vigilance between age and sex classes of California ground squirrels (Spermophilus beecheyi) persisted during responses to two types of alarm calls and during non-calling periods.

California ground squirrels emit both nonrepetitive chatters and repetitive chatter-chats in the presence of terrestrial predators (mammals and snakes; Owings and Virginia, 1978). Chatters are thought to function as an "alarm" signal, being elicited by important environmental events (e.g., the first sight of a predator or changes in the predator's direction or speed of movement, see Owings et al., 1986). Repetitive calling usually occurs after warning chatters have been emitted and is thought to maintain vigilance in already alerted perceivers.
Both types of calling increase vigilance in perceivers, and repetitive calling has been shown to increase vigilance over that elicited by chatters alone (Loughry and McDonough, 1988). However, not all individuals may respond in the same way upon hearing a call (Leger and Owings, 1978). Thus, the identity of call perceivers may be a source of constraint on signalling effectiveness. In this study, we hoped to identify whether such constraints, manifested as differences in vigilance among call perceivers, existed for either signal. Additionally, seasonal differences in responses to calls were analyzed (before vs. after the first emergence of pups—young of the year—from their natal burrows) as another potential contextual influence on vigilance.

METHODS

California ground squirrels were studied in an abandoned walnut orchard at Camp Ohlone, Sunol Regional Wilderness, Alameda County, California from 11 April through 27 June 1987 for a total of 172 h of observation. Data were collected for 2 days each week during this period and half these days occurred prior to the first emergence of pups from their natal burrows. Most individuals within the colony were marked (29 adult males and 26 adult females in 1987) and observations were made from two elevated blinds approximately 50 m apart.

Whenever calling occurred, we immediately began a focal animal sample of an individual other than the caller. The amount of time spent in quadrupedal and bipedal forms of vigilance was continuously monitored for the duration of the call and for 5 min after calling had stopped. Vigilance was defined as occurring when a squirrel was stationary and had its head at or above a horizontal plane with the ground. Control observations on the same individual were obtained after an interval of at least 15 min had passed in which no calling occurred. Control samples were of the same duration as call length or at least 5 min long for brief calling bouts.

Only apparently spontaneously emitted calls for which the elicitor was unknown were used to avoid confounding vigilance evoked by the call with that evoked by the disturbance itself. In addition, observations were terminated if a second individual began calling before the end of the first call bout. California ground squirrels use similar repetitive and non-repetitive calls in agonistic social interactions (Owings and Virginia, 1978; Owings and Leger, 1980) and it may be that our calls were socially rather than predator-evoked. If so, then our results are a conservative test of the impact of these calls on vigilance since one would predict a minimal increase in vigilance to socially evoked calls. However, most calling occurred at a considerable distance from the focal animal, so that the individual we observed probably had little information about the circumstances eliciting calling. Depending on how much information is potentially extractable from the calls (Owings and Leger, 1980), perceivers may treat predator and socially evoked calls similarly when the elicitor can not be seen.

Squirrels were selected for observation in such a way that we avoided biasing our data toward conspicuously vigilant individuals. Usually this was done by preselecting an individual prior to any calling. Individuals were chosen to provide approximately equal samples of all age/sex classes. In all, 16 different adult males, 22 adult females, and 17 pups were sampled in 95 bouts of calling. Some of these individuals contributed twice to the data set: once in response to repetitive calls and once in response to chatters.

For both call and control samples, the initial number and distance of other squirrels within 10 m of the focal animal were recorded as well as the distance of the focal animal from the caller. These data are not presented here because the results indicated weak and inconsistent effects. Similarly, even though vigilance in California ground squirrels can vary
with microhabitat location (Leger et al., 1983), no attempt was made to examine this. The orchard seemed relatively uniform to us and focal animals often moved through large areas of the study site during observations, thus removing any bias in vigilance due to remaining in a particular microhabitat location.

Vigilance data were calculated as the percentage of time spent in bipedal, quadrupedal and total (bipedal + quadrupedal) vigilance during the call, the 5-min postcall, and control periods. Initial analyses indicated that pup emergence influenced adult vigilance, so data for the same individual from before and after pup emergence were not pooled (n = two individuals). Data for individuals sampled more than once for a particular call type within either of these time periods were pooled and average values used in the analysis (n = 11 individuals; no individual was sampled for the same call type more than three times). For pup-adult comparisons, only adult data from after pup emergence were used. The effect of parental status was not examined because we did not know paternity of pups and the sample sizes for mothers and nonmothers were small. Percentages were arcsine-transformed prior to analysis to homogenize variances among groups. However, untransformed data are presented in the figures. t-tests were used for between-group comparisons and all tests were two-tailed.

**RESULTS**

**Vigilance during control periods.**—Squirrels were primarily engaged in feeding, resting or social activities during noncalling periods. No sex differences in vigilance were found for adult squirrels (Fig. 1); however, adults tended to be more vigilant than pups (total vigilance, $t = 1.96, P < 0.06, df = 50$; Fig. 1). There were no differences in the time adult females spent in the various forms of vigilance before and after pup emergence ($P > 0.30, df = 31$ in all cases), but adult males increased the proportion of time spent in bipedal vigilance and decreased time spent in quadrupedal vigilance after pup emergence ($P < 0.01$ for bipedal vigilance, $P < 0.06$ for quadrupedal vigilance, $df = 18$; Fig. 1). The total proportion of time males spent vigilant did not change seasonally ($P < 0.97, df = 18$).

**Vigilance after nonrepetitive chatters.**—Most individuals responded to chatters in the same way, with a short-lived increase in bipedal vigilance (compare Fig. 2 with Fig. 1; see also...
Loughry and McDonough, 1988). In contrast to noncalling periods, pups and adults had similar levels of vigilance upon hearing a chatter (Fig. 2). Sex differences in responses to chatters were only apparent prior to pup emergence, with adult females spending more time bipedally vigilant than did males (t = 2.41, P < 0.04, df = 10). However, males spent more time quadrupedally vigilant than did females (t = 2.58, P < 0.03) and thus total levels of vigilance for each sex were roughly equivalent (t = 1.80, P < 0.10). Male and female levels of vigilance did not differ after pups emerged (Fig. 2). Separate examination of males and females showed no seasonal influences on vigilance, although there was a marked decline in the time females spent bipedally vigilant after pup emergence (Fig. 2). This difference is probably not significant because of small sample sizes (see legend to Fig. 2).

Vigilance during repetitive calling bouts.—Like chatters, repetitive calling increased vigilance in perceivers by increasing the proportion of time spent bipedally vigilant (at least during the call bout, compare Fig. 3 with Fig. 1; see also Loughry and McDonough, 1988). There were few age differences in how squirrels responded to repetitive calling bouts (Fig. 3A). Pups spent less time in quadrupedal vigilance during a calling bout than did adults (t = 2.16, P < 0.04, df = 32). Pups also tended to spend less time in all forms of vigilance during the 5-min postcall period than did adults, although these differences were not statistically significant (P > 0.09, df = 26, for variables in Fig. 3A).

Sex differences in responsiveness to repetitive calling were more prominent, but only occurred prior to pup emergence (Fig. 3B). Males spent far more time in quadrupedal vigilance than did females both during the call bout (t = 4.43, P < 0.0006, df = 14) and the postcall period (t = 3.26, P < 0.006). Consequently, males also spent more time in total vigilance than did females, at least during a calling bout (t = 2.95, P < 0.01). No sex differences in responses to repetitive calling were found after pup emergence (Fig. 3B). Separate examination of each sex showed that pup emergence had little impact on how females responded to repetitive calls, but males spent less time in total vigilance during a calling bout after pup emergence (t = 3.32, P < 0.01, df = 9), primarily because they spent less time in quadrupedal vigilance (Fig. 3B).

Repetitive calling bouts vary in duration and the number of calls per bout and it could
Fig. 3.—Vigilance by California ground squirrels during and after a repetitive calling bout. A. Age differences in responsiveness to calling. B. Sex differences in responsiveness to calling before and after pup emergence. Significant differences (P < 0.05) between groups for each variable are indicated. QD and BP refer to the proportion of time spent in quadrupedal and bipedal vigilance respectively, otherwise the legend is the same as in Figure 1. Sample sizes were: adult males before—3, after—8; adult females before—13, after—7; pups—16.

be that the results just presented were due to a nonrandom distribution of call lengths among classes of individuals or between seasons. To assess the importance of this problem, we split repetitive calls into two groups: bouts shorter and longer than the median duration (350 sec). There was no evidence of a biased distribution of call lengths between ages or sexes of squirrels, or before vs. after pup emergence ($\chi^2$, P > 0.71, df = 1 in all cases). A 2-way ANOVA of vigilance variables by age and call duration (short, long) resulted in no significant interaction terms, indicating that pups and adults responded similarly to short and long calls. A similar analysis using sex and call duration as the two factors yielded only one
Responses to repetitive vs. nonrepetitive calls.—Repetitive calling has been shown to act "tonically" in maintaining vigilance at levels higher than those evoked by nonrepetitive chatters alone (Loughry and McDonough, 1988). This was demonstrated by comparing vigilance during the first 5 min of a repetitive call with that observed during the 5 min after a chatter. Here we examine whether this effect is maintained when pups, adult males and adult females are examined separately, and whether the same effect was produced before and after pup emergence.

Pups.—Figure 4 shows that pups spent more time vigilant during repetitive calling than

significant interaction term, for total vigilance during a call bout ($F = 6.19$, $P < 0.02$, df = 1, 24).

**Fig. 4.—** Differences in vigilance elicited by repetitive and nonrepetitive calls. Legend is the same as in Figure 1. First 5 min and entire call refer to vigilance during repetitive calling. Significant differences ($P < 0.05$) between vigilance evoked by chatters and that evoked by repetitive calling are indicated. See Figures 2 and 3 for sample sizes.
after a nonrepetitive call, but these differences were not significant (P > 0.17, df = 17 in all cases). Total vigilance over the entire duration of a repetitive call bout vs. total vigilance after a chatter was almost significantly different (t = 1.96, P < 0.06, df = 24), but this does not represent a test of the tonic hypothesis. In sum, then, pups showed only a tendency for repetitive calling to act tonically on their vigilance.

**Adult females.**—There was no evidence that repetitive calling acted tonically on female vigilance (Fig. 4). Females behaved similarly to both types of calls and actually spent slightly less time vigilant over the entire course of a repetitive call bout than after a chatter (see Fig. 4).

**Adult males.**—Males showed increased vigilance during the 1st 5 min of a repetitive call compared to that elicited by a chatter alone (total vigilance, t = 2.16, P < 0.05, df = 17, Fig. 4). This was true when bipedal and quadrupedal vigilance during this time were examined separately, although the differences were not significant (P < 0.09 for bipedal, P < 0.19 for quadrupedal vigilance). Total vigilance was also higher over an entire repetitive calling bout than after a chatter (t = 2.59, P < 0.02, df = 20, Fig. 4).

**Pup emergence.**—Pooling data from both adult males and adult females, a 2-way ANOVA was run on the variables in Figure 4 with time of year (before and after pups) and type of call (repetitive and nonrepetitive) as the two factors. No significant interaction terms were found, but time of year did influence vigilance to both call types. Time spent in bipedal vigilance declined after pup emergence, but quadrupedal vigilance increased (bipedal, F = 8.79, P < 0.005, df = 1,38; quadrupedal, F = 5.79, P < 0.02). Total vigilance remained relatively similar before and after pup emergence for each call type.

**DISCUSSION**

The results presented here document age, sex and seasonal differences in the vigilance of California ground squirrels in several different contexts. Age differences in vigilance were more apparent during noncalling periods and diminished during calling. On the other hand, there were no sex differences in vigilance during control periods, but there were pronounced differences during calling. However, these sex differences were apparently influenced by the time of year since they were only observed prior to the first emergence of pups from their natal burrows.

The effectiveness of repetitive and nonrepetitive calls in promoting increased vigilance may thus depend on the identity of call perceivers and the context in which calling occurs (e.g., time of year). Many discussions of animal communication systems have pointed out the importance of contextual constraints on signalling behavior (e.g., Owings and Leger, 1980; Morton, 1982; Krebs and Dawkins, 1984; Owings and Hennessy, 1984; Markl, 1985). This paper has shown that such constraints do in fact exist for California ground squirrel callers. It remains to be discussed as to why or how such constraints might have arisen.

**Age differences.**—Carey and Moore (1986) found juvenile yellow-bellied marmots (*Marmota flaviventris*) to be more vigilant than adults while foraging, but Devenport (1986) found no age differences in time spent vigilant by black-tailed prairie dogs (*Cynomys ludovicianus*). In the present study, California ground squirrel pups were slightly less vigilant than adults during noncalling periods. During their first weeks above ground pups are especially vulnerable to both snake predation and attacks by infanticidal adult females (Trulio et al., 1986; Hennessy and Owings, 1988; pers. observ.), and one might have expected pups to be highly vigilant as a result. However, it may be that pups parasitize the vigilance of adults. Given the susceptibility of pups to attacks by conspecifics, the only adult whose vigilance could be so utilized would seem to be the pups’ mother (see below).
Age differences in vigilance were minimal during repetitive calling and after a chatter. This suggests that calling represents an important situation for which pups cannot rely on the vigilance of adults. Note that pup responses to both types of calls were primarily in the form of bipedal vigilance (see Fig. 4). This might be expected since pups are smaller and may need to remain bipedal in order to scan the environment effectively. However, for repetitive calls, pups did not maintain high levels of vigilance after calling had ceased, unlike adults. This suggests that pup vigilance may be constrained by other considerations, so that calling is only effective while it proceeds.

**Sex differences.**—Sex differences in vigilance have rarely been documented. In ground squirrels, Devenport (1986) found that male black-tailed prairie dogs were more vigilant than females while foraging. Adult male and female California ground squirrels spent about the same amount of time vigilant during control periods. One might have predicted female California ground squirrels to have been more vigilant than males, especially after pup emergence, because of the extreme vulnerability of pups (see above). Yet this was not observed. It may be that separate analysis of mothers and nonmothers would reveal such differences, but we were unable to evaluate this possibility. However, perhaps the question should not be why females are not more vigilant than males, but why males are so vigilant in the first place. Because paternity of pups may be uncertain (D. Boellstorff and D. H. Owings, pers. comm.), protection of young seems unlikely for males and it may be that males are vigilant in order to detect intruders into their home range, while females are vigilant in order to protect their vulnerable young.

Fairly pronounced sex differences were observed during calls although these differences were only apparent prior to pup emergence. Females were more vigilant than males after chatters, spending more time bipedal than did males. Females may have been more vigilant than males in order to protect vulnerable young (see also Leger and Owings, 1978). Males were more vigilant than females during repetitive calling, but this may be an artifact of small sample sizes (see legend to Fig. 3). In any case, males were primarily quadrupedally vigilant. Quadrupedal vigilance seems less likely to be effective in spotting potential predators than bipedal vigilance, and may reflect some other contingency of those situations (e.g., close proximity of other adults).

**Seasonal differences.**—It is difficult to devise an explanation for the decrease in vigilance shown by adults after pup emergence. It may be that adults habituate to calls to some extent, and indeed calling was much more frequent after pup emergence (34 call bouts before vs. 61 bouts after pup emergence, repetitive and nonrepetitive calls combined, \( \chi^2 = 7.68, P < 0.01 \)). Since we only analyzed calls with no known elictor, then habituation to these calls may have been especially likely. Additionally, the seasonal decline in male vigilance may be due in part to a general decline in male activity as the summer approaches (Owings et al., 1979).

**Tonic signalling.**—Previous work had shown that repetitive calling acted tonically to increase vigilance over that produced by nonrepetitive calls alone (Loughry and McDonough, 1988). In the present study only males showed a significant increase in vigilance during repetitive calling, although pups also tended to do so. Repetitive calling apparently did not act tonically on adult females. However, examination of Figure 4 shows that females responded with higher levels of vigilance to chatters than did pups or males, so that vigilance during repetitive calling could not exceed these values by very much. Thus, repetitive calling may not act tonically on females because females respond with high levels of vigilance regardless of call type. Females may treat both types of calls equivalently because of the need to protect vulnerable young.

In summary, vigilance by California ground squirrels was quite variable. Differences
between age or sex classes of squirrels were not necessarily consistent across different circumstances, implying that these differences may be context-dependent. This variability in vigilance further suggests that there may be constraints on the effectiveness of alarm signalling in this species. It is possible that other constraints on signalling effectiveness also exist, such as the identity and reliability of the caller (e.g., Cheney and Seyfarth, 1988). The existence of such constraints suggests a potential conflict of interest between signaler and perceivers over the level and duration of vigilance elicited by a particular bout of calling. Since calling is an ongoing process during these interactions, resolution of this conflict might be viewed as a form of negotiation between the participants (e.g., Penman, 1980; Hinde, 1985).

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LITERATURE CITED


