Anim. Behav., 1988, **36**, 1533-1540

Calling and vigilance in California ground squirrels: a test of the tonic communication hypothesis

W. J. LOUGHRY* & COLLEEN M. McDONOUGH†

**Ethology Program, Department of Zoology, University of Tennessee, Knoxville, TN 37996, U.S.A.*
†Animal Behavior Graduate Group, Division of Environmental Studies, University of California, Davis, CA 95616, U.S.A.

Abstract. Owings & Hennessy (1984) proposed that repetitive calling by ground squirrels, i.e. long bouts of calling wherein the same vocalization is uttered repeatedly, might act as a tonic signal to promote vigilance in perceivers. This idea was tested by comparing the effect of naturally occurring repetitive and non-repetitive calls on the behaviour of California ground squirrels, *Spermophilus beecheyi*. Both types of calls increased the amount of time spent vigilant by perceivers, especially in bipedal postures. More time was spent vigilant after repetitive than non-repetitive calls, thus supporting the tonic communication hypothesis. However, longer bouts of repetitive calling did not promote proportionately increased vigilance over that evoked by shorter calls. In fact, the reverse was true and the increase in vigilance to repetitive calls began to wane during the later stages of a calling bout. Repetitive calling may represent a case of 'persuasion', in which the signaller continues signalling in an attempt to maintain some state in resistant perceivers.

Schleidt (1973) first proposed a possible 'tonic' function for some aspects of animal signalling behaviour. These tonic signals were hypothesized to modify the behaviour of perceivers over an extended period of time rather than producing some immediate and short-lived behavioural response. For example, Schneider et al. (1986) have proposed that the vibration dance of the honeybee, *Apis mellifera*, acts tonically to regulate foraging activity within the hive.

Owings & Hennessy (1984) applied Schleidt's hypothesis to some instances of calling in ground squirrels. Many ground squirrels utter the same vocalization repeatedly in long, rhythmic bouts of calling (e.g. Balph & Balph 1966; Waring 1966, 1970; Melchior 1971; Barash 1973; Betts 1976; Matocha 1977; Smith et al. 1977; Taulman 1977; Koeppl et al. 1978; Owings & Virgina 1978; Robinson 1981; Leger et al. 1984). These calls are often heard during or in the aftermath of an encounter with a predator (e.g. Owings et al. 1986). Owings & Hennessy (1984) proposed that these repetitive calls might act tonically to promote vigilance in perceivers, the signaller thus obtaining lookouts for detecting the predator should it return. There is anecdotal evidence that some ground squirrel calls may function in this manner (e.g. Betts 1976; Smith et al. 1977), but the hypothesis has not yet been tested rigorously.

We attempted to test this tonic communication hypothesis by examining the repetitive calling of California ground squirrels, *Spermophilus beecheyi*. California ground squirrels utter both non-repetitive chatters and repetitive chatter-chats during and after encounters with mammalian predators (Owings & Virginia 1978; Leger et al. 1980; Owings & Leger 1980; Owings et al. 1986). Owings et al. (1986) argued that non-repetitive chatters served primarily a warning function since they occurred early in an encounter, and that repetitive calling might serve some other function since these calls were acting on individuals that had already been alerted. They hypothesized that repetitive calling might function to maintain visual vigilance in perceivers and thus produce lookouts in case the predator should return.

Several predictions can be made in order to test this tonic function of repetitive calling. First, repetitive calling should elicit more persistent or sustained vigilance than that evoked by non-repetitive calls alone. In other words, vigilance in response to non-repetitive calls should decay while the additional calling during repetitive calls should maintain higher levels of vigilance. Second, one might also predict that longer bouts or higher rates of repetitive calling would produce more prolonged increases in the vigilance of perceivers (cf. Harris et al. 1983). Finally, longer bouts of repetitive calling might also prevent a decay in vigilance, so that perceivers would have lower levels of vigilance after completion of a short call bout than during the later stages of a long bout. In this paper, we test these predictions and present data on the effect of each type of call on the behaviour of perceivers.

METHODS

The study was conducted on a population of California ground squirrels located in an abandoned walnut orchard at Camp Ohlone, Sunol Regional Wilderness, Alameda County, California. This population has been studied continuously since 1982 and a general description of the study site and methods are published elsewhere (e.g. Trulio et al. 1986).

Squirrels were observed 2 days each week beginning 11 April and ending 27 June 1987, for a total of 172 h of observation. Half of the observation days occurred prior to the first emergence of pups (young of the year) from their natal burrows.

During observations, a Uher 4400 tape-recorder was kept running at a tape speed of 4·7 cm/s in order to record any vocalizations that occurred. These tapes were analysed subsequently to obtain information on the duration, number of calls and call rate in each recorded bout of calling. Some calls could not be analysed due to high levels of background noise, although it was usually at least possible to obtain information on call duration.

When a repetitive or non-repetitive call occurred, we immediately selected a squirrel other than the caller and began a focal-animal sample of that individual (Altmann 1974). If another caller began calling before the first caller had stopped, we abandoned data collection. We avoided biasing our data towards conspicuously vigilant squirrels by either selecting the animal closest to the caller or, more often, pre-selecting an individual prior to any calling. Individuals were selected so as to provide an approximately equal sample of all age/sex classes (Loughry & McDonough, unpublished data). Focal samples were collected only when the elicitor of the call was unknown. This was done to avoid confounding vigilance produced by calling with that elicited by the disturbance itself. We assumed that calls for which we did not know the cause were also perceived as such by the squirrels, thus making the methodology a form of natural playback experiment (e.g. Robinson 1981). This may or may not have been a valid assumption depending on how much information about the eliciting situation was potentially extractable from the calls (e.g. Leger et al. 1980; Owings & Leger 1980).

Focal samples centred on whether the animal was vigilant. Vigilance is defined here as including any instance in which the squirrel was stationary and its head was at or above a horizontal plane passing through its shoulders. We distinguished between bipedal and quadrupedal forms of vigilance, hypothesizing that bipedal vigilance would be more important in detecting or monitoring predators and thus more likely to be influenced by repetitive calling. The time of onset and termination of each bout of vigilance was recorded and the percentage of time spent in bipedal and quadrupedal vigilance was then calculated. Focal samples were continued for the duration of the call and for 5 min after the end of the call. Control samples were then obtained for the focal animal after at least 15 min had elapsed in which no calling occurred. These control samples were taken for the same length of time as during the call or for a minimum of 5 min for calls of short duration. Not all individuals could be relocated and observed on the day the call was uttered. When this happened, the control sample was taken at the same time of day during the next observation session.

The focal animal's vigilance may have been influenced by the number of other squirrels and their distance from the focal individual (Loughry & McDonough, unpublished data). However, we found no evidence that the distributions of these variables were different for repetitive versus non-repetitive calls, or for calls versus control periods, so they do not influence the comparisons made here. Vigilance in California ground squirrels can also vary with microhabitat location (Leger et al. 1983), but no attempt was made to control for this. In part this was because the focal squirrels usually moved through large areas of the colony during sampling (both during calls and control periods), thus removing any bias from remaining in a particular microhabitat location.

Data on vigilance were calculated as the percentage of time spent in either quadrupedal or bipedal vigilance. These percentages were arcsine transformed prior to analysis. The data for individuals who were sampled more than once for a particular type of call were pooled for each individual and the average values were used in analyses. Matched-

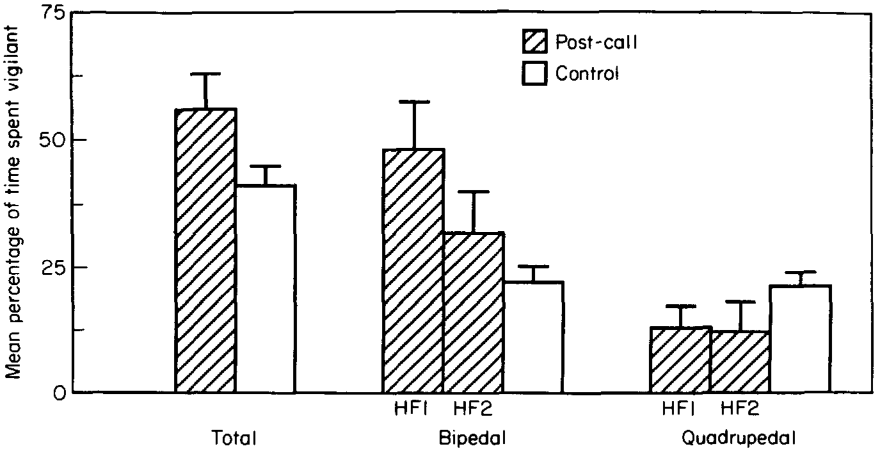

Figure 1. Percentage of time spent vigilant after hearing a non-repetitive chatter. Variance estimates of 1 SE from the mean are also presented. HF1 and HF2 refer to the first and second half of the post-call period, respectively. Total is the total percentage of time spent vigilant during the observation period and includes both bipedal and quadrupedal (quad) components.

pairs *t*-tests were used to investigate the effect of repetitive and non-repetitive calling on vigilance. Unpaired *t*-tests were used to compare repetitive and non-repetitive calling with one another. All tests are two-tailed.

RESULTS

We first examine the effects of non-repetitive and repetitive calls on vigilance separately and then test the predictions of the tonic communication hypothesis.

Non-repetitive Calls

All non-repetitive calls were chatter vocalizations. California ground squirrels also give non-repetitive 'whistles' to avian predators (Owings & Virginia 1978; Leger et al. 1979), but we did not record any of these, since raptors are rare in the orchard. Non-repetitive calls usually consisted of a single chatter lasting less than 1 s, although bouts of up to five chatters lasting almost 2 min were also recorded ($\bar{X}=1{\cdot}74$ calls per bout, duration range= <1–110 s, $N=36$).

After hearing a chatter, squirrels significantly increased the percentage of time they spent vigilant and this increase was largely due to an increase in the time squirrels spent bipedally vigilant (Fig. 1). Matched-pairs *t*-tests revealed significant differences between post-call and control periods for total ($t=2{\cdot}07$, $P<0{\cdot}03$), total bipedal ($t=3{\cdot}05$, $P<0{\cdot}003$) and total quadrupedal ($t=2{\cdot}19$, $P<0{\cdot}02$) vigilance. In all cases, $df=31$. In fact, the percentage of time spent in quadrupedal vigilance declined during this time (Fig. 1), suggesting that squirrels may make some trade-off in the time allocated to different forms of vigilance.

However, the impact of a chatter was not long lasting. We split the 5-min post-call period into two halves and examined vigilance in each half. Figure 1 shows that the increase in bipedal vigilance was only apparent during the first half of the post-call period. Indeed, the percentage of time spent in bipedal vigilance was significantly higher in the first half than in the second half of the post-call period ($t=2{\cdot}67$, $df=28$, $P<0{\cdot}02$). Bipedal vigilance during the second half of the post-call period was only marginally different from that observed during control observations ($t=1{\cdot}64$, $df=27$, $P<0{\cdot}06$). Focal squirrels spent more time bipedally than quadrupedally vigilant during the first half of the post-call period ($t=3{\cdot}02$, $df=30$, $P<0{\cdot}01$), but by the second half they spent equal amounts of time in each type of vigilance ($t=1{\cdot}36$, $df=28$, $P<0{\cdot}19$, this was also the case during control periods, $t=0{\cdot}59$, $df=80$ for quadrupedal versus bipedal vigilance).

In sum, non-repetitive chatters did increase vigilance, largely by increasing the proportion of time perceivers spent bipedally vigilant. This effect lasted for only a few minutes before perceivers returned to baseline levels of visual vigilance.

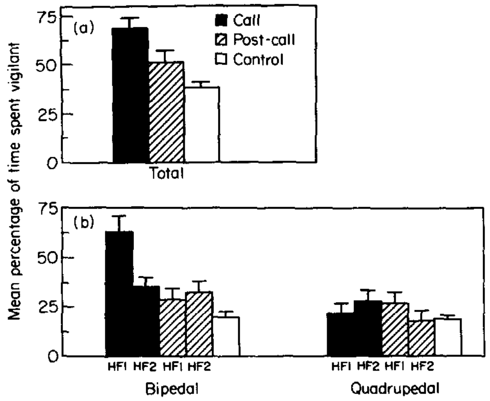

Figure 2. Percentage of time spent vigilant during and after a repetitive calling bout. (a) The total percentage of time spent vigilant. (b) Vigilance in the first and second halves of the call and post-call periods. Legend is the same as in Fig. 1. See text for discussion of statistical comparisons.

Repetitive Calls

Repetitive calls were usually initiated by one or more chatter vocalizations, followed by a variable number of rythmically uttered single-note 'chats' (Owings & Virginia 1978). The inclusion of a series of chats distinguished repetitive from non-repetitive calls and no repetitive calling bout consisted solely of chatters. Repetitive calling bouts were long ($\bar{X}$ duration $=394{\cdot}5$ s, range $=21$–1462 s, $N=56$) and contained a large number of vocalizations ($\bar{X}$ number of calls per bout $=264{\cdot}9$, range $=6$–1596, $N=49$). The rate of calling within a bout was faster initially and declined as the bout progressed (call rate during the first half of the bout versus overall call rate, paired $t=5.22$, $df=34$, $P<0{\cdot}0001$, means $=0{\cdot}70$ versus 0.55 calls/s, respectively). Also, bouts of longer duration tended to have higher overall rates of calling (Pearson's $r=0{\cdot}65$, $N=43$, $P<0{\cdot}01$).

Repetitive calling did increase vigilance over that observed during control periods. Figure 2a shows that total vigilance during a repetitive call bout was significantly different from that observed both during the control ($t=5.81$, $df=46$, $P<0{\cdot}0001$) and during the 5-min post-call periods ($t=3.39$, $df=43$, $P<0{\cdot}001$). Total vigilance was also significantly higher during the 5 min after the call than during the control period ($t=2.43$, $df=42$, $P<0{\cdot}01$, see Fig. 2a). As Fig. 2b demonstrates, this increased vigilance during repetitive calling was due to an increase in the percentage of time spent bipedal during the first half of the bout (time spent bipedal in first versus second half $t=4{\cdot}34$, $df=49$, $P<0{\cdot}0001$). By the second half of a call bout, bipedal vigilance had declined to post-call levels ($t=0{\cdot}50$, $df=43$), but was still significantly greater than control levels ($t=2{\cdot}67$, $df=46$, $P<0{\cdot}02$). This effect seems independent of the duration of calling. We split repetitive calls into two groups: those with durations shorter ($\bar{X}$ duration $=184$ s) and longer ($\bar{X}$ duration $=654$ s) than the median (350 s). Separate examination of these short and long repetitive calls showed the same pattern of decline in bipedal vigilance from the first to the second half of a calling bout ($P<0{\cdot}004$ in both cases). This effect may be due to the fact that in both short and long calling bouts, the rate of calling declined as the bout progressed (call rate in the first half of the bout versus overall call rate), though for short call bouts this difference was not significant ($t=1{\cdot}74$, $df=10$, $P<0{\cdot}12$).

Squirrels spent approximately the same percentage of time in quadrupedal vigilance during and after calling as during the control period, although there was a significant decline from the first to the second half of the post-call period ($t=1{\cdot}68$, $df=40$, $P<0{\cdot}05$, Fig. 2b). It was only during the first half of a repetitive call bout that squirrels spent more time bipedally than quadrupedally vigilant ($t=4{\cdot}12$, $df=49$, $P<0{\cdot}0001$). For the rest of the bout and throughout the post-call period, squirrels spent approximately equal percentages of time in each form of vigilance and this was also true of control periods (see above and Fig. 2b, note also that control levels of vigilance did not differ for repetitive and non-repetitive calls, compare Figs 1 and 2). These findings did not change when short and long bouts were examined separately.

These data indicate that repetitive calling does increase visual vigilance in perceivers, but that this effect diminishes as the bout progresses. Given the seemingly limited impact of repetitive calling, it could be argued that either (1) the repetitive component of the call is unimportant and it is actually the initiating chatter(s) that promote increased vigilance, or (2) there are unmeasured effects of repetitive calling on perceiver behaviour. The former argument can be tested by comparing the effects of repetitive and non-repetitive calls on perceiver vigilance. If repetitive calling acts tonic-

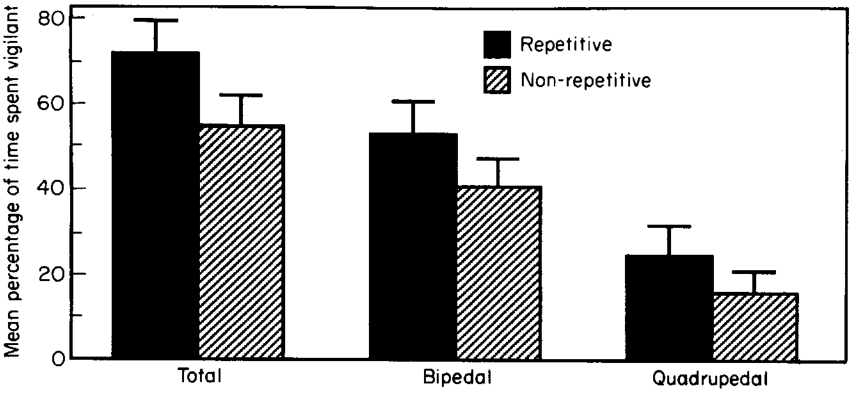

Figure 3. Effect of repetitive and non-repetitive calls on percentage of time spent vigilant by perceivers. Values represent the percentage of time spent vigilant during the first 5 min of a repetitive calling bout and the 5 min after a non-repetitive call. Legend is the same as in Fig. 1. Only total vigilance was significantly different between call types, see text.

ally, one would predict increased vigilance to repetitive calls over that elicited by a non-repetitive call alone.

Tests of the Tonic Hypothesis

We tested the above prediction by comparing vigilance during the 5-min post-call period for chatters with vigilance during the first 5 min of a repetitive call. If the additional cells in a repetitive call did not have an effect on visual vigilance, then the values should be similar. If repetitive calling acted tonically to maintain higher levels of such vigilance, then the values should be higher than those for chatters alone. The results of this analysis are presented in Fig. 3. As predicted, total vigilance in this 5-min period was increased by repetitive calling ($t=2{\cdot}23$, $df=61$, $P<0{\cdot}03$). This was a cumulative effect since neither bipedal nor quadrupedal levels of vigilance were significantly different between the two call types (although the trends were in the appropriate direction, see Fig. 3). These results represent a strong test of the tonic communication hypothesis and provide support for its primary prediction.

Comparison of the levels of vigilance over the entire duration of a repetitive calling bout with vigilance after a chatter revealed the same pattern: bipedal and quadrupedal vigilance were not different when examined separately, but total vigilance was marginally higher for repetitive calls ($t=1{\cdot}91$, $df=81$, $P<0{\cdot}06$; repetitive calls: $\bar{X}=68{\cdot}9\%$, non-repetitive calls: $\bar{X}=55{\cdot}6\%$). Thus, although visual vigilance declined as a repetitive calling bout progressed (see above), calling was not completely futile since it did elicit more vigilance from perceivers than did chatters. Additionally, absolute (rather than proportional) levels of vigilance were significantly related to call duration (e.g. total bipedal vigilance during a call bout, $r=0{\cdot}45$, $N=41$, $P<0{\cdot}01$; total vigilance during a call bout, $r=0{\cdot}50$, $N=41$). Thus, longer repetitive calling bouts produced longer periods of vigilance in perceivers, but the percentage of time perceivers spent in vigilance declined as the bout progressed.

There was little support for the second prediction derived from the tonic hypothesis. Only one significant correlation of vigilance with call rate or duration was found, and this was negative (percentage of time in quadrupedal vigilance in the first half of the call bout with call rate in the first half of the bout, $r=-0{\cdot}37$, $N=30$, $P<0{\cdot}05$). Recall that we predicted that longer calling bouts should promote a prolonged increase in vigilance over that produced by shorter bouts, but the data do not support this prediction.

We attempted to test this prediction further by comparing short and long repetitive calls (defined above). Again, the prediction was not supported. While no comparison reached statistical significance, even the trends were in the direction opposite that predicted. For example, both total vigilance during a bout and in the post-call period tended to be higher for short than for long calls (total vigilance during call: short = 74·5%, long = 64·4%, $t = 1{\cdot}32$, $df = 45$, $P < 0{\cdot}19$; post-call: short = 60·5%, long = 44·4%, $t = 1{\cdot}49$, $df = 40$, $P < 0{\cdot}14$).

A final prediction from the tonic hypothesis can be made if one assumes that repetitive calling acts to retard the rate of decay in perceiver vigilance. If so, then the percentage of time spent in vigilance should be greater in the later stages of a long calling bout than in the post-call period of a short bout. We attempted to test this by comparing vigilance in the second half of long calling bouts with vigilance in the post-calling period of short bouts. Again, there was no support for this prediction (bipedal, quadrupedal and total vigilance, $P < 0{\cdot}77$, $df = 47$ in all cases).

DISCUSSION

In total, the results presented here partially support the tonic communication hypothesis for repetitive calling by California ground squirrels. Both repetitive and non-repetitive calling increased the percentage of time perceivers spent visually vigilant, but repetitive calling maintained this increase in vigilance for a longer period of time. However, repetitive call bouts were only effective at maintaining high levels of such vigilance in perceivers over the first half of the bout's duration. Indeed, increased call duration did not lead to an increase in the percentage of time perceivers spent vigilant (see also Harris et al. 1983). Long repetitive call bouts may have been less effective than shorter ones at maintaining proportionately high levels of vigilance in perceivers, but long calling bouts were not completely futile since they did produce higher absolute levels of vigilance than did short bouts. These findings indicate that, while better than non-repetitive calls, there may be some limit to the effectiveness of repetitive calling at maintaining visual vigilance.

This constraint may arise from the conflict of interest between signaller and perceiver inherent in many communicatory systems (Dawkins & Krebs 1978; Morton 1982; Krebs & Dawkins 1984; Owings & Hennessy 1984; Markl 1985; Owings & Loughry 1985). Repetitive calling is a time-consuming activity; some bouts lasted more than 20 min and we observed one to go on for more than an hour. Recall that, in this study, only calls for which the elicitor was presumably unknown were used. Thus, perceivers of these call bouts could potentially have spent considerable amounts of time scanning for a disturbance that did not exist or was of uncertain significance. It is clearly in the best interests of a perceiver to scan the environment at the onset of a call, but it seems reasonable to assume that willingness to maintain this activity will decline as calling continues and nothing happens. The particular 'giving up' time will probably depend on the constraints imposed on the time budget of an individual. For instance, one might predict that adult females with vulnerable young might remain vigilant longer (e.g. Leger & Owings 1978). Recently emerged pups face an interesting trade-off in that they are probably more vulnerable individuals and so should remain vigilant for a long time, but they also need to feed in order to put on the weight necessary for successful overwintering (e.g. Murie & Boag 1984). Of course, some activities are not fully incompatible with vigilance. It was common to observe squirrels begin feeding while still remaining bipedal and scanning the surroundings (see also Devenport 1986).

Repetitive calling by California ground squirrels may represent a form of 'persuasion' (Dawkins & Krebs 1978; Krebs & Dawkins 1984), wherein signallers attempt to maintain or induce, by repeated signalling, some outcome in perceivers. Chatter vocalizations, either alone or as initiators of a repetitive calling bout, seem effective in temporarily increasing vigilance in perceivers. Repetitive calling might then be necessary to persuade perceivers to remain vigilant for longer than they otherwise would if a non-repetitive call had been used. The effectiveness of this persuasion is then constrained by the interests of the particular perceiver. Thus, longer repetitive call bouts may become less effective than shorter ones (see above). The mechanism for this loss of effectiveness might be some form of habituation. California ground squirrels may be able to circumvent this constraint and induce longer periods of vigilance by inserting non-repetitive calls intermittently into a repetitive calling bout (see also Beletsky et al. 1986). We have observed this on a few occasions and it seemed to increase the vigilance of perceiving squirrels, although the effect was usually short-lived. Alternatively, a signaller might increase the rate of repetitive calling in an attempt to maintain vigilance during long call bouts (e.g. Morton & Shalter

1977). Although we found no positive correlation between call rate and vigilance, we did not attempt to correlate vigilance with changes in call rate. It was our impression that sudden increases in call rate evoked temporary increases in vigilance by conspecifics. Thus, in order to remain an effective persuader within a repetitive calling bout, signallers may have to vary their signalling output (in effect, dishabituating perceivers). The effectiveness of such a strategy would then also be imbedded within longer time-scale constraints such as the signaller's past history of reliability with perceivers (Cheney & Seyfarth 1988).

An alternative to the interpretation of repetitive calling as persuasion might be that such calling allows perceivers to go on with their normal activities while remaining auditorily alert with the caller acting as a kind of sentinel (e.g. Morton & Shalter 1977). This alternative seems consistent with the decline in visual vigilance associated with long bouts of repetitive calling. This view would also seem to predict increased visual vigilance to deviations from the established calling pattern (e.g. alterations in call rate or insertion of non-repetitive elements). However, this view would not seem to predict the tonic effect of repetitive calling documented in this paper. Indeed, one might predict the opposite effect, that visual vigilance would decline at the onset of a repetitive call and thus be less than that elicited by a non-repetitive call alone.

These two alternatives could be distinguished experimentally. The persuasion view argues that callers continue calling repetitively in order to gain lookouts should the predator return. The sentinel view argues that call perceivers reduce their vigilance and rely on the signaller to be a sentinel. Thus, the persuasion view would predict that a predator would be detected by non-calling individuals earlier in trials in which calling occurred than during non-calling trials. The sentinel view would predict that non-calling individuals would detect the approach of a predator no earlier, and possibly later, than during non-calling control periods. In addition, the sentinel hypothesis would not predict changes in call patterning in the absence of changes in the eliciting situation. Remember that the calls under study here were apparently not evoked by the actual presence of a predator and changes in call patterning did not appear to us to be correlated with any obvious change in environmental conditions. If callers often alter call patten in the absence of situational changes, then the sentinel hypothesis would seem less explanatory. Finally, whether one interprets repetitive calling as persuasive or as the outcome of the signaller attempting to inform conspecifics about changes in the eliciting situation, seems to us to depend on whether one opts for an informational or non-informational view of communicatory systems (e.g. Smith 1977; Dawkins & Krebs 1978; Green & Marler 1979; Morton 1982; Owings & Hennessy 1984; Owings & Loughry 1985). It is not clear whether empirical information can resolve this larger issue.

Repetitive and non-repetitive forms of calling are ubiquitous among ground squirrels (see references in Introduction) and are probably common among other species as well. So far as we are aware, this is the first study to demonstrate empirically a function for repetitive calling. It seems unlikely that repetitive calling necessarily serves the same function in all other ground squirrels. Indeed, repetitive calling may not function in the same way for all individuals within a species. There is some evidence of age, sex and seasonal differences in individual responsiveness to repetitive and non-repetitive calls in California ground squirrels (Leger & Owings 1978; Loughry & McDonough, unpublished data). We await further testing of the tonic communication hypothesis in other species, which will undoubtedly deepen our understanding of this form of calling.

ACKNOWLEDGMENTS

We thank Don Owings for permitting us to carry out this project at his study site. NSF grant BNS 8210065 to D. H. Owings and D. F. Hennessy made the establishment of this study site possible. Special thanks to Marta Hersek and Diane Boellstorf for providing help, advice and friendship in the field. Don Owings and W. J. Hamilton III graciously lent us the necessary equipment. D. W. Leger, D. H. Owings, W. J. Smith, C. T. Snowdon and an anonymous reviewer made many useful comments on an earlier version of this paper. Preparation of the manuscript was made possible while W.J.L. held an N.I.H. post-doctoral traineeship in Ethology at the University of Tennessee.

REFERENCES

Altmann, J. 1974. Observational study of behaviour: sampling methods. *Behaviour*, **49**, 227–265.

Balph, D. M. & Balph, D. F. 1966. Sound communication of Uinta ground squirrels. *J. Mammal.*, **47**, 440–450.

Barash, D. P. 1973. The social biology of the Olympic marmot. *Anim. Behav. Monogr.*, **6**, 171–245.

Beletsky, L. D., Higgins, B. J. & Orians, G. H. 1986. Communication by changing signals: call switching in red-winged blackbirds. *Behav. Ecol. Sociobiol.*, **18**, 221–229.

Betts, B. J. 1976. Behavior in a population of Columbian ground squirrels, *Spermophilus columbianus columbianus*. *Anim. Behav.*, **24**, 652–680.

Cheney, D. L. & Seyfarth, R. M. 1988. Assessment of meaning and detection of unreliable signals by vervet monkeys. *Anim. Behav.*, **36**, 477–486.

Dawkins, R. & Krebs, J. R. 1978. Animal signals: information or manipulation? In: *Behavioral Ecology: An Evolutionary Approach* (Ed. by J. R. Krebs & N. B. Davies), pp. 282–309. Sunderland, Massachusetts: Sinauer.

Devenport, J. A. 1986. Foraging and behavioral ecology of black-tailed prairie dogs. Ph.D. thesis, University of Oklahoma, Norman, Oklahoma.

Green, S. & Marler, P. 1979. The analysis of animal communication. In: *Handbook of Behavioral Neurobiology. Vol. 3, Social Behavior and Communication* (Ed. by P. Marler & J. G. Vandenbergh), pp. 73–158. New York: Plenum Press.

Harris, M. A., Murie, J. O. & Duncan, J. A. 1983. Responses of Columbian ground squirrels to playback of recorded calls. *Z. Tierpsychol.*, **63**, 318–330.

Koeppl, J. W., Hoffman, R. S. & Nadler, C. F. 1978. Pattern analysis of acoustical behavior in four species of ground squirrels. *J. Mammal.*, **59**, 677–696.

Krebs, J. R. & Dawkins, R. 1984. Animal signals: mind reading and manipulation. In: *Behavioral Ecology: An Evolutionary Approach* (Ed. by J. R. Krebs & N. B. Davies), pp. 380–402. Sunderland, Massachusetts: Sinauer.

Leger, D. W., Berney-Key, S. D. & Sherman, P. W. 1984. Vocalizations of Belding's ground squirrel (*Spermophilus beldingi*). *Anim. Behav.*, **32**, 753–764.

Leger, D. W. & Owings, D. H. 1978. Responses to alarm calls by California ground squirrels: effects of call structure and maternal status. *Behav. Ecol. Sociobiol.*, **3**, 177–186.

Leger, D. W., Owings, D. H. & Boal, L. M. 1979. Contextual information and differential responses to alarm whistles in California ground squirrels. *Z. Tierpsychol.*, **49**, 142–155.

Leger, D. W., Owings, D. H. & Coss R. G. 1983. Behavioral ecology of time allocation in California ground squirrels (*Spermophilus beecheyi*): microhabitat effects. *J. comp. Psychol.*, **97**, 283–291.

Leger, D. W., Owings, D. H. & Gelfand, D. L. 1980. Single-note vocalizations of California ground squirrels: graded signals and situation-specificity of predator and socially evoked calls. *Z. Tierpsychol.*, **52**, 227–246.

Markl, H. 1985. Manipulation, modulation, information, cognition: some riddles of communication. In: *Experimental Behavioral Ecology and Sociobiology* (Ed. by B. Holldobler & M. Lindauer), pp. 163–194. Sunderland, Massachusetts: Sinauer.

Matocha, K. G. 1977. The vocal repertoire of *Spermophilus tridecemlineatus*. *Am. midl. Nat.*, **98**, 482–487.

Melchior, H. R. 1971. Characteristics of Arctic ground squirrel alarm calls. *Oecologia (Berl.)*, **7**, 184–190.

Morton, E. S. 1982. Grading, discreteness, redundancy and motivation–structural rules. In: *Acoustic Communication in Birds. Vol. 1. Production, Perception and Design Features of Sounds* (Ed. by D. E. Kroodsma, E. H. Miller & H. Ouellet), pp. 183–212. New York: Academic Press.

Morton, E. S. & Shalter, M. D. 1977. Vocal response to predators in pairbonded Carolina wrens. *Condor*, **79**, 222–227.

Murie, J. O. & Boag, D. A. 1984. The relationship of body weight to overwinter survival in Columbian ground squirrels. *J. Mammal.*, **65**, 688–690.

Owings, D. H. & Hennessy, D. F. 1984. The importance of variation in sciurid visual and vocal communication. In: *The Biology of Ground-Dwelling Squirrels* (Ed. by J. O. Murie & G. R. Michener), pp. 169–200. Lincoln: University of Nebraska Press.

Owings, D. H., Hennessy, D. F., Leger, D. W. & Gladney, A. B. 1986. Different functions of 'alarm' calling for different time scales: a preliminary report on ground squirrels. *Behaviour*, **99**, 101–116.

Owings, D. H. & Leger, D. W. 1980. Chatter vocalizations of California ground squirrels: predator- and social-role specificity. *Z. Tierpsychol.*, **54**, 163–184.

Owings, D. H. & Loughry, W. J. 1985. Variation in snake-elicited jump-yipping by black-tailed prairie dogs: ontogeny and snake-specificity. *Z. Tierpsychol.*, **70**, 177–200.

Owings, D. H. & Virginia, R. A. 1978 Alarm calls of California ground squirrels (*Spermophilus beecheyi*). *Z. Tierpsychol.*, **46**, 58–70.

Robinson, S. R. 1981. Alarm communication in Belding's ground squirrels. *Z. Tierpsychol.*, **56**, 150–168.

Schleidt, W. M. 1973. Tonic communication: continual effects of discrete signs in animal communication systems. *J. theor. Biol.*, **42**, 359–386.

Schneider, S. S., Stamps, J.A. & Gary, N. E. 1986. The vibration dance of the honeybee. I. Communication regulating foraging on two time scales. *Anim. Behav.*, **34**, 377–385.

Smith, W. J. 1977. *The Behavior of Communicating*. Cambridge, Massachusetts: Harvard University Press.

Smith, W. J., Smith, S. L., Oppenheimer, E. C. & DeVilla, J. G. 1977. Vocalizations of the black-tailed prairie dog, *Cynomys ludovicianus*. *Anim. Behav.*, **25**, 152–164.

Taulman, J. F. 1977. Vocalizations of the hoary marmot, *Marmota caligata*. *J. Mammal.*, **58**, 681–683.

Trulio, L. A., Loughry, W. J., Hennessy, D. F. & Owings, D. H. 1986. Infanticide in California ground squirrels. *Anim. Behav.*, **34**, 291–294.

Waring, G. H. 1966. Sounds and communications of the yellow-bellied marmot. *Anim. Behav.*, **14**, 177–183.

Waring, G. H. 1970. Sound communications of black-tailed, white-tailed, and Gunnison's prairie dogs. *Am. midl. Nat.*, **83**, 167–185.

(Received 12 November 1987; revised 22 January 1988; MS. number: A5173)