Ethology 101, 25—32 (1995)

ISSN 0179-1613

Animal Behavior Program, Section of Evolution and Ecology, University of California, Davis

Golden-marmot Alarm Calls. II. Asymmetrical Production and Perception of Situationally Specific Vocalizations?

DANIEL T. BLUMSTEIN

BLUMSTEIN, D. T. 1995: Golden marmot alarm calls. II. Assymetrical production and perception of situationally specific vocalizations. Ethology **101**, 25—32.

Abstract

Many species produce alarm calls that vary according to situation. An implicit assumption for these species is that production and perception of situationally specific alarm calls is symmetrical: perceivers respond to variation produced by signalers. The companion paper to this one (BLUMSTEIN 1995) showed that golden marmots (*Marmota caudata aurea*) produce variable alarm calls that vary in proportion to the degree of risk the caller perceives. Calls produced in higher-risk situations have fewer notes than calls produced in lower-risk situations. In this study, to determine the salience of the number of notes per call in eliciting different responses in conspecific perceivers, I played back three-note alarm calls, eight-note alarm calls, and the non-alarm vocalization of a local bird to adult golden marmots. Although marmots responded differently to bird calls and alarm calls, vigilance responses to the different alarm calls were similar. Several explanations may account for the apparent insensitivity to alarm-call variation: golden marmots may require additional contextual cues to properly interpret alarm calls, perceptual abilities do not parallel production abilities, or calls may serve a generalized alerting function.

D. T. BLUMSTEIN, Department of Systematics and Ecology, University of Kansas, Lawrence, KS 66045, USA.

Introduction

An implicit assumption for species which produce situationally specific alarm calls is that production and perception of variable alarm calls is symmetrical: perceivers respond differently according to signal type (OWINGS 1994). Golden marmots (*Marmota caudata aurea*) produce situationally specific alarm calls. The results of my companion study (BLUMSTEIN 1995) suggest that the number of notes per call is inversely related to the degree of risk a calling marmot experiences when it calls. If call variation communicates the degree of risk or type of predator, then marmots who hear alarm calls should, in some way, respond differently to

U.S. Copyright Clearance Center Code Statement: 0179-1613/95/1011-0025$11.00/0

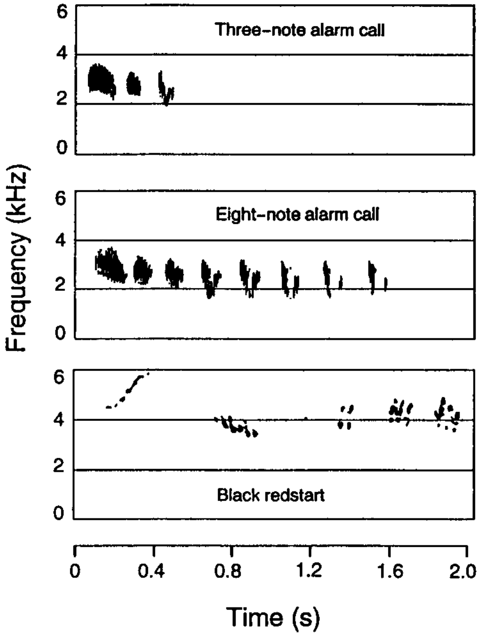

Fig. 1: Representative spectrograms of the two marmot alarm calls and the bird call played back to marmots

variants (SMITH 1977; HARRIS et al. 1983; CHENEY & SEYFARTH 1990; MACEDONIA & EVANS 1993). I conducted playback experiments to determine whether marmots had overtly different responses to higher risk (three-note) and lower risk (eight-note) alarm calls.

Methods

High-quality human-elicited marmot calls recorded from different individuals were used for this experiment (recording details in BLUMSTEIN (1995)). Calls were sampled at 44 kHz using an AudioMedia AD-DA board then filtered (1000–5000 kHz three-pole Butterworth bandpass filter) using Signalyze software (KELLER 1992) to remove environmental noise. Longer calls were shortened to three or eight notes using AudioMedia, and playback tapes were made using AudioMedia software (DIGIDESIGN 1990).

A total of 10 three-note and 11 8-note examples (Fig. 1), exhibiting 'natural' variation in other acoustic parameters (bandwidth, minimum and maximum frequencies, duration, inter-note intervals), were used for the experiments. By using multiple examples of alarm calls, I was able to test the hypothesis that marmots respond to different types of alarm calls and not to different examples of alarm calls (MCGREGOR et al. 1992).

Marmots did not produce other loud vocalizations (e.g. food or territorial calls) that could be used as a suitable control sound. Instead, I used a single 1.21-s song of a common alpine bird (black redstart: (*Phoenicurus ochruros*) as a control stimulus (Fig. 1). A redstart song was selected because, while it is not an alarm call, it is pulsed like marmot alarm calls. The control sound was used to test the hypothesis that marmots respond to alarm calls and not just to the experimental setup, and/or to a sudden pulsed sound.

Each experimental marmot heard all three stimuli: a three-note call, an eight-note call, and the redstart song. Between marmots, playback order was systematically varied. To avoid possible habituation to played-back alarm calls, I attempted to limit playbacks in a given day to the number that a marmot might normally hear ($\bar{X} = 2.67$ playbacks per playback day, range 1–8 c.f.; marmots naturally hear 6–22 natural 'bouts' of alarm calls per day; BLUMSTEIN 1995)

Before marmots emerged from their burrows in the morning, the speakers and cables were set up and left in place throughout the morning (and occasionally afternoon) experimental period. Stone boxes to camouflage the speaker (between one and several per marmot group) were constructed at least 1 wk prior to experiments and were left throughout the season. I sat with the video camera (with an attached telephoto lens) and tape deck in one of four hides between 180 and 460 m from the speaker. Different stone boxes were used in playbacks conducted on subsequent days.

Several additional criteria, to ensure maximal responsiveness, had to be met prior to a playback. Firstly, no natural alarm calls could have occurred in the past 30 min. Secondly, if a previous playback had been conducted, I waited at least 7 min before playing back another sound. Thirdly, since behavior, and potentially location, can influence responsiveness to a played-back alarm call (BLUMSTEIN 1994), I attempted to control for behavior by conducting playbacks only to marmots that were sitting and looking or standing and looking from their main burrows ($\bar{X}$ distance to main burrow = 0.36 m, range 0–4 m).

Examples of calls were played back on a Sony WM-D6C tape deck. The audio signal was split leaving the Sony headphone jack, sending the exemplar directly to a video camera (Sony SP-7, video 8) and also through an unbalanced-to-balanced line-conversion box (Countryman Type-85 Direct Box), across 365–455 m of balanced microphone cable, into a line amplifier (Sure FP11) that also converted the signal back to an unbalanced one, and finally to a Sony SRS-77G powered speaker with a relatively flat frequency response.

Since playback volume may influence responsiveness (BLUMSTEIN 1994), line levels on the tape deck, line amplifier, and powered speaker were adjusted until the sound-pressure level, 0.1 m in front of the speaker, was about 100–104 dB (measured using a Realistic model 33–2050 sound-level meter). In fact, the average playback volume was 104.8 dB (range: 97–112 dB), and the speakers were 13.4 m from the marmots (range: 5.4–25.5 m).

The playback situation mimicked the situation of a distant marmot alarm calling. Depending on the exact location of the speaker, the hypothetical 'caller' could have been from the same or an adjacent social group. Marmots routinely responded to alarm calls produced throughout the meadow.

Single-frame analysis of the video (temporal resolution = 0.033 s) permitted marmots' responses to playbacks to be measured. From the videotape, variables hypothesized to reflect responsiveness on different temporal scales were measured to search for differential responsiveness. Immediate responses were quantified by measuring: 1. The delay in responding to the played-back stimulus, defined as the time between the beginning of the playback and the beginning of the first look; and 2. The duration of the first look following the playback. Short-term responses were quantified by recording the number and duration of each bout of looking in the first 17 s. This time was chosen because the average time between alarm calls was 17 s (BLUMSTEIN 1995). Longer-term responses were quantified by recording the number and duration of each bout of looking in the first 59 s following the playback. While any differential responsiveness to alarm-call variants would have been telling, I anticipated the number of looks and the time spent looking to be positively associated with the degree of risk 'encoded' in the call. Moreover, I anticipated shorter response times to alarm calls than to bird song.

Friedman non-parametric ANOVAs (with no interaction effects) were used to test for differences in the responsiveness to these acoustic stimuli while controlling for individual variation. Pairwise post-hoc multiple comparisons were calculated using equation 7.5a from SIEGEL & CASTELLAN (1988).

Results

Marmots responded differently to alarm calls than to the bird song, but did not respond differently to three-note and eight-note alarm calls (Fig. 2). Between 24 May and 16 Aug. 1993, I played back the three different acoustic stimuli to 15 adult marmots (nine males/six females) in six different social groups. Overall, the

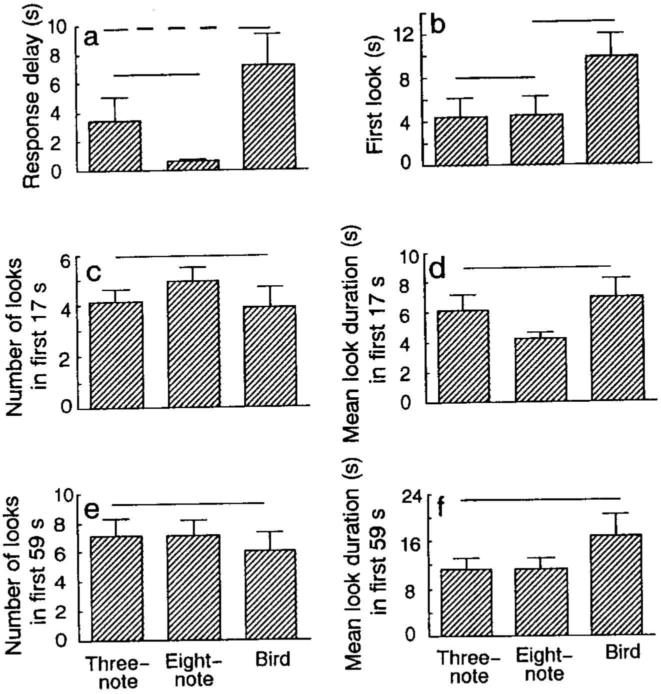

Fig. 2: Responsiveness (±SE to played back acoustic stimuli in terms of: a. Response time following the played back stimulus; b. Duration of the first look following the played back stimulus; c. The number of looks in the first 17 s following the playback; d. The number of looks in the first 59 s; e. The average duration of each look during the first 17 s; and f. The average duration of each look during the first 59 s. Significance tested with Friedman's nonparametric ANOVA, blocked by individual. Solid lines above graphs illustrate non-significantly different pairwise comparisons ($p > 0.05$). Response delays of marmots to the bird song and the three-note alarm call were not significantly different

average time between playbacks was 1.91 d; individual marmots averaged 3.6 d between playbacks of different acoustic stimuli.

Response delays to different acoustic stimuli differed significantly ($p = 0.031$). Multiple pairwise comparisons revealed that marmots had indistinguishable response delays to alarm calls but took longer to respond to bird song than to eight-note alarm calls.

The duration of the first look following playbacks also differed among treatments ($p = 0.017$). Multiple comparisons suggested that marmots only differentiated three-note alarm calls from bird song. However, the comparison of eight-note alarm calls to bird song was close to the significantly different multiple-comparison criteria. The duration of the first look was indistinguishable between three-note and eight-note alarm calls. A longer first look in response to bird song than to alarm calls was expected since bird song was not supposed to be alarming: alarmed marmots appeared 'agitated' and looked around frequently. Marmots 'responding' to bird song tended to 'casually' look around and did not appear agitated.

None of the short-term or long-term measurements of responsiveness differed significantly between treatments.

Discussion

Why Perceivers May Not Respond to Call Variation

Given the apparently robust relationship between the number of notes per call and the degree of risk the caller experiences when calling (BLUMSTEIN 1995), it is somewhat surprising that marmots did not respond differently to the played-back three-note and eight-note alarm calls. That marmots responded differently to alarm calls and the bird song suggests that marmots were not simply responding to sound coming from the speaker, nor to the pulsed playback. There are several non-mutually exclusive explanations of why marmots appeared not to differentiate alarm-call types.

Firstly, measurements of vigilance may not be sensitive enough to detect slight, but perceptually meaningful, evidence of stimulus discrimination (HAUSER 1994). Yet, other investigators have found vigilance patterns to be sensitive measurements of response differences to acoustic stimuli (LEGER & OWINGS 1978; OWINGS & LEGER 1980; HARRIS et al. 1983; HAUSER 1986; CHENEY & SEYFARTH 1990; EVANS et al. 1993). Different measures of responsiveness such as tail-pilo-erection onset time (COSS 1995), specific cardiac responses (EVANS & GAIONI 1990), or other autonomic nervous-system responses (BROOKS 1983), might have revealed significantly different responses to variants.

Secondly, alarm calls alone may not have provided sufficient context for perceivers to properly interpret the meaning of the calls (SMITH 1977; LEGER 1993). Some species are able to recognize individuals by their vocalizations (GREEN & MARLER 1979; CONNER 1985; CHENEY & SEYFARTH 1990). Golden marmots live in sufficiently stable social groups for perceivers to have the opportunity to learn the special characteristics of their neighbors' calls and to include that knowledge in their assessment of a call's meaning: adding marmot identity increased the total explained variation in the number of notes per call; BLUMSTEIN (1995). Additionally, volume-related potential cues may have aided marmots' interpretation of an alarm call. Since these contextual cues were, by design, absent in this experiment, marmots might normally – with appropriate contextual cues – be able to differentiate alarm-call variants. Nevertheless, if these cues are required to respond differently, then the number of notes per call alone cannot communicate variation in predation risk. If so, the opportunity for asymmetrical production and perception seems plausible.

Thirdly, previous studies that found an ability for species to perceive temporal differences in calls have been conducted on species that have the ability to produce structurally different calls (LEGER & OWINGS 1978; HARRIS et al. 1983; STONE & TROST 1991; studies of Eurasian marmots by NIKOL'SKII & NESTEROVA 1988, 1989, 1990 (loc. cit. NIKOL'SKII et al. 1994) are apparent exceptions). However, some species, such as golden marmots, produce only temporally different calls. If the ability to produce structurally distinct call types was correlated with the ability to differentiate call types, then species producing only temporally variable calls would be less able to differentiate alarm-call variants. This potential evolutionary constraint must be studied by investigating production and perception in the entire genus. Specifically, to determine whether perceptual abilities are correlated with production abilities, the order of trait evolution must be studied (BROOKS & MCLENNAN 1991).

Fourthly, it is probable that marmots use simple rules-of-thumb to assess predation risk (BOUSKILA & BLUMSTEIN 1992). An example of an assessment rule might be where perceivers treat any alarm call as representing an equivalent threat. If so, different calls would elicit identical responses. Assessing calls similarly might be a reasonably inexpensive strategy because: 1. The immediate response to an alarm call is looking and presumably assessing the situation; and 2. Alarm calls are not that common. It is worth noting that calls may have been perceived differently but have had equivalent meanings to the marmots (see discussion of 'just meaningful difference' in NELSON & MARLER (1990).

Finally, the first alarm call might serve a generalized alerting function (BALPH & BALPH 1966). Perceivers might use changes in the number of notes in subsequent calls to assess the relative risk of predation (sensu BELETSKY et al. 1986). Given that a substantial amount of variation in the number of notes per call may be explained by knowing the caller's identity, a perceiver might pay less attention to the absolute number of notes per call in the first call than to how the number of notes from the same caller changes over time. If the change in the number of notes in subsequent calls is used to assess predation risk, degree of risk is not communicated immediately. While calls may be repeated to track risk, an alternative explanation of repeated calls is that they are used to maintain vigilance (SCHLEIDT 1973; OWINGS & VIRGINIA 1978; HARRIS et al. 1983; OWINGS & HENNESSY 1984; LOUGHRY & MCDONOUGH 1988). Yet, if risk is communicated over a larger time scale, then the inter-call interval would be a variable requiring additional study (see NIKOL'SKII et al. 1994).

Conclusions

This study underscores the importance of conducting playback experiments to study the meaning of alarm calls (GREEN & MARLER 1979). Many studies have looked for correlations between alarm call variation and stimulus variation. Such studies can be used to define what potential information is made available to perceivers. Relatively few investigators have played back alarm call variants to a species to determine whether variants are able to elicit different responses (but see: LEGER & OWINGS 1978; LEGER et al. 1979; SCHWAGMEYER & BROWN 1981; HARRIS et al. 1983; BROWN 1985; CHENEY & SEYFARTH 1990; MACEDONIA 1990; STONE & TROST 1991; NIKOL'SKII & NESTEROVA 1988, 1989, 1990 cited in NIKOL'SKII et al. 1994; BLUMSTEIN & ARNOLD 1995). Studies that only correlate call types with situation may erroneously assume that perceivers respond to call variation. Playback experiments must be conducted to determine whether their subjects respond to different call types (MACEDONIA & EVANS 1993). It is theoretically possible that subjects do not respond differently to call variants. Communication can be understood only by studying the behavior of both the signaler and the receiver (SMITH 1977).

Acknowledgements

I thank the government of Pakistan and the Khunjerab Village Organization for permission to work in Khunjerab, and for their hospitality while in Pakistan. I also thank Walter ARNOLD, Don OWINGS, Susan PERLOFF, Brad SHAFFER, W. John SMITH, and, especially, Judy STAMPS for comments on previous versions of this paper.

Funding was generously provided by The National Geographic Society, the Fulbright-Hayes programme, the University of California-Davis (Graduate Fellowships, Graduate Research Awards, Jastro-Shields Research Scholarships), The American Institute of Pakistan Studies, the NSF Training Grant in Animal Behavior to UC Davis, the World Wide Fund for Nature-Pakistan, the World Pheasant Association-Pakistan, the US National Park Service – International Division, Sigma Xi, The Explorers Club, The American Society of Mammalogists, and the Max-Planck-Gesellschaft (through Wolfgang WICKLER). Commercial support was provided by Bushnell – a division of Bausch and Lomb, Deckers Corporation (Teva), Delta Airlines, Hi-Tec Sports, Sterigenics, and The North Face.

Literature Cited

BALPH, D. M. & BALPH, D. F. 1966: Sound communication of Uinta ground squirrels. J. Mammal. **47**, 440—450.

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.

BLUMSTEIN, D. T. 1994: Predation hazard assessment and management in golden marmots (*Marmota caudata aurea*). PhD Diss., Univ. of California, Davis.

— — 1995: Golden marmot alarm calls: I. The production of situationally-specific vocalizations. Ethology **100**, 113—125.

— — & ARNOLD, W. 1995: Situational-specificity in alpine marmot alarm communication. Ethology **100**, 1—13.

BOUSKILA, A. & BLUMSTEIN, D. T. 1992: Rules of thumb for predation hazard assessment: predictions from a dynamic model. Am. Nat. **139**, 161—176.

BROOKS, C. M. 1983: Newer concepts of the autonomic system's role derived from reductionist and behavioral studies of various animal species. J. Auton. Nerv. Syst. **7**, 199—212.

BROOKS, D. R. & MCLENNAN, D. A. 1991: Phylogeny, Ecology, and Behavior. Univ. of Chicago Press, Chicago.

BROWN, E. D. 1985: Functional interrelationships among the mobbing and alarm caws of common crows (*Corvus brachyrhynchos*). Z. Tierpsychol. **67**, 17—33.

CHENEY, D. L. & SEYFARTH, R. M. 1990: How Monkeys See the World. Univ. of Chicago Press, Chicago.

CONNER, D. A. 1985: The function of the pika short call in individual recognition. Z. Tierpsychol. **67**, 131—143.

COSS, R. G. 1995: Evolutionary persistence of behavior: restraints on geographic variation and phenotypic plasticity. In: Geographic Variation of Behavior: an Evolutionary Perspective (FOSTER, S. A. & ENDLER J. A., eds). Oxford Univ. Press, Oxford, in press.

DIGIDESIGN 1990: AudioMedia User's Guide. Digidesign Inc., Menlo Park.

EVANS, C. S. & GAIONI, S. J. 1990: Conspecific calls evoke characteristic cardiac responses in mallard ducklings. Anim. Behav. **39**, 785—796.

— —, EVANS, L. & MARLER, P. 1993: On the meaning of alarm calls: functional reference in an avian vocal system. Anim. Behav. **46**, 23—38.

GREEN, S. & MARLER, P. 1979: The analysis of animal communication. In: Handbook of Behavioral Neurobiology, Vol. 3. Social Behavior and Communication (MARLER, P. & VANDENBERGH, J. G., eds). Plenum Press, New York. pp. 73—158.

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.

HAUSER, M. D. 1986: Male responsiveness to infant distress calls in free-ranging vervet monkeys. Behav. Ecol. Sociobiol. **19**, 65—71.

— — 1994: How monkeys feel about how they see the world. Language Commun. **14**, 31—36.

KELLER, E. 1992: Signalyze, Vers. 2. InfoSignal Inc., Lausanne.

LEGER, D. W. 1993: Contextual sources of information and responses to animal communication signals. Psych. Bull. **113**, 295—304.

— — & 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.

— —, — — & BOAL, L. M. 1979: Contextual information and differential responses to alarm whistles in California ground squirrels. Z. Tierpsychol. **49**, 142—155.

LOUGHRY, W. J. & MCDONOUGH, C. M. 1988: Calling and vigilance in California ground squirrels: a test of the tonic communication hypothesis. Anim. Behav. **36**, 1533—1540.

MACEDONIA, J. M. 1990: What is communicated in the antipredator calls of lemurs: evidence from playback experiments with ringtailed and ruffed lemurs. Ethology **86**, 177—190.

— — & EVANS, C. S. 1993: Variation among mammalian alarm call systems and the problem of meaning in animal signals. Ethology **93**, 177—197.

MCGREGOR, P. K., et al. 1992: Design of playback experiments: the Thornbridge Hall NATO ARW consensus. In: Playback and Studies of Animal Communication: Problems and Prospects (MCGREGOR, P. K, ed.). Plenum Press, New York. pp. 1—9.

NELSON, D. A. & MARLER, P. M. 1990: The perception of birdsong and an ecological concept of signal space. In: Comparative Perception (BERKLEY, M. & STEBBINS, W., eds). Wiley & Sons, New York. pp. 443—478.

NIKOL'SKII, A. A., NESTEROVA, N. L. & SUCHANOVA, M. V. 1994: Situational variations of spectral structure in *Marmota bobac* Müll. alarm signal. In: Actual Problems of Marmots Investigation (RUMIANTSEV, V. Y., ed.). ABF Publ. House, Moscow. pp. 127—148.

OWINGS, D. H. 1994: How monkeys feel about the world: a review of how monkeys see the world. Language Commun. **14**, 15—30.

— — & HENNESSY, D. F. 1984: The importance of variation in sciurid visual and vocal communication. In: The Biology of Ground-dwelling Squirrels (MURIE, J. O., & MICHENER, G. R., eds). Univ. of Nebraska Press, Lincoln. pp. 169—200.

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

— — & VIRGINIA, R. A. 1978: Alarm calls of California ground squirrels (*Spermophilus beecheyi*). Z. Tierpsychol. **46**, 58—70.

SCHLEIDT, W. M. 1973: Tonic communication: continual effects of discrete signs in animal communication systems. J. Theor. Biol. **42**, 359—386.

SCHWAGMEYER, P. & BROWN, C. H. 1981: Conspecific reaction to playback of thirteen-lined ground squirrel vocalizations. Z. Tierpsychol. **52**, 25—32.

SIEGEL, S. & CASTELLAN, N. J., Jr. 1988: Nonparametric Statistics for the Behavioral Sciences. McGraw-Hill, New York.

SMITH, W. J. 1977: The Behavior of Communicating. Harvard Univ. Press, Cambridge.

STONE, E. & TROST, C. H. 1991: Predators, risks and context for mobbing and alarm calls in black-billed magpies. Anim. Behav. **41**, 633—638.

Received: September 13, 1994

Accepted: January 13, 1995 (W. Wickler)