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Vocalizations of the Townsend chipmunk (Eutamias townsendii)

Greig Michael Warner
Portland State University

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[redacted]

Richard B. Forbes, Chairman

[redacted]

Denzel E. Ferguson

[redacted]

John H. Wirtz

This study describes an analyzes the vocalizations of the Townsend chipmunk (Eutamias townsendii) in Oregon. Tape recordings of calls were collected primarily from Forest Park in Portland (Oregon) during 1970 and 1971, and sonograms of these recordings were produced. Findings were compared with those of Brand (1970) who investigated E. townsendii vocalizations in California.

The prominent calls in the vocal repertoire of townsendii are the quist, the quirt, and the chipper. These calls all appear to be warning calls. The quist note is a chevron-shaped (Λ) figure representing a sound which begins at a low frequency (1-2 KC), sharply rises to a peak at about 11 KC, and then drops sharply to the lower frequencies again. Quists are arranged into bursts, and bursts into sequences. The number of quists per burst and the

frequency of the top of the note decreased significantly over time. The interval between burst increased significantly. Quist rate and burst rate appear to decrease, while the interval between quists seems to increase over time.

The variation in the quist rate and related characteristics between Oregon and California *townsendii* populations is probably a result of subspecific differences.

There seems to be a trend in the sciurids from the specific vocal system (one definite meaning per call) of the forest dwellers towards the unspecific vocal systems of animal groups which live in the more open habitats. *E. townsendii* displays a specific vocal system in which each call seems to have a specific function.

VOCALIZATIONS OF THE TOWNSEND CHIPMUNK (EUTAMIAS TOWNSENDII)

by

GREIG MICHAEL WARNER

A thesis submitted in partial fulfillment of the requirements for the degree of

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TO THE OFFICE OF GRADUATE STUDIES:

The members of the Committee approve the thesis of Greig Michael Warner presented September 13, 1971.

[redacted]

Richard B. Forbes, Chairman

[redacted]

Denzel E. Ferguson

[redacted]

John H. Wirtz

APPROVED:

[redacted]

Earl Fisher, Head, Department of Biology

[redacted]

David T. Clark, Dean of Graduate Studies

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INTRODUCTION

While extensive research has been focused upon the spectrographic analysis of avian vocalizations (Lanyon, 1960; Marler, 1960; Bremand, 1963; and Marler and Hamilton, 1966) relatively little bioacoustical information is available for mammals (Tembrock, 1963 and 1968 for summaries). Recent investigations on sciurid rodent vocalizations include studies on the eastern chipmunk (Dunford, 1970; Brand, 1970); ten species of the western chipmunks (Brand, 1970); the yellow-bellied marmot (Waring, 1966); the Uinta ground squirrel (Balph and Balph, 1966); the 13-lined ground squirrel, Mexican ground squirrel, golden-mantled ground squirrel, and antelope ground squirrel (Harris, 1967); the black-tailed, white-tailed, and Gunnison's prairie dogs (Waring, 1970); the Douglas squirrel (Smith, 1968) and the red squirrel (Embry, 1970; Smith, 1968); and the fox squirrel (Zelley, 1971).

The Townsend chipmunk (*Eutamias townsendii*) ranges from northern California to southern British Columbia (Hall and Kelson, 1959). As with other chipmunks, this species is highly vocal when disturbed in the field. Its calls were first described by Grinnell and Storer (1924), and Miller (1944). Recently Brand (1970) analyzed and discussed the calls of Townsend chipmunks in northern California.

This thesis is primarily concerned with the description of the vocalizations of the Townsend chipmunk in Oregon and insofar as possible, a comparison of my findings with those of Brand.

MATERIALS AND METHODS

This study was based on 35 tape recordings of chipmunk calls. The recordings were obtained between September 1970 and July 1971.

Most work was conducted in Forest Park, which is inside the city limits of Portland (Multnomah Co., Oregon). I concentrated on roughly a triangular area bounded by Dogwood, Wildwood, and Wild-cherry trails. This humid transition zone forest, at an altitude of 700 feet, is mainly comprised of Douglas fir (*Pseudotsuga menziesii*), western hemlock (*Tsuga heterophylla*) and bigleaf maple (*Acer macrophyllum*). The understory contains vine maple (*A. circinatum*), thimbleberry (*Rubus parviflorus*), salal (*Gaultheria shallon*), red alder (*Alnus rubra*), Pacific red elder (*Sambucus callicarpa*), lady fern (*Athyrium filix-femina*), and western sword-fern (*Polystichum munitum*).

Recordings of a few *E. townsendii* were obtained at secondary study areas in different geographical locations within Oregon. One area was the first mile of the Hidden Lake Trail, which lies near Barlow Campground within the Mt. Hood National Firest (Clackamas Co.). This site is 2½ miles west of Government Camp. A second area was the first 4 miles of trail along Eagle Creek, also within the Mt. Hood National Firest (Hood River Co.). The base of the trail is 2 miles southwest of Cascade Locks. Observations were also made at the Longview Fiber Company site along Clear Creek (Washington Co.), and

Lost Prairie Campground in the Willamette National Forest (Linn Co.). The chipmunks of the Forest Park and Clear Creek study areas are *E. townsendii*; those of the other three areas are *E. t. cooperi*.

I walked along a trail within a study area with the tape recorder running. When a chipmunk called, I would attempt to get as close to the caller as possible. Locality, date, and behavior of vocalizing animals were noted for recorded and some nonrecorded individuals.

Tape recordings were obtained with a Uher 4000 Report-L tape recorder. A Sony Electret Condenser Microphone (ECM-19B) was used. All recordings were made at a tape speed of 7.5 inches per second.

Visual representations of the vocalizations were produced by a Kay Electric Company sound spectrograph (Model 6061-A Sonograph; see Borror and Reese, 1953, for detailed description). The machine was set to analyze frequencies between 160 and 16,000 cycles per second, using a wide band analysis. Using the sonograms, datas were collected on duration of interval between notes, duration of notes, frequencies of parts of the notes, and chipper rates. Using a stop watch and ¼ tape speed, calling rates of quist notes and bursts, distance between bursts, and notes per burst were noted. Frequency was measured to the nearest 0.5 kilocycles (KC) and time duration to the nearest 0.005 second.

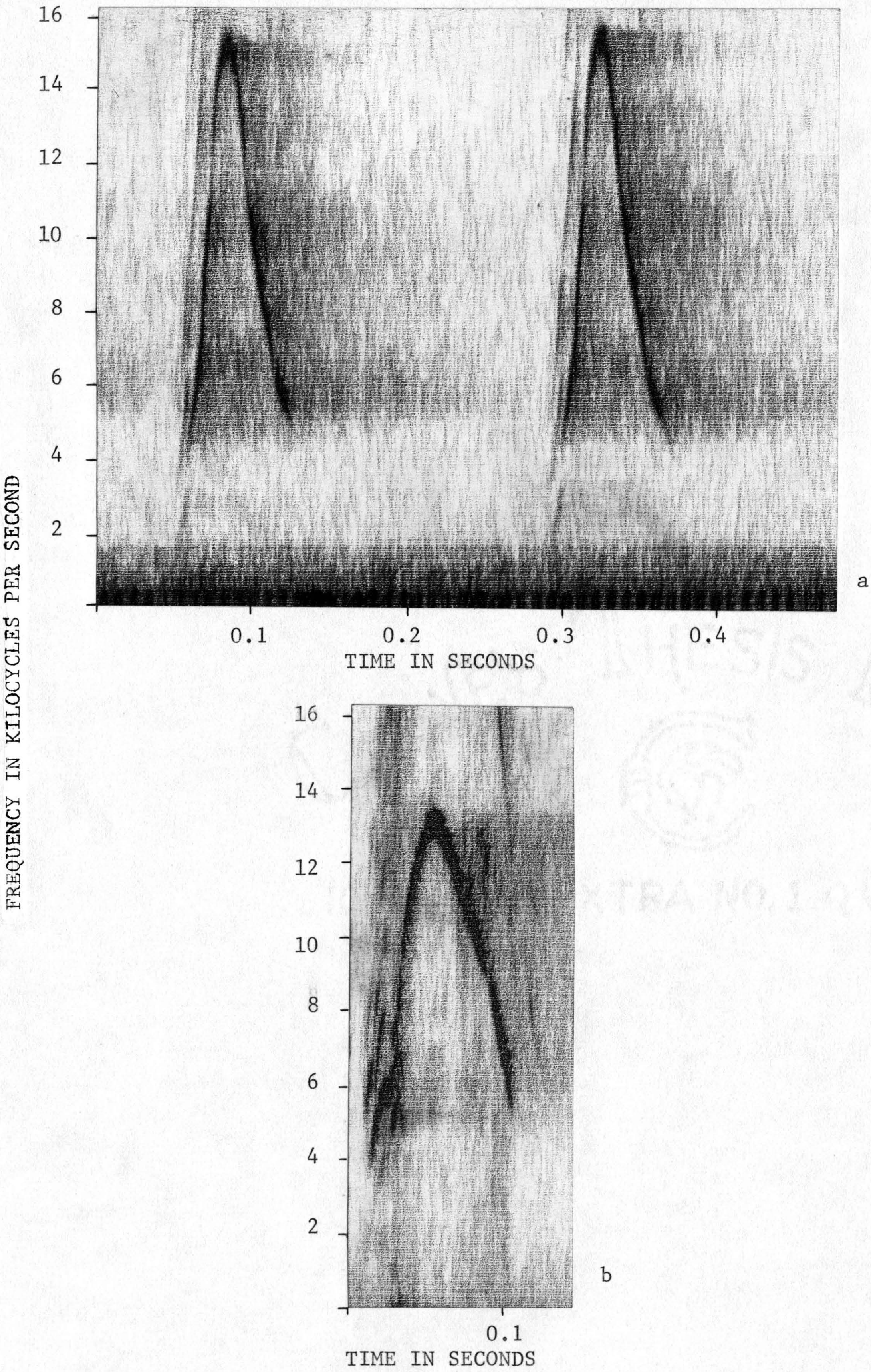
RESULTS

I. THE QUIST VOCALIZATION

The quist note or "chip" of Brand (1970) and Miller (1944) of the Townsend chipmunk appears on a sonogram as a chevron-shaped figure ($\wedge$) of about six harmonics (Figures 1, 2). The upswing of the note arises between 0.5 and 2.0 KC ($\bar{x}$= 1.1) and carries little energy, until at 2.5-5.5 KC ($\bar{x}$= 3.7) when a second harmonic carrying more energy enter in. The apex of the note ranges from 9.5 to over 16 KC ($\bar{x}$= 11.6) with the downswing ending at 2.5-8.5 KC ($\bar{x}$= 4.5). The quist note is 0.025-0.100 second long ($\bar{x}$= 0.068). Tables I, II, and III summarize the quist vocalization data. Often extra chevrons or lines will enclose or top the basic quist note (Figure 2a, b). These begin at approximately 5 KC and apparently often rise to frequencies above 20 KC.

Quists are arranged into bursts containing between one and seven notes. The average time between two notes in 0.171 second (range= 0.085-0.395); the average time between two bursts is 6.8 seconds (range= 1.1-25.6). The bursts are arranged into sequences which may last less than a minute or more than 20 minutes. Two of the recorded sequences (12%) contained only bursts of one quist each; i.e., each sequence was a series of quist notes. Brand (1970) also observed a frequency of 12% for this phenomenon. The average number

Figure 1. Sonograms of *E. townsendii cooperi* quist note: *a* is a two-quist burst from Barlow Campground; *b* is a quist from a two-quist burst from Lost Prairie Campground.



FREQUENCY IN KILOCYCLES PER SECOND
16
14
12
10
8
6
4
2
0.1
0.2
0.3
0.4
TIME IN SECONDS
a
16
14
12
10
8
6
4
2
0.1
TIME IN SECONDS
b

Figure 2. Sonograms of *E. townsendii townsendii* quist notes from Forest Park: Note in *a* and *b* that more than one chevron makes up the call. Notes *d* and *e* are single quists emitted by chipmunks on the ground and running away. These notes seem mainly to be emitted by juveniles.

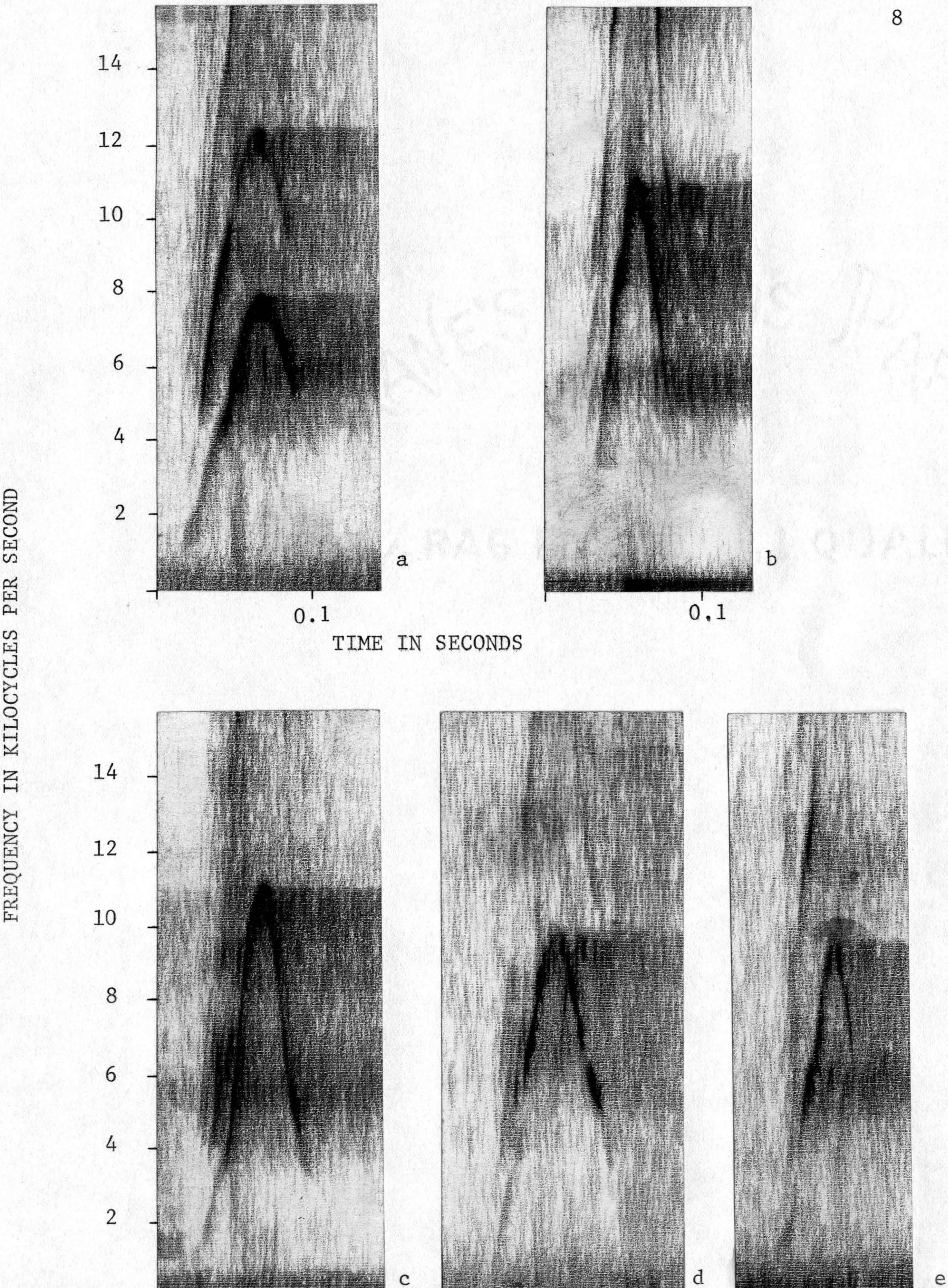

FREQUENCY IN KILOCYCLES PER SECOND
14
12
10
8
6
4
2
a
b
0.1
0.1
TIME IN SECONDS
c
d
e
0.1
0.1
0.1
TIME IN SECONDS

TABLE I

INDIVIDUAL DATA FOR THE QUIST CALL*

Chipmunk	Interval Between Bursts (sec.)	Interval Between Quists (sec.)	Quist Duration (sec.)	Bottom of Upswing (KC)	Higher Harmonic of Upswing (KC)	Top of Upswing (KC)	Bottom of Downswing (KC)
Forest Park							
1	8, 5.7	7, .230	5, .076	4, .9	5, 3.8	5, 11.5	4, 4.6
2	26, 4.4	19, .234	17, .033	16, 1.5	17, 4.0	17, 12.2	
3	47, 3.5	14, .202	25, .063	25, .9	25, 3.5	25, 10.7	25, 4.0
4	9, 4.8	9, .140	6, .072	4, 1.0	6, 3.9	6, 13.2	6, 4.3
5	15, 9.0	16, .133	11, .064	10, .8	10, 4.1	11, 11.6	9, 4.7
6	10,10.2	9, .163	7, .078	7, 1.0	7, 3.6	7, 11.6	7, 3.6
7	16, 7.9	13, .157	10, .076	10, 1.0	10, 3.8	10, 8.6	10, 3.2
8	16, 7.2	10, .193	9, .064	6, .8	9, 4.0	9, 10.3	6, 3.8
9	23, 4.0	10, .159	14, .068	14, 1.2	14, 3.8	14, 11.5	14, 4.8
10	4, 7.4	–	2, .080	2, 1.0	2, 3.2	2, 10.5	2, 5.0
11	14, 4.4	4, .224	7, .072	7, 1.0	7, 3.9	7, 11.6	7, 4.7
12	4,13.5	4, .232	2, .072	2, 1.2	2, 3.5	2, 12.5	2, 5.8
Lost Prairie (1)	16, 7.6	11, .144	9, .072	10, 1.2	10, 3.5	10, 12.1	10, 5.4
Barlow Camp.							
1	35, 5.7	17, .189	17, .072	10, 1.5	18, 4.3	18, 12.6	18, 5.3
2	22, 7.5	19, .128	14, .073	11, 1.4	13, 3.5	14, 13.5	14, 4.7
Clear Ck. (1)	18, 6.6	23, .139	15, .060	13, 1.0	15, 3.7	15, 11.8	9, 4.0

* n, the number of items analyzed, is given first followed by the $\bar{x}$ for each individual

TABLE II

QUIST CALL DATA FOR FOREST PARK STUDY AREA

	Interval Between Bursts (sec.)	Interval Between Quists (sec.)	Quist Duration (sec.)	Bottom of Upswing (KC)	Higher Harmonic of Upswing (KC)	Top of Upswing (KC)	Bottom of Downswing (KC)
n	12	11	12	12	12	12	11
$\bar{G}$	6.8	.188	.068	1.0	3.7	11.3	4.4
R of the $\bar{x}$'s	3.5-13.5	.133-.234	.033-.080	.8-1.5	3.2-4.1	8.6-13.2	3.2-5.8
SE	.864	.012	.004	.056	.075	.343	.220
R of all items	1.1-25.6	.085-.395	.025-.100	.5-2.0	2.5-5.5	8.0-16+	2.5-8.5
$\bar{x}$ of all items	5.6	.184	.063	1.1	3.8	11.2	4.2

Continues on page 11

TABLE II (continued)

QUIST CALL DATA FOR FOREST PARK STUDY AREA

	Quists/Burst	Quist Rate (Quists/min.)	Burst Rate (Bursts/min.)
n	17	16	16
$\bar{x}$	2.5	24	11
R	1.0-4.4	9-50	5-19
SE	.257	2.72	1.07

TABLE III

QUIST CALL DATA FOR OTHER STUDY AREAS*

	Quists/Burst	Quist Rate (Quists/min.)	Burst Rate (Bursts/min.)
Lost Prairie	1, 2.4	1, 20.7	1, 8.7
Barlow Camp.	2, 2.8	2, 24.4	2, 9.4
Clear Ck.	1, 4.4	1, 34.1	1, 7.8

* n, the number of individual chipmunks, appears first followed by $\bar{x}$

of quists per minute (quist rate), which is primarily influenced by the number of quists per burst and the distance (time) between bursts, is 24.6 (range= 8.9-50.4). The number of bursts per minute (burst rate) ranges between 5.0 and 18.9 ($\bar{x}$= 10.3).

Quists are warning vocalizations, and are the most frequently emitted vocalization of the E. townsendii repertoire. The quists I recorded probably were elicited by my presence, although on Eagle Creek trail my dog may have acted as a stimulus. Of the quists recorded, 88% were emitted by stationary animals in trees or more than 3 feet above ground in bushes (Table IV). When vocalizing on the ground or below 3 feet in bushes, individuals are nearly always stationary and well-camouflaged in dense brush. An individual chipmunk may emit a chipper (p. 18) just prior to a quisting sequence, but never during nor following it.

Long sequences of quists (e.g., over 10 minutes) seem to show a basic pattern, only parts of which are heard in shorter recorded sequences. These long sequences begin with a high number of quists per burst, relatively small intervals between bursts, and a rapid quist and burst rate. Near the end of the first one-third of these sequences, the characteristics slowly change, and the end of the sequence is usually marked by single-quist bursts, larger interburst intervals, and smaller quist and burst rates. Thus, shorter sequences with large numbers of quists per burst or a short series of one-quist bursts may represent parts of the larger sequence. Factors such as previous events or the level of chipmunk anxiety may dictate the area of the large sequence from which a smaller sequence will be selected.

TABLE IV

LOCATION OF CHIPMUNKS EMITTING QUIST, CHIPPER, AND SINGLE QUIST VOCALIZATION

Vocalization	Percent of All Calls Chipmunk on Ground or Below 3 Feet in Brush	Chipmunk in Trees or Above 3 Feet in Brush
Quist	6	48
Chipper	39	0
Single quist	13	0

To test whether variation within a given sequence longer than 5 minutes actually occurs in a definite pattern over time, the characteristics of the first five quists and bursts were compared to those of the last five using a four (chipmunks) by two (first versus last quists and bursts) analysis of variance with five replications (Table V). It was found that the top of the note upswing decreased significantly ($p < 0.01$) over time, as did notes per burst ($p < 0.05$). Interval between bursts increased ($p < 0.01$). It also appears that the interval between notes increases, while quist rate and burst rate decrease over time. Zelley (1971) has recently shown that fox squirrel (Sciurus niger rufiventer) barks decrease in duration and intensity over time, and that the interval between barks increases.

Variations in different characteristics of the quist note produce variations in the shape of the first upstroke as well as the overall shape of the chevron. Several chevrons may compose one note. Also, one of the chipmunks recorded (6%) had only the upswing of the quist note. Brand (1970) reported that the quist notes of 33% of all E. *townsendii* individuals studied had no downswing.

TABLE V

COMPARISONS OF THE FIRST AND LAST FIVE QUISTS AND BURSTS OF FOUR SEQUENCES LASTING FIVE MINUTES OR LONGER

Quisting Characteristic	$\bar{x}$ of First Five Quists (Bursts)	$\bar{x}$ of Last Five Quists (Bursts)	F^{3}_{12} Value
Bottom of upswing (KC)	1.3	1.0	1.5
Top of upswing (KC)	11.7	9.1	4.9 **
Second harmonic (KC)	3.8	3.7	5.5 **
Quist Duration (sec.)	.058	.060	2.3
Interval between quists (sec.)	.192	.312	-
Quist per burst	2.9	1.2	3.2 *
Interval between bursts (sec.)	3.9	5.7	6.2 **
Quist rate (quists/min.)	36.2	11.0	-
Burst rate (bursts/min.)	12.5	9.5	-

* $p < 0.05$
** $p < 0.01$

While inadequate sample sizes were obtained from the Clear Creek, Barlow Campground, and Lost Prairie study areas to permit any conclusions regarding interpopulational variation in quist characteristics in Oregon, it appears that no obvious variations in chevron shape and size exist between these areas.

Brand (1970) collected data for E. *townsendii* from five locations in northern California: Crescent City (elevation 100 ft., latitude 41 45' N, longitude 124 30' W), Arcata (100 ft., lat. 40 45' N, long. 124 15' W), Burney (4300 ft., lat. 40 45' N, long. 122 00' W), Almanor (4500 ft., lat. 40 15' N, long. 121 30' W), and Yosemite

(8400 ft., lat. 37 45' N, long. 119 45' W). Townsend chipmunks in the Crescent City and Arcata study areas are represented by E. townsendii ochrogenys; E. t. senex is found in the other areas (Hall and Kelson, 1959). The quist rate was shown by Brand to decrease from Yosemite to Crescent City. Means for quists given in bursts for the five study areas are 16, 21, 37, 55, and 69 quists per minute, respectively. The decrease in call rate between these areas is related to a Yosemite-to-Crescent City decrease in frequency of the bottom of the downswing of the quist note. Burst rate and number of quists per burst also decrease, while note duration and the interval between quists increase. Brand suggests that his data demonstrate a decrease in call rate from south to north. However, his data could as easily be interpreted to demonstrate an altitudinal or longitudinal cline. That is, call rate increases as altitude increases and as longitude decreases. The latter two trends are supported by the data from Forest Park (elevation 700 ft., latitude 45 30' N, longitude 122 30' W; mean quist rate= 24 notes per minute).

A single quist vocalization is a lone note which is to be distinguished from a series of single quist notes. This note is usually emitted by juveniles shortly after emerging from their nests in late spring and early summer. Single quists were heard between June 10, the first day juveniles were observed, and July 8. Several times during this period I heard startled juveniles emit this call as they ran for cover. No single quists were heard during my last three observation periods, between July 20 and 26, nor during the week prior to June 10 (Figure 3). Interestingly, Forbes and Turner (1971) found that the first adult-type call given by an 18-day old caged chipmunk was a single quist. Single quists seem to be functional equivalents of chippering by adult chipmunks. Like chippering, single quists are exclusively given by chipmunks on the ground (Table IV). I heard only one adult chipmunk emit this call.

II. THE QUIRT VOCALIZATION

The quirt, or "chuck" of Brand (1970) or "bark" of Miller (1944), was heard only occasionally, and never in Forest Park. It seems to be associated with the least amount of alarm (or warning), and is usually given when the chipmunk is a relatively long distance from the observer. Brand (1970) reports that is is a slightly convex note with its fundamental frequency between 0.7 and 1.8 KC. Each quirt is between 0.03 and 0.05 second long, and is given in a series of 50 to 178 per minute. The average distance between 10 quirts of a series recorded at Clear Creek was 0.49 second (n= 6).

The absence of quirting in Forest Park is puzzling when comparison is made to northern California, or even other areas in Oregon. Most of the study areas in northern California were in parks or near logged areas, where chipmunks could presumably see and hear for relatively long distances. Forest Park lacks such areas. It would seem that quirting, which appears to be a mild warning or alert call, would be more common in areas where a potential predator could be sighted from a long distance. By the time a chipmunk in Forest Park

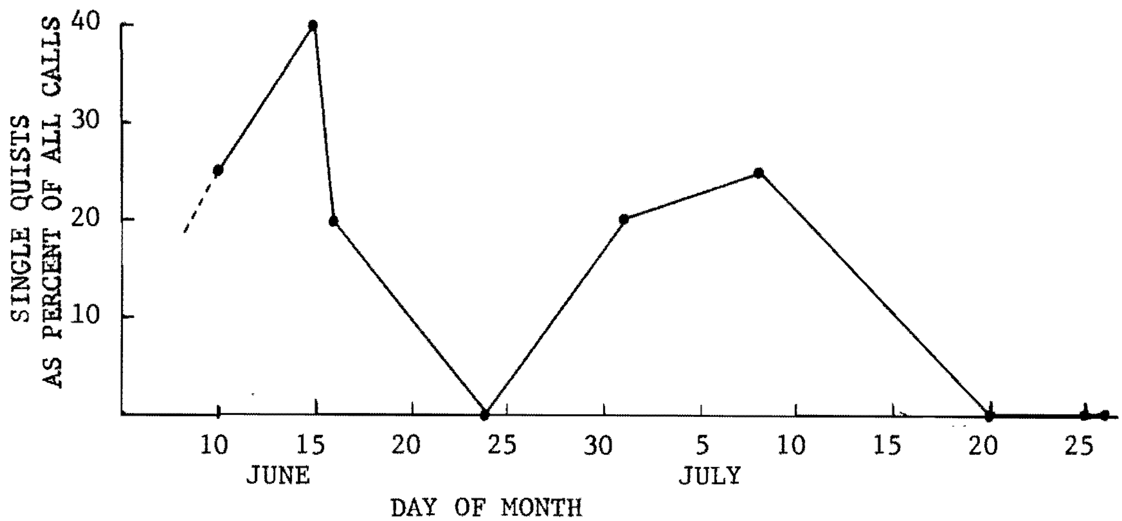


Figure 3. Percent of calls which are single quist notes. Juvenile chipmunks were first sighted on June 10. No single quists were heard prior to June 10 nor subsequent to July 20. These single quists appear to be used primarily by juveniles and serve a warning function analogous to the chipper of adults.

discerns a potential enemy it is in close proximity, and the vocalizations of greater alarm would seem to be more adaptive.

III. THE CHIPPER VOCALIZATION

The chipper is the warning call displaying the greatest amount of alarm or anxiety. It is exclusively given by chipmunks which are on the ground (Table IV), usually as they are running for cover. Chipper notes appear to be modified quist notes (Figure 4). Many appear to be nearly indistinguishable from quist notes, while others show little resemblance to quists. The note is composed of an upswing which begins at 1.4 KC (range= 0.5-3.5), is met at approximately 2.5 KC by a second harmonic, and peaks at 10.1 KC (range= 4.5-16+). The downswing ends at 3.8 KC (range= 1.5-7.0). The note duration is 0.058 second (range= 0.035-0.105), and the interval between notes averages 0.121 second (range= 0.025-0.860). The chipper call, which contains between four and 21 notes ($\bar{x}$= 8.8) and lasts between 0.6 and 4.0 seconds ($\bar{x}$= 1.4), has 6.7 chipper notes per second (chipper rate). This is a rate of 402.0 notes per minute. (Tables VI, VII, and VIII summarize the chipper call data.) Roughly 55% of the chipper calls I recorded preceded quisting sequences. (This represents 25% of all quist sequences.) Individual chipmunks never emitted the chipper during or after their own quist sequences.

In general, chippering can be differentiated from quisting by its more rapid note rate, and its lack of bursts and sequences. The chipper notes are much more variable than quists or quirts in all

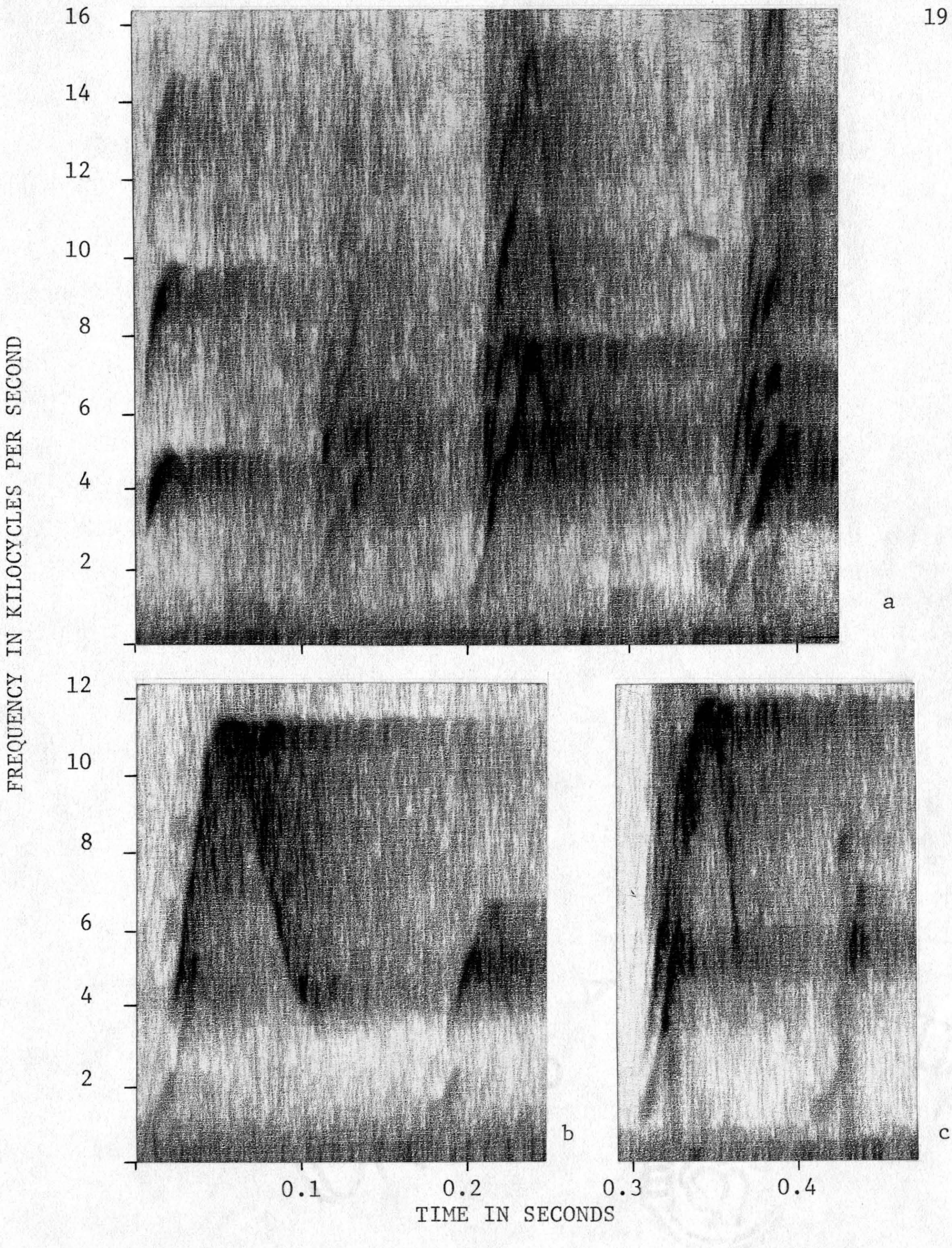


Figure 4. Chipper notes of Forest Park chipmunks. With the exception of a, the notes are very similar to quist notes. Observe variability of size and shape of consecutive notes in b and c, broken structure of a notes, and lack of downswing in d.

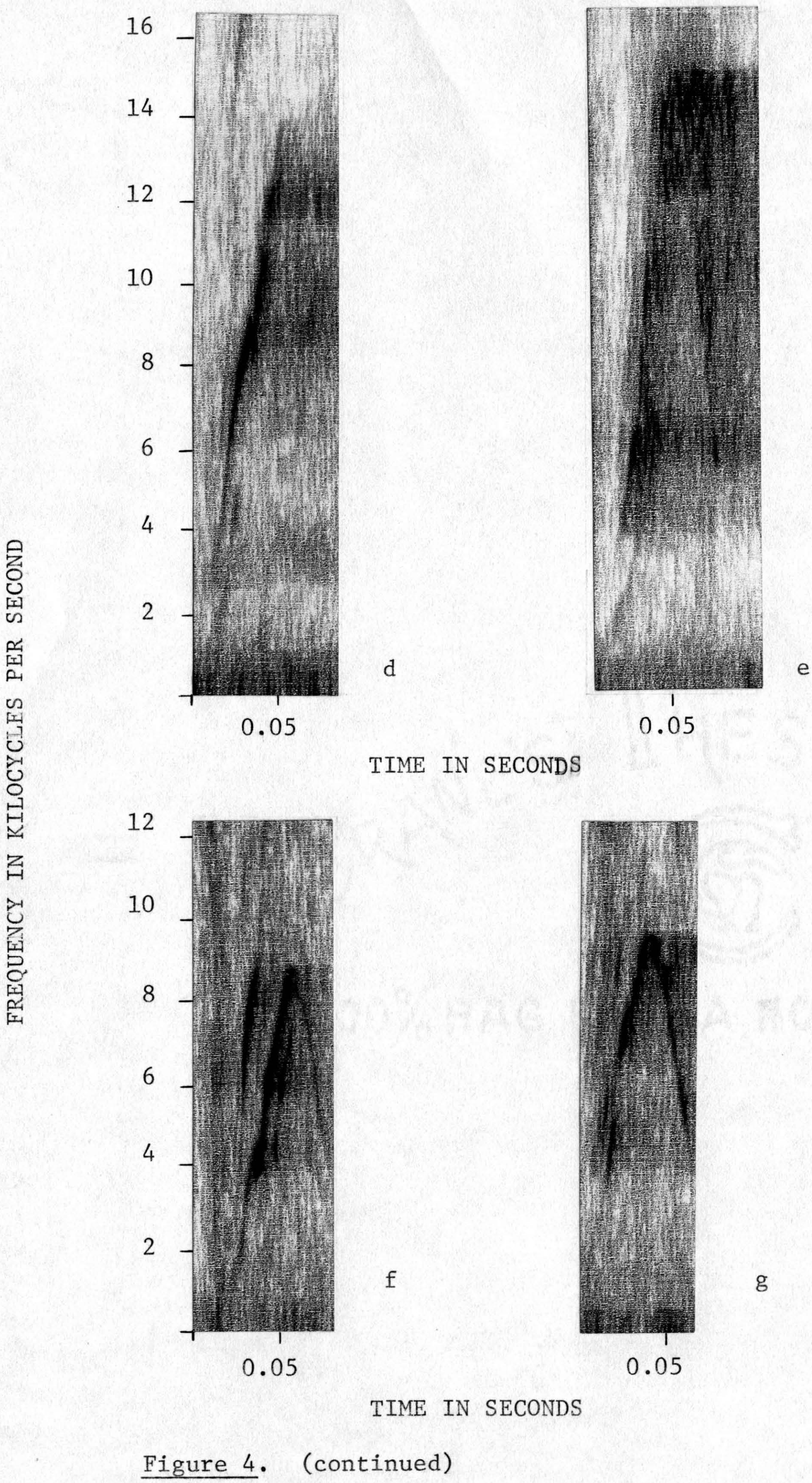


Figure 4. (continued)

TABLE VI

INDIVIDUAL DATA FOR THE CHIPPER CALL*

Chipmunk	Bottom of Upswing (KC)	Top of Upswing (KC)	Bottom of Downswing (KC)	Duration of Note (sec.)	Interval Between Notes (sec.)
Forest Park					
1	4, 1.6	4, 7.2	4, 3.9	4, .050	3, .125
2	7, 1.2	8, 10.5	5, 4.1	8, .064	7, .179
3	9, 1.2	8, 11.1	7, 4.8	8, .068	8, .095
4	12, 1.1	13, 8.8	13, 3.4	13, .070	12, .140
5	8, 1.8	8, 11.8	8, 4.4	8, .070	7, .100
6	10, 1.2	10, 8.5	8, 3.4	10, .057	8, .138
7	6, 1.4	6, 11.7	6, 3.4	6, .049	5, .065
8	11, 1.7	12, 11.1	12, 4.2	12, .045	11, .105
9	5, 1.6	5, 9.8	5, 3.5	5, .050	4, .175
10	9, 1.3	9, 10.6	6, 3.2	9, .058	8, .144
11	6, .9	6, 10.2	5, 3.1	6, .064	5, .104
Eagle Creek					
1	-	4, 11.2	-	4, .059	3, .073
2	6, 1.5	8, 8.7	6, 2.8	8, .046	7, .101
Barlow Camp.	(1)9, 1.5	21, 10.2	19, 4.7	20, .056	19, .146

* n, the number of items analyzed, is given first followed by the $\bar{x}$ for each individual

TABLE VII

CHIPPER CALL DATA FOR FOREST PARK STUDY AREA*

	Bottom of Upswing (KC)	Top of Upswing (KC)	Bottom of Downswing (KC)	Duration of Note (sec.)	Interval Between Notes (sec.)
G	1.4	10.1	3.8	.059	.124
R of $\bar{x}$'s	.9- 1.8	7.2- 11.8	3.1- 4.8	.045- .070	.065- .179
SE	.085	.389	.166	.003	.010
R of all items	.5- 3.5	4.5- 15.5	1.5- 7.0	.035- .105	.025- .860

	Total Time (sec.)	Notes/Call	Rate of Notes (notes/sec.)
$\bar{x}$	1.4	8.2	6.4
R	.6- 2.5	4.0- 13.0	4.4- 10.0
SE	.177	.853	.445

* n= 11 individuals

TABLE VIII

CHIPPER CALL DATA FOR OTHER STUDY AREAS*

	Total Time (sec.)	Notes/Call	Rate of Notes (notes/sec.)
Eagle Ck.	2, 6.7	2, 6.0	2, 9.0
Barlow Camp.	1, 4.0	1, 21.0	1, 5.2

* n, the number of individual chipmunks, appears first followed by $\bar{x}$

specific characteristics as well as the overall note shape (for instance, the great variability in two consecutive notes in Figure 4b, c). In comparison with quists, chipper notes have a smaller frequency range (from bottom of upswing to top of upswing), higher bottom of upswing (1.4 vs. 1.1 KC in quists), lower second harmonic (2.5 vs. 3.7 KC), lower top of upswing (10.1 vs. 11.6 KC), and lower bottom of downswing (3.8 vs. 4.5 KC). The duration of the chipper note is shorter (0.058 vs. 0.068 second), as is the interval between notes (0.121 vs. 0.171 second). These differences between chipper and quist call notes are probably a reflection of the greater chipper note rate, combined with the requirements for the localization of these notes.

IV. OTHER VOCALIZATIONS

Brand (1970) discusses and presents sonograms for four more *E. townsendii* vocalizations. Trills are a rapid series of quist-like notes emitted during quisting sequences, which seem to be functionally equivalent to quists. Trills are rarely emitted by *townsendii*.

Chattering is given during agonistic encounters and courtship. It is emitted by the pursued chipmunk during 10% of all chases that occur in the field. It is rarely accompanied by harmonics, although harmonic structure is more common in courtship than in agonistic chattering. I was able to record a chipmunk emitting this call as I was moving its cage. The growl is also associated with agonistic behavior, being emitted by chipmunks in traps, when unable to escape attack, when being restrained, and in encounters with dominant individuals. Finally, squeals were commonly emitted in the laboratory by chipmunks being attacked. Squeals are high-pitched sounds containing several harmonics.

DISCUSSION

The vocal repertoire of *E. townsendii* is dominated by three warning calls: the quirt, the quist, and the chipper. Each is a response to a greater degree of alarm. The quirt is often heard when there is no apparent alarm stimulus, or when the calling animal is a relatively great distance from the observer. The quirt sounds similar to the chuck of the eastern chipmunk, *Tamias striatus* (Forbes, personal communication).

The quist is usually emitted when the intensity of alarm is intermediate between that which elicts the quirt and that which elicts the chipper. Spectrographically, its form is that of a chevron. This call is harmonic and carries for a considerable distance. Brand (1970) has shown that the quists ofother chipmunks are also chevron-shaped or are a modification of that shape. He has proposed a scheme outlining the possible way that different quists have arisen from the basic chevron shape. This involves changes in the action of the vocal apparatus. The sonogram of the eastern chipmunk's quist represents a chevron without the upswing (\ ) (Brand, 1970; Dunford, 1970). This type of quist is no more variable than the quists of several other *Eutamias* species, and, according to Brand's hypothesis, represents an intermediate stage leading to the inverted chevron (V) quist of *E. sonomae*. These data, and those of Moore (1959), Nadler and Block (1962), and Nadler (1964) cast doubt on

White's (1953) proposed parallel evolution of Eutamias and Tamias from separate sciurid tribes (Callosciurini and Marmotini, respectively). While Nadler and Block (1962) and Nadler (1964) demonstrated that both Eutamias and Tamias have 38 chromosomes (other sciurids are extremely variable) and that the two basic karyotypes of Eutamias are no more similar than either is to that of Tamias, the former workers evoke Simpson's axiom that somatic changes are more important than genetic changes in assessing phylogeny. Since sonograms are visual representations of the emissions of the vocal apparatus, they should be considered in determining phylogenetic relationships. It is hard to imagine that numerous morphological characteristcs, chromosomes, and the vocal apparatus of Eutamias and Tamias have all evolved in such an exactly parallel manner.

Brand (1970) suggested that the variation of the quist call rate of E. townsendii in California represents a north-south character displacement allowing townsendii and E. quadrimaculatus, which are sympatric and possibly closely related, to recognize conspecifics. As mentioned, this variation between Yosemite and Crescent City (and Forest Park) could be the result of an altitudinal or longitudinal cline. If this is a latitudinal phenomenon, however, the call rate from Forest Park would seem to support a character displacement theory. That is, since E. quadrimaculatus is not found in Oregon we would not expect the south to north rate decrease to continue and it does not. Actually, the call rate variation observed by Brand probably represents the variation between different California subspecies, E. t. ochrogenys in the northwest and E. t. senex in the northeast. Most of the data from Brand's California study sites can be placed in one of these groups. Almanor and Yosemite lie in the senex range and have high call rates, while Crescent City and Arcata lie in the range of ochrogenys and have relatively low quist rates. Other related characteristics seem to be arranged in this manner also. Chipmunks from Burney do not consistently belong to either group and is often intermediate. Perhaps this is because in an area in California, near Burney, the senex and ochrogenys subspecies are not strictly isolated from one another, allowing chipmunks in the Burney area to be influenced by gene flow from both subspecies, as well as from E. t. siskiyou to its west. Interestingly, the quist of the Forest Park population is most similar to the Arcata chipmunk population in six of eight measurements including call rate. The range of the Forest Park chipmunks, E. t. townsendii, and the range of ochrogenys merge in southern Oregon.

Chippering expresses the greatest amount of alarm. It is given by animals which are disturbed while on the ground as they dash for cover. Brand (1970) claims that chippering is the same as the chip-trill of Tamias striatus, but the relationship is probably only functional since the two sound distinctly different (Forbes, personal communication).

With the exception of the trill the other calls in the chipmunk repertoire serve a function other than warning. They include agonistic and sexual chattering, growls, and squeals. Generally these calls are only slightly harmonic, relatively soft, and they do not cover large frequency ranges. Thus, the system of vocalizations in the Townsend chipmunk adheres to the general system of physical sounds proposed by Collias (1960). That is, it contains alarm calls which are harsh (wide spread of frequencies and several harmonics), loud, and high pitched, enabling sound localization. The system also contains sexual and agonistic vocalizations which have few of these characteristics and are more difficult to localize.

Marler (1959) points out that harsh repetitive vocalizations allow for sound location by intensity differences, phase differences, and temporal differences. Intensity differences at the two ears are brought about as the head creates a "sound shadow" on the side opposite to the sound source. This can only result from sounds which are high pitched. Phase differences at the two ears can only be perceived when the sound is low pitched, so that the wavelength is longer than the distance between the ears. Sharp discontinuities are necessary if time differences are to act as a cue in sound localization. The ideal sound for localization purposes is one that has a wide range of frequencies, is broken, and is repetitive. Thus, the quist and chipper notes of the Townsend chipmunk are easily localized. The chipper note is less easily localized by intensity and phase differences since its range of frequencies is less than that of quists; but the brokenness and the variability of the chipper notes, as well as their rapid rate probably compensates via enhancing temporal cues. Localization of the quirt note must depend primarily on binaural phase differences.

The fact that the alarm notes of adults are so easily localized may explain why juvenile chipmunks which have recently left the nest rarely emit warning vocalizations, or emit only a single quist note. These juveniles appear extrememly vulnerable to predation at this early age and the emission of easily localized alarm calls would increase this vulnerability.

Vocal localization in the adult chipmunk probably functions by focusing attention upon a potential predator. In 57% of the quist sequences observed chipmunk vocal interactions occurred. Either two or more chipmunks would quist alternately, or one quisting individual would be superseded by another. Thus a predator could be followed through an area of forest with most chipmunks aware of its presence. It appeared to me that quisting chipmunks, Douglas squirrels (Tamiasciurus douglasii), and certain birds communicated a certain amount of alarm to one another in Forest Park.

The relationship between the behavior and ecology of a species is known to be intimate (see Eibl-Eibesfeldt, 1970, Chapter 15). Thus, it is not surprising that the Townsend chipmunk, which is confined to relatively dense forests or brush where surprise predation may be a constant problem, has a vocal repertoire dominated by warning calls. Chipmunks are relatively asocial animals displaying dominance hierarchies under certain conditions (Brand, 1970; Forbes, unpublished data), and, rarely, territorial behavior (Broadbooks, 1970). Thus, western chipmunks have little need for prominent non-warning signals. This vocal system is specific in that each call seems to have a definite meaning.

The function of the communication signals appears to vary with the type of social organization. Thus, the eastern chipmunk, Tamias striatus, appears to be slightly more territorial than Eutamias if we accept "reversal of dominance with difference in space" as a criterion of territorial behavior. Related to this is the fact that chipping (one of its three warning calls) has taken on a secondary function as an agonistic signal inhibiting the approach of non-resident (subordinate) chipmunks (Dunford, 1970).

Individuals of the genus Tamiasciurus defend definite territories, allowing for the acquisition, storage, and defense of a food supply which will last throughout the year; and they maintain a territory with a minimum of time and energy (Smith, 1968). Of its five calls, four are territorial, and one functions in warning and courtship (Embry, 1970; Smith, 1968).

Prairie dogs studied by Waring (1970) (Cynomys ludovicianus, C. leucurus, and C. gunnisoni) have only one alert call, and seven, four, and three non-warning calls, respectively. Each has a unique group cohesion call. This vocal repertoire is what would be expected of a highly social animal living in relatively open areas, and is a specific vocal system with each vocalization appearing to have a restricted meaning.

Another social animal that has been studied is the yellow-bellied marmot, Marmota flaviventris (Waring, 1966). The marmot's vocal system appears to be somewhat unspecific in that two of the eight calls are used in both alert and threat situations, the other six calls are divided evenly between alert and non-alert types. Waring points out that many communication signals (for instance the "all-clear" signal) are performed by body posture and movements. Also, olfactory and tactile stimulation have important signaling functions (e.g., greeting).

The Uinta ground squirrel (Spermophilus armatus) is a highly aggressive, asocial species which lives in aggregations in open habitats (Balph and Balph, 1966). All six calls are used in agonistic behavior, two of these also functioning as warning calls. This is a simple, unspecific vocal system in which the different calls only seem to draw attention to a stimulus, and have no inherent meaning. Balph and Balph point out that this unspecific system may be the result of reliance on visual and olfactory signals in an open habitat.

It is difficult to make general conclusions concerning the sciurid vocal systems, except that the number of calls does not seem to increase with increased social organization, and that there seems to be a trend toward unspecific vocal communication systems in animal groups living in open habitats. The Towsend chipmunk, which must rely on vocal communication in the dense forest, employs a specific meaning for each signal. On the other had, species living in groups in open habitats are free to develop signals through various non-vocal modalities and may develop unspecific systems of communication. However, one may question why the highly social prairie dogs have relatively specific vocal systems. Fisler's (1970) hypothesis that the number and complexity of vocal and visual signals increases with more complex social relationships appears to be unsupported within the sciurid family. The quist call of Eutamias *townsendii* appears to be a more complex signal than the unspecific marmot whistle, which can be given in a number of contexts. The whistle requires more complex behavior on the part of the receiver, who must decide whether the whistle signals an agonistic encounter between two marmots or the presence of a predator. In chipmunks the meaning of a vocal signal is probably more restricted.

SUMMARY

This study describes and analyzes the vocalizations of the Townsend chipmunk (Eutamias townsendii) in Oregon. Tape recordings of calls were collected primarily from Forest Park in Portland (Oregon) during 1970 and 1971, and sonograms of these recordings were produced. Findings were compared with those of Brand (1970) who investigated E. townsendii vocalizations in California.

The prominent calls in the vocal repertoire of townsendii are the quist, the quirt, and the chipper. These calls all appear to be warning calls. The quist note is a chevron-shaped (Λ) figure representing a sound which begins at a low frequency (1-2 KC), sharply rises to a peak at about 11 KC, and then drops sharply to the lower frequencies again. Quists are arranged into bursts, and bursts into sequences. The number of quists per burst and the frequency of the top of the note decreased significantly over time. The interval between burst increased significantly. Quist rate and burst rate appear to decrease, while the interval between quists seems to increase over time.

The variation in the quist rate and related characteristics between Oregon and California townsendii populations is probably a result of subspecific differences.

There seems to be a trend in the sciurids from the specific vocal system (one definite meaning per call) of the forest dwellers

towards the unspecific vocal systems of animal groups which live in the more open habitats. *E. townsendii* displays a specific vocal system in which each call seems to have a specific function.

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