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Postcopulatory mate guarding by vocalization in the Formosan squirrel

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Abstract The Formosan squirrel, *Callosciurus erythraeus thaiwanensis*, emitted different vocalizations in response to terrestrial and aerial predators and snakes. Each vocalization caused nearby individuals to adopt a different type of anti-predator behaviour. In mating bouts, males produced two types of loud calls: precopulatory calls, emitted before copulations, and postcopulatory calls, emitted after copulations. The latter continued for 17 min on average. The estrous female and other males attending the mating bouts stopped moving during the postcopulatory call, so that the calling male was able to tend the female without interruption. The sound characteristics of anti-terrestrial-predator and postcopulatory calls recorded in the captivity were compared, and none of the ten characters of duration and frequency measured differed between the two calls. Playback experiments also showed that responses to the sounds in two different contexts, escape behaviour and defensive immobility, did not differ. The similarity between anti-predator and postcopulatory calls is discussed with reference to the possibility of manipulation and other explanatory hypotheses.

Key words Squirrel · Postcopulatory call
Alarm call · Manipulation

Introduction

Discrimination of sounds directed to different situations and targets is important for social animals. Some species, in fact, use sounds with different acoustic structures corresponding to the target, for example, warning calls toward different predator species in the vervet monkey (Seyfarth et al. 1980). Nonetheless, in some cases, sounds which appear similar to the human ear are used in different contexts. For example, sounds evoked by predators were also produced in agonistic social interactions among conspecifics in ground-dwelling squirrels (Balph and Balph 1966; Smith et al. 1977; Owings and Hennessy 1984).

Four hypotheses have been presented to explain the similarity of sounds produced in different contexts. According to Smith (1991), multiple targeting might be a regular feature in communication, and animals may use signals with multiple functions. He emphasized the importance of contextual information for recipients in assessing the message of signals. Even when the caller uses the same signals, recipients identify the appropriate message by assessing the circumstances (hypothesis 1). This hypothesis would be supported if the sounds induced different reactions in recipients in different contexts.

The second hypothesis is that animals can distinguish the sounds by differences in sound characteristics, even though they appear similar to humans (hypothesis 2). In such cases, detailed analyses of sound structures will show the existence of differences between similar sounds produced in different contexts (Leger et al. 1980, 1984; Owings and Leger 1980).

Similarity of sounds produced in different contexts has also been explained by the manipulation hypothesis (hypothesis 3) proposed by Dawkins and Krebs (1978). For example, the alarm calls for predators were given deceptively in feeding situations in order to monopolize food by avian species and by the arctic fox

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(Matsuoka1980; Munn 1986; Rüppell 1986; Møller 1988). Food calls were also used by the male domestic fowl to attract the female in situations without food (Gyger and Marler 1988). According to the manipulation hypothesis, the audience cannot use the sound characteristics and/or the circumstances to discriminate between the signals in the two different contexts. Thus, animals will react similarly towards the sounds recorded in different contexts.

A fourth hypothesis is also a possible explanation when animals show the same reaction towards similar sounds produced in different contexts. Animals may in fact receive different messages from the same sounds from the different contexts, but they may react similarly in some cases. For example, the female domestic fowl may already know of the absence of food, but she approaches the male to mate (Gyger and Marler 1988). In this case, the sounds which may originally have been produced for deception have already lost their deceptive function, but encode a new "honest" message. The existence of individual differences in calling behaviour and sound characteristics would be important to support this hypothesis.

Here I examined the similarity of the sound produced in the anti-predator and mating calls in the Formosan squirrel, *Callosciurus erythraeus thaiwanensis*, and try to distinguish among the four hypotheses. First, I described the sounds produced in the field when squirrels encountered various predators and during attended mating bouts. Next, the alarm and mating calls were recorded in captivity and the acoustical structures were compared. Playback experiments were conducted to examine the possibility that squirrels discriminate the signals between the alarm and mating calls. The aim of these investigations was to determine whether or not squirrels manipulate competitors by signalling deceptively.

Materials and methods

Field observation

The Formosan squirrel, *Callosciurus erythraeus thaiwanensis*, of southern Formosa (Chu and Yie 1970) was introduced to Izu-ohshima island, Tokyo Prefecture, Japan in 1933 (Udagawa 1954). Some squirrels were transferred from Izu-ohshima to other parts of Japan, for example, Enoshima island and Kamakura, Kanagawa Prefecture. Subsequently, the squirrels have reproduced in the wild on several islands and in coastal areas of central to southern Japan since about 40 years ago.

The 7-ha study area was located in the woods of Kamakura City. From October 1982 to March 1988, I patrolled census routes of 2.3 km on 2 or 3 days per week at four times each day: at dawn, in the morning (c. 10:00 a.m.), in the afternoon (c. 15:00 p.m.), and at dusk. Squirrels were captured by live traps set in a 3-ha trapping area in the centre of the census area. A stainless steel collar with one or two plastic rings of various colour combinations was attached to each squirrel for individual identification. Body weight, sex, and maturity were recorded each time that squirrels were captured. Further information on the study site and trapping methods is available in Tamura et al. (1988, 1989).

When I encountered a squirrel along the census routes, individual identification, location, time, and behaviour were recorded. When vocalizations were detected, I recorded the location and behaviour of the caller, the target of calling, the total duration of calling, and the reactions of neighbouring squirrels. Each observation started from the moment I first saw the squirrel and continued until I lost sight of it. On the day of estrus, several males assembled near the female and began calling and chasing early in the morning, as reported in other species of tree squirrels (Farentinos 1972; Thompson 1977; Koford 1982; Koprowski 1993a, b), so I was able to detect the mating bouts. If I found a mating bout in the morning, the entire bout was observed and the following points were recorded: identity of males that tended the estrous female, whether or not he vocalized, how long he continued calling, and how many males copulated with the female. Tending behaviour was defined as one male chasing other males away from a female and remaining with her to copulate.

Recording of vocalizations in captivity

Three adult females and four adult males were captured from a population on Izu-oshima Island, Tokyo, central Japan in May 1988, and kept in an outdoor cage (6 × 6 × 3 m high) on the campus of Tokyo Metropolitan University. Each individual was marked by a different pattern of trimmed hair on the tail. Sunflower seeds and water were available ad libitum, and peanuts, bananas and other kinds of fruit were also given.

A total 256 h of observation was conducted from 12 October 1988 to 9 January 1990. I recorded all behaviours during the 1-h observation period each day from a shelter 2 m from the cage. When the squirrels vocalized, the position and behaviour of the caller, the target of calling, the total duration of calling, and the reactions of other individuals in the cage were noted. Females (A, B, C) were checked for vaginal swelling, indicating estrus. All males (Bo, An, Ci, Kb) had mature reproductive organs (scrotum length >25 mm; T'sui et al. 1982). On the day of mating, I started observation at sunrise and continued until the estrous female entered the nest box.

Recording was conducted from the shelter using a cassette tape recorder (Sony TC-D5M) and a directional condensor microphone (Victor MU-5100). Recordings were analysed using a Kay DSP Sonagraph Model 5500, covering a frequency range of 0–16000 Hz. I selected 20 notes for every 2 min in each calling bout for acoustic analysis. Indistinct notes were omitted from the analyses.

Playback experiments

The postcopulatory calls of three males in the cage and the alarm calls of two females and one male in the cage were used for playback experiments. For comparison, white noise with the same amplitude as the playback calls (about 80 dB at 5 m from the sound origin) were prepared. Each of the recorded sounds was played back to free-living squirrels in Kamakura. The speaker was located at 5 m from an artificial feeding stand established in the centre of the 7-ha study area. At least 15 different individuals used the feeding stand, and the maximum number of squirrels observed at one time near the feeding stand was nine (Tamura et al. 1988). The feeding stand was 1 m in height and surrounded by several large trees (*Castanopsis cuspidata*, *Camellia japonica*, *Hovenia dulcis*, and *Cryptomeria japonica*) clustered into a stand (10 × 10 m) separated from surrounding forests. All the squirrels in the stand were observed 15 m from the feeding stand using 7.5 × binoculars. The duration of playback was 3, 5, and 10 min for each type of sound. Trials were repeated up to four times per day and the interval between experiments was more than 1 h to prevent habituation.

Results

Vocalization toward predators

Interactions between feral cats and squirrels were observed 96 times in Kamakura. On 9 occasions, cats attacked squirrels, but a successful attack occurred only once. In 79 cases, the cat used a sit-and-wait tactic. When squirrels detected hidden cats, they climbed trees to escape the cat, and at that time produced repetitive alarm calls in 77 cases (Fig. 1a, b). Squirrels did not produce such alarm calls when the cat was trotting or eating (6 cases). The alarm calls was audible from about 100 m away from the source. Calls continued for 7.3 min on average (n = 77, range 2–20). This type of call was also produced toward humans (4 cases), dogs (3 cases), and terrestrial birds, *Bambuscicola thoracica* (1 case), which were probably due to mistakes in recognising the species. The calling, in such cases, terminated within 2 min. In response to the calls, other squirrels escaped from the ground to the trees, and then stopped moving until the calls terminated.

Squirrels were frightened by large flying birds, such as *Milvus migrans* (7 times), *Corvus levaillantii* (7 times), and *Garrulus glandarius* (1 time). The squirrels that noticed an approaching large bird produced a single-note alarm call different from the sound produced in response to cats (Fig. 1c).

Snakes, especially the species known to climb trees, such as *Elaphe climacophora*, were also potential predators of young squirrels. Although I did not observe predation by snakes, 36 cases of snake-directed mobbing by squirrels were observed. When squirrels encountered a snake in a tree, they produced screams (Fig. 1d) which were audible from at least 100 m. When neighbouring squirrels heard the calls, some of them congregated near the source of the call and started mobbing in a group (Tamura 1989).

Vocalization in mating bouts

Detailed behaviour in mating bouts was summarized in Tamura et al. (1988) based on 19 mating bouts observed from 1982 to 1985. The following description is based on 28 mating bouts (19 bouts in 1982–1985 and 9 bouts of 1986–1988) observed in Kamakura. In the early morning of the day of mating 9–17 neighbouring males assembled near the home range of the estrous female. Two or three dominant males chased each other while following the female at the start of mating bouts. After chasing, the most dominant male tended the female for 29.4 min ± 13.5 SD (n = 28) during which he copulated 1–4 times. After he left the female, the next most dominant male tended and copulated. The replacements of tending males occurred in accordance with the dominance order, but the tending duration did not differ with order of tending (F = 1.09, df = 10, 224, $P > 0.05$ by ANOVA). The mating bouts terminated in the afternoon. The average duration of total mating bouts was 8.5 ± 1.0 h (n = 28). As a result, the female mated with 7.9 ± 2.0 (n = 28) different males.

Males produced two types of loud calls during mating. While waiting for the opportunity to tend, lower-ranking males repeatedly gave specific calls consisting

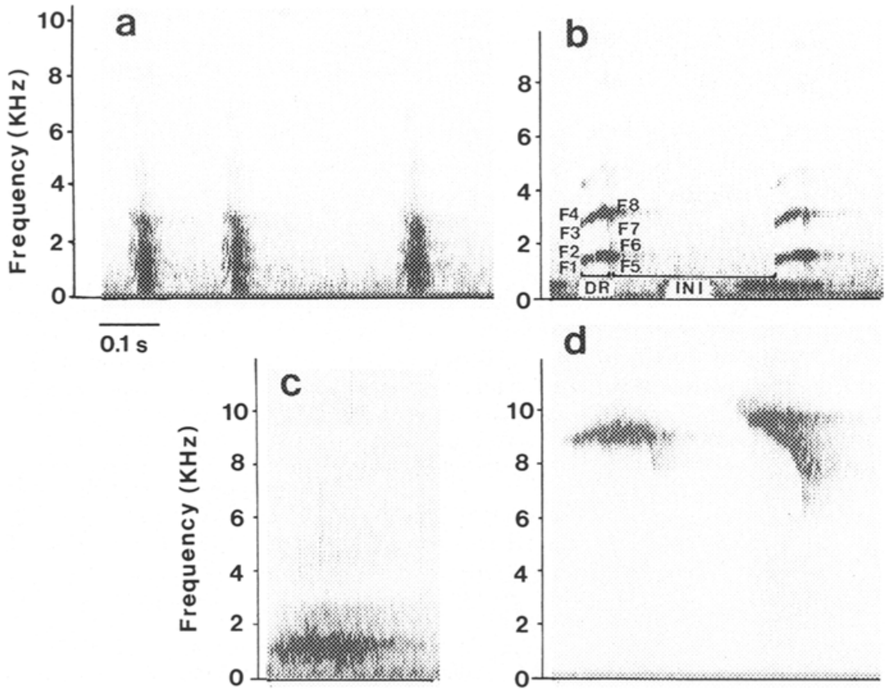

Fig. 1 Sonagraphs of the anit-predator calls: the continuous barking at terrestrial predators in **a** the starting phase and **b** the main phase, **c** the single bark at aerial predators, and **d** the screams at snakes. *Scales* are all the same (abbreviations: *INI* internote interval, *DR* duration of note, *F1* lowest frequency of basic note at starting, *F2* highest frequency of basic note at starting, *F3* lowest frequency of 1st harmonic at starting, *F4* highest frequency of 1st harmonic at starting, *F5* lowest frequency of basic note at ending, *F6* highest frequency of basic note at ending, *F7* lowest frequency of 1st harmonic at ending, *F8* highest frequency of 1st harmonic at ending

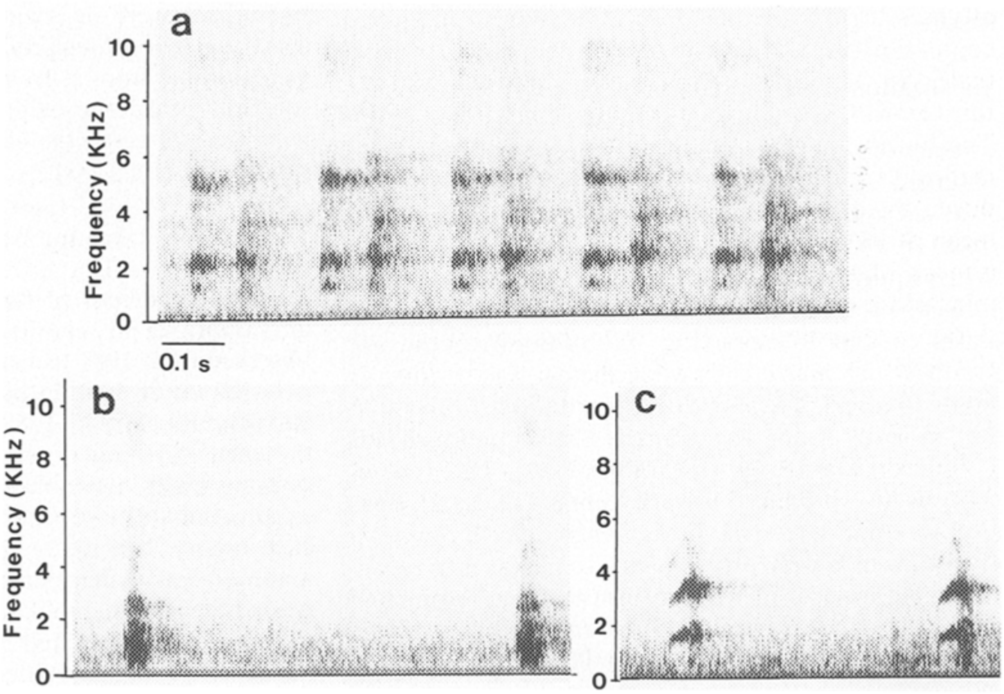

Fig. 2 Sonagraphs of the mating calls: **a** the precopulatory calls, **b** the postcopulatory calls in the starting phase, and **c** in the main phase. *Scales* are all the same

of two to eight notes (Fig. 2a). This call was audible from 50 m. As males who assembled to the mating bouts called frequently near the female home range, I easily found the site of mating bouts during the morning census. Once the male had started to tend the female, he occasionally followed the female giving small nasal sounds. After copulations, however, he suddenly barked loudly (Fig. 2b, c) and continued for 17.0 ± 10.0 min ($n = 130$, range 1–51 min). This sound was audible from more than 100 m. Of 238 males who tended the estrous female, 193 males (81%) produced the loud barking after copulations, 19 males (8%) did not, and for 26 males (11%) the result was unknown.

Recording of vocalizations in captivity

Alarm calls at feral cats and postcopulatory calls sounded similar to the human ear, and the responses of squirrels toward the calls were also similar in the field. To ascertain how similar the sound characteristics were for the calls produced in two different contexts, I recorded both sounds in captive individuals.

I observed warning behaviour and vocalizations on 42 occasions in the cage; 39 were directed at feral cats, 1 at a group of crows and 2 at snakes. Sounds and reactions to these predators were similar to responses in natural conditions. The repetitive alarm calls (Fig. 1a, b) were solely produced in response to feral cats. The first squirrel that located the cats wandering around the cage produced the alarm call. The mean duration of calling was 7.0 ± 4.1 min. All other squirrels in the cage climbed trees or high places and stopped moving during the call. The duration of immobility was strictly related to the duration of calling ($y = 1.03x + 0.02$, $r^2 = 0.99$, $r = 0.99$, $n = 39$, $P < 0.01$). Ten bouts of 39 alarm calls by three females and two males were recorded in their entirety.

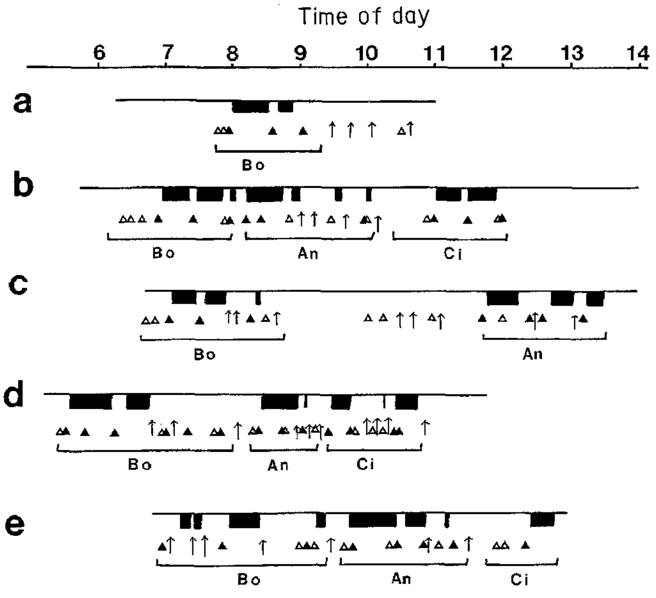

Fig. 3 Tending sequences of five mating bouts: **a**, **c** by female A, **b**, **d** by female B, and **e** by female C (abbreviations: *letters* identification of the male tending the female, *horizontal brackets* tending duration, *open triangles* mountings, *filled triangles* copulations, *arrows* chasing among males, *black bars* duration of the postcopulatory calls

A total of five mating bouts were observed, twice involving female A, twice involving female B, and once involving female C. Figure 3 shows the sequences in which males tended the female in each mating bout. In all cases, male Bo first tended the female and attempted copulation several times. In four mating bouts, the next male, An, tended the female and copulated, and the third male, Ci, also tended the female in three of them. The fourth male, Kd, did not tend the female in any mating bout. After copulations, the males usually produced the postcopulatory calls for 1–31 min, with a mean of 13.6 ± 8.8 min ($n = 14$) for Bo, 1–35 min with a mean of 14.9 ± 12.0 min ($n = 12$) for An, and 1–22 min with a mean of 15.2 ± 6.8 min ($n = 6$) for Ci. The duration of postcopulatory calls did not differ with the order of males ($F = 0.07$, $df = 2, 29$, $P > 0.05$ by ANOVA). The call was not produced after only 4 of 18 copulations (22.2%) by Bo, 2 of 14 copulations (14.3%) by An, and 2 of 8 copulations (25.0%) by Ci. The mean tending duration was 110.0 ± 27.0 min ($n = 5$) by Bo, 98.0 ± 17.0 min ($n = 4$) by An, and 66.0 ± 8.7 min ($n = 3$) by Ci.

The female and males that were not calling stopped moving during the postcopulatory calls. The duration of immobility was strongly related to the duration of postcopulatory calls ($y = 1.02x + 0.51$, $r^2 = 0.98$, $r = 0.99$, $n = 72$, $P < 0.01$). Eleven series of postcopulatory calls delivered by three males (Bo, An, and Ci) were recorded during the mating bouts of the female A, B, and C.

Analysis of sound characteristics

The total duration of ten bouts of alarm calls directed to cats recorded in captivity was 4.8 ± 3.2 min and that of 11 bouts of the postcopulatory call was 6.9 ± 4.3 min. The total duration was not significantly different between the two calls ($t = 1.26$, $df = 19$, $P > 0.05$). Both calls consisted of two types of sounds: type 1 were noisy sounds with a broad frequency range (Figs. 1a, 2b), and type 2 were harmonic sounds (Figs. 1b, 2c). All calls started with sound type 1, but changed to sound type 2 after 2.8 ± 1.5 min ($n = 8$) in alarm calls and 3.6 ± 2.5 min ($n = 11$) in postcopulatory calls. The time when sounds changed to type 2 was not significantly different between the two calls ($t = 0.91$, $df = 17$, $P > 0.05$). However, two alarm calls continued for less than 2 min and were constructed only of sound type 1 until the last note.

Before comparing the sound characteristics of the alarm and the postcopulatory calls, I examined whether or not the sound characteristics changed with the duration of calling. The values of internote interval (INI), note duration (DR) and F1–F8 (constituent frequencies, Fig. 1) were compared among starting notes, notes at 2 min, 4 min, 6 min, 8 min, 10 min, and 12 min after calling in the alarm and the postcopulatory calls, respectively. INI and DR changed with time, while F1–F8 did not differ significantly with time either in the alarm or the postcopulatory calls (ANOVA: Table 1). Thus, the values of F1–F8 recorded in different time series was accumulated in the following analysis, while INI and DR have to be analysed separately in each time series. I chose two series for analysis of INI and DR; one was the starting notes (type 1 sounds) and the other was the notes just after changing to type 2 sounds. The results are summarized in Table 1.

Discriminant analysis of F1–F8 showed that the alarm calls and the postcopulatory calls did not differ significantly (Mahalanobis $D^2 = 0.33$; correct discrimination rate was 0.66 for the alarm calls and 0.59 for the postcopulatory calls). INI did not differ significantly between the two calls either in the starting ($t = 0.97$, $P > 0.05$) or the changing phases (Welch's $t = 1.54$, $P > 0.05$). DR also did not differ significantly in the starting ($t = 0.96$, $P > 0.05$) or the changing phases (Welch's $t = 1.76$, $P > 0.05$).

Table 1 Statistical analysis (ANOVA) of the change in sound characteristics with time of calling, and the mean ± SD (number of notes measured) of ten variables of sound characteristics in the alarm and the postcopulatory calls (*INI* internote interval, *DR* duration of note, *F1* lowest frequency of basic note at start, *F2* highest frequency of basic note at start, *F3* lowest frequency of 1st harmonic at start, *F4* highest frequency of first harmonic at start, *F5* lowest frequency of basic note at end, *F6* highest frequency of basic note at end, *F7* lowest frequency of 1st harmonic at end, *F8* highest frequency of 1st harmonic at end)

Variables	ANOVA		Variables	Mean ± SD (n)	
	Alarm calls	Postcopulatory calls		Alarm calls	Postcopulatory calls
INI	$F = 7.37$ ($df = 5,27$)**	$F = 2.46$ ($df = 6,42$)**	INI start (s)	0.88 ± 0.45 (181)	0.84 ± 0.45 (189)
			change (s)	0.74 ± 0.18 (159)	0.78 ± 0.33 (187)
DR	$F = 2.84$ ($df = 5,27$)**	$F = 6.00$ ($df = 6,31$)**	DR start (ms)	124.9 ± 29.50 (75)	120.7 ± 30.9 (130)
			change (ms)	44.9 ± 28.0 (126)	40.2 ± 15.0 (220)
F1	$F = 1.79$ ($df = 4,19$)	$F = 2.00$ ($df = 5,23$)	F1 (kHz)	0.92 ± 0.01 (290)	0.97 ± 0.04 (530)
F2	$F = 2.59$ ($df = 4,15$)	$F = 1.73$ ($df = 5,23$)	F2 (kHz)	1.40 ± 0.01 (290)	1.45 ± 0.04 (530)
F3	$F = 0.26$ ($df = 4,15$)	$F = 1.37$ ($df = 5,21$)	F3 (kHz)	2.10 ± 0.07 (290)	2.19 ± 0.20 (530)
F4	$F = 0.33$ ($df = 4,15$)	$F = 0.97$ ($df = 5,22$)	F4 (kHz)	2.58 ± 0.07 (290)	2.69 ± 0.18 (530)
F5	$F = 0.48$ ($df = 4,14$)	$F = 1.72$ ($df = 5,22$)	F5 (kHz)	1.29 ± 0.01 (290)	1.29 ± 0.03 (530)
F6	$F = 0.22$ ($df = 4,14$)	$F = 2.38$ ($df = 5,23$)	F6 (kHz)	1.76 ± 0.02 (290)	1.78 ± 0.02 (530)
F7	$F = 0.33$ ($df = 4,13$)	$F = 2.00$ ($df = 5,22$)	F7 (kHz)	2.72 ± 0.04 (290)	2.78 ± 0.07 (530)
F8	$F = 0.44$ ($df = 4,13$)	$F = 2.37$ ($df = 5,22$)	F8 (kHz)	3.22 ± 0.05 (290)	3.30 ± 0.07 (530)

**$P < 0 .01$

Table 2 Correct discrimination rates by the discriminant analysis using F1–F8 (see Table 1). The number of notes measured for each individual is shown in parentheses. Females A, B, C, and males An, Bo, Ci are the names of individual squirrels

	Squirrel identification					
	Female A	Female B	Female C	Male Bo	Male An	Male Ci
Female A (185)	–	0.83	0.91	0.91	0.87	0.93
Female B (37)	0.78	–	0.87	0.81	0.81	0.89
Female C (28)	0.89	0.82	–	0.89	0.89	0.96
Male Bo (280)	0.86	0.78	0.81	–	0.98	0.98
Male An (190)	0.73	0.87	0.92	0.86	–	0.83
Male Ci (100)	0.80	1.00	1.00	1.00	0.80	–

Table 3 The t-value (equal variance) and Welch's t-value (unequal variance) of INI and DR between pairs of individuals; *df* in parentheses

			Female A	Female B	Female C	Male Bo	Male An	Male Ci
Female A	INI	start		3.87** (96)	6.47** (96)	6.16** (113)	4.27** (156)	11.66** (80)
		change		6.65** (98)	9.56** (98)	16.42** (138)	0.54 (158)	4.79** (84)
	DR	start		2.73** (76)	2.28* (89)	2.18* (69)	0.40 (107)	1.96 (58)
		change		7.30** (88)	3.01** (94)	4.74** (158)	4.69** (158)	0.35 (98)
Female B	INI	start			4.23** (78)	8.58** (95)	1.05 (138)	14.46** (62)
		change			2.05* (78)	9.94** (118)	8.20** (138)	2.69** (64)
	DR	start			3.83** (65)	1.78 (45)	2.41* (76)	3.86** (34)
		change			8.96** (64)	8.99** (128)	8.69** (128)	9.44** (68)
Female C	INI	start				9.92** (95)	2.47* (138)	15.92** (62)
		change				9.05** (118)	14.5* * (138)	2.08* (64)
	DR	start				4.26** (58)	2.41* (96)	0.85 (47)
		change				3.60** (134)	3.36** (134)	3.42** (74)
Male Bo	INI	start					8.73** (155)	2.84** (79)
		change					18.77** (178)	1.20 (104)
	DR	start					1.42 (76)	4.34** (27)
		change					0.08 (198)	5.90** (138)
Male An	INI	start						16.16** (122)
		change						4.97** (124)
	DR	start						1.65 (65)
		change						5.83** (138)

*$P < 0.05$, **$P < 0.01$

The individual differences in F1–F8 were examined by discriminant analysis (Table 2). Individuals were well assigned, but sexual differences were not apparent. INI and DR were also compared among individuals (Table 3). For INI, 14 out of 15 pairs of individuals differed significantly in the starting phase and 13 in the changing phase. For DR, 9 to 15 pairs of individuals differed significantly in the starting phase and 13 in the changing phase. Although individual differences in sound characteristics were detected, no characteristics were related to the dominance order of the three males (Table 4).

Playback experiments

Before the experiments, squirrels were searching for and eating food on and around the feeding stand. Because the feeding stand was small and occupied by

Table 4 The mean (± SD) value of sound characteristics of the three males in captivity

Variables		Bo	An	Ci
F1 (kHz)		0.80 ± 0.13	1.14 ± 0.14	1.05 ± 0.08
F2 (kHz)		1.27 ± 0.13	1.62 ± 0.14	1.58 ± 0.07
F3 (kHz)		1.79 ± 0.23	2.51 ± 0.33	2.52 ± 0.12
F4 (kHz)		2.30 ± 0.21	2.99 ± 0.32	3.02 ± 0.13
F5 (kHz)		1.18 ± 0.15	1.39 ± 0.14	1.36 ± 0.09
F6 (kHz)		1.68 ± 0.13	1.87 ± 0.14	1.83 ± 0.10
F7 (kHz)		2.58 ± 0.21	2.94 ± 0.27	2.90 ± 0.17
F8 (kHz)		3.11 ± 0.24	3.45 ± 0.28	3.39 ± 0.19
INI (s)	start	1.25 ± 0.49	0.64 ± 0.22	1.49 ± 0.27
	change	1.14 ± 0.27	0.55 ± 0.09	1.02 ± 0.48
DR(ms)	start	115.3 ± 12.4	122.4 ± 32.1	140.6 ± 18.5
	change	36.9 ± 9.7	37.0 ± 10.4	56.9 ± 20.5

the dominant individual who chased the subordinates (Tamura et al. 1988), some squirrels were waiting in the trees near the feeding stand. All the squirrels near the feeding stand was able to see each others, movements. Before the experiments, 21.6%, 30.7% and 47.7% of a total of 88 squirrels were on the ground, the feeding stand, and in the trees, respectively (Table 5). The positions of squirrels before the experiments were not different among the playbacks of white noise, alarm calls, and postcopulatory calls ($\chi^2 = 6.39$, $P > 0.05$). Between one and five squirrels were near the feeding stand at once, and the mean number of squirrels examined at once did not differ among the three experiments ($F = 0.05$, $df = 2, 41$, $P > 0.05$ by ANOVA).

Squirrels glanced at the speaker when the sound of white noise was played back, but soon continued moving during the playback. They continued eating not only on the feeding stand but also on the ground. In contrast, when the playback of alarm and postcopulatory calls started, squirrels looked at the speaker, and individuals on the ground and on the feeding stand ran up the trees. Individuals on the tree also climbed up to a higher branch. These movements occurred within 1 s after the start of the playback, and squirrels then remained immobile in the trees until the playback sounds diminished.

The duration of immobility clearly increased with the duration of playback (Table 5), and the mean duration of the pause did not differ between the two calls within each experimental duration ($t = 0.96$ in 3 min, $t = 1.78$ in 5 min, and $t = 0.55$ in 10 min; all Ps > 0.05).

Soon after the experiment, the squirrels started moving one by one. Some individuals went back to the feeding stand and resumed feeding. Self-grooming or chasing behaviour also resumed on the trees. However, no squirrel went down on the ground for at least 10 min after the playback of the alarm and the postcopulatory calls.

Table 5 Responses induced by the playback sound and the duration of immobility

Call types	Duration of	No. squirrels		Position of squirrels			Duration of stop (min)
played back	playback	examined		Before exp.	During exp.	After exp.	mean ± SD, range
White noise	3 min	8	ground	2	3	3	–
			feeding stand	2	1	1	
			tree	4	4	4	
	5 min	5	ground	1	2	1	–
			feeding stand	2	2	3	
			tree	2	1	1	
	10 min	7	ground	2	2	0	–
			feeding stand	2	5	6	
			tree	3	0	1	
Alarm call	3 min	10	ground	2	0	0	4.35 ± 1.31, 3.0–7.0
			feeding stand	3	1	2	
			tree	5	9	8	
	5 min	12	ground	3	0	0	5.83 ± 0.65, 5.0–7.0
			feeding stand	3	0	7	
			tree	6	12	5	
	10 min	11	ground	6	0	0	12.18 ± 1.25, 10.0–14.0
			feeding stand	3	0	5	
			tree	2	11	6	
Postcopulatory call	3 min	11	ground	0	0	0	5.05 ± 1.94, 3.0–8.0
			feeding stand	3	0	4	
			tree	8	11	7	
	5 min	12	ground	2	0	0	6.58 ± 1.31, 5.5–10.0
			feeding stand	5	0	9	
			tree	5	12	3	
	10 min	12	ground	1	0	0	12.47 ± 1.27, 11.0–15.5
			feeding stand	4	0	5	
			tree	7	12	7	

Discussion

The Formosan squirrels produced predator-specific alarm calls toward terrestrial and aerial predators and snakes, as reported for the vervet monkey (Seyfarth et al. 1980), ground-dwelling Sciuridae (Balph and Balph 1966; Melchior 1971; Owings and Virginia 1978; Owings and Leger 1980; Halpin 1983; Davis 1984) and other species of *Callosciurus* in Malaysia (Tamura and Yong 1993). Neighbouring individuals adopted different movements toward each signal, and the reaction seemed suitable for escape from the various predators.

Among the three types of calls, only the sound directed to anti-terrestrial predators was repeatedly emitted for several minutes. Loughry and McDonough (1988) tested the effect of a long call, constructed by repeating of the same sound, and concluded that results supported the tonic information hypothesis. That is, the repetitive calling functions to maintain vigilance behaviour in perceivers and thus produces lookouts in case the predator should return or remain close by. This type of call would be advantageous for escaping from the sit-and-wait hunting tactic of the feral cats. At the start of repetitive calls, the sounds had a broad frequency range with a long note duration (type 1 in Results). As this type of sound is easily localized by the recipients (Marler 1955), it may be useful for conveying information to neighbouring squirrels about the location of predators. However, after about 3 min, the sound changed to harmonic structures (type 2 in Results). This type of sound propagates more widely than type 1 sounds with the same energy. Thus, the changing of sounds from type 1 to type 2 may save energy for the long bouts of calling. A similar example was reported in African tree squirrels with extended calling periods (Viljoen 1983).

During mating bouts, male Formosan squirrels gave two types of loud call. Vocal communication is often used in various contexts during mating by male and female sciurids (Smith 1968; Farentinos 1974; Callahan 1981; Lishak 1982; Viljoen 1983; Leger et al. 1984; Grady and Hoogland 1986; Blake and Gillett 1988; Sherman 1989; Tamura 1993). Sounds emitted by the female before mating attract neighbouring males, which will lead to male-male competition (Callahan 1981; Blake and Gillett 1988). Precopulatory calls by males may reduce the aggressiveness of the estrous female and increase receptivity of the female (Farentinos 1974). On the other hand, the functions of the postcopulatory call by males are so far uncertain. Grady and Hoogland (1986) examined the relationships of calling frequencies in the black-tailed prairie dog versus the number of competitor males, the order of copulation, and the number of young, but the results did not support any functional interpretation.

In the present study, the alarm calls in response to terrestrial predators were similar to the postcopulatory calls, and the similarity was examined in the light of the four hypotheses (Introduction). Behavioural observations in the field and captivity showed that squirrels reacted similarly to the alarm and postcopulatory calls; they remained immobile in trees during the calls. Such escape behaviours may be advantageous for call recipients in the anti-predator contexts, but not in mating situations. Thus, squirrels are unlikely to discriminate the two sounds by differences in the contexts (hypothesis 1).

Leger et al. (1984) tested the similarity between the sounds evoked by predators and those produced in mating in Belding's ground squirrels. They analysed the sound characteristics in detail and concluded that squirrels might be able to distinguish the two calls by differences in sound characteristics. In Belding's ground squirrels, the sound characteristics of trills were different in the alarm and the postcopulatory calls, but chirps given in the two situations had the same sound characteristics. In this study, however, the sound characteristics of the alarm and the postcopulatory calls did not differ significantly. Although some of the measurements were individually different, they could not be classified into the two groups by their contexts, the anit-predator and the mating bouts. Thus, hypothesis 2 is also rejected in this study.

Playback experiments also indicated that the squirrels did not discriminate the postcopulatory calls from the alarm calls. Do Formosan squirrels recognize the postcopulatory calls as the signal warning of predators even in mating situations? If the squirrels are really on the alert for predators during the postcopulatory calls, the manipulation hypothesis would be supported, and it could then be said that the postcopulatory call is deceptively emitted to prevent interruption by other males (hypothesis 3). Alternatively, the squirrels may already know that there is no predator, based on the context and their experience. The function of the postcopulatory calls in such cases may be that the caller advertises his energy in order to deter other males, and this signal may cause recipients to refrain from wasteful challenges. In this case the call is not manipulative, but it conveys new information as "honest advertisement" (hypothesis 4). If hypothesis 4 is true, the duration of calling might increase with the dominance order of males, and/or the sound characteristics should differ with the order of callers. However, since no characteristics of the sounds were related to the order of males in this study, the possibility of hypothesis 4 might be low. In conclusion, the similarity of the sounds between different contexts in the Formosan squirrel seems to be explained by manipulation (hypothesis 3).

What is the advantage to the callers of producing the alarm calls deceptively after mating? The adaptive explanation of the postcopulatory calls may be that they increase the probability of paternity of the caller. In thirteen-lined ground squirrels, delay of the second mating is an important factor in ensuring paternity of the first male (Schwagmeyer and Foltz 1990). Therefore, immobility of other males and then delay of consecutive copulation may increase probability of paternity of the caller in the Formosan squirrel. Furthermore, the male Formosan squirrels often remated several times during the tending period. The postcopulatory calls functioned to retain the female nearby and then increase the opportunity for multiple copulation. In promiscuous mating systems, these tactics will be advantageous in sperm competition. The males of other species of tree squirrels actively guard the female after copulation by chasing other males (Farentinos 1972; Thompson 1977; Benson 1980; Koford 1982; Koprowski 1993a, b), rather than by postcopulatory calls as in the Formosan squirrel. Such direct guarding by males was shown to extend the duration of tending and increase the opportunity for copulation.

Further studies will be necessary to know the effect of postcopulatory calling on probability of paternity in the Formosan squirrel, through paternity identification by biochemical analyses.

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