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GRADED AGGRESSIVE CALLS OF THE SPRING PEEPER, *PSEUDACRIS CRUCIFER*

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ABSTRACT: Broadcasts of synthetic advertisement and aggressive calls to male spring peepers, *Pseudacris crucifer*, demonstrated that aggressive call duration is not a static feature. Frogs increased call duration as well as the number and proportion of aggressive calls that they gave in response to increases in stimulus intensity. Increases in the duration of aggressive call stimuli, independent of changes in sound intensity, also elicited elevations in call duration and other measures of aggressive response. Data on calling effort indicate that males may be energetically constrained during bouts of vocal activity, and that aggressive calls are given at the expense of advertisement calls if a male's calling effort is near its upper limit. Use of graded aggressive calls may be a form of honest signalling, enabling males to advertise their own endurance and assess that of potential opponents.

Key words: Anura; *Pseudacris crucifer*; Communication; Aggressive calls

STUDIES of anuran communication have demonstrated that chorusing male frogs can display considerable flexibility in their use of vocalizations (Wells, 1988). Males may shift between advertisement and aggressive calls or even modify diphasic calls in response to changes in their acoustic and social milieu. Some species also appear to utilize graded signals, perhaps because such signalling enables them to make fine scale adjustments which influence the message of their calls (sensu Smith, 1977) during close range interactions. For example, the Central American treefrogs *Hyla ebraccata*, *H. microcephala*, and *H. phlebodes* increase the duration of aggressive call introductory notes while simultaneously dropping secondary notes as interacting males move closer together or when prerecorded calls are increased in playback intensity (Schwartz and Wells, 1984; 1985; Wells and Schwartz, 1984). Use of graded aggressive calls may also occur in other species of frogs (Arak, 1983; Littlejohn and Harrison, 1985; Pengilley, 1971), but because research specifically designed to test for it has been so limited, knowledge of the ubiquity and function of such signalling behavior is superficial at best. The use of graded calls probably has gone undetected, even in species for which there is considerable information from descriptive and empirical studies of vocal behavior.

The spring peeper, *Pseudacris crucifer* (Hedges, 1986), is a very abundant frog of the northeastern United States, and males form dense breeding choruses in the early spring. Males utilize a tone-like, slightly frequency modulated advertisement call; a trilled aggressive call is employed during close range male-male encounters. The communication system of *P. crucifer* has been studied by a number of workers over the past 25 yr (Brenowitz et al., 1984; Doherty and Gerhardt, 1984; Forester and Czarnowsky, 1985; Forester and Harrison, 1987; Jones and Brattstrom, 1961; Lemon and Struger, 1980; Rosen and Lemon, 1974; Schmidt, 1964; Schwartz, 1987*a*), but use of graded signals has not been reported. Rosen and Lemon (1974) reported that the aggressive calls of interacting males exhibit considerable variation in duration, but they did not indicate whether these changes in duration were correlated with any characteristic of the acoustic environment. While analyzing recordings that I made during a previous study of this species (Schwartz, 1987*a*), I noticed that males frequently gave longer aggressive calls to more intense synthetic advertisement calls. Moreover, aggressive call duration appeared to vary continuously. In the present study, I set out to examine this phenomenon in a systematic fashion using both advertisement and aggressive call stimuli.

Specifically, I wanted to know how stimulus call intensity influences the level of male aggressive response and to test the hypothesis that males could differentiate between aggressive calls differing solely in duration. Would males, for example, give longer aggressive calls in response to longer aggressive calls independent of stimulus intensity; that is, would they respond to graded signals with graded responses? If variation in aggressive call duration is important in the communication system of *P. crucifer*, receivers should, at least, be able to distinguish between calls selected from opposite extremes of the distribution of durations of natural aggressive calls (Green and Marler, 1979).

MATERIALS AND METHODS

Playback experiments with male *P. crucifer* were conducted at ponds near Storrs, Connecticut and in Rehoboth, Massachusetts from April through June of 1986 and 1987, respectively. Fieldwork was usually conducted between 2000 and 2230 h, because calling of individuals often ceased or dropped to low levels after 2200. Males establish calling sites on the ground or emergent vegetation, and if growth is not too dense, it is fairly easy to present acoustic stimuli and record vocal responses of frogs. Because choruses can be quite dense, it was often necessary to remove males calling near the test subject prior to experiments.

Experimental acoustic stimuli were generated by a portable frog call synthesizer constructed by the author (Schwartz, 1987*a*). Tone stimuli as well as pulsed calls could be created, and stimulus duration, pulse shape, rate of amplitude modulation, and frequency could be independently varied. This device was used, rather than a tape recorder-based stimulus presentation system, because it made possible the presentation of synthetic calls in a manner which mimicked the timing of natural calls (see Narins, 1982, for a field study which also employed a frog call synthesizer). Male *P. crucifer* in choruses alternate calls with neighboring conspecifics, so the closest individuals rarely exhibit acoustic interference, nor do they differ much in their calling rates (Rosen and Lemon, 1974). The frog call synthesizer was designed so that it could be set to be triggered by the onset of a frog's call after an adjustable preset time delay and thus "behave" like a real animal interacting with the experimental subject.

At the field sites, the output of the synthesizer was amplified and recorded with a Marantz PMD 360 stereo cassette tape recorder. Calls were broadcast at a distance of 1 m to males from a University 4401 horn speaker mounted on wooden baffles. The output of this speaker is essentially flat (±3 dB) over the frequency range of 1.1–14.5 kHz. Response calls of males were taped on the second channel of the tape recorder using a Realistic 33-1062 directional microphone. The output of the microphone was split using a Y-cord so that it could also be used to trigger the synthesizer. Prior to conducting the playbacks, the settings on the synthesizer were calibrated using both a Tektronix 5111 storage oscilloscope and a Unsican Model 4500 real-time spectrum analyzer. During the field season, frequent checks were made on the synthesizer output to determine if frequency, pulse rate, or duration had shifted from values obtained during the initial calibration. Because values did not change, recalibration was unnecessary. Sound intensities were pre-calibrated with either a calibrated Gen Rad 1982 or Bruel and Kjaer 2230 precision sound level meter equipped with a random incidence microphone. Measurements were made with the meter set for flat weighting and peak SPL (sound pressure level; dB re 20 μPa) at a distance of 1 m in a room lined with anechoic wedges. During experiments, stimulus broadcasts were made to frogs unobstructed by vegetation. Sound intensities, periodically checked in the field at the calling site of subjects, were found to be within 2 dB of the pre-calibrated values.

Experimental stimuli were synthetic advertisement and aggressive calls of 2880 Hz designed to correspond closely to the natural calls of *P. crucifer*. Advertisement calls were unmodulated tones and aggressive calls were pulsed signals (Fig. 1). Because call duration and pulse rate are func-

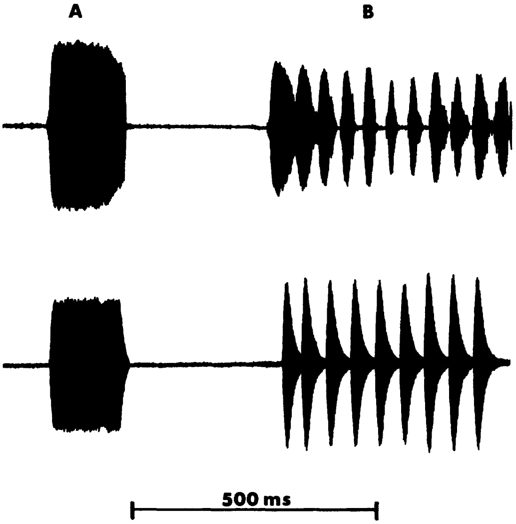

FIG. 1.—Oscillograms of natural calls (above) and synthetic stimuli (below) presented to males of *P. crucifer*. (A) An advertisement call; (B) an aggressive call. Natural calls were recorded at 9 C.

TABLE 1.—Parameters of synthetic advertisement (ADV) and aggressive (AGG) call stimuli broadcast to male *P. crucifer*. Values shown were used at or near 10 C. Durations of aggressive calls were chosen to encompass the range of durations that I had found in calls recorded during a previous experiment.

	Pulses/s	Duration (ms)			Frequency (Hz)
		Short	Medium	Long	
ADV	—	—	144	—	2880
AGG	22	223	440	648	2880

tions of temperature in this species (Lemon and Struger, 1980), these parameters were adjusted according to pre-calculated regression equations after air temperature adjacent to the subject was measured. Values of pulse rate and duration used are shown for 10 C in Table 1. Three experiments were conducted. In experiment 1, advertisement calls were presented at intensities of 90, 95, 100, and 105 dB SPL (dB re 20 μPa). For a male on the ground calling at a realistic intensity of 85 dB SPL at a distance of 100 cm, these stimulus intensities correspond to intermale distances of approximately 59, 35, 21, and 12 cm as calculated from Brenowitz et al. (1984). In experiment 2, medium duration aggressive calls (Table 1) were presented at these same intensities. In experiment 3, aggressive calls of short, medium, and long duration were presented at an identical peak intensity. This was 100 dB SPL for all but three animals for which 105 dB SPL stimuli were used. The order in which experiments were conducted and aggressive call stimuli presented in experiment 3 was determined using a table of random numbers. It was not possible to complete the entire series of experiments for every subject because call rates and response levels often dropped to low levels later in the evening. This was the major reason why two seasons were required to acquire an adequate sample size to complete the study. Prior to presentations, all frogs were recorded for a 2-min no-stimulus period to determine baseline levels of aggressive calling. Each stimulus type was presented for 2 min. Between playback level changes and experimental shifts, I waited 2 min or until a frog had returned to his pre-stimulus pattern of calling.

The number, proportion, and duration of aggressive calls given by each male to the different stimulus treatments were determined using a Commodore Amiga 1000 computer equipped with an Applied Visions FutureSound (TM) audio digitizer and accompanying software. Recordings were digitized at 10 kHz and call duration measured to the nearest 1 ms. Data obtained from different males were not pooled during statistical analyses, because temperature effects could render such tests meaningless. Rather, data were analyzed using the Friedman test and Wilcoxon signed rank test (Noether, 1976). Because frogs that gave no aggressive calls during any treatment in an experiment were not included in tests for stimulus effects on call duration, sample sizes are considerably lower in such tests than in those evaluating effects on number and proportion of aggressive calls.

RESULTS

Advertisement call intensity had a significant effect on the number of aggressive call responses (Friedman test; $Q = 28.5$, $P < 0.01$, $n = 17$ males), the proportion of aggressive calls ($Q = 27.4$, $P < 0.01$, $n = 17$), and their average duration ($Q = 16.3$, $P < 0.01$, $n = 8$). With increasing intensity, males gave numerically (Fig. 2A) and proportionately (Fig. 2B) more aggressive calls as well as longer aggressive calls (Fig. 2A, Table 2). Intensity also had a significant effect on these response measures when aggressive calls were used as stimuli (number: $Q = 15.9$, $P < 0.01$, $n = 13$; proportion: $Q = 19.6$, $P < 0.01$, $n = 13$; duration: $Q = 10.6$, $P < 0.025$, $n = 6$); however, there was not a consistent rise in either number or average duration of aggressive calls with intensity (Fig. 3, Table 3). Seven of 13 males gave fewer aggressive calls at 95 than at 90 dB SPL and four of six males gave shorter calls at 105 than at 100 dB SPL. Duration of aggressive call stimuli had a significant effect on number ($Q = 14.8$, $P < 0.01$, $n = 18$) and proportion ($Q = 15.8$, $P < 0.01$, $n = 18$) of aggressive calls and aggressive call duration ($Q = 13.8$, $P < 0.01$, $n = 11$). For all three measures, the most dramatic response differences occurred between the short and medium duration stimulus (Fig. 4, Table 4). Responses to the long and medium duration calls did not differ significantly at an overall $P = 0.20$ (nonparametric multiple comparisons: Noether, 1976). I also compared responses to advertisement calls with responses to aggressive calls at the same intensity. Males gave significantly longer and significantly more aggressive calls to the medium and long duration aggressive calls than to advertisement calls at 100 dB (Wilcoxon signed rank test; $P < 0.05$). At 90 dB, they also gave longer aggressive calls to the medium duration aggressive call; however, at 105 dB they did not do so.

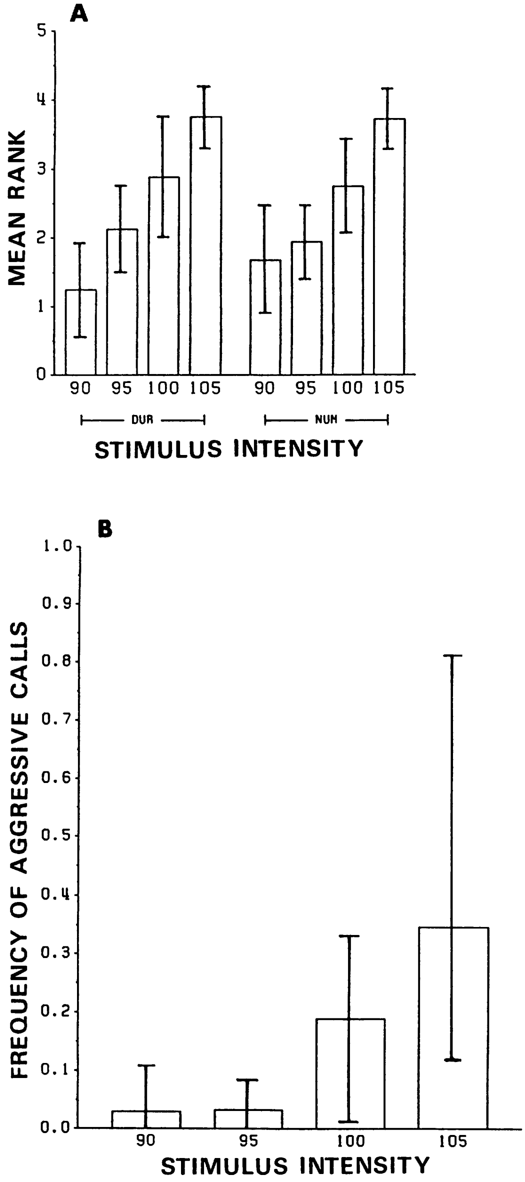

FIG. 2.—Responses to advertisement calls presented at four intensities. (A) The average aggressive call duration and number of aggressive calls given by each male were ranked by stimulus intensity. Bars show the mean ranks ± 1 SE. (B) Proportion of aggressive calls. Data presented as medians and approximate 95% C.I.

DISCUSSION

The results of the playback experiments demonstrate that male *P. crucifer* employ an aggressive call which is graded in duration, and the stimulus treatments did produce significant effects on this call feature. On average, the increases in duration were not great; in experiment 3, most males exhibited increases of <30%. Some males did show substantial changes, however. For example, for frog 24, the increase in average call duration from short to long stimulus was 77%. In response to increases in stimulus intensity, most increases in av-

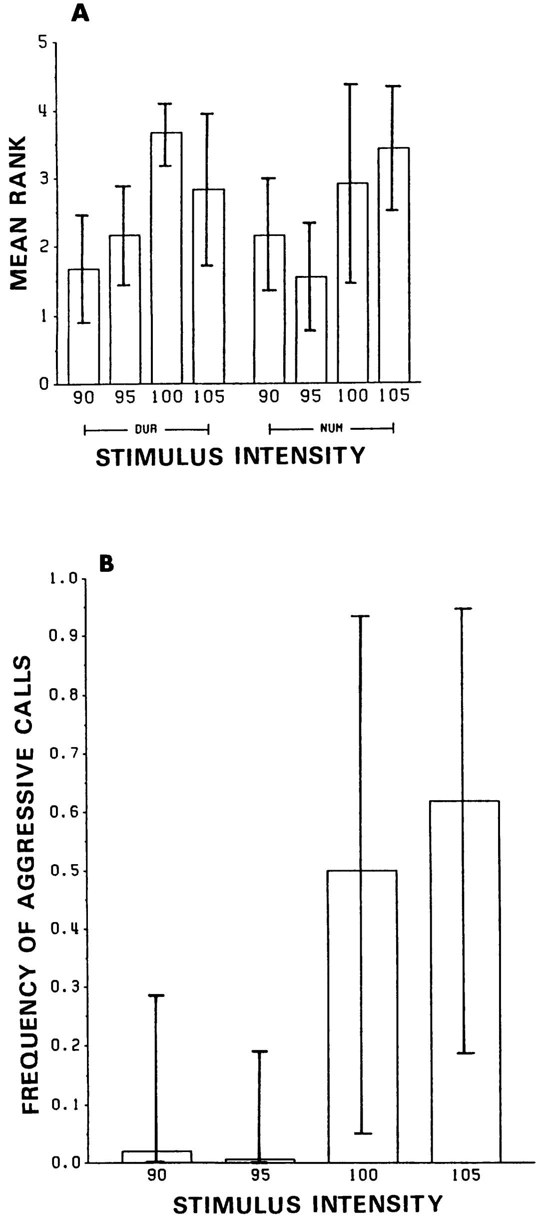

FIG. 3.—Responses to medium duration aggressive calls presented at four intensities. (A) Ranks of average aggressive call duration and number of aggressive calls given by each male. Data presented as means ± 1 SE. (B) Frequency of aggressive calls. Data presented as medians and approximate 95% C.I.

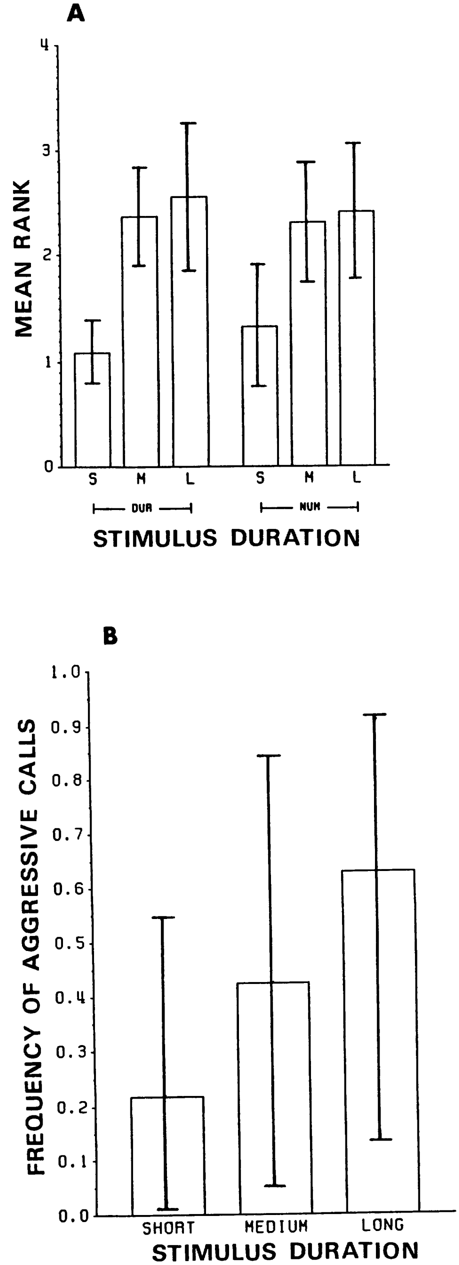

FIG. 4.—Responses to short (S), medium (M), and long (L) duration aggressive calls. (A) Ranks of average aggressive call duration and number of aggressive calls given by each male. Data presented as means ± 1 SE. (B) Frequency of aggressive calls. Data presented as medians and approximate 95% C.I.

erage aggressive call duration were also <30%. However, the range in the duration of calls given by individual males was often considerable (frog 2: 342–947 ms at 9 C), and the longest calls were usually given in response to the loudest stimuli (calls 100 dB SPL or above). Therefore, the data are similar to those reported for *H. ebraccata*

TABLE 2.—Mean duration of aggressive calls (ms) given to synthetic advertisement calls at intensities of 90, 95, 100, and 105 dB SPL. Standard errors and sample sizes are shown in parentheses. Median and mean of mean durations are given at the bottom of the table.

Frog	90	95	100	105
7	523 (15, 6)	556 (9, 9)	557 (12, 13)	629 (11, 20)
12	349 (13, 13)	373 (10, 16)	357 (11, 13)	411 (5, 44)
14	383 (21, 4)	400 (13, 6)	467 (10, 18)	530 (10, 27)
15	352 (13, 9)	411 (7, 16)	437 (4, 18)	448 (5, 18)
20	698 (15, 8)	607 (17, 2)	620 (20, 6)	717 (34, 9)
23	549 (29, 2)	554 (—, 1)	610 (21, 6)	583 (16, 7)
25	431 (34, 2)	440 (24, 3)	520 (20, 7)	528 (29, 7)
26	276 (23, 6)	387 (18, 8)	432 (11, 21)	422 (10, 12)
Median	407.5	425.5	493.5	529
$\bar{x}$	445	466	500	534

(Wells and Schwartz, 1984), but the shifts in duration are not as dramatic as reported for *H. microcephala* (Schwartz and Wells, 1985) and *H. phlebodes* (Schwartz and Wells, 1984).

It is noteworthy that call duration increased less in response to increases in aggressive call intensity (mean increase = 11.2%) than to elevations in advertisement call intensity (23.5%). A possible explanation is that aggressive call stimuli, even at low intensities, elicit longer calls than advertisement call stimuli in *P. crucifer*. Aggressive calls, in general, may simply be a more potent agonistic stimulus than advertisement calls, as has been demonstrated in other species (Lopez et al., 1988; Wells, 1988). The relative numbers of aggressive calls given in response to these two stimulus types at 100 dB SPL support this view (median response to advertisement call = 5, median response to medium duration aggressive call = 15; $n = 10$, $P < 0.05$, Wilcoxon signed rank test), as do the mean and median values of aggressive calling effort (total of call durations) at all intensities (Table 5).

The most interesting result of this study is that male *P. crucifer* can discriminate differences in aggressive calls based solely on call duration, a capability which has recently been demonstrated in *H. ebraccata* (Wells, 1989). Therefore, it seems likely that the graded changes that spring peepers make in this call feature are of significance during male-male vocal interactions. Whether individuals perceive these graded changes in a graded fashion is not entirely clear, however. The numbers and durations of aggressive response calls to the medium and long duration stimuli did not differ significantly, suggesting that aggressive calls above a certain duration may be "lumped together" in one category (Green and Marler, 1979). It also is possible that males perceived the differences between calls in these two stimulus categories but were not able to in-

TABLE 3.—Mean duration of aggressive calls (ms) given to synthetic medium duration aggressive calls at intensities of 90, 95, 100, and 105 dB SPL. Standard errors and sample sizes are shown in parentheses. Median and mean of mean durations are given at the bottom of the table.

Frog	90	95	100	105
2	513 (14, 8)	517 (24, 5)	633 (38, 13)	661 (17, 18)
7	538 (15, 7)	499 (65, 2)	666 (7, 23)	558 (24, 6)
14	466 (10, 31)	529 (7, 28)	578 (9, 38)	511 (11, 24)
23	561 (—, 1)	598 (22, 10)	653 (13, 17)	614 (22, 12)
24	411 (19, 14)	420 (15, 10)	451 (11, 19)	476 (11, 32)
25	540 (7, 29)	584 (13, 26)	587 (9, 25)	532 (8, 28)
Median	525.5	523	610	545
$\bar{x}$	505	525	595	595

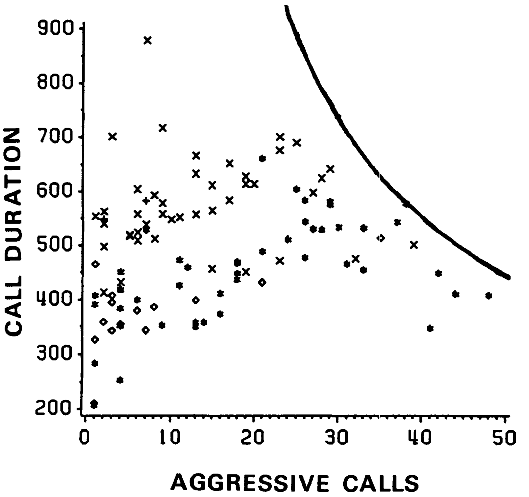

FIG. 5.—Average aggressive call duration (ms) plotted against number of aggressive calls given in each 2-min stimulus presentation. The line above the data is part of a hyperbola delineating an aggressive calling effort of 660 s/h (22 s/2 min). Different symbols indicate data obtained at temperatures of: 0–5 C (plus), 6–10 C (x), 11–15 C (asterisk), and 15–20 C (diamond).

TABLE 4.—Mean duration of aggressive calls (ms) given to synthetic aggressive calls of short, medium, and long duration. All stimulus presentations were at 100 dB SPL except those to frogs 21, 24, and 26 which were at 105 dB SPL. Standard errors and sample sizes are shown in parentheses. Median and mean of mean durations are given at the bottom of the table.

Frog	Short	Medium	Long
2	551 (33, 11)	633 (38, 13)	729 (20, 19)
5	565 (—, 1)	631 (26, 10)	663 (30, 17)
6	564 (15, 15)	567 (21, 9)	614 (10, 19)
9	474 (34, 9)	686 (12, 19)	552 (9, 19)
14	543 (6, 37)	578 (9, 38)	478 (7, 26)
19	345 (57, 2)	433 (47, 4)	519 (41, 5)
21	348 (10, 41)	408 (7, 48)	455 (6, 33)
23	610 (20, 15)	653 (13, 17)	625 (11, 28)
24	208 (19, 4)	476 (11,32)	369 (19, 19)
25	547 (14, 18)	587 (9, 25)	605 (11, 25)
26	342 (40, 3)	354 (29, 4)	446 (24, 3)
Median	543	578	552
$\bar{x}$	463	546	550

crease the strength of their response much beyond that given to the medium duration calls. If aggressive calls are energetically costly, then the frogs may have been close to some upper limit on their rate of production, duration, or product of the two.

The presence of some constraint is supported if we examine the relationship between the rate at which males gave aggressive calls and the average duration of these calls (Fig. 5). As the number of aggressive calls in different 2-min stimulus periods increases from 1–23 calls, the mean duration of calls rises slowly. However, further increases in the rate of aggressive calling are accompanied by reductions in the mean duration of aggressive calls. A stepwise multiple regression analysis revealed that for the low rates, temperature explained over 45% of the variation in call duration, while calling rate explained an additional 7%. For rates of aggressive calling of 23 calls/2 min and greater, the picture is quite different. When a multiple linear regression analysis is performed, call rate accounts for 44% of the variation in duration and temperature only an additional 11%. This suggests that when males give a strong aggressive response to another male, they do not or cannot increase their calling effort above a certain level. In fact, all frogs had aggressive calling efforts below 660 s/h.

TABLE 5.—Mean (above) and median (below) values of aggressive calling effort for all tests. Values in parentheses are SE of means or approximate 95% C.I. for medians. Data are total ms of calling in 2 min. ADV = advertisement call stimuli, AGG = aggressive call stimuli, n = number of tests.

Stimulus	90	95	100	105
ADV	1373 (426)	1732 (532)	3347 (770)	7334 (1779)
$n = 17$	862 (0–1656)	1078 (0–2400)	3622 (307–4641)	5064 (1406–12,580)
AGG	3663 (1497)	3398 (1522)	7410 (1893)	8241 (1246)
$n = 13$	1222 (0–5754)	410 (0–5980)	6307 (1280–14,675)	8274 (3348–12,264)
	Short	Medium	Long	
AGG	4197 (1400)	7948 (1680)	8514 (1392)	
$n = 18$	761 (0–8460)	5832 (1416–14,675)	9472 (2595–13,851)	

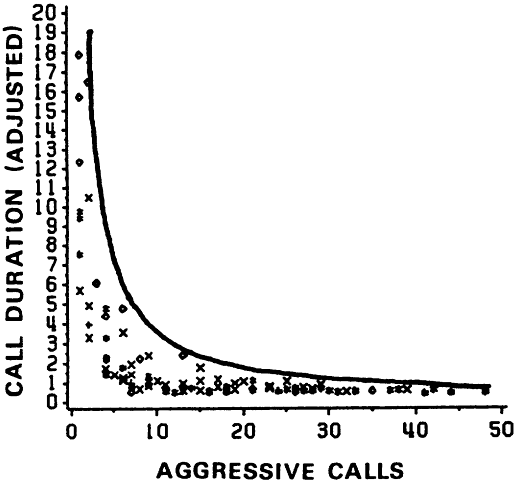

FIG. 6.—Adjusted average aggressive call duration (s) plotted against number of aggressive calls given in each 2-min stimulus presentation. The product of these two variables equals the calling effort. The hyperbola above the data delineates an upper bound on calling effort of 34 s. Different symbols indicate data obtained at temperatures of: 0–5 C (plus), 6–10 C (x), 11–15 C (asterisk), and 15–20 (diamond).

Most males gave a mixture of aggressive and advertisement calls, and any argument based on energetic constraints must consider the contribution of advertisement calls to energy expenditure. Figure 6 shows the data of Fig. 5 after the contribution of advertisement calling is included by taking the total duration of all calls given in each 2-min stimulus period and dividing by the number of aggressive calls given. In calculating this adjusted mean call duration, I assume that the cost of producing advertisement and aggressive calls in the spring peeper is equivalent at equal calling efforts. The adjusted data follow a hyperbolic curve and reveal that calling effort had an upper bound of 990 s/h (just five playback tests elicited calling efforts above 780 s/h). For comparison, Taigen et al. (1985) obtained maximum calling efforts in spring peepers of under 600 s/h. In that study, animals were tested in the laboratory and gave advertisement calls only.

The results of this study demonstrate that male *P. crucifer* can both detect differences in the duration of aggressive calls given by other males and shift the duration of their own aggressive calls in response to changes in the acoustic milieu. When a male gives aggressive calls to a neighboring male, he can increase the strength of his agonistic response by elevating the rate at which he gives aggressive calls, by lengthening his own aggressive calls, or both. However, the maximum calling effort of males appears to be constrained, and aggressive calls may be given at the expense of advertisement calls if a male's calling effort is near its upper limit. Therefore, if aggressive calls are less attractive to females than advertisement calls, as is the case in some other species of treefrogs (Oldham and Gerhardt, 1975; Schwartz, 1987*b*; Wells and Bard, 1987), aggressive calling may entail additional costs besides high energy expenditure (see Wells, 1988, for a discussion of this issue). A question that remains unanswered is why males modify the duration of their aggressive calls at all. Longer calls may signal a higher level of aggressive motivation and probability of physical attack; although on theoretical grounds, it seems unlikely that males would reveal such information to rivals (Caryl, 1979; Dawkins and Krebs, 1978). Alternatively, aggressive calls may contain information about the physical strength of a male and so facilitate assessment of opponents. Males of *Hyla versicolor* increase the duration of their advertisement calls in response to the calls of other males (Wells and Taigen, 1986) and females find these longer calls more attractive (Klump and Gerhardt, 1987). Wells and Taigen (1986) speculated that the production of these longer pulsed advertisement calls leads to more rapid depletion of glycogen reserves than production of shorter calls at equal calling efforts. Therefore, production of longer calls may limit the length of time a male can call. A similar argument may be relevant to aggressive calling in the spring peeper. By giving longer aggressive calls, a male could reflect some biochemical attribute of muscles used in call production, such as a high level of the substrate glycogen. If there is a positive correlation between substrate levels in those muscles used in fighting and those used in calling, he could communicate his potential endurance in a physical encounter. If this is so, aggressive calling in this species would constitute a form of honest advertisement (Clutton-Brock and Albon, 1979; Kodric-Brown and Brown, 1984).

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VARIATION IN CLUTCH SIZE AND EGG SIZE IN THE GREEN TURTLE NESTING POPULATION AT TORTUGUERO, COSTA RICA

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ABSTRACT: Data on clutch size for green turtles, *Chelonia mydas*, nesting at Tortuguero, Costa Rica, for a period spanning over 30 yr, and data on egg size from one nesting season are analyzed to determine sources of variation in clutch parameters. Mean clutch size is 112.2 (SD = 24.2, n = 2544) with a range from 3–219 eggs. Female body size is significantly correlated with clutch size but accounts for only a small proportion of the variation in clutch size. At the population level, clutch size increases significantly throughout a nesting season, but at the individual level, the increase in clutch size is not significant. Annual variation in mean clutch size was significant only between the years with the highest and lowest mean values. Clutch size increases significantly with age of the female; increase in body size with age is not significant. Number of days between clutches within a nesting season, number of years between nesting seasons, and egg size are not significantly related to clutch size. Egg size, which is significantly correlated with female body size, is less variable than clutch size. Apparently clutch size is not under strong environmental control.

Key words: *Chelonia mydas*; Clutch size; Egg size; Green turtle; Reproduction; Reptilia

REPRODUCTIVE output in the green turtle, *Chelonia mydas*, is a function of clutch size, number of clutches per nesting season, interval between nesting seasons, and length of reproductive life (survivorship and senescence). The first three parameters vary widely within and among individual green turtles nesting at Tortuguero, Costa Rica, the largest green turtle colony in the Atlantic (Carr et al., 1978). Almost certainly the fourth parameter has similar variation. Data collected from 1956–1987 for green turtles nesting at Tortuguero are used to assess possible sources of variation in one of these parameters—clutch size. The number of eggs deposited by a female green turtle when she ventures onto the beach varies considerably. Identifying the sources of this variation is important for determining what factors control reproductive output in green turtles and for understanding their life history patterns.

The potential sources of variation in clutch size investigated in this paper are female body size, female relative age, egg size, number of years between nesting seasons, and number of days between successive nests. Annual variation and seasonal variation in clutch size are analyzed at both individual and population levels.

In addition to clutch size, we also examined variation in egg size. The relationship between female body size and egg size is determined, and seasonal variation