Territorial and Reproductive Behavior of the Tropical American Frog Centrolenella fleischmanni

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Tadpoles of *I. acarpicus* were kept in an aquarium (15–18 C) from 3 January 1979 until metamorphosis was completed on 12 February 1979. On completion of metamorphosis the froglets were 20–22 mm ($\bar{x}$ = 21 mm) in snout–vent length. The young animals showed the same ectosomatic morphology as the adults which were described by Barrio (Physis 30:331–341, 1970). Females with mature white ovarian eggs (34–61) have been collected during January and May. The existence of mature females in these months and juveniles during December–May suggests that the larval period may be 11–12 months in nature.

SPECIMENS EXAMINED

All specimens were collected at the type locality (Mehuín, Valdivia Province, Chile). They are located in the collection of the Instituto de Zoología, Universidad Austral de Chile (IZUA) and the private collection of Nelson Díaz (ND).

Insuetophrynus acarpicus.—ND 2, 4, and 6 collected 3 July 1978; ND 82, 83, 85, and 89 collected January 1977; ND 113 and 114 collected 4 December 1977; ND 187 and 215 collected 23 January 1978; IZUA 1815-A collected 5 July 1978; IZUA 1816-A collected 23 November 1978; IZUA 538-A (12 specimens) collected 12 December 1978; IZUA 1817-A (5 specimens) collected 2 March 1979.

Acknowledgments.—We thank: P. Castro for field assistance, M. A. Vera for preparing the illustrations, and S. Lacrampe for typing the MS. This work was supported by Proyecto RS 77-47, Dir. Invest. Univ. Austral Chile, and Proyecto B 705-791, Serv. Desarrollo Científico-Artístico y Cooperación Int., Univ. Chile.

RESUMEN: Se describe la larva de la rana *Insuetophrynus acarpicus* y se agregan notas ecológicas de adultos y renacuajos de esta especie.

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TERRITORIAL AND REPRODUCTIVE BEHAVIOR OF THE TROPICAL AMERICAN FROG *CENTROLENELLA FLEISCHMANNI*

BEVERLY J. GREER AND KENTWOOD D. WELLS

ABSTRACT: Movements of marked male *Centrolenella fleischmanni* were monitored for 1.5 months along a small stream on Barro Colorado Island, Panama. Males were territorial and most occupied no more than two sites during the study. Females laid eggs at calling sites of males and males obtained 1–11 matings. Mating success of males was positively correlated with the number of days males occupied calling sites. Sites more than 0.6 m high were occupied on more days and used for oviposition more frequently than sites below 0.6 m. Males at high sites obtained matings at a faster rate than those at low sites. Males showed no parental care. There was relatively little predation on eggs and overall survival of eggs to hatching was 61–71%.

Key words: Amphibia; Salientia; Centrolenidae; *Centrolenella*; Behavior; Reproduction; Territoriality; Vocalizations; Panama

MEMBERS of the family Centrolenidae are small, arboreal frogs found in lowland and mid-elevation forests of Central and South America. During the rainy season, males call at night from leaves overhanging streams. Females deposit eggs at or near calling sites, which are defended as territories by males of some species.

Males may return to the same calling sites on successive nights and fertilize the eggs of several females. In some species, males attend eggs for varying lengths of time, but in others there is no evidence of parental care (Duellman and Savitsky, 1976; Duellman and Tulecke, 1960; McDiarmid, 1975, 1978; McDiarmid and Adler, 1974; Villa, 1972, 1977).

We report the results of a 1.5-month study of territoriality and reproductive behavior in a small population of *Centrolenella fleischmanni*. We monitored movements of marked males to determine how long they remained in territories, and we investigated the relationship between territoriality and individual mating success. We observed the behavior of females approaching calling males and attempted to determine factors influencing female choice of oviposition sites. We also followed the development and survival of egg clutches.

MATERIALS AND METHODS

We studied *C. fleischmanni* in a lowland tropical forest with pronounced wet (May–December) and dry (January–April) seasons. The study plot was an area approximately 13 × 17 m along Lutz Stream on Barro Colorado Island, Panama (BCI). Most male *C. fleischmanni* called from vegetation over the main stream channel or over intermittent drainage courses that contained a few centimeters of water during most of the study. We marked 21 calling sites with plastic flags. Each site consisted of a single plant or a branch of a large shrub. We measured distances between adjacent sites and we characterized each site by measuring distances to the ground and nearest water. In our analysis we compare sites above and below 0.6 m in height. This was a natural division because *Dieffenbachia* plants formed a relatively even layer at about 0.6 m, whereas other plants formed a second layer starting at about 1.0 m. Daily rainfall data were obtained from the Panama Canal Company BCI station.

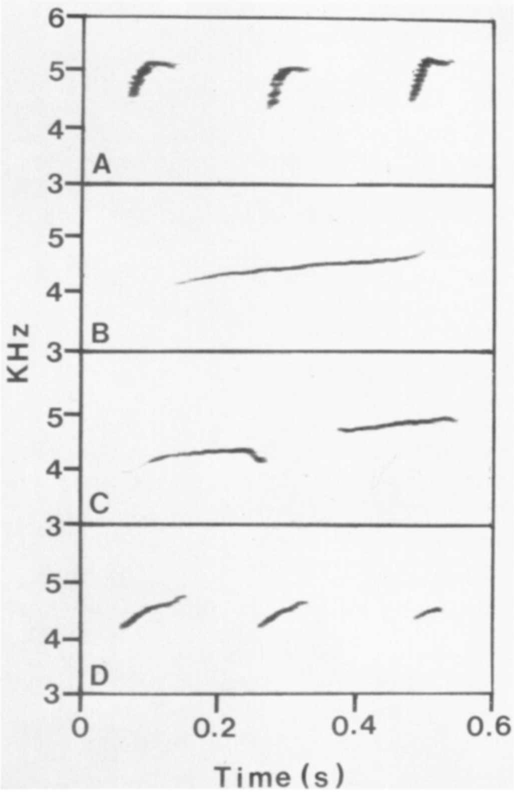

FIG. 1.—Sonagrams of calls of *Centrolenella fleischmanni* (45 Hz narrow band filter). A. Advertisement peeps from three different males; B. aggressive mew; C. courtship mews from two different males; D. courtship chirps from three different males. Calls were recorded at air temperatures of 25–26 C.

We visited the area between 1900 and 2400 on 30 nights between 18 June and 3 August 1978, and we returned almost every day to check egg clutches. Observations at night totalled over 50 h. On each nocturnal visit we censused all males and toe-clipped and measured unmarked individuals. We marked 24 males and observed, but did not mark, gravid females. On each visit we recorded (1) weather conditions, (2) number of calling and noncalling males, (3) number of clutches in each territory, (4) number of eggs or tadpoles in each clutch, (5) any evidence of predation on eggs, and (6) descriptions of any male-male or male-fe-

TABLE 1.—Summary of temporal and spectral features of calls of *Centrolenella fleischmanni*. N_i = number of individuals recorded. N_c = number of calls. Values are means ±SD. Numbers in parentheses are ranges. All calls were recorded at air temperatures of 25–26 C.

Call	Context	N_i	N_c	Duration (s)	Lowest frequency (Hz)	Highest frequency (Hz)
Peep	advertisement	5	26	0.10 ± .01 (0.08–0.14)	4383 ± 135 (4165–4582)	5216 ± 78 (5081–5331)
Mew	encounters	3	8	0.45 ± .07 (0.32–0.52)	4238 ± 206 (3998–4582)	4852 ± 182 (4758–5248)
Mew	courtship	3	14	0.27 ± .03 (0.21–0.33)	4194 ± 363 (3665–4748)	4546 ± 318 (4165–4998)
Chirp	courtship	3	24	0.10 ± .04 (0.02–0.18)	4002 ± 267 (3582–4248)	4387 ± 402 (3582–4748)

male interactions. We recorded vocalizations on a Uher® 4200 tape recorder with a Uher® M517 microphone and analyzed recordings on a Kay® 6061 Sona-Graph spectrum analyzer.

RESULTS

Behavior of males.—Males usually called from the undersurfaces of broad-leaved plants such as *Dieffenbachia*, or shrubs, ground bromeliads, and epiphytes on tree trunks. Calling sites were approximately 0.5–10 m above the ground and 0–6 m from water (all of our marked sites were within 2.5 m of the ground). Individual males called almost continuously from sunset until midnight or later. We found no correlation ($r = 0.29$, $n = 30$, $P > .05$) between number of males calling each night and amount of rainfall that day (midnight to midnight), although the entire population became inactive on very dry nights.

The advertisement call was a peep approximately 0.1 s long and was delivered every 6–16 s (4–10 calls per min). Calls were between 4300–5300 Hz, with no clear dominant frequency (Fig. 1; Table 1). We detected no alternation of calls by near neighbors at normal spacing distances (about 1–2 m), in contrast to Duellman's (1967) report of "trios" of calling males in this species. We played recordings of advertisement calls to several males at close range (15–30 cm), but we were unable to elicit any change in calling behavior.

During agonistic encounters, males gave advertisement calls interspersed with a call which we termed a mew. This was a single note approximately 0.45 s long with more gradual frequency change than the advertisement call (Fig. 1; Table 1). During some encounters, males gave mostly mews with few peeps. However, in one encounter, 14 of 16 mews (88%) were preceded by single peeps with about 0.4 s between the two calls. Apparently mews function as encounter calls (McDiarmid and Adler, 1974; Wells, 1977*a*) and are given primarily when a male detects another frog on his leaf. In tests with several males we were unable to elicit mews in response to playbacks of either peeps or mews, even at high volumes.

We observed four male-male interactions. In one interaction two males 15 cm apart on different plants alternated peeps for about 30 min and approached one another, but never gave encounter calls and never came into physical contact. In two other encounters, two males only a few millimeters apart on the same leaf exchanged mews and peeps. Most calls were given by the resident male. The males moved around on their leaves while calling. Each encounter ended after about 30 min without physical contact when the intruder withdrew.

We observed a fourth interaction for 2 h. When we arrived the resident male was sitting on top of the intruder and was giving peeps and mews. After a few seconds the intruder moved from under the resident. Both males moved around on leaves within 25 cm of each other, giving both peeps and mews. At one point the resident approached the intruder and performed a four-legged push-up with no response from the intruder. The males remained within 5–10 cm of one another for 1.5 h, but no additional contact or displaying occurred.

Male-female interactions.—We found pairs in amplexus 16 times and observed 9 courtship interactions, of which 7 were successful. We do not know how long females took to locate calling sites, but events leading to amplexus lasted 10–165 min ($\bar{x} = 55$, SD = 55, $n = 7$) after females reached the plants on which the males were calling. Females appeared to inspect calling sites carefully before amplexus. Once a female reached a male's leaf, she moved around on the upper and lower surfaces, often moving to the edge and peering toward the ground.

When a female was on the same surface as a calling male, she assumed a low, flattened posture and circled the male, sometimes brushing against parts of his body with no apparent response from the male. A female sometimes circled a male for several minutes before moving to the upper surface of the leaf or to another leaf, only to return a few minutes later for additional circling. Eventually the female initiated amplexus by moving toward the male in a crouched position and backing her body under his until he clasped her. We never saw a male attempt to clasp a female or change his position before the female backed under him.

Males gave three types of calls during courtship. When a male first detected a female nearby, either visually or through tactile cues, he would begin interspersing mews with peeps. The mews we recorded during courtship were shorter than mews recorded during aggressive encounters, but had essentially the same frequency structure (Fig. 1; Table 1). However, because of our small sample size, we do not know whether the different durations of aggressive and courtship mews are real.

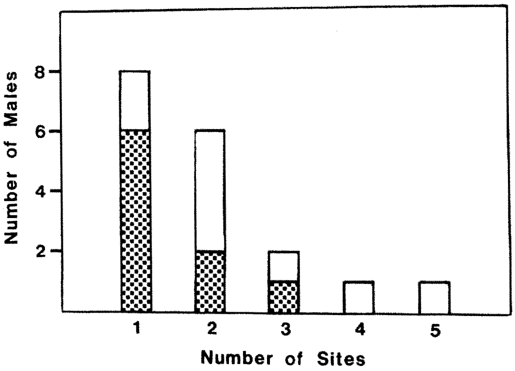

FIG. 2.—Number of calling sites occupied by individual males over a 6.5-week period. Open columns indicate males at sites ≤ 0.6 m from the ground; checkered columns indicate males at sites > 0.6 m.

Courting males also gave chirp calls about 0.1 s long (Fig. 1; Table 1). These were given most frequently when a female was on the same surface as a male. We were able to elicit chirps and mews from some males by tapping lightly on the male's leaf, but other males gave no response. As courtship progressed, males usually stopped giving peeps and gave mostly chirps. Immediately before amplexus each male gave a rapid series of brief chirps.

In three instances we observed a second female approaching a courting pair. The females showed no reaction to each other. In each case the second female stopped her approach when the male clasped the first female; she then reoriented toward another calling male.

Spacing of males.—Calling males in our population were spaced at distances of 0.9–2.1 m ($\bar{x} = 1.5$, SD = 0.4). Few new calling sites were established during

TABLE 2.—Expected and observed mating frequencies for male *Centrolenella fleischmanni* at high and low sites. We assumed that each night a male was present in a territory represented one potential mating opportunity for a female. Expected frequencies are the numbers of matings males would have obtained if their mating success were proportional to the number of mating opportunities they controlled.

Male	Site	Nights present	Proportion of mating opportunities	Number of matings Expected	Number of matings Observed	Deviation from expected
10	high	15	.13	7.8	11	>
14	high	13	.11	6.6	10	>
1	high	10	.08	4.8	7	>
2	high	6	.05	3.0	5	>
13	high	3	.03	1.8	3	>
8	high	11	.09	5.4	3	<
6	low	3	.03	1.8	4	>
3	low	9	.08	4.8	4	<
9	low	20	.17	10.2	4	<
5	low	6	.05	3.0	3	=
4	low	9	.08	4.8	3	<
22	low	6	.05	3.0	2	<
12	low	7	.06	3.6	1	<
Totals		118	1.01	60.6	60	

the study; in general, for every new site occupied, a nearby site was abandoned. Of 18 males seen more than twice, 8 (44%) occupied only one site during the 6.5-week study, and 14 (78%) occupied no more than two sites (Fig. 2). Seven of 10 males (70%) that occupied more than one site spent most of their time at sites below 0.6 m, whereas 6 of 8 males (75%) that occupied only one site spent most of their time at sites above 0.6 m (Fig. 2). However, the difference was not statistically significant ($G = 3.74$, df $= 1, 0.5 < P < .1$).

Males did not remain in their territories continuously throughout the study. Some males were present at the same sites for up to 10 consecutive capture nights over a 15–20 day period. Others left for periods of 1–18 nights and then returned to the same sites. These data are rough approximations because we were not present every night. When males moved to new sites, they usually moved less than 2 m, although occasionally they moved as far as 5 m.

Mating success of males.—Females deposited eggs at calling sites on the undersurfaces of leaves. Because there was little movement of males between sites, it was possible to monitor individual mating success. Of 14 males at sites low enough to be monitored accurately, 13 obtained at least one mating. These males obtained 60 matings (range = 1–11, $\bar{x} = 4.6$) at 19 different sites. The number of clutches fertilized was significantly correlated with the number of nights each male was present in a territory ($r_s = 0.49$, df $= 11$, $P < .05$) indicating that at least part of the variance in male mating success can be attributed to differences in time spent in territories.

The height of territories above the ground also appeared to affect male mating success. Sites above 0.6 m were occupied on more nights than those below 0.6 m (high—5–18 nights, $\bar{x} = 11$, $n = 7$; low—1–15 nights, $\bar{x} = 6$, $n = 12$; $U = 17$, $P < .025$, one-tailed Mann-Whitney U-test) and were used more often for oviposition (high—1–11 clutches, $\bar{x} = 5.7$, $n = 7$; low—0–4 clutches, $\bar{x} = 2.4$, $n = 12$; $U = 19$, $P < .05$). Males that spent most of their time at high sites obtained more matings than those at low sites (high—3–11 clutches, $\bar{x} = 6.5$, $n = 6$; low—1–4 clutches, $\bar{x} = 3$, $n = 7$; $U = 8$, $P = .037$).

Much of the difference in male mating

success at high and low sites might be attributable to more frequent occupation of high sites by males. To correct for this, we divided the number of clutches each male fertilized by the number of nights the male was observed in a territory. Although we were not present every night, we assume that our observations were a proportional sample of the total nights on which males were present. Males at high sites obtained significantly more clutches per night ($\bar{x} = 0.67$, median = 0.75, $n = 6$) than those at low sites ($\bar{x} = 0.35$, median = 0.33, $n = 7$; Median Test, $P = .024$). We also calculated expected mating frequencies for males if females selected males in proportion to their occurrence at calling sites, and we compared these values with observed mating frequencies (Table 2). Five of 6 males at high sites obtained more matings than expected, whereas only 1 of 7 males at low sites did so (Fisher's Exact Test, $P = .02$). These data indicate that males at high sites not only occupied sites for longer periods, but also attracted females at a faster rate than those at low sites.

Development and survival of eggs.—Males in our population sometimes had up to five clutches of eggs in a territory at one time, but we found no evidence of parental care. In general, males calling from very large leaves remained on the same leaf after eggs were laid and continued to attract females, whereas males on small leaves usually moved to another leaf on the same plant. Males did not remain at calling sites during the day.

Clutch size was 20–40 ($\bar{x} = 27$, SD = 5, $n = 35$). Time from oviposition to complete hatching was 8–21 days ($\bar{x} = 13$, SD = 2, $n = 32$). Sometimes all tadpoles in a clutch hatched on one day, but often tadpoles disappeared over 2–3 days. Tadpoles changed from yellow to orange to red during development and nearly all hatched in the orange or red stage. Yellow tadpoles appeared to have substantial yolk reserves and probably could not survive independently. We assumed that any disappearance of yellow tadpoles was due to predation. However, once tadpoles reached the orange stage (usually day 8 or 9), it was impossible to distinguish tadpoles that had hatched from those taken by predators.

We followed 32 clutches from oviposition to the disappearance of all tadpoles. Two clutches (6%) were destroyed before day 5 by drosophilid fly larvae as described by Villa (1977). Seven additional clutches showed signs of disturbance by predators (i.e., crushed embryos, rapid disappearance of yellow tadpoles) and had less than 25% of their tadpoles surviving by day 8. However, we made over 500 inspections of individual egg clutches during the day and at night, and we never observed predators attacking eggs.

We estimated survival of the remaining 23 clutches by counting surviving embryos at three stages: (1) on day 5, (2) on day 8, and (3) on the day before we observed a substantial decrease in the number of orange or red tadpoles (we designated this as the start of hatching). We also counted the maximum number of dead embryos observed in each clutch to estimate the amount of mortality due to causes other than predation. Mean survivorship estimates were 97% for day 5, 90% for day 8, and 81% for the day before the start of hatching. The last figure probably is a minimum estimate because some tadpoles may have hatched one or two days before the rest of a clutch. Approximately 30% of the apparent mortality to the day before the start of hatching could be accounted for by dead embryos in the clutches. Hence, maximum predation was about 13% (70% of the 19% mortality).

For all 32 clutches we estimated survival to hatching at 61–71%. Considering only survival to day 8, we estimated that of 865 embryos originally present, 43 (5%) were destroyed by fly larvae, 67 (8%) died during development, and 137 (16%) were taken by predators or disappeared due to unknown causes. There were no significant differences in survival of clutches at high and low sites.

DISCUSSION

Territoriality and courtship.—Males in our population showed a strong tendency to remain at the same sites for several weeks, but they rarely defended their territories with overt aggression. Even when males were within a few centimeters of one another they generally settled disputes with vocal challenges rather than physical contact. Our brief observations of agonistic behavior were similar to McDiarmid and Adler's (1974) report for *C. viridissima* (=*C. fleischmanni*) in Mexico. They described a "preep" call corresponding to the mew we recorded, and "jerky rocking motions" similar to the push-up display we observed.

The only previously published description of courtship in centrolenid frogs is McDiarmid's (1975) general account, so it is impossible to compare the behavior of *C. fleischmanni* with that of other species. The most striking feature of courtship was the tendency for a male to remain stationary and not attempt to initiate amplexus even when touched by a female. There may be little advantage to a male in attempting to clasp females quickly, because the wide spacing of males would reduce the chances of interference during courtship. Premature clasping attempts might drive away a female and cause her to seek another male. This sit-and-wait courtship behavior is similar to that reported for many North American hylids (Fellers, 1979) and other territorial frogs (Wells, 1977*a*,*b*).

Female choice of mates.—During our brief study, the most successful males obtained more than 10 times as many matings as the least successful males. Although much of this variance was due to differences in the amount of time males spent in territories, our data also indicate that female choice probably influences male mating success. However, we were not able to determine precisely the criteria used by females to select mates. Theoretically, female choice of mates could be influenced by morphological or behavioral features of the males themselves, by characteristics of territories held by males, or by a combination of these factors (Howard, 1978; Trivers, 1972; Wells, 1977*a*).

We found it impossible to separate completely characteristics of males themselves from characteristics of their territories because most sites were occupied by only one male for most of the study period. Hence, the sites used most frequently for oviposition tended to be occupied by males that obtained the most matings. However, because all males were nearly the same size (21–23 mm, $\bar{x}$ = 21.5, CV = 2.6%), size differences probably were relatively unimportant. We were unable to detect any consistent differences in calling behavior which might have served as cues for female choice. Although calling rates varied from night to night, we found that males called at similar rates on any given night. Nevertheless, the calling behavior of individual males needs to be studied in a more quantitative way before it can be eliminated as a factor in mate selection.

There are at least two ways that characteristics of a male's territory might influence female choice. First, the location of a territory might enhance the effectiveness of a male's vocal signals (Fellers, 1979). Second, some feature of the territory might enhance survivorship of eggs or tadpoles and females might detect differences in territory quality.

There are several reasons to suspect that males calling from high sites would be detected by females more readily than those at low sites. First, excess attenuation of all sound frequencies is greatly increased within 1 m of the ground (Marten and Marler, 1977; Marten et al., 1977). All of our low sites were below this level, whereas most of our high sites were well above it. Second, dense vegetation may produce scattering of sounds, resulting in additional attenuation (Marten and Marler, 1977; Wiley and Richards, 1978). Most of our low sites were in a dense stand of *Dieffenbachia* at a relatively uniform level. In contrast, all of our high sites were in relatively open areas.

Finally, the tendency of males at both high and low sites to call from the undersides of leaves may affect the directionality of their signals. The leaf may serve as a sound reflector, so a female below the leaf would perceive a male's call more readily than one above the leaf. Therefore, signals originating from high sites should be audible over a larger area than those originating from low sites. Females that we observed approaching males appeared to come from shrubs and other vegetation, but not from the ground.

If females choose oviposition sites on the basis of features enhancing survival of offspring, then apparently only post-hatching survival is affected because we found no difference in pre-hatching survival of eggs at high and low sites. One might expect sites directly over water to be most favorable for oviposition, but this did not appear to be the case. Two of our most frequently used high sites were on trees 3–4 m from the nearest standing water. Tadpoles from these sites could not have reached suitable pools unless they hatched during heavy rains. In contrast, every low site used at least once for oviposition was within a few centimeters of standing water and most were directly over pools.

We conclude that males calling from high sites were more successful in attracting females than males at low sites. We suspect that female choice of mates is influenced by some feature of a male's territory, but we cannot rule out the possibility that some aspect of male behavior is also important. Whether females derive a reproductive advantage from mating with males at certain sites, or simply mate with males whose signals are most easily perceived, is a question which requires further investigation. Although we found no differences in survival of eggs at high and low sites which might explain a female preference for high sites, it is possible that such differences would emerge in a longer study. Furthermore, it may be that the relative advantages for males calling in different locations change seasonally or vary with the number of males calling at high and low sites. Such variation would go undetected in a short-term study such as ours. Hence, a complete understanding of the basis of female choice in these frogs depends on additional studies of populations under a variety of ecological conditions.

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HEART RATE-VENTILATORY RESPONSE OF SEVEN TERRESTRIAL SPECIES OF NORTH AMERICAN SNAKES

James S. Jacob

Abstract: Simultaneous electrocardiograms and impedance pneumograph tracings were recorded from seven species of unrestrained terrestrial snakes (families Colubridae and Viperidae) at 24 ± 1 C. Heart rates recorded during ventilatory periods were significantly higher than heart rates during apneas. Electrocardiographic changes between apneic and ventilatory periods consisted primarily of an increase in length of the diastolic period with little or no change in atrioventricular conduction time or duration of ventricular depolarization. Ventilatory tachycardia began at the start of a ventilatory period and terminated within 2–4 heart beats. Artificial lung inflation produced a ventilatory tachycardia essentially identical to that observed during normal breathing. The heart rate-ventilatory response appears to be a basic reptilian feature which functions to allow rapid equilibration of gas tensions between blood and tissue during the brief ventilatory periods characteristic of terrestrial reptiles.

Key words: Reptilia; Serpentes; Colubridae; Viperidae; *Crotalus; Elaphe; Pituophis;* Heart Rate; Ventilation

Coupling of cardiac and ventilatory activity in vertebrates (see Andersen, 1966, for a review) has been seen in fishes (Capra, 1976; Garey, 1962; Johansen, 1970; Reynolds, 1977; Satchell, 1960), amphibians (Shelton, 1970), reptiles (White, 1976), birds (Jones and Johansen, 1972), and mammals (Hoff and Geddes, 1965; Irving et al., 1941; Kilgore, 1920; McCrady et al., 1966). The heart rate-ventilatory response in reptiles, consisting of an increase in heart rate associated with ventilatory activity, has been documented in crocodilians (Huggins et al., 1970), aquatic turtles (Ackerman and White, 1979; Belkin, 1964; Gaunt and Gans, 1969*a*; Johansen et al., 1977; Weathers and White, 1971; White and Ross, 1965, 1966), semi-aquatic lizards (Millard and Johansen, 1974), marine snakes (Heatwole, 1977; Heatwole et al., 1979; Heatwole and Seymour, 1975), and freshwater snakes (Irvine and Prange, 1976; Jacob and McDonald, 1976; Pough,