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Source: *Herpetologica*, Vol. 41, No. 4, (Dec., 1985), pp. 396-404
Published by: Herpetologists' League
Stable URL: http://www.jstor.org/stable/3892108
Accessed: 30/04/2008 08:36

Herpetologica, 41(4), 1985, 396-404

REPRODUCTIVE BEHAVIOR AND MALE MATING SUCCESS IN TWO SPECIES OF GLASS FROGS (CENTROLENIDAE)

SUSAN K. JACOBSON

ABSTRACT: Reproductive behavior and male mating success were compared between two sympatric species of glass frogs exhibiting different degrees of parental care. During some nights, male *Centrolenella fleischmanni* called continuously from vegetation overhanging streams and maintained greater nearest neighbor distances than did male *C. prosoblepon*. Female *C. fleischmanni* initiated amplexus and deposited eggs that were attended by males. Males generally attended eggs late in the evening, when few additional females were available, thus minimizing lost mating opportunities. Male *C. prosoblepon* called sporadically, moved actively, initiated amplexus, and showed no paternal care of clutches. Female *C. prosoblepon* attended eggs immediately after deposition. Egg attendance did not appear to enhance larval survivorship significantly in either species. For both species, male reproductive success was correlated with length of residency at the site, but snout-vent length and call pitch or duration were not correlated with male success in obtaining mates. Larval survivorship was enhanced by the choice of wet microhabitats for oviposition by *C. prosoblepon*.

Key words: Amphibia; Anura; Centrolenidae; Parental care; Reproductive behavior; Sexual selection

CENTROLENIDS are small, arboreal frogs inhabiting forests from sea level to 2000 m in Central and South America (Duellman and Savitsky, 1976; Savage, 1967; Savage and Starrett, 1967; Starrett and Savage, 1973; Villa, 1977, 1984). Two species of centrolenids (*Centrolenella fleischmanni* and *C. prosoblepon*) occur sympatrically along the Gaucimal River in Monteverde, Costa Rica. Males of both species defend calling sites and attract females to mate. Females appear throughout the breeding season from May through September and deposit eggs on leaves overhanging the river. Hatching tadpoles drop into the river and live in the bottom silt. Though these species are ecologically sympatric and morphologically similar, their reproductive behavior and degree of parental care are markedly different. This study compares the reproductive behavior of *C. fleischmanni* and *C. prosoblepon*. I evaluate behavioral and phenotypic characteristics correlated with male reproductive success and examine the influence of parental behavior on larval survivorship.

MATERIALS AND METHODS

The study was conducted from May through September 1982, on the Gaucimal River in Monteverde, Puntarenas Province, Costa Rica, at an elevation of 1360 m. The river varied from 3–7 m in width and 0.2–1.1 m in depth, depending on location and rainfall. The surrounding area is lower montane wet forest (Holdridge, 1967). Daily rainfall was measured with a gauge at 0800 h every day. Relative humidity was determined with a hydrothermograph 500 m away, and air temperature (±0.1 C) was taken each time that I recorded frog calls.

An 80 m section of the river was marked with flagging tape at 2 m intervals along both shores so that nightly locations of individual frogs could be mapped. I monitored frogs found up to 3 m above the river and up 3 m of each shore. I censused between 2100 h and 0300 h on 123 nights for 2–4 h depending on frog density. I conducted additional behavioral observations both before and after these times, resulting in 610 h of study. Nightly census data for each frog included (1) activity (calling, egg attendance, moving, fighting), (2) location (height above ground), and (3) straight-line distance to nearest conspecific neighbor. All 536 *C. fleischmanni* and 353 *C. prosoblepon* found at the site were (1) sexed by presence of eggs in females, spines in *C. prosoblepon* males and male vocalizations in both species, (2) measured to the nearest 0.5 mm snout–vent length (SVL), (3) weighed to the nearest 0.1 g with a 5 g Pesola scale, and (4) toe-clipped for permanent identification. For short-term behavioral observations, I sprinkled differently colored powdered acrylics on the frogs. This lasted throughout the night with no apparent effect on frog behavior. Observations were made with a Minespot headlamp and red filter which also did not affect frog behavior.

Male behavior was compared between species using 1 h time budgets of calling rates and distances moved for 25 male *C. fleischmanni* and 27 male *C. prosoblepon*. Calling rates were extrapolated from 5 min intervals for *C. fleischmanni* and from 20 min intervals for *C. prosoblepon*. Additionally, time budgets of 16 pairs of *C. fleischmanni* in amplexus and 14 pairs of *C. prosoblepon* were compared to determine interspecific differences in reproductive activity.

Observations of egg clutches being fertilized and males attending clutches were used as evidence of male mating success. To determine any differences in phenotypic attributes characterizing successful versus unsuccessful males, SVL and calling characteristics were compared between these two groups. Calls of 27 *C. fleischmanni* and 10 *C. prosoblepon* were recorded with a Sony TC55 tape recorder when air temperature was between 17–18.5 C. These were analyzed on a Kay 7029A Sonagraph. The duration and frequency of calls given by successful and unsuccessful males were compared.

Larval survivorship was monitored for 80 of 124 *C. fleischmanni* egg clutches and 30 of 50 *C. prosoblepon* clutches. Tadpoles changed from yellow to red during development (Villa, 1984). I defined clutch survivorship as clutches with more than 70% of the larvae turning red and dropping from the leaf. Average heights above ground were compared between surviving and dying clutches to determine if certain sites enhanced survivorship. In *C. fleischmanni*, the fate of clutches attended by males on subsequent nights was compared with clutches not subsequently attended. Standard nonparametric techniques were used in data analysis (Siegel, 1956).

RESULTS

Vocal and Territorial Behavior of Males

Vocalizations.—Male *C. fleischmanni* could be heard calling from dusk until dawn of some nights. In general, they called from the undersides of leaves, remaining in the same position for the duration of their calling period. Characteristics of their advertisement calls are given in Table 1. The calling rate (calls/h) of individual males decreased as the evening progressed. Before 0100 h, the average rate was 579 calls/h. After 0100 h, the average rate dropped to 178 calls/h for six males. Males in amplexus or attending eggs did not call, with one exception. *Centrolenella fleischmanni* courtship and aggressive calls are described by Greer and Wells (1980).

In contrast to *C. fleischmanni*, *C. prosoblepon* males gave advertisement calls at irregular intervals from the tops of leaves. They usually faced a different direction for each call and averaged only 17 calls/h. The advertisement call of *C. prosoblepon* consisted of three short beeps, with occasional two to five beep sequences (Table 1). Males often gave a series of rapid short beeps when encountering another frog within 0.15 m. Unlike *C. fleischmanni*, males of *C. prosoblepon* called vigorously while in amplexus and also immediately after egg deposition.

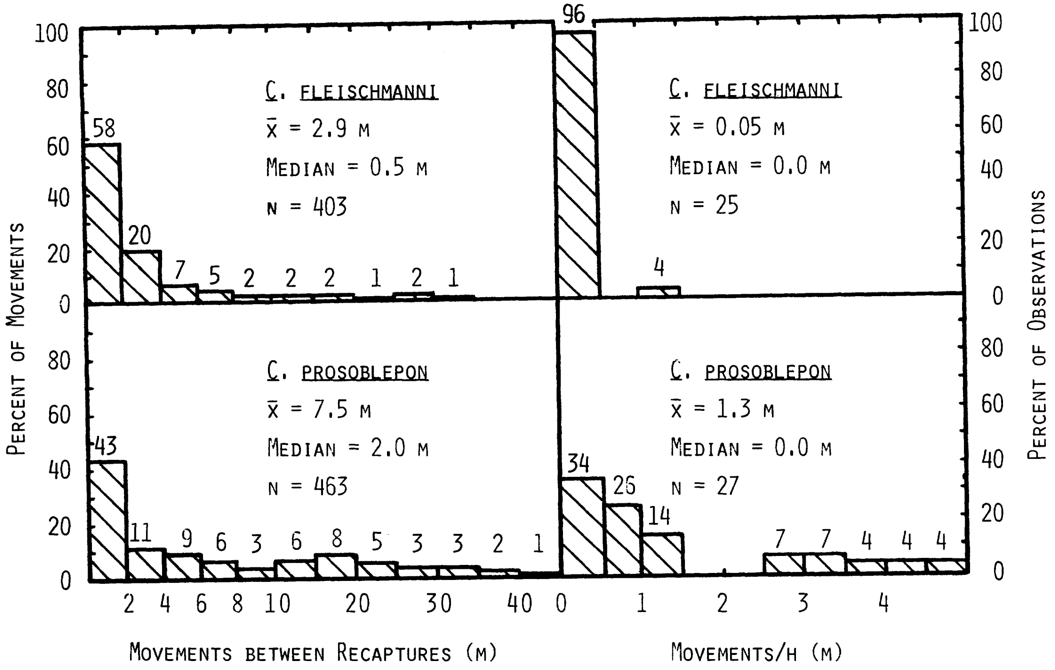

FIG. 1.—Average distances moved by males between sites of recapture and movements of calling males during 1-h time budgets.

Movements.—After the initial marking, individual male *C. fleischmanni* were recaptured from 0–13 times (65% were seen only once). Male *C. prosoblepon* were recaptured from 0–23 times (37% were seen only once). On subsequent nights, recaptured *C. fleischmanni* males were usually found at their original sites, while *C. prosoblepon* males moved greater distances (Mann Whitney *U*-test, $P < 0.001$) (Fig. 1). One hour time budgets were used to determine average distances moved by calling males of both species. Males of *Centrolenella fleischmanni* were generally sedentary, in contrast to the more active *C. prosoblepon* males (Fig. 1).

Aggressive behavior.—Nearest neighbor distances of all males were measured nightly during August. For 265 *C. fleischmanni* males, the average nearest conspe-

TABLE 1.—Characteristics of calls and calling behavior of *C. fleischmanni* and *C. prosoblepon*. Spearman rank correlation (r_s) between pitch and SVL is shown.

Species	Pitch (Hz)	Duration (ms)	r_s	Calling rate (calls/h)
C. fleischmanni				
$\bar{x}$ ± SD	4294 ± 291	0.21 ± 0.03	−0.61**	579 ± 210
Range	3880–4800	0.15–0.30		240–1120
n	27	27		25
C. prosoblepon				
$\bar{x}$ ± SD	5758 ± 232	0.04 ± 0.01	−0.16	17 ± 12
Range	5300–6000	0.025–0.05		1–43
n	10	10		27

** $P < 0.01$.

cific neighbor distance was 4.1 m (SD = 5.4). This was significantly greater than the average nearest conspecific neighbor distance for 324 *C. prosoblepon* males of 3.2 m (SD = 4.2) (Mann Whitney *U*-test, $P < 0.01$).

Violent aggression was rarely observed in either species. I observed 70 occurrences of *C. fleischmanni* males within 0.5 m of each other for longer than 10 min. Physical combat occurred in seven of these cases. Three complete fights lasted from 1–26 min; the remainder were discovered after combat had begun (described by Greer and Wells, 1980). *Centrolenella prosoblepon* males were observed 109 times within 0.5 m of each other for more than 10 min. Of these, only seven encounters resulted in combat, and the one complete fight witnessed lasted only 3 min. Incomplete fights were 3–26 min in duration. All *C. prosoblepon* fights consisted of one or both frogs dangling upside down while holding the vegetation by their hind legs, grappling with each other. This is similar to behavior described for *C. griffithsi* (Duellman and Savitsky, 1976). In both species, combat usually ended when one male dropped to lower vegetation or flattened its body against a leaf. The victor usually continued calling. No physical damage was evident as a result of any of the battles, although several of the contestants moved away slowly and with difficulty.

Courting and Mating Behavior

Behavior of females and mated pairs.— Most females of both species were observed on only one night. Amplexus and egg deposition often occurred at this time. Behavior leading to amplexus in *C. fleischmanni* females consisted of moving around the vegetation and remaining motionless near calling males. This behavior resulted in amplexus 17% of the time ($n = 35$). In these cases, the female nudged the male on his side and crawled beneath him; the male then clasped the female in amplexus (described by Greer and Wells, 1980).

Centrolenella prosoblepon females were never observed surveying the vegetation in the manner of *C. fleischmanni* females. In two observations of activity prior to mating, *C. prosoblepon* males initiated amplexus. In each case, a male jumped onto a nearby female's back. This behavioral difference between species was supported by manipulations, dislodging amplectant pairs and placing the frogs 0.15 m apart. Four *C. fleischmanni* males displaced from amplexus began calling (interspersing advertisement with mating calls) and were again approached and nudged by the females. Four *C. prosoblepon* males also called, but upon detection of the females, leaped onto their backs.

I measured the time and distances moved by many of the amplectant pairs encountered. *Centrolenella fleischmanni* pairs remained in amplexus for an average of 129 min (SD = 111, range = 38–385 min, $n = 14$) and moved 0.8 m (SD = 0.71, range = 0.0–1.9 m, $n = 14$) before oviposition. *Centrolenella prosoblepon* pairs were in amplexus for an average of 174 min (SD = 100, range = 75–321 min, $n = 14$) and moved 4.5 m (SD = 4.7, range = 0.9–17 m, $n = 13$). The time that the two species remained in amplexus was not significantly different (Mann Whitney *U*-test, $U = 73$, $P > 0.05$), but pairs of *C. prosoblepon* moved significantly greater distances ($U = 31$, $P < 0.001$). For *C. fleischmanni*, 82% of the pairs in amplexus were observed before 1230 h. I observed oviposition between 2200 h and 0600 h; 91% occurred between midnight and 0300 ($n = 23$). Nineteen pairs of *C. fleischmanni* observed did not deposit eggs. After remaining in amplexus throughout the night, the male released the stationary female and hopped into the canopy. All oviposition in *C. prosoblepon* occurred after 0230 h. When eggs were deposited, males of both species usually rubbed their hind legs alternately over the females' sides for approximately 10 s. All *C. fleischmanni* eggs were deposited on the undersides of leaves. In contrast, *C.*

TABLE 2.—Comparison of body size, call characteristics, and number of nights in a chorus for successful males (those that obtained at least one mate) and unsuccessful males for *C. fleischmanni* and *C. prosoblepon*. Median values are given.

Species	SVL (mm)	Call pitch (Hz)	Call duration (ms)	No. of nights
C. fleischmanni				
Successful	25.5	4200	0.20	5
Unsuccessful	25.5	4180	0.20	1
P (*U*-test)	>0.05	>0.05	>0.05	<0.001
r_s with no. of matings				0.39**
C. prosoblepon				
Successful	26.5	5900	0.03	5
Unsuccessful	26.5	5650	0.03	2
P (*U*-test)	>0.05	>0.05	>0.05	

** $P < 0.01$.

prosoblepon clutches were deposited on leaf tops and on moss-covered rocks or branches.

Correlates of male mating success.—Mean mating success for 376 male *C. fleischmanni* was 0.14 matings (SD = 0.54) distributed as follows: no matings, 337 (90%); 1 mating, 33 (9%); 2 matings, 5 (1%); 8 matings, 1 (1%). Mean mating success for 257 male *C. prosoblepon* was 0.09 matings (SD = 0.30) distributed as follows: no matings, 234 (91%); 1 mating, 22 (9%); 2 matings, 1 (1%). Table 2 compares body size, calling characteristics, and number of nights at the study site for successful (those that obtained at least one mate) and unsuccessful males for *C. fleischmanni* and *C. prosoblepon*. In both species, successful males were not significantly larger than unsuccessful males, nor were their calling pitch or duration significantly different. Male reproductive success in both species seemed to be primarily determined by the number of nights a male occupied a site. Successful males occupied sites for longer periods. For males of *C. fleischmanni*, there was also a significant correlation between the number of nights spent at a site and the number of matings obtained (Spearman rank correlation, r_s = 0.39, $P < 0.01$).

Parental Care and Larval Survivorship

Parental behavior.—Male behavior after fertilization differed markedly between species. *Centrolenella fleischmanni* males slowly backed off as the female moved upward on the leaf. The males settled on the eggs and began a series of turning movements probably to hydrate the egg clutch (M. Hayes, personal communication). The males spent an average of 30 min (SD = 12.27, n = 17) on the eggs after oviposition. The jelly matrix surrounding the eggs visibly swelled between the time that the eggs were deposited and the male finished his movements. On subsequent nights after oviposition, 35% of the male *C. fleischmanni* returned to their egg clutches and repeated the rotating motions. Twenty-eight instances of egg attendance on subsequent nights were observed between 2000 h and 0230 h, 71% of these occurring after midnight.

This form of paternal care was not displayed by *C. prosoblepon*. Once fertilization was achieved, *C. prosoblepon* males moved ahead of the females and hopped upward into the canopy while giving advertisement calls. All the females remained with their eggs, though their subsequent behavior was variable. Of nine instances of behavior observed after oviposition, four females remained on top of all of the eggs for 10, 45, 124, and 131 min. In the remaining cases, the females covered only part of the clutch for an average of 72 min. During these observations, the females remained motionless. They did not demonstrate the rotating movements exhibited by *C. fleischmanni* males on eggs, nor was there a visible

TABLE 3.—Reproductive biology of four species of *Centrolenella*.

	C. valerioi[1]	*C. colymbiphyllum*[1]	*C. fleischmanni*[2] in Panama	*C. fleischmanni*	*C. prosoblepon*
Number of males	43	83	14	376	257
Number of clutches	112	152	32	124	50
Average clutch size	29	50	27	26	20
Percent of males producing larvae	63	57	—	5	5
Percent of clutches surviving	86	74	72	32	47

[1] Data from McDiarmid, 1978.

[2] Data from Greer and Wells, 1980.

change in the clutch due to a female's attendance. Neither parent returned to the egg clutch on subsequent nights.

Larval survivorship.—Larval survivorship was followed from a sample of clutches, and the effects of parental care and site of egg deposition were evaluated. *Centrolenella fleischmanni* deposited 124 egg clutches from mid-May through late September. *Centrolenella prosoblepon* did not begin ovipositing until later in the season. The first *C. prosoblepon* clutch was deposited 21 June, though 80% of the total 50 clutches were deposited after 15 August. Clutch characteristics are given in Table 3. Clutch deposition was not correlated with daily rainfall in either species (Spearman rank correlation, *C. fleischmanni* $r_s = 0.16$, $P > 0.05$; *C. prosoblepon* $r_s = 0.04$, $P > 0.05$).

During embryonic development, centrolenid larvae became active, turned red, and finally dropped from the leaf. Of 80 *C. fleischmanni* clutches that I followed through development, only 32% (26) were successful (defined as having more than 70% of the larvae disappear from the leaf after turning red). Larval survivorship of *Centrolenella fleischmanni* was not significantly increased by paternal care on nights after the initial laying occurred; 11 of 23 clutches attended by males survived, and 15 of 42 subsequently unattended clutches survived ($\chi^2 = 2.25$, $P > 0.05$, 1 df, $n = 80$). Egg deposition site varied from 0.1–3 m above the ground ($\bar{x} = 1.49$ m, SD = 0.87) and did not influence the fate of a clutch (Mann Whitney *U*-test, $U = 790$, $P > 0.05$).

Of the 50 *C. prosoblepon* clutches deposited in the study site, 30 were followed throughout development. Of these, 47% (14) were successful. In contrast to *C. fleischmanni*, larval survivorship was related to egg deposition site. The average height of egg deposition was 1.13 m (SD = 0.81, range = 0–3 m, $n = 30$). Clutches that survived were significantly lower than those that did not (surviving clutches, $\bar{x} = 0.8$ m, SD = 1.0; dying clutches, $\bar{x} = 1.4$ m, SD = 0.5; Mann Whitney *U*-test, $U = 164.5$, $P < 0.01$). In part, this was due to the choice of moist microhabitats for egg deposition. Five clutches were deposited on a mossy rock bank of the river that had a perpetual water runoff from the surrounding forest. In addition, three clutches were deposited in water-laden moss growing in forked branches of trees.

DISCUSSION

Male Reproductive Success

In some anuran species, it has been demonstrated that male body size or calling characteristics influence reproductive success (e.g., Berven, 1981; Davies and Halliday, 1979; Howard, 1978; Ryan, 1980; Wells, 1979). Neither size nor call pitch or duration increased reproductive success in either centrolenid species. Male reproductive success was simply correlated with the number of nights a male was at the site. Males at the study site for more than one night enjoyed greater reproductive success than those observed only once. Increased success with increased length of

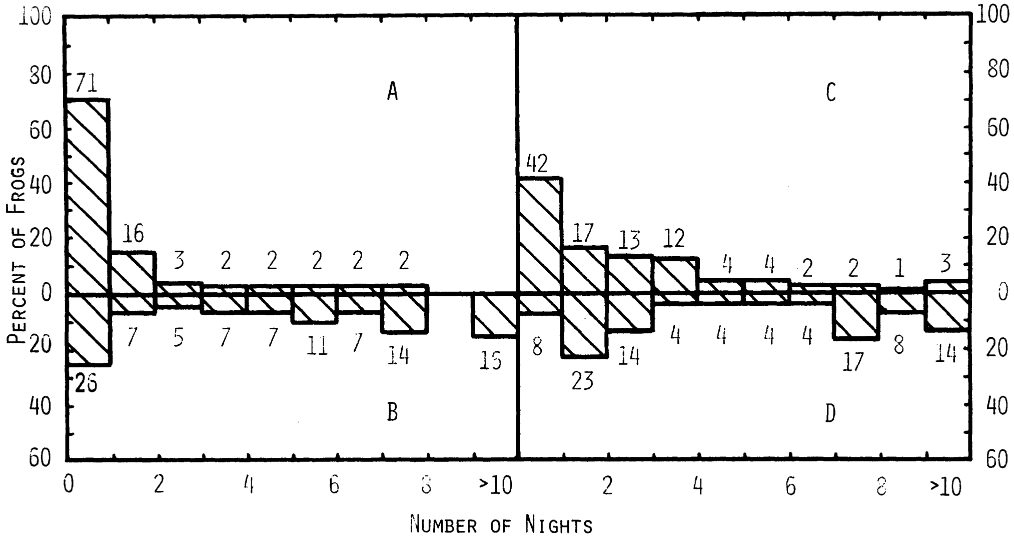

FIG. 2.—Number of nights frogs were observed at the site, by species and reproductive success. (A) *C. fleischmanni* unsuccessful males ($n = 337$). (B) *C. fleischmanni* successful males ($n = 39$). (C) *C. prosoblepon* unsuccessful males ($n = 234$). (D) *C. prosoblepon* successful males ($n = 23$).

residency also was significant for *C. fleischmanni* (Fig. 2). Greer and Wells (1980) observed this association in *C. fleischmanni* in Panama, and it has been reported in other anurans (Kluge, 1981; Woodward, 1982).

Table 3 compares the reproductive success of *C. fleischmanni* and *C. prosoblepon* with two other species of glass frogs (*C. valerioi* and *C. colymbiphyllum*). Males of these species both attend eggs (McDiarmid, 1978). A population of *C. fleischmanni* studied in the lowlands is also included for comparison (Greer and Wells, 1980). The majority of males in these studies produced larvae. In contrast, only 5% of the males in my study successfully produced larvae.

Reproductive Behavior and Larval Survivorship

Egg attendance has been reported in 12 anuran families (Lamotte and Lescure, 1977; McDiarmid, 1978; Salthe and Mecham, 1974; Wells, 1981). Male attendance of eggs has been reported in three species of glass frogs (McDiarmid, 1978; M. Clark, personal communication). Female attendance, as I observed in *C. prosoblepon,* has never been reported in centrolenids. Parental care probably incurs different costs for each sex. The main costs for females may be diminished opportunities to renew energy reserves necessary for producing more offspring (Trivers, 1972; Williams, 1975). Males may have diminished opportunities to mate. Male *C. fleischmanni* did not call while attending eggs, potentially diminishing their opportunity to attract a female. However, males minimized this disadvantage by attending eggs after midnight, when pair formation was less likely. Therefore the chances of missing an opportunity to mate were reduced.

Gross and Shine (1981) found that Williams' (1975) hypothesis that territoriality preadapted a sex for parental care was most consistent with empirical data from amphibians, and Wells (1981) concurred. In a review of *Eleutherodactylus* demonstrating egg attendance, he found an association between male parental care and territorial defense of oviposition sites. In species where females gave parental care, the males called from areas away from oviposition sites. This hypothesis was supported by my study as well. I found a stronger association between males and their embryos among *C. fleischmanni* than among *C. prosoblepon*. Male *C. fleischmanni* showed greater site tenacity. They returned nearer to the same site on subsequent nights relative to *C. prosoblepon*, and they maintained larger nearest neighbor distances. This trend was reflected in their hourly time budgets. *C. fleischmanni* called from one site whereas *C. prosoblepon* were more mobile. Female amplectant behavior also lends credence to the "association" hypothesis. *C. fleischmanni* females seldom moved once in amplexus and deposited eggs at the male's calling site. *C. prosoblepon* females moved greater distances, often ovipositing several meters from the male's calling site.

During the course of this study, paternal care by *C. fleischmanni* did not significantly increase larval survivorship. However, under a different climatic regime it may be significant. In 1982, the month of May was the wettest in 22 years (J. Campbell, personal communication). The rainy season usually gets progressively wetter until it reaches a peak in September–October. This typical weather pattern may be reflected in the dates of clutch deposition of the two species. *C. fleischmanni* deposited eggs throughout the study. If their paternal care functions in hydrating the eggs (M. Hayes, personal communication), this permits an extended breeding period. Reliance on rain is diminished. In contrast to this, most eggs of *C. prosoblepon* were deposited from mid-August to mid-September, a time of more consistent rain. It is also possible that a certain number of rainy days must pass before *C. prosoblepon* are stimulated to lay eggs. The relatively extended breeding period of *C. fleischmanni* may confer an advantage to the offspring born early in the season. Villa (1977) found that larval parasitism by frogflies (*Drosophila* sp.) increased as the season progressed. Egg attendance by *C. prosoblepon* females was highly variable and appeared ineffectual. Eggs seemed unchanged after female care. This behavior may be insignificant, as Woodruff (1976) has suggested for *Pseudophryne* egg attendance. Table 3 shows that larval survivorship was relatively higher for *C. prosoblepon* than for *C. fleischmanni*.

Acknowledgments.—I thank M. Crump for advice in the field and helpful comments on various drafts of this manuscript. K. Wells, J. Robinson, C. Lanciani, B. Patterson, R. Jaeger, and an anonymous reviewer provided critical review of the manuscript. I am grateful to N. Hamilton for field assistance, M. Hayes for rainfall data and fieldwork, J. Campbell for humidity data, P. May for computational assistance, T. Webber for sound advice, C. Saltzman for field assistance, B. Jacobson for graphics work, and B. Busby, B. Alverson, and B. Lawton for botanical identification. I also thank S. Wermen for working with me on a preliminary study, and R. Buskirk and O.T.S. for introducing me to centrolenids. This research was funded by a Noyes Foundation grant and a travel award from the Department of Zoology, University of Florida. Sound recording equipment was provided by the Florida State Museum.

LITERATURE CITED

BERVEN, K. A. 1981. Mate choice in the woodfrog, *Rana sylvatica*. Evolution 35:707–722.

DAVIES, N. B., AND T. R. HALLIDAY. 1979. Competitive mate searching in male common toads, *Bufo bufo*. Anim. Behav. 27:1253–1267.

DUELLMAN, W. E., AND A. H. SAVITSKY. 1976. Aggressive behavior in a centrolenid frog, with comments on territoriality in anurans. Herpetologica 32:401–404.

GREER, B. J., AND K. D. WELLS. 1980. Territorial and reproductive behavior of the tropical American frog *Centrolenella fleischmanni*. Herpetologica 36:318–326.

GROSS, M. R., AND R. SHINE. 1981. Parental care and mode of fertilization in ectothermic vertebrates. Evolution 35:775–793.

HOLDRIDGE, L. 1967. Life Zone Ecology. Tropical Science Center, San Jose, Costa Rica.

HOWARD, R. D. 1978. The evolution of mating strategies in bullfrogs, *Rana catesbeiana*. Evolution 32:850–871.

KLUGE, A. G. 1981. The life history, social organization, and parental behavior of *Hyla rosenbergi* Boulenger, a nest-building gladiator frog. Misc. Publ. Mus. Zool. Univ. Michigan 160:1–170.

LAMOTTE, M., AND J. LESCURE. 1977. Tendances adaptives à l'affranchissement du milieu aquatique chez les amphibiens anoures. Terre Vie 31:225–311.

McDiarmid, R. W. 1978. Evolution of parental care in frogs. Pp. 127–147. *In* G. M. Burghardt and M. Bekoff (Eds.), The Development of Behavior. Garland Press, New York.

Ryan, M. J. 1980. Female mate choice in a neotropical frog. Science 209:523–525.

Salthe, S. N., and J. S. Mecham. 1974. Reproductive and courtship patterns. Pp. 309–521. *In* B. Lofts (Ed.), Physiology of the Amphibia, Vol. 2. Academic Press, New York.

Savage, J. M. 1967. A new tree-frog (Centrolenidae) from Costa Rica. Copeia 1967:325–331.

Savage, J. M., and P. H. Starrett. 1967. A new fringe-limbed tree-frog (family Centrolenidae) from lower Central America. Copeia 1967:604–609.

Siegel, S. 1956. Nonparametric Statistics for the Behavioral Sciences. McGraw-Hill, New York.

Starrett, P., and J. M. Savage. 1973. The systematic status and distribution of Costa Rican glassfrogs, genus *Centrolenella* (family Centrolenidae), with description of a new species. Bull. So. California Acad. Sci. 72:57–78.

Trivers, R. L. 1972. Parental investment and sexual selection. Pp. 126–179. *In* B. Campbell (Ed.), Sexual Selection and the Descent of Man, 1871–1971. Aldine, Chicago.

Villa, J. 1977. A symbiotic relationship between frog (Amphibia, Anura, Centrolenidae) and fly larvae (Drosophilidae). J. Herpetol. 11:317–322.

———. 1984. Biology of a neotropical glass frog, *Centrolenella fleischmanni* (Boettger), with special reference to its frogfly associates. Milwaukee Public Mus. Contrib. Bio. Geol. 55:1–60.

Wells, K. D. 1979. Reproductive behavior and male mating success in a neotropical toad, *Bufo typhonius*. Biotropica 11:301–307.

———. 1981. Parental behavior of male and female frogs. Pp. 184–197. *In* R. D. Alexander and D. W. Tinkle (Eds.), Natural Selection and Social Behavior: Recent Research and New Theory. Chiron Press, New York.

Williams, G. C. 1975. Sex and Evolution. Princeton University Press, New Jersey.

Woodruff, D. S. 1976. Courtship, reproductive rates, and mating systems in three Australian *Pseudophryne* (Amphibia, Anura, Leptodactylidae). J. Herpetol. 10:313–318.

Woodward, B. D. 1982. Male persistence and mating success in Woodhouse's toad (*Bufo woodhousei*). Ecology 63:583–585.

Accepted: 8 April 1985
Associate Editor: Kentwood Wells

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Herpetologica, 41(4), 1985, 404–407

CALL RATE AND AEROBIC CAPACITY IN WOODHOUSE'S TOAD (*BUFO WOODHOUSEI*)

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Abstract: In *Bufo woodhousei*, females prefer as mates males with high call rates. We determined call rate and maximum aerobic capacity ($\dot{V}_{O_2}$ max) for 16 male *B. woodhousei*. $\dot{V}_{O_2}$ max was not significantly correlated with call rate. Our results do not support the hypothesis that male call rate is limited by aerobic capacity.

Key words: Amphibia; Anura; Bufonidae; *Bufo woodhousei*; Female choice; Call rate; Aerobic capacity

Woodhouse's toad (*Bufo woodhousei*) provides an example of female choice in mate selection. In the population that we studied in central Arizona, a lek mating system is used during a prolonged breeding period (typically February–June; see Sullivan, 1982). On each night of breeding activity, 2–25 males will form a chorus