
Breeding Biology of the Gopher Frog, *Rana capito*, in Western Florida

Author(s): John G. Palis

Source: *Journal of Herpetology*, Jun., 1998, Vol. 32, No. 2 (Jun., 1998), pp. 217-223

Published by: Society for the Study of Amphibians and Reptiles

Stable URL: <https://www.jstor.org/stable/1565300>

REFERENCES

Linked references are available on JSTOR for this article:

https://www.jstor.org/stable/1565300?seq=1&cid=pdf-reference#references_tab_contents

You may need to log in to JSTOR to access the linked references.

JSTOR is a not-for-profit service that helps scholars, researchers, and students discover, use, and build upon a wide range of content in a trusted digital archive. We use information technology and tools to increase productivity and facilitate new forms of scholarship. For more information about JSTOR, please contact support@jstor.org.

Your use of the JSTOR archive indicates your acceptance of the Terms & Conditions of Use, available at <https://about.jstor.org/terms>



is collaborating with JSTOR to digitize, preserve and extend access to *Journal of Herpetology*

JSTOR

Breeding Biology of the Gopher Frog, *Rana capito*, in Western Florida

JOHN G. PALIS

529 North Main Street, Jonesboro, Illinois 62952, USA

ABSTRACT.—The breeding biology of *Rana capito* was studied for one breeding season at a 1.2 ha pond in Okaloosa County, Florida. Frog movement was monitored with a drift fence and pitfall traps and egg deposition site selection was examined using wading surveys. A total of 301 unmarked adult frogs was captured, nearly half in February. Movement of immigrating frogs was positively correlated with rainfall. Frogs that entered and exited the pond only once, exited within an average of 38.5 m from the point of entry. Males spent more time in the basin than females and multiple-recaptured males stayed in the basin longer than single-recaptured males. Overall, the sex ratio did not differ from parity; however, nightly operational sex ratios were overwhelmingly male-biased. The eight-month breeding season (October through May) encompassed three major breeding events (one each in October, February, and April). A total of 146 complete egg masses was found, 67 of which contained an average of 2210 eggs. Frogs oviposited non-randomly, preferring rigid, vertical stems upon which to lay eggs. Each female deposited one egg mass.

The gopher frog, *Rana capito*, is considered rare throughout its range (Martof, et al. 1980; Means, 1986; Dundee and Rossman, 1989; Godley, 1992), with habitat loss regarded as the greatest threat to its existence (Bailey, 1991). The terrestrial stage of the life cycle is threatened by habitat degradation or loss resulting from fire suppression, or habitat loss as a consequence of conversion for agriculture, plantation forestry, and real estate development. The larval stage is threatened by breeding site degradation due to drainage, siltation from road run-off, stocking of predatory fishes, and off-road vehicle use.

Although various facets of its ecology have been investigated (Volpe, 1958; Franz, 1986; Bailey, 1990; Semlitsch et al., 1995), the natural history of *R. capito* remains poorly known. The only quantitative ecological study of *R. capito* was by Bailey (1990), who examined population size and structure, and environmental factors influencing movement of *R. capito* at a breeding site in Alabama. A better understanding of the breeding biology of *R. capito* is needed to address its conservation needs. My study was designed to gather data on (1) *R. capito* breeding migrations and breeding population size and structure, (2) the number of egg masses deposited per female, and (3) female oviposition site selection.

MATERIALS AND METHODS

Rana capito breeding biology was examined at Holley Pond, an isolated 1.2 ha depression marsh (Florida Natural Areas Inventory, 1990) on Eglin Air Force Base, Okaloosa County, Florida. Holley Pond is dominated by herbaceous vegetation, principally maidencane (*Panicum hemitomon*), spikerushes (*Eleocharis* spp.), hatpins

(*Eriocaulon compressum*), bog-moss (*Mayaca fluviatilis*), floating hearts (*Nymphoides aquatica*), centella (*Centella erecta*), yellow-eyed grass (*Xyris* sp.), and panic grass (*Panicum* sp.). Holley Pond typically dries annually, and is comprised of three sub-basins that are connected at high water. Holley Pond occurs within an extensive, fire-suppressed longleaf pine (*Pinus palustris*)-turkey oak (*Quercus laevis*) sandhill, and is immediately bordered by a narrow band of longleaf pine-live oak (*Quercus virginiana*) flatwoods.

Frog movement into and out of Holley Pond was studied from 20 October 1994 to 19 May 1995 using a drift fence and pitfall traps. The drift fence was constructed from 30.5 m long \times 0.9 m high rolls of black polypropylene silt-fencing, the bottom 15 cm of which was buried in the soil to prevent animals from burrowing beneath the fence. The ends of adjoining rolls were overlapped and secured with staples. Wooden stakes were used to support the fence. The fence, which completely encircled the pond, was 483 m long and an average of 15 m (range = 6–26 m) from the pond edge. Forty-seven pairs of 19 l plastic buckets were sunk flush against both sides of the fence at approximately 10 m intervals. Each bucket was filled with water to a depth of approximately 2.5 cm and furnished with a sponge to provide cover for trapped animals and moisture if the water evaporated.

With few exceptions, traps were checked daily in the morning and occasionally at night during peaks of frog migration. Buckets were covered on days when pitfalls were not checked. Frogs were measured with a plastic rule to the nearest mm (SVL) while flattened on their back, weighed to the nearest 0.5 gram with Pesola

spring scales, and individually marked with a unique combination of toe clips. Scissors were dipped in alcohol before and after each use to prevent infection (Donnelly, et al., 1994). Thumbs and adjacent toes on the forelimbs were not clipped. Sex was determined by presence or absence of vocal sacs. Sex was recorded as unknown if sex could not positively be determined. Using external appearance, females were scored as gravid (taut, fully distended abdomen) or non-gravid (flaccid, attenuated abdomen). Immigrating frogs were released into the pond, emigrating frogs were released outside the fence. Recaptures were identified, reweighed, and immediately released on the opposite side of the fence. Water temperature, maximum water depth (measured at a permanent gauge), total precipitation, and maximum and minimum air temperatures from the previous 24 h, were recorded at the study site each trap day.

Surveys for egg masses were made from 3 October 1994 to 26 April 1995. Egg masses were located by slowly wading through the pond following immigration of gravid females. Maximum water depth (cm), depth of the top of the egg mass from the surface (cm), distance of the bottom of the egg mass from the substrate (cm), distance from the nearest egg mass (m), and the plant species used for support were recorded for each egg mass. The distance between egg masses was measured to discern whether *R. capito* behaved similarly to *R. utricularia* and deposited eggs closer together in colder water than warmer water (Caldwell, 1986). To determine whether females oviposited preferentially on particular plant species or oviposited on vegetation in proportion to its availability, I compared plant species used by frogs with those identified at 100 randomly chosen points along ten 25-m transects arranged to include all microhabitat types. Clutch size was determined by volumetric displacement of egg masses (Davis and Folkerts, 1986). Volumetric displacement was obtained by placing an egg mass into a 1-L graduated cylinder containing a known volume of water. The volume of water displaced by each egg mass was multiplied by a standard displacement volume, previously determined by counting the number of eggs necessary to displace one ml of water in a 100 ml graduated cylinder. Actual clutch counts of six egg masses differed from volumetric estimates by an average of $\pm 16.0\%$ (range = 1.9–25.1%). Egg masses were returned to their original location attached to wire survey flags.

I used Spearman-Rank correlations to examine associations between frog movement and weather variables, t-tests and chi-square tests to make pairwise comparisons, and ANOVA to test for differences in egg mass parameters among months. Non-parametric tests were used

TABLE 1. Summary of monthly captures of immigrating and emigrating adult *Rana capito* captured at the Holley Pond drift fence.

Month	Immigration			Emigration		
	Cap-tures	Recap-tures	Total	Cap-tures	Recap-tures	Total
Oct	12	3	15	16	5	21
Nov	0	4	4	10	6	16
Dec	11	3	14	5	7	12
Jan	38	8	46	0	3	3
Feb	144	31	175	4	170	174
Mar	4	3	7	0	35	35
Apr	39	47	86	1	40	41
May	2	1	3	3	11	14
Total	250	100	350	39	277	316

when the assumption of normality was violated. Using cumulative captures and recaptures of frogs entering and exiting the basin, I estimated nightly operational sex ratios (OSR; the “ratio of fertilizable females to sexually active males” [Emlen and Oring, 1977]) for each night frogs moved. Unmarked frogs captured exiting the pond through 11 December were presumed to have entered the basin in October prior to the emplacement of the drift fence and were added to nightly sex ratio estimates of previous dates. Although unmarked males emigrating in February (N = 1) and April (N = 4) may have entered the basin in October, they were not added to previous nightly totals because had they entered in October, their stay in the basin extended beyond the documented length of time other recaptured frogs stayed in the basin. Using the compass orientation of each pitfall trap, I used the Raleigh test (Batschelet, 1981) to determine if the 146 frogs that entered and exited the basin only once immigrated randomly. I applied the methodology of Shoop and Doty (1972) to determine if these same frogs emigrated in the direction of immigration.

RESULTS

Movement Patterns.—A total of 301 adult *R. capito* was captured at Holley Pond, 12 initially in the pond before the drift fence was complete and 289 initially at the drift fence (Table 1). Frogs bred just prior to the emplacement of the drift fence in response to a tropical storm which passed over Eglin AFB on 1–2 October. The largest documented movement of adult frogs occurred in February when nearly half (49.1%) of all unmarked frogs were captured. Adult frogs moved in and out of the basin on 60 nights, but large immigrations (>10 frogs) occurred on only nine nights. Males and females immigrated simultaneously but males typically arrived in greater numbers than females (Table 2). Thirty-

TABLE 2. Number of adult male and female *R. capito* entering Holley Pond during relatively large ($N > 10$ frogs) immigration waves.

	Oct	Dec	Jan	Feb				Apr	
	14	04	28	12	15	16	18	12	13
Males	7	11	25	26	10	43	5	48	6
Females	4	1	2	6	3	44	9	16	5

one metamorphs were captured emigrating between 2–19 May.

Adult frogs migrated principally on rainy (mean rain accumulation = 18.6 mm, range = 0–120 mm) nights. Rain, the only environmental variable significantly correlated with the number of adults (unmarked and marked) intercepted at the drift fence, was correlated with the total number of adults and the number of immigrating adults, but not with the number of emigrating adults (Table 3). Catches of 10 or more adult frogs occurred on 18 nights when 0–120 mm (mean = 16.1 mm) of rain fell.

Examination of arrival and departure dates of frogs that entered and exited the basin only once revealed that males (mean ± 1 SD = 14.6 \pm 18.11 d, range = 1–78 d, $N = 56$) spent more time than females (mean = 9.5 \pm 13.85 d, range = 1–95 d, $N = 85$) in the basin (Mann-Whitney U-test, $U = 2.2$, $P = 0.02$). Of 66 males that reentered the basin 1–3 times, 11 (16.6%) that were first captured in October were recaptured as late as April. Twenty-one of these had a com-

TABLE 3. Spearman-Rank correlations among environmental variables and the number of adult *R. capito* captured at Holley Pond. Significant correlations ($P < 0.01$) are indicated by an asterisk.

	Rain	Max. temp.	Min. temp.
Total frogs ($N = 166$)	0.395*	0.013	0.163
Immigrating frogs ($N = 166$)	0.439*	0.006	0.127
Emigrating frogs ($N = 166$)	0.134	0.025	0.110

plete known history of entry/exit dates. These males spent a mean of 27 \pm 27.61 d (range = 5–135 d) in the basin, which is significantly longer than males that entered and exited once (Mann-Whitney U-test, $U = 3.2$, $P = 0.001$).

Population structure.—The sex ratio for all adult frogs (0.85:1; F:M) did not differ significantly from 1:1 ($\chi^2 = 1.96$, $df = 1$, $P > 0.5$). Estimates of nightly OSRs, however, were male-biased on 56 nights (0.17:1–0.63:1; $\chi^2 = 3.85$ –37.09, $df = 1$, $P < 0.05$), but no different from parity on four nights (0.5:1–0.66:1; $\chi^2 = 1.33$ –3.35, $df = 1$, $P > 0.05$).

Adult females were significantly larger than adult males ($t = 18.61$, $df = 291$, $P < 0.001$; Table 4). Females were significantly heavier than males whether gravid ($t = 18.8$, $df = 275$, $P < 0.001$) or not gravid ($t = 6.3$, $df = 253$, $P < 0.001$; Table 4). Single-captured males (entered

TABLE 4. Measurements of adult *R. capito* captured at Holley Pond (SVL in mm, mass in g). For each category the mean is followed by ± 1 SD, the range, and the sample size in parentheses. The mass of females and males is that at initial capture. The weight loss of multiple-recaptured males is their greatest weight loss.

Sex	Mean SVL	Mean mass	Mean mass loss	Mean % mass loss
Females	93.5 \pm 7.00	93.0 \pm 22.46	—	—
	78.0–112.0	54.5–151.0	—	—
	(135)	(134)	—	—
Gravid females	93.5 \pm 6.85	95.5 \pm 22.46	24.3 \pm 10.76	26.6 \pm 8.08
	79.0–111.0	56.0–151.0	8.5–54.0	10.5–44.0
	(119)	(119)	(76)	(76)
Spent females	91.8 \pm 6.32	66.4 \pm 12.01	—	—
	76.0–110.0	43.0–94.0	—	—
	(96)	(96)	—	—
Males	80.2 \pm 5.24	57.6 \pm 10.08	—	—
	61.0–93.0	29.0–84.0	—	—
	(158)	(158)	—	—
Single-recap males	79.9 \pm 5.30	57.0 \pm 10.56	3.2 \pm 2.20	5.8 \pm 4.19
	69.0–93.0	33.0–82.0	0.0–9.0	0.0–16.3
	(53)	(53)	(49)	(49)
Multiple-recap males	80.6 \pm 5.35	59.3 \pm 10.30	5.7 \pm 3.37	9.7 \pm 5.50
	61.0–90.0	29.0–77.5	0.0–14.0	0.0–22.8
	(55)	(55)	(53)	(53)

TABLE 5. Summary of egg mass parameters measured at Holley Pond. For each category the mean is followed by ± 1 SD and the range. All values are in cm except for the gap between egg masses (m).

Month	Water depth	Egg mass depth from surface	Egg mass depth from substrate	Gap between egg masses
Oct (N = 66)	59.1 \pm 11.18 33.0–78.0	4.6 \pm 4.58 0.0–20.0	44.5 \pm 11.36 22.0–71.0	2.8 \pm 1.91 0.6–9.4
Feb (N = 76)	30.3 \pm 6.97 19.0–49.5	3.7 \pm 3.77 0.0–20.0	18.3 \pm 6.00 8.0–36.0	2.5 \pm 3.00 0.0–18.0
Apr (N = 17)	33.5 \pm 10.41 17.0–62.0	2.1 \pm 2.74 0.0–8.0	21.9 \pm 8.68 7.0–40.0	3.7 \pm 3.96 1.3–16.9

and exited once) did not differ from multiple-captured males in SVL or weight (SVL: $t = -0.68$, $df = 106$, $P = 0.5$; weight: $t = -1.11$, $df = 106$, $P = 0.26$; Table 4). Snout-vent length and weight were significantly correlated for both males ($r = 0.66$, $P < 0.001$, $N = 158$) and females ($r = 0.64$, $P < 0.001$, $N = 134$).

Pre- and post-oviposition weights were obtained for 76 females captured entering the basin gravid and exiting spent. Females were significantly heavier when gravid (mean = 88.7 \pm 17.83 g, range = 56.0–137.0 g) than spent (mean = 64.4 \pm 11.65 g, range = 43.0–93.0 g; $t = 9.94$, $df = 150$, $P < 0.001$). On average, females lost 24.3 \pm 10.76 g after oviposition, or 26.6% of their pre-oviposition body weight (Table 4). Combined, single- and multiple-recaptured males lost a mean of 4.5 \pm 3.12 g (7.8%) of their initial capture weight. Multiple-recaptured males lost significantly more weight than single-recapture males ($t = -4.41$, $df = 100$, $P < 0.001$) (Table 4).

A total of 31 metamorphs was captured emigrating from 2–19 May. The mean SVL and weight of metamorphs was 34.2 \pm 1.61 mm (range = 31.0–38.0 mm) and 4.1 \pm 0.62 g (range = 3.0–5.5 g). Metamorphs were likely from eggs deposited in October (developing tadpoles were periodically dipnetted and examined from October through May). Additional tadpoles remained in the pond when the drift fence was removed.

Homing and Habitat Preference.—I compared the observed average number of traps between arrival and departure points (mean = 3.85 \pm 3.841 traps) for frogs that entered and exited only once to the expected average number of traps between entry and exit points if the direction of departure was random (mean = 11.74 traps). Frogs exited in directions significantly closer to their entry points than if departure was random ($t = 24.8$, $df = 145$, $P < 0.001$). Nearly 9% of frogs ($N = 13$) exited at their entry point, 22% ($N = 32$) were captured 10 m from their point of entry, and 12% ($N = 18$) exited 20 m of their entry point. Sixty percent of the frogs ($N = 88$) departed within 30 m of their entry point. Distance between entry and exit points

did not differ between males (mean = 3.1 \pm 2.65 traps, $N = 56$) and females (mean = 4.4 \pm 4.43 traps, $N = 85$; Mann-Whitney U-test, $U = 1.6$, $P = 0.11$). Frogs immigrated non-randomly with respect to direction (Raleigh $R = 0.147$, $Z = 3.17$, $P < 0.05$); proportionally more frogs immigrated from the west (42%) than from any other direction.

Oviposition Site Selection and Clutch Size.—Frogs did not oviposit on vegetation in proportion to its availability in October ($\chi^2 = 83.02$, $df = 3$, $P < 0.001$), February ($\chi^2 = 117.59$, $df = 2$, $P < 0.001$), or April. Sixty-six egg masses were located between 3 and 6 October (Table 5). These egg masses were most commonly attached to stems of beakrush (*Rhynchospora inundata*; 33%), maidencane (28%), and spikerush (*Eleocharis elongata*; 22%), but also to yellow-eyed grass, broomsedge (*Andropogon* sp.), and St. John's-wort (*Hypericum myrtifolium*). Between 8 and 19 February, egg masses were attached principally to stems of maidencane (59%) and spikerush (26%). The remaining 15% were affixed to stems of beakrush, yellow-eyed grass, hatpins, and floating hearts. One egg mass was attached to a metal flag marking the location of an egg mass laid in October. Between 15 and 26 April, all egg masses but one were attached to newly sprouted flowering scapes of hatpins (94%), which was encountered 57% of the time during random sampling. The remaining egg mass was affixed to the stem of maidencane.

Average clutch size of 67 egg masses volumetrically displaced between October and April was 2210 \pm 1114.1 eggs (range = 540–4825 eggs). Multiplying the average number of eggs per mass by the 146 complete egg masses found (fourteen smaller, partial egg masses excluded), yields approximately 322,660 eggs laid between October and May.

In October, egg masses were deposited in deeper water ($F_{2,156} = 178.0$, $P < 0.001$) and further from the pond bottom ($F_{2,155} = 159.6$, $P < 0.001$) than in February or April (Table 5). This is apparently a result of deeper water in October (>1 m) than at any other time during the study

period. In February, mean water depth during the eight-day egg laying period averaged 71.5 cm (range = 69–73 cm), whereas in April, water depth was 84 cm on the 17th, the day 88% of the eggs were laid. Even though frogs oviposited in deeper water in October than during February or April, egg mass depth below the surface did not vary significantly among months ($F_{2,155} = 2.5$, $P = 0.08$; Table 5). Overall, egg masses ($N = 159$) were deposited 3.94 cm (range = 0–20 cm) below the surface.

Water temperature was not measured when eggs were laid in October. In February, water temperature averaged 18 C (range = 15–22 C) during the eight-day egg laying period, and in April, water temperature averaged 24 C (range = 23–26 C) on the three days eggs were laid. The distance between egg masses differed significantly among months (Kruskal-Wallis test, $P = 0.02$; Table 5).

Comparing the number of complete egg masses observed in February ($N = 71$) with the number of females that entered gravid between December and February, and then emigrated spent in February and the beginning of March ($N = 71$), suggests that each female deposits a single egg mass. The following observations, however, indicate that the number of egg masses observed do not necessarily equal the number of breeding females: five emigrating females were still gravid; the sex of four emigrating frogs could not be positively determined (i.e., they may have been females), and 12 females that entered the basin were not recaptured emigrating (possible mortality).

DISCUSSION

Rana capito bred during three temporally discrete periods during the eight-month breeding season at Holley Pond. Bailey (1990) and Semlitsch et al (1995) observed four and two *R. capito* migration pulses, respectively. As documented by Bailey (1990), *R. capito* moved on damp (usually rainy) nights. Gibbons and Bennett (1974) also determined that terrestrial movement of 16 frog species was correlated with rainfall.

Throughout much of its range, the breeding season of *R. capito* is typically described as December through April (Mount, 1975; Franz, 1986; Ashton and Ashton, 1988; Dundee and Rossman, 1989; Bailey, 1991; Semlitsch et al., 1995; A. Braswell, pers. comm.). In northern Florida and southern Alabama, however, *R. capito* has been observed breeding in September (M. Bailey, pers. comm.) and November (C. K. Dodd, Jr., pers. comm.). *Rana capito* often breeds in summer in central and southern Florida (Godley, 1992), and has been heard calling year-round in South Carolina (S. Bennett, pers. comm.). At

Holley Pond, *R. capito* bred from October through May, the period of study. Although the typical breeding season of *R. capito* throughout most of its range may be December–April, some individuals are apparently capable of breeding at other times of the year following heavy rains as suggested by Means (1986).

Corroborating Bailey's (1990) observations, I found that male *R. capito* remained in the pond longer than females. Similar observations have been made with the congeners *R. temporaria* (Elmberg, 1990) and *R. aurora* (Calef, 1973). The greater number of days males spent in the pond, combined with the number of males that re-entered the pond, contributed to the male-biased OSR. Males may have spent more time in the basin to increase their chance of obtaining a mate (Woodward, 1982; Godwin and Roble, 1983; Gerhardt, et al., 1987) and/or because they may be capable of mating more than once a year (Wells, 1977; Howard, 1978). Male-biased sex ratios can induce aggressive male encounters (Howard, 1980), for which there is anecdotal evidence in *Rana capito* (Doody et al., 1995).

Like Holley Pond frogs, *R. capito* studied by Bailey (1990) emigrated in the direction of immigration. The tendency to emigrate in the direction of immigration suggests that *R. capito* possesses the ability to home to and from a particular terrestrial retreat. This would be advantageous because *R. capito* inhabits burrows of other animals outside the breeding season (Gentry and Smith, 1968; Lee, 1968; Franz, 1986). Proportionally more frogs immigrated to Holley Pond from the west, the direction of an extensive bombing range maintained in an early successional, graminaceous oldfield stage by roller chopping. Perhaps more frogs found shelter there than elsewhere in the surrounding uplands due to the presence of a relatively large number of *Peromyscus polionotus* burrows (Palis, unpubl. data).

If, as it appeared, metamorphs captured emigrating in May were from eggs deposited in October, then the larval period was seven months, the longest observed for *R. capito* (Volpe, 1958; Semlitsch et al., 1995). Volpe's (1958) laboratory-raised larvae metamorphosed in 141–155 d (4.7–5.16 mo) at an average water temperature of 20 ± 3 C. The longer larval period at Holley Pond may be due to cooler water temperatures (18.1 ± 4.9 C). Applying the average growth rate of *R. capito* (1.5 mm per mo; Franz, 1986) to Holley Pond metamorphs, while assuming that growth rates of males and females do not differ and that all frogs entering Holley Pond were sexually mature, suggests that males are capable of attaining sexual maturity as early as approximately 18 months following metamorphosis and females in approximately 29 months.

Although there was a significant difference in

the average distance between egg masses among months, egg masses were never deposited close enough to be considered communal (Caldwell, 1986). The difference in distance between egg masses among months may be the result of variation in the distribution of rigid vertical supports and the number of egg masses deposited.

Female *R. capito* appeared to choose similar egg mass attachment substrates throughout the breeding season, but in different proportions depending upon availability of particular vegetation types. For example, beakrush was used frequently in October because it was inundated by high water and it had not yet decomposed. During the February and April egg laying periods, however, very little beakrush was inundated so other plant species were used for egg mass attachment. A parallel example exists for hatpins. Very few flowering scapes of hatpins persisted into October and February but, by April, newly sprouted flowering scapes were ubiquitous throughout the pond. As observed in other studies (Wright, 1931; Bailey, 1990; J. Young, pers. comm.), Holley Pond *R. capito* chose rigid, vertical supports upon which to oviposit.

Rana capito oviposits near the surface in relatively shallow water (this study; Wright, 1931; Bailey, 1990). Oviposition near the surface may confer some advantage to embryos because surface water warms faster than subsurface water hastening the development rate of embryos (Brodman, 1995). Oviposition on rigid supports would keep egg masses at depths chosen by the females.

Determining the number of egg masses laid by each female has practical applications to *R. capito* surveys because such surveys often rely on counts of egg masses. Because each female deposits one egg mass, counting the number of egg masses may provide an inexpensive means of estimating the number of females that oviposited. However, because the number of egg masses observed may be less than the number of females present (this study; R. Seigel, pers. comm.), egg mass counts should be considered only a rough estimate of the total number of females that entered the pond to breed.

Clearly, additional studies of the breeding biology of *R. capito* are needed. The advantages of oviposition site selection to embryos needs to be determined, and male-male and male-female interactions at the breeding site needs study.

Acknowledgments.—Funds were provided by the U.S. Department of Defense Legacy Resource Management Program through a contract with The Nature Conservancy administered by the Florida Natural Areas Inventory. I thank C. Petrick and D. Atencio for on-site sup-

port; J. Hamilton, J. Jensen, J. Johnson, L. Philips, S. Pritchard, and D. Teague for constructing the drift fence; J. Jensen for routinely checking pitfall traps and collecting other data; J. Bell, P. Gault, C. Nordman, and D. Printiss for occasional field assistance; R. Seigel and C. K. Dodd, Jr. for advice on data analysis; M. Bailey, K. Dodd, M. Parris, R. Semlitsch, and two anonymous reviewers for commenting on an earlier draft of this manuscript; and P. York for support during manuscript preparation. Portions of the manuscript, presented as a report to Eglin Air Force Base, benefited from the comments of D. Jackson. This work was authorized under Florida Game and Fresh Water Fish Commission permit WV93057.

LITERATURE CITED

- ASHTON, R. E., JR., AND P. S. ASHTON. 1988. Handbook of Reptiles and Amphibians of Florida, Part Three: The Amphibians. Windward Publishing, Miami, Florida.
- BAILEY, M. A. 1990. Movement of the dusky gopher frog (*Rana areolata sevosia*) at a temporary pond in the lower coastal plain of Alabama. In C. K. Dodd, Jr., R. E. Ashton, Jr., R. Franz, and E. Wester (eds.), Proc. Eighth Ann. Mtg. Gopher Tortoise Council, pp. 27–43. Florida Mus. Nat. Hist., Gainesville.
- BAILEY, M. A. 1991. The dusky gopher frog in Alabama. *J. Alabama Acad. Sci.* 62:28–34.
- BATSCHLEET, E. 1981. Circular Statistics in Biology. Academic Press, London.
- BRODMAN, R. 1995. Annual variation in breeding success of two syntopic species of *Ambystoma* salamanders. *J. Herpetol.* 29:111–113.
- CALDWELL, J. P. 1986. Selection of egg deposition sites: a seasonal shift in the southern leopard frog, *Rana sphenoccephala*. *Copeia* 1986:249–253.
- CALEF, G. W. 1973. Spatial distribution and “effective” breeding population of red-legged frogs (*Rana aurora*) in Marion Lake, British Columbia. *Can. Field Nat.* 87:279–284.
- DAVIS, M. S., AND G. W. FOLKERTS. 1986. Life history of the wood frog, *Rana sylvatica*, Le Conte (Amphibia: Ranidae) in Alabama. *Brimleyana* 12:29–50.
- DONNELLY, M. A., C. GUYER, J. E. JUTERBOCK, AND R. A. ALFORD. 1994. Techniques for marking amphibians. In W. R. Heyer, M. A. Donnelly, R. W. McDiarmid, L. C. Hayek, and M. S. Foster (eds.), Measuring and Monitoring Biological Diversity: Standard Methods for Amphibians, pp. 277–284. Smithsonian Institution Press, Washington, D.C.
- DOODY, J. S., J. E. YOUNG, AND G. N. JOHNSON. 1995. *Rana capito*. combat. *Herpetol. Rev.* 26:202–203.
- DUNDEE, H. A., AND D. A. ROSSMAN. 1989. The Amphibians and Reptiles of Louisiana. Louisiana State Univ. Press, Baton Rouge.
- ELMBERG, J. 1990. Long-term survival, length of breeding season, and operational sex ratio in a boreal population of common frogs, *Rana temporaria* L. *Can. J. Zool.* 68:121–127.
- EMLEN, S. T., AND L. W. ORING. 1977. Ecology, sexual selection, and the evolution of mating systems. *Science* 197:215–223.

- FLORIDA NATURAL AREAS INVENTORY. 1990. Guide to the Natural Communities of Florida. Florida Natural Areas Inventory and Florida Dept. of Natural Resources, Tallahassee, Florida.
- FRANZ, R. 1986. The Florida gopher frog and Florida pine snake as burrow associates of the gopher tortoise in northern Florida. In D. R. Jackson and R. J. Bryant (eds.), Proc. Fifth Ann. Mtg. Gopher Tortoise Council, pp. 16–20. Florida State Museum, Gainesville.
- GENTRY, J. B., AND M. H. SMITH. 1968. Food habits and burrow associates of *Peromyscus polionotus*. J. Mammal. 49:562–565.
- GERHARDT, H. C., R. E. DANIEL, S. A. PERRILL, AND S. SCHRAMM. 1987. Mating behaviour and male mating success in the green treefrog. Anim. Behav. 35: 1490–1503.
- GIBBONS, J. W., AND D. H. BENNETT. 1974. Determination of anuran terrestrial activity patterns by a drift fence method. Copeia 1974:236–243.
- GODLEY, J. S. 1992. Threatened: Gopher frog *Rana capito* Le Conte. In P. E. Moler (ed.), Rare and Endangered Biota of Florida, Volume 3. Amphibians and Reptiles, pp. 15–19. Univ. Press of Florida, Gainesville.
- GODWIN, G. J., AND S. M. ROBLE. 1983. Mating success in male treefrogs, *Hyla chrysoscelis* (Anura: Hylidae). Herpetologica 39:141–146.
- HOWARD, R. D. 1978. The evolution of mating strategies in bullfrogs, *Rana catesbeiana*. Evolution 32: 850–871.
- . 1980. Mating behaviour and mating success in wood frogs, *Rana sylvatica*. Anim. Behav. 28:705–716.
- LEE, D. S. 1968. Herpetofauna associated with central Florida mammals. Herpetologica 24:83–84.
- MARTOF, B. S., W. M. PALMER, J. R. BAILEY, AND J. R. HARRISON. 1980. Amphibians and Reptiles of the Carolinas and Virginia. Univ. of North Carolina Press, Chapel Hill.
- MEANS, D. B. 1986. Threatened: Dusky gopher frog. In R. H. Mount (ed.), Vertebrate Animals in Need of Special Attention in Alabama, pp. 30–31. Alabama Agric. Exp. Sta., Auburn, Alabama.
- MOUNT, R. H. 1975. The Reptiles and Amphibians of Alabama. Auburn Univ. Agricultural Exp. Sta., Auburn, Alabama.
- SEMLITSCH, R. D., J. W. GIBBONS, AND T. D. TUBERVILLE. 1995. Timing of reproduction and metamorphosis in the Carolina gopher frog (*Rana capito capito*) in South Carolina. J. Herpetol. 29:612–614.
- SHOOP, C. R., AND T. L. DOTY. 1972. Migratory orientation by marbled salamanders (*Ambystoma opacum*) near a breeding area. Behav. Biol. 7:131–136.
- VOLPE, E. P. 1958. The early development of *Rana capito sevosa*. Tulane Stud. Zool. 5:207–225.
- WELLS, K. D. 1977. Territoriality and male mating success in the green frog (*Rana clamitans*). Ecology 58:750–762.
- WOODWARD, B. D. 1982. Male persistence and mating success in Woodhouse's toad (*Bufo woodhousei*). Ecology 63:583–585.
- WRIGHT, A. H. 1931. Life Histories of the Frogs of the Okefinokee Swamp, Georgia. MacMillan Co, New York.

Accepted: 16 January 1998.

Journal of Herpetology, Vol. 32, No. 2, pp. 223–229, 1998
Copyright 1998 Society for the Study of Amphibians and Reptiles

A New Species of *Rana* from the Terai of Nepal

INDRANEIL DAS¹

Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts 02138, USA

ABSTRACT.—A new species of *Rana* is described from the terai region of Nepal on the basis of three specimens. The new species is diagnosable from known congeners in possessing the following characteristics: head longer than wide; tympanum rounded, smaller than orbit diameter; supratympanic fold absent; finger I longer than finger II; a series of large, flat glands on lateral aspect of body; broad webbing on toe IV to penultimate subarticular tubercle, reaching tip of toes as a narrow sheath; tips of digits flattened to form disks with distinct circummarginal grooves separating dorsum of disks from ventrum; tibia length/snout–vent length ratio 47.23–54.15; and absence of humeral gland on forelimb of males. The snout–vent length range shown by the type series is 30.4–32.5 mm.

The Terai region of Nepal, at the foothills of the Himalayan range, comprises extensive

marshes and associated grasslands, formed by the seepage of the larger streams (Mani, 1974a). Once 80–100 km in width, the Terai, which is dominated by tall grass and *Tamarix*, with patches of *Shorea* forest, has been reduced to a relatively narrow belt through anthropogenic

¹ Present Address: Centre for Herpetology, Madras Crocodile Bank Trust, Post Bag 4, Mamallapuram, Tamil Nadu 603 104, India.