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Natural History and Reproductive Behavior of *Nyctibatrachus cf. humayuni* (Anura: Ranidae)

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The genus *Nyctibatrachus* Boulenger 1882 (family Ranidae) is endemic to the Western Ghats mountain chain of southwestern India, and comprises ten described species (Dutta 1997; Krishnamurthi et al. 2001). Species of *Nyctibatrachus* are found mainly in the rocky streams of montane and submontane evergreen and semi-evergreen forests. Apart from taxonomic descriptions and distributional records there is little information on these frogs and the observations reported herein are the first accounts of natural history and reproductive behavior of any *Nyctibatrachus* species.

I observed *Nyctibatrachus cf. humayuni* at various localities (elevational range 75–300 m) in the states of Goa and Karnataka in southern India, but mainly between Castle Rock and Dudhsagar (15.41°N, 74.33°E to 15.35°N, 74.3°E). Annual precipitation here is 3000–5000 mm. The main rainy season, resulting from a southwest monsoon, is from June to September. There are a few showers from a northeast monsoon in November and early December. The forest is semi-evergreen and evergreen, ca. 15–25 m tall, and undergrowth is thick. Numerous small streams cut through these forests, often forming steep rocky watercourses with abundant overhanging vegetation. These streams are the natural habitat of this frog and the overhanging vegetation provides oviposition sites.

My observations span monsoonal seasons over a five-year period (1997–2001). During my study I captured individual frogs on first sighting, recorded snout–vent lengths (SVLs) to the nearest 0.1 mm using a vernier caliper, and noted sex. I marked each individual by fixing a narrow, uniquely colored strip of balloon around the waist and released each frog at point of capture. Marking with balloon strips did not seem to harm the frogs or disrupt their activities. Marked frogs neither abandoned their calling posts nor stopped vocalizing. Moreover, they seemed to attract females and fertilize eggs just as efficiently as they did before marking. I measured mating success of males (Fig. 3) over a period of 8 nights in the years 1998 and 2001 (total 16 nights). I considered only neighboring males to make direct comparisons meaningful, and excluded very old egg-clutches from male territories for this analysis because they could have been fertilized by other males in cases of territory takeovers. During the nights of direct observations I counted new clutches fertilized by territorial males. Therefore, although my measurements may be slight underestimates, they are corrected for temporal (number of days the males were observed) and spatial (micro-spatial variation in mating success) biases.

I collected all the marked frogs from 1998 and 1999 and preserved them in 10% formaldehyde solution when field observations were terminated. Hemant Ghate in the Department of Zoology, Modern College, Pune, is currently studying the taxonomic status of *N. cf. humayuni*. Morphometric measurements and certain behavioral details pertaining to individual frogs observed in the field are described elsewhere (Kunte 2001).

Sexual dimorphism.—Sexes in *N. cf. humayuni* are subtly dimorphic. SVL of calling adult males was 42.08 ± 3.24 mm (range 32–47 mm; N = 29) and that of adult females, 41.42 ± 2.61 mm (range 37–45.5 mm; N = 15). Males lack the nuptial pads which are present in many male anurans; I attribute their absence to the lack of amplexus. Only adult males had femoral glands colored pale orange to bright orange or pink. Males also had larger toe-discs as compared to females. Toe-discs are known to offer firm hold on smooth substrates, such as leaves. Therefore, larger toe-discs of males probably help them hold onto smooth leaves during the extended vocalization periods.

Vocalization.—Breeding activity commenced by the end of May or early June at the onset of the southwest monsoon and continued until mid-September. Thereafter, occasional rains and the northeast monsoon triggered short spurts of breeding. Males vocalized throughout the breeding season. The vocalizations began at dusk. The call was a soft and melodious, prolonged note—OORRsss—with an occasional faint "OA" preceding the call. Males vocalized with an average frequency of 6 calls/min. They perched at a height of up to 1 m on leaves overhanging flowing water of forest streams. When overhanging vegetation was absent they positioned themselves on slanting moss-free faces of wet rocks flanking the streams.

Vocalization continued until ca. 2130–2200 h. Then some of the males stopped vocalizing while others vocalized less frequently or occasionally. The males foraged afterwards, as evidenced by gut contents of males that had been vocalizing for as long as 8 nights. After foraging, the males took refuge before dawn in crevices or under rocks.

Territoriality.—Males maintained large territories in which oviposition took place. An individual territory consisted of suitable calling posts on over-hanging vegetation or moss-free rock and the underlying portion of the stream. The average inter-male (between calling posts) distance was 7.92 ± 3.28 m (N = 32), with a mode at 5 m (N = 11). A minimum distance of 5 m was always maintained between two calling posts. The calling posts later served as oviposition sites.

Territories were exclusive, in which only one calling male reigned. In two instances new males replaced the territorial males; in both occurrences larger males seemed to have dominated (Kunte 2001). Adult males not engaged in reproductive activities were never seen close to territories of calling males. It is possible that these males have short non-reproductive spells of a few days or weeks during which they forage away from the territorial males, gain weight or mass and later replace territorial males. My search for silent satellite males, which associate themselves with calling territorial male frogs and intercept gravid females (Arak 1988; Bourne 1993; Howard 1978), did not reveal any in *N. cf. humayuni*.

Egg-laying.—I observed seven complete egg-laying sequences. The following was a standard egg-laying process. Males vocalized usually from leaves ca. 10–100 cm above flowing water 2–30 cm deep. Observations on marked females revealed that females foraged in the territories of several males, which probably provided them time and opportunity to rank males and their territories. When a female was ready to lay a clutch of eggs she climbed to the spot from where a chosen male had been vocalizing. The male vocalized with slightly higher frequency of calling when the female approached. The male moved a few centimeters away from its calling post when the female approached but continued vocalizing. The female reached the exact original calling post and deposited eggs. If the female laid part of her clutch in another spot, it was always the second spot to which the calling male had shifted upon the female's arrival. Thus, the male, rather than the female, determined oviposition sites, with the female laying eggs exactly at the spot from where the male had been calling. There was no amplexus or any physical contact between the sexes (however, in another egg-laying sequence I observed 'pseudo-amplexus.' This preceded oviposition by 5 min and therefore did not serve the pur-

FIG. 1. This figure shows oviposition behavior and lack of amplexus in *Nyctibatrachus cf. humayuni*. The female to the right was laying eggs without the male being in amplexus while another gravid female waited beside it (note the bulging abdomen). The male on the lower part of the leaf was waiting for the female to finish oviposition, it fertilized the eggs after the female left. Note the old clutch at an advanced stage of development beside the male. Egg-clutches fertilized by a male are often clumped. Also note much larger toe-discs and thicker digits of male as compared to the females.

pose of fertilization [Kunte 2001]). Vocal communication on the part of the female was not perceptible. After laying its clutch, the female immediately entered the water and moved away. The male then stopped vocalizing and positioned itself over the eggs to enable fertilization. For the same purpose, sometimes the male also moved a little over the clutch, apparently ensuring that all the eggs received sperm. When it had released semen the male resumed vocalization within a few minutes from a different post only a few centimeters away from the freshly laid eggs, often on the same leaf. On successive nights the male continued vocalizing from the new post until another female visited. Thus, eggs laid by different females but fertilized by the same male tended to be spatially clumped on the same leaf or on neighboring leaves on the same branch (Fig. 1).

Clutch size, fertilization success, hatching success, and multiple clutching.—I observed a total of 1937 eggs comprising 85 clutches. Egg diameter at the time of oviposition was 2.5–3 mm (N = 15, from 3 clutches). Clutch size ranged from 10 to 55 eggs, with a median of 21 and mean of 22.79 ± 8.84 eggs **(**Fig. 2**).** Fertilization success in all 85 clutches was 100%. The length of the egg stage in the developmental process was approx. 12–15 days. When tadpoles were ready to hatch they wriggled violently in the egg-jelly, which burst, releasing the tadpoles. The ejected tadpoles fell in the flowing water below where they fed at the bottom close to the banks. I did not observe any pre-hatching mortality; tadpoles from over 700 eggs (ca. 30 observed clutches) ejected out of the jelly capsules successfully.

Six females were dissected for ovarian examination. Females preserved 1–4 days post-oviposition had a new batch of eggs developing in their ovaries; these would have matured in 10–15 days. Females that were caught close to calling males had a batch of eggs ready to be laid and yet another batch developing, which would have been ready after 10–15 days. It is evident, therefore, that females lay a minimum of two clutches. Judging from the prolonged breeding season of this species and assuming that eggs are produced throughout the breeding season, females can potentially produce as many as 6 egg-clutches per breeding season.

Male mating success and sexual dimorphism.—Most of the calling males were successful in obtaining at least one but typically multiple matings (Fig. 3). As a consequence, variance in reproductive success of male *Nyctibatrachus* may not be as high as in those species in which a few males monopolize all matings (Cherry 1993; Table 3.3 in Duellman and Trueb 1986). Also, many individual females possibly laid multiple clutches in a season. Hence, it would be interesting to work out reproductive success of both sexes in this species, which will perhaps be comparable. Thus, low variance in reproductive success of males and comparable fitness of both sexes may be the two reasons why sexes are similar in size, and only subtly dimorphic, in *Nyctibatrachus*.

The reproductive biology of *N. cf. humayuni* has remarkable features. Of particular interest is the lack of amplexus. In anurans amplexus has been considered an adaptive behavior that facilitates juxtaposition of cloacae of male and female during oviposition, which is important for success in external fertilization (Duellman and Trueb 1986). The total lack of amplexus has so far been reported only in Central and South American arrow-poison frogs (family Dendrobatidae) (Crump 1972; Limerick 1980) and Darwin's frog (*Rhinoderma darwinii*) (Busse 1991). These frogs have a different set of reproductive behaviors and life history traits as compared to *N. cf. humayuni.* For example, dendrobatids usually lay less than half a dozen eggs (some species, just one), and exhibit parental care unlike *Nyctibatrachus*. Darwin's frogs also have parental care. Interestingly, despite the evolutionary advantages usually attributed to the presence of amplexus, *Nyctibatrachus* has achieved 100% fertilization success in its total absence. Loose, abbreviated, or otherwise crude forms of amplexus are reported in many anurans, e.g., in *Discoglossus* (Knoepffler 1962) and Madagascan *Mantidactylus* (Blommers-Schlösser 1975) and *Mantella* (Arnoult 1966; Heying 2001). Therefore, *Nyctibatrachus* is only the third anuran group in which amplexus is totally absent and the first record of such a frog from the Old World.

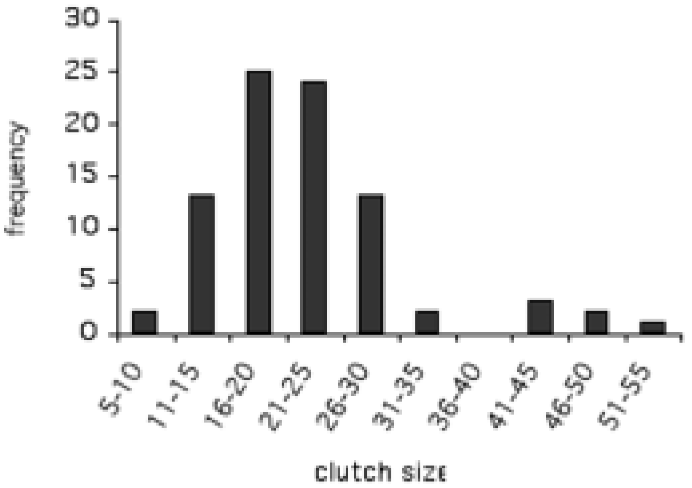

FIG. 2. Clutch size in *Nyctibatrachus cf. humayuni.*

Another notable feature of the breeding biology of this species is the nature of oviposition sites and clutch sizes. *Nyctibatrachus* is among the rare anurans that deposit eggs outside water—on ground or vegetation but not in a foam-nest, and whose larvae drop into water when they hatch (other examples in Duellman and Trueb 1986). Many of these species lay small clutches of large eggs. Central and South American glass frogs (family Centrolenidae) have similar breeding habits to *Nyctibatrachus*,

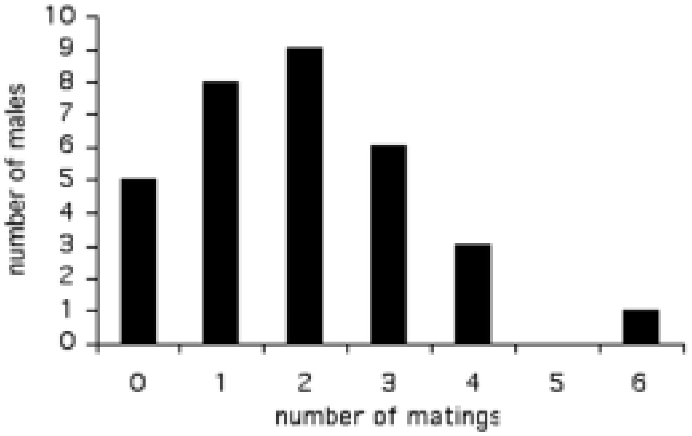

FIG. 3. Mating success of male *Nyctibatrachus*. Most males get at least one, typically multiple, matings.

although they have amplexus and parental care (Mc Diarmid 1978). *Phyllomedusa* and related genera (Kenny 1966; Vaira 2001) also have similar eggs, clutch sizes, and oviposition sites. It would be interesting to compare reproductive behaviors and mating success of these frogs.

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The Origins of the Anuran Interdigital Webbing Formula

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An established and useful part of anuran descriptions is the webbing formula, which expresses the extent of the webbing between fingers and toes in a standardized manner. This formula enumerates those phalanges which are free of webbing, rather than those which are webbed; this obviates the problem of whether to include metacarpals and metatarsals in the count of "phalanges." The development of the formula for expressing interdigital webbing has an interesting history, and its origin has often gone unacknowledged.

Many early authors used descriptors such as "¼ webbed" or "½ webbed." The major drawback to this system is that it requires a subjective assessment of the extent of the webbing, there being no clear, objective criteria upon which the fractions are based.

Edwards (1974) developed a formula which enumerated the number of phalanges which are covered by webbing. This system was used to describe webbing in *Colostethus* by La Marca (1985, 1997).

Loveridge appears to have been the first to quantify the extent of the webbing by enumerating the phalanges that are free of webbing. Loveridge (1933, p. 90) described the toes of *Glauertia* [*Uperoleia*] *russelli* as: "...strongly webbed, at most a single joint free with the exception of the fourth which has three joints free...." This method was elaborated upon in later work; "...of its toes only the first has a single joint free, the second, third and fifth are webbed to the disks on at least one side, the fourth has one and a half (right) to 2 (left) joints free of web" (Loveridge 1941, p. 129). Loveridge used "joint" as the equivalent of phalanx. Although Loveridge's descriptive method is useful and objectively quantifiable, no notation formula was established.

Rivero also described webbing using the number of free phalanges, but in his method "...the fingers and toes are placed close together and the extension of the webbing is determined by considering the middle, not the margins, of the membrane" (Rivero 1961, p. 15). Although Rivero stated that "Loveridge's system of measuring the amount of webbing by giving the number of free phalanges has been adopted here...." (*ibid*, p. 15), Rivero's system departs from Loveridge's in that Loveridge measured webbing by counting the number of free phalanges ("joints") to the point of contact between web and digit, while Rivero counted free phalanges to a point corresponding to the deepest emargination of the webbing between adpressed digits. An example of Rivero's notation is "...toes taken in order from first to fifth exhibit the following phalanges free of web: 1⅔, 1, 1½, 2½ to 3, 1 to 1¼;..." (*ibid*, p. 106). Although it is not explicitly stated, Rivero appears to offer a range of variation in the extent of the webbing, but makes no distinction between the inner and outer sides of the toes.

Savage and Heyer (1967) established a formula similar to that