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Source: *Herpetologica*, Vol. 32, No. 4 (Dec., 1976), pp. 401-404

Published by: [Herpetologists' League](#)

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for the hypertrophied CCS was provided without notable change on the bony ribs, but the cartilage ribs in their normal slender form proved to be inadequate to the demands imposed by hypertrophy of the CCI. In the course of evolution, selection for improvement was undoubtedly strong, leading to compensatory hypertrophy of the cartilage ribs and thereby to greater rigidity and area for attachment of the CCI.

Once the flared costal cartilages evolved, they were not lost in those colubroids reverting to small ventrals, e.g., certain sea snakes. However, the ventrals are enlarged, not only in most colubroids, but also in some of the more primitive Alethinophidia, independent of the colubroid evolution, or at least independent of the correlated evolution of the flared costal cartilages. It is quite possible, of course, that some of the primitive Alethinophidia, and perhaps all, evolved from a common ancestor with colubroids—but a common ancestor in which the flared rib cartilages had not yet differentiated. Obviously the ventrals of non-colubroid snakes, even if enlarged, cannot be as ef-

fective in locomotory roles as those of most colubroids.

Acknowledgments.—We are greatly indebted to Dr. Alice G. C. Grandison, British Museum (N.H.), for the loan of the bolyeriid snakes, and to Dr. Richard G. Zweifel, American Museum of Natural History, for the loan of the tropidophiid and xenodermine snakes.

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Received: 17 October 1975

Accepted: 25 February 1976

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AGGRESSIVE BEHAVIOR IN A CENTROLENID FROG, WITH COMMENTS ON TERRITORIALITY IN ANURANS

WILLIAM E. DUELLMAN AND ALAN H. SAVITZKY

ABSTRACT: *Centrolenella griffithsi* (Goin) ♂♂ exhibit aggressive behavior consisting of grasping one another with the forelimbs while suspended from vegetation. Aggressive behavior and territoriality are well developed in certain species having specialized reproductive modes that require limited resources.

FROGS of the genus *Centrolenella* are small, delicate species. Characteristically males call at night from vegetation overhanging streams, and eggs are deposited on vegetation over water. Observations on several South American species and reports by McDiarmid (1975) on some

Central American species reveal that males have calling sites that are utilized on succeeding nights and that egg clutches are deposited on or near the leaf used as a calling site.

McDiarmid and Adler (1974) reported on territorial behavior in *Centrolenella*

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viridissima [= *fleischmanni*] and *Centrolenella valerioi*. In these species the intrusion of a male at the calling site of another male evoked a series of responses by the resident male, consisting of (1) an encounter call, (2) jerky motions, and (3) axillary claspings. These encounters resulted in the intruder twisting away and departing from the calling site of the resident.

We report here a different kind of apparent territorial behavior in *Centrolenella griffithsi* (Goin). Observations were made on the nights of 9 and 10 April 1975 at a stream 9 km SE of Tandayapa, Provincia Pichincha, Ecuador. This locality is at an elevation of 2150 m on the Pacific slopes of the Cordillera Occidental of the Andes. The area supports cloud forest and contains many streams and many more rivulets. Cliffs with continuously dripping water support an abundance of ferns. *Centrolenella griffithsi* were very numerous on vegetation over the stream and on ferns on the cliff. In many cases calling males were no more than 50 cm apart.

On 9 April two males were found dangling from a fern overhanging a rivulet; an egg clutch was present on the same frond. The frogs were grasping one another belly to belly, each with the forelimbs wrapped about the other's neck. One frog was holding onto the fern with both feet, whereas the other was holding on with one foot; the other hind limb was folded against the body in a resting position. The frogs repeatedly flexed and extended their outstretched hind limbs so as to move their bodies up and down. The frogs were collected subsequent to the original observations on their position.

On 10 April a male was accidentally frightened from a perch \approx 2 m above the stream; it jumped to a fern \approx 1.5 m above the water. The fern was occupied by a calling male. Almost immediately the resident and the intruder were dangling by their feet from an horizontal herbaceous stem \approx 10 cm below the fern. The position

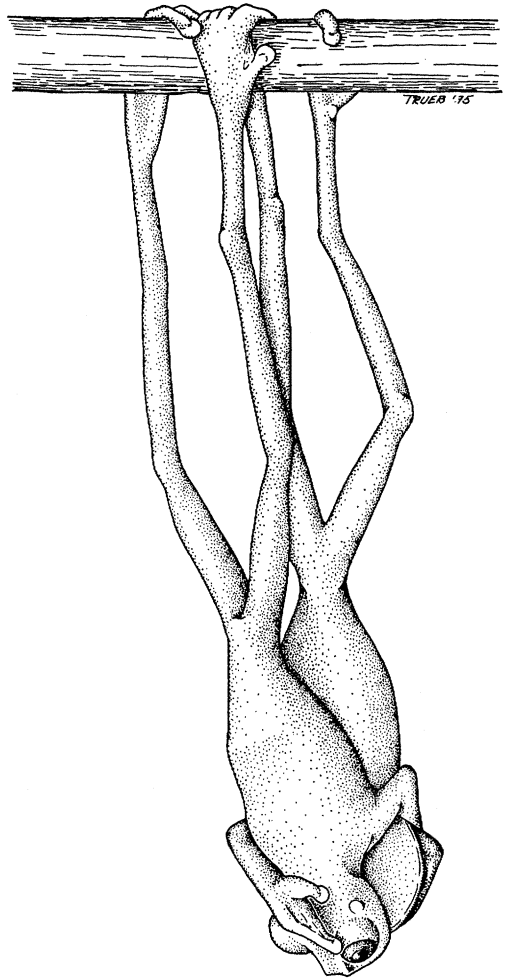


FIG. 1.—Grappling $\delta\delta$ of *Centrolenella griffithsi*, drawn from photograph.

of the frogs was the same as those observed the night before except that each frog grasped the stem with both feet (Fig. 1). During the following 5–6 min each frog periodically flexed one leg causing the pair to swing laterally. Subsequently the frogs simply hung from the stem for another 5 min, after which time they were collected.

At the initiation of the second confrontation there was no audible change in the call of the resident. If there was a change

it most likely was not noticed due to the large number of calling males in the immediate vicinity. Two different calls were traced to males of *C. griffithsi*. The most commonly heard call consisted of two short notes, whereas less frequently a single note was heard. Possibly the single note is a territorial call or, in using the terminology of McDiarmid and Adler (1974) an encounter call. The occurrence of scores of high-pitched peeps every minute precluded accurate determination of which individual was producing what kind of note. The only other *Centrolenella* found along the stream is a much larger species with a distinctly different call.

DISCUSSION

The occurrence of two or more egg clutches in different stages of development at a calling site suggests that male *Centrolenella* are instrumental in selecting the oviposition site (McDiarmid, 1975; *personal observation*). Not all sites along a stream are equally well suited for the survival of the eggs and tadpoles. Ideal sites must be shaded during the day and must be directly over the stream, so as to insure that the hatchling tadpoles will drop into the water. Survival rates of eggs and hatchlings will be higher for those located at the best sites; thus, the defense of these sites by the resident male enhances the survival of his genes in the population.

McDiarmid and Adler (1974), who summarized the growing but still meager literature on territoriality and aggressive behavior in anurans, suggested that ". . . territorial behavior has evolved in many different frog species representing several diverse lineages, not as the result of peculiar or specialized life histories as suggested by Duellman (1966), but rather because of the temporal and spatial permanency of breeding or feeding sites or both and the local densities of frogs." Certainly, at least to some degree, territorial and aggressive behavior is dependent upon the density of the frogs; density increases the

likelihood for territorial encounters. Likewise, a restricted number of calling sites could result in increased territorial interactions even among relatively few frogs. There is a growing amount of evidence for the existence of aggressive behavior and territoriality in migratory pond-breeding species. Frogs that call from scattered nonaquatic sites and lay terrestrial eggs that undergo direct development are not yet known to be territorial.

Although territoriality and its attendant aggressive behavior is not limited to frogs that remain at the breeding site throughout the breeding season (possibly throughout the year in the tropics), such behavior is well developed in many of these species. Presumably males call from the same sites for at least part, if not all, of the season; most recorded cases of territoriality in these species involve the defense of the calling site. Vegetation overhanging ponds or streams provides both calling and ovipositional sites for *Agalychnis callidryas* (Pyburn, 1964) and for centrolenids, both of which exhibit territoriality. Dendrobatids defend calling sites, which also are, or are presumed to be, near ovipositional sites (Duellman, 1966; Goodman, 1971; Crump, 1972). Nest-building frogs, such as *Hyla faber* (Lutz, 1960) and those that call from constructed burrows, which also serve as ovipositional sites, such as *Leptodactylus melanonotus* (Brattstrom and Yarnell, 1968) and *Pseudophryne* (Pengilley, 1971), also exhibit territorial behavior. Sexton (1962) observed defense of foam nests (constructed at calling site) by *Leptodactylus insularum* [= *bolivianus*]. In all but the dendrobatids, the territorial behavior is associated with constructed calling and nesting sites (*Hyla faber*, *Leptodactylus*, *Pseudophryne*) or suitable ovipositional sites over water (*Centrolenella*, *Agalychnis*).

The limited observations suggest that the occurrence of territoriality is frequent in those frogs which, by the nature of their specialized modes of life history, utilize limited resources for calling and/or nest-

ing. These frogs, and some with generalized reproductive modes which also demonstrate territoriality, tend to call from the same sites throughout the season. Thus, as suggested by McDiarmid and Adler (1974:77), they would have an opportunity to establish territories, whereas migratory breeders would not. Therefore, we view territoriality in these anurans as having resulted from intraspecific competition for one or more limited resources requisite to the successful completion of the life cycle of the species. Finally, territoriality has been documented more frequently in species that deposit their eggs at the calling site. The dual role of such sites may enhance the selective advantage of agonistic behavior in males.

Nearly all reports on territoriality and aggressive behavior in anurans have been based on incidental field observations. Although casual field observations will continue to increase the taxonomic breadth of our knowledge of anuran territoriality, intensive field and experimental studies are prerequisite to an understanding of the behavioral mechanisms involved.

Acknowledgments.—Duellman's fieldwork in Ecuador was supported by the National Geographic Society and the National Science Foundation (GB 42481). Savitzky's travel to Ecuador was made possible by a Watkins Museum of Natural History Grant, University of Kansas. We thank Linda Trueb for rendering the illustration.

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Received: 26 January 1976

Accepted: 17 May 1976

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