Plasticity and geographic variation in the reproductive ecology of gladiator frogs, particularly *Hypsiboas rosenbergi*

Plasticidad y variación geográfica en la ecología reproductiva de ranas gladiadoras, especialmente *Hypsiboas rosenbergi*

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Abstract: The reproductive strategy of most male anurans involves merely providing sperm. In a few species, like the neotropical gladiator frogs, males sometimes provide additional resources in the form of nests used as oviposition sites and parental care of the freshly laid clutch. Because providing resources entails additional costs, reproductive strategies should be modulated by resource availability. Studies involving different gladiator frog species, as well as different populations of the same species have revealed a great deal of geographic variation in various aspects of their reproductive ecology. In this chapter I argue that this variation is largely due to plasticity in response to local differences in the availability of one important resource – potential nest sites. Nest-guarding and fighting behaviour may be rare or absent under conditions in which a nest is easily obtained, but frequent under conditions in which a nest is a difficult to obtain commodity.

Key words: nest-building, basin, parental care, fighting behaviour.

Resumen: La estrategia reproductiva de los machos de la mayoría de los anuros involucra simplemente proveer espermatozoides. En algunas especies, como en las ranas gladiadoras del neotrópico, los machos a veces proveen recursos adicionales, en la forma de nidos y de protección a la camada recién puesta. Debido a que proveer estos recursos involucra costos adicionales para los machos, las estrategias reproductivas deberían ser moduladas por la disponibilidad de recursos. Estudios con diferentes especies de ranas gladiadoras, así como con diferentes poblaciones de la misma especie, han revelado un alto nivel de variación geográfica en varios aspectos de su ecología reproductiva. En este capítulo, argumento que esta variación se debe en gran medida a plasticidad en la respuesta a diferencias en la disponibilidad local de un importante recurso – sitios de anidación. El cuido parental de nidos y el comportamento de pelea entre machos pueden ser escasos o ausentes cuando es fácil obtener un nido, y frecuentes cuando los nidos son escasos.

Palabras clave: construcción de nido, concavidad, cuido parental, comportamiento de pelea.

Introduction

Gladiator frogs are medium to large tree frogs (Family Hylidae) that occur from Costa Rica into northern South America. The name Gladiator frogs is a reference to their highly pugnacious behaviour and well developed prepollical spine that they use when fighting (Lutz 1960a, Kluge 1981, Martins et al. 1998). They were formerly grouped together in the *Hyla boans* species group (Kluge 1979). Based on molecular data, Faivovich et al. (2005) recently split this group of frogs into two, not closely related, species groups. The *Hypsiboas faber* group – consisting of *H. albomarginata, H. crepitans, H. exastis H. faber, H. lundii, H, pardalis, H. pugnax,* and *H. rosenbergi* – and the *Hypsiboas semilineatus* group – which includes *H. boans, H. geographicus, H. pombali, H. semilineatus,* and *H. wavrini*. All of these species except for *H. albomarginata* build nests for egg deposition (Lutz 1960b, Duellman 1970, 1973, Crump 1974, Kluge 1981, Martins & Moreira 1991, Caldwell 1992, Martins 1993). These nests are constructed from wet clay or sand along the margins of ponds or streams. They are almost circular, and often have a rampart of material that the constructing male transported out of the nest (Kluge 1981, Martins 1993). Nest building constitutes a substantial investment by the males, since they spend from 30 minutes to several hours in constructing a nest (Kluge 1981, Martins 1993). When a male has finished his nest, he will start calling to attract a female. Males generally call from within the nest, but sometimes they may call

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Fig. 1: Close-up of the hands of a male gladiator frog, showing the prepollical spines on their thumbs. The spines are covered by a fleshy sheath that is retracted when the spines are used as weapons during fights.

Fig. 2: An adult gladiator frog *Hypsiboas rosenbergi*.

next to it or even from elevated positions in the vegetation around it (KLUGE 1981, MARTINS & HADDAD 1988, MARTINS 1993, HÖBEL 2000). Once the male has attracted a female, she will enter the nest and the male will amplex her. Sometimes the female will further modify or renovate the nest before finally laying eggs (KLUGE 1981, MARTINS & HADDAD 1988, MARTINS 1993). Eggs are laid as a monolayer floating on the surface of the nest (KLUGE 1981, MARTINS 1993, HÖBEL 2000). Until the tadpoles hatch, this surface film may not be disturbed; once the eggs or embryos become submerged and sink to the bottom of the nest they will quickly die (KLUGE 1981). Parental care in the form of nest construction for oviposition is thought to have evolved as a means of isolating the vulnerable eggs and developing embryos from water current and potential aquatic predators like fish, aquatic insects of cannibalistic conspecific tadpoles (BREDER 1946, CRUMP 1974, KLUGE 1981). In some species parental care goes one step further: Males of *H. rosenbergi* and *H. faber* may return to their clutches the nights following oviposition. During this time they sit next to the nest that contains a clutch, and keep other frogs from entering the nest (KLUGE 1981, MARTINS et al. 1998). Clutch guarding lasts a few nights, until the tadpoles hatch. After hatching, rainfall or flooding will wash the tadpoles into the adjacent body of water, where they conclude their development.

Fig. 3: A gladiator frog pair in their basin (puddle-type), prior to oviposition.

Geographic variation in reproductive behaviour of *H. rosenbergi*

The reproductive ecology of *H. rosenbergi* has been studied in two sites with very different physical conditions. One study was conducted in the canal zone of Panama (KLUGE 1981), the other at La Gamba Field Station in the Golfo Dulce Region of Costa Rica (HÖBEL 2000). At the Panamanian study site, frogs were breeding along a creek in the forest. The substrate along the creek was soft sand, and it was largely free of vegetation (KLUGE 1981). At La Gamba, frogs were breeding next to a small swamp in the middle of a large cattle pasture (HÖBEL 1999, 2000). The substrate was earth or mud, and most of the area was covered by dense vegetation (mainly short pasture grasses and sedges). Another important difference between the two sites was the presence of cattle at La Gamba, which left the area littered with footprints that quickly filled with water, either through rainfall or seepage of the moist ground.

The reproductive behaviour of *H. rosenbergi* differed substantially between the two study sites. The first difference was that while all males in Panama built their own nests, only a fraction of the males at La Gamba did so. Of 198 basins (basin = every depression, natural or built by the frogs, that contained a calling male or a clutch) marked during a 4 month study period, only 29% were male-built nests. Most of the time a calling male or a clutch was found in small puddles or one of the many cattle footprints found at the site. Although the three basin types (male-built nest, puddle, cattle footprint) differed in some physical characteristics (e.g.

depth, surface area), the volume of water contained in each basin type was similar (HÖBEL 1999). Interestingly, male-built nests were found mainly in an area of the study site to which cattle had no access, i.e. where easily occupiable basins were lacking (HÖBEL 1999).

The second difference observed in the two studies was that most males at the Panamanian site performed clutch guarding (KLUGE 1981), while at La Gamba practically none of the males guarded their clutches (HÖBEL 2000). Of 43 instances, 39 males were not observed the night after oviposition, three males were found calling from a new basin, and only one male was found on a perch near his clutch the night after oviposition, presumably guarding it (HÖBEL 2000).

The third difference was that while males in Panama frequently engaged in violent fights with conspecifics (KLUGE 1981), males at La Gamba did not fight (HÖBEL 2000). Fighting in gladiator frogs is a conspicuous and noisy affair, involving much jumping and splashing and specialised aggressive vocalisations (KLUGE 1981, MARTINS et al. 1998). During playback experiments that simulated the approach of a rival by confronting males with conspecific calls, males at La Gamba did respond with aggressive vocalisations (HÖBEL pers. obs.). But during the 4-month long study period, no fight was ever observed (HÖBEL 2000). KLUGE (1981) reported that 38% of males at his Panamanian site exhibited conspicuous wounds after only a few nights of residency, but only 2% of the males had wounds when first encountered. This suggests that the majority of wounds were inflicted during fights between males, and that an indirect assessment for whether fights occur might be made by looking for males with scars. At La Gamba 31% of males had some kind of scratch or scar. However, 25% of females also had scars, and the proportion of frogs with scars did not differ significantly between the sexes, as would be expected if scars originated mainly from fights between males (HÖBEL 2000). The lack of direct observation of fights, combined with the failure to attribute scars in males to fights as an indirect measure of violent aggression indicate that at La Gamba fighting was indeed absent, or at least much less frequent than in Panama.

Plasticity in gladiator frog nest-acquisition behaviour

Because female gladiator frogs will only mate with males that provide a nest, occupying one is of primary importance for a male gladiator frog. To obtain a nest, a male may do one of three things: First, he may build a nest; second, he may find and occupy a natural waterfilled depression that can serve as a nest, or third, he may take over another males nest. All three strategies have been observed in nature (KLUGE 1981, MARTINS & HADDAD 1988, CALDWELL 1992, MARTINS 1993, HÖBEL 1999).

Fig. 4: The eggs of gladiator frogs are laid as a one-layer film on the surface of small, waterfilled basins.

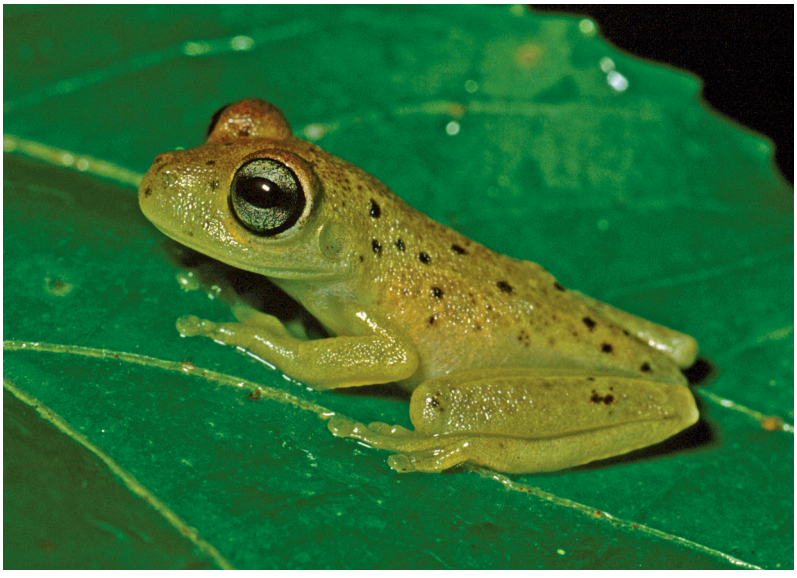

Fig. 5: Juvenile *H. rosenbergi* are green with black dots. As they mature, the brown colour of the adults slowly displaces the green colour of the juveniles.

Nest construction is a time and energy consuming activity that can take the better part of a night (KLUGE 1981, MARTINS 1993), and not every habitat contains substrates suitable for nest construction (CALDWELL 1992). Studies on several gladiator frog species have revealed that males will often take advantage of local conditions that help them decreased nest construction time. Panamanian *H. rosenbergi* (BREDER 1946, KLUGE 1981) and Brazilian *H. faber* (MARTINS 1993) readily accept pre-existing depressions in the sand or mud from which to initiate nest-building. Males also often re-use

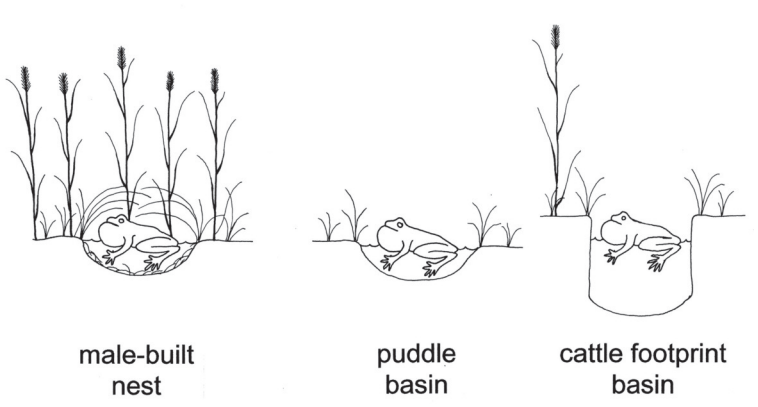

Fig. 6: Basin types used by *H. rosenbergi* at La Gamba, Costa Rica.

abandoned nests that they then only have to renovate a little (KLUGE 1981, MARTINS 1993), or males occupy naturally occurring waterfilled depressions (HÖBEL 1999). Also, nest construction behaviour, as well as the architecture of the finished nest seems to depend to a large degree on the substrate that is locally available to the frogs. CALDWELL (1992) studied two gladiator frog species (*H. boans, H. creptians*) along small streams in Brazil that had very different microhabitats. In parts of the study site the substrate was sandy , i.e. suitable for nest construction. But in the main channel of the stream rocky outcrops with small backwater pools dominated. She found that when the substrate was suitable for nest construction, males would construct nests. When the substrate was rocky, however, pairs would use rocky pools for oviposition, or even use leaf circles that delimited a small private pool from the rest of the river. MARTINS et al. (1998), studying the gladiator frog *H. faber* in different habitats in Brazil, also report that nest architecture differed depending on the nature and hardness of the substrate. Although males will normally construct almost circular mud nests, on occasion they will just pushed away aquatic vegetation at the pond margins to create a nest. Evidently, male gladiator frogs show behavioural plasticity in nest-building and nest-acquisition behaviour. They adjust their behaviour to local conditions, and may even resort to adopting naturally occurring depressions of suitable size if they are available.

Plasticity in nest building behaviour may be possible because female gladiator frogs do not seem to have preferences for specific basin shapes. Females of Panamanian *H. rosenbergi* (KLUGE 1981) and Brazilian *H. faber* (MARTINS & HADDAD 1988) seem to inspect the nests of males prior to amplexus, and once in amplexus may swim around in the nest, seemingly renovating it more to their liking. But so far no study has yielded conclusive evidence that females discriminate among males on the basis of some physical characteristic of their nests. The substrate, architecture and size of basins can vary greatly. For example, mean diameter of basins can vary from 121mm to 3719mm (HÖBEL 1999, CALDWELL 1992). At La Gamba, no basin type (male-built nest, puddle, cattle footprint) was preferred for oviposition, and basins with and without clutches did not differ in size (HÖBEL 2000). Other authors report similar results (KLUGE 1981; MARTINS & HADDAD 1988), suggesting that basin parameters per se may not matter to female gladiator frogs. Gladiator frog clutches have been observed in basins as different as cattle footprints, puddles, leaf circles, depression delimited by tree roots, rock pools as well as male constructed nests (e.g. KLUGE 1981, MARTINS & HADDAD 1988, MARTINS 1993, HÖBEL 1999), but never outside a basin in open water. Apparently, what counts is that a male owns a basin and not so much how it looks like.

Plasticity in gladiator frog reproductive and social behaviour

Whenever males use the third nest-acquisition strategy, that is hostile take-overs of another males nest, than this may have implications for other aspects of reproductive behaviour. An important thing to remember is that during occupation of a nest that contains a clutch, the new male will invariably disturb the delicate surface film, and the eggs fathered by the previous owner will sink to the bottom of the nest and die. KLUGE (1981) therefore suggested that the highly aggressive behaviour towards other males during the breeding season, for which gladiator frogs are so famous for, may result from the need for nest guarding and aggressive nest defence. Thus, ecological conditions that affect nest-acquisition behaviour may be directly linked to the prevalence of nest guarding and fighting behaviour. Similar to the behavioural plasticity in nest-building behaviour, differences in local ecological conditions may also lead to behavioural plasticity of the social and reproductive behaviour of the frogs. Hostile take-overs of other male's nest should be rare when potential nest sites are abundant, i.e. in habitats with many waterfilled natural depression, in habitats with substrate suitable for nest construction, or at sites with low densities of reproductively active males. Under these conditions, clutch guarding may not be as vital for a male's reproductive success, and fights between males should be infrequent. On the other hand, hostile take-overs may be more common in conditions in which nest sites are limited, i.e. in habitats where natural depression are scarce, in habitats that contain few areas with substrate suitable for nest construction, or at sites with high densities of reproductively active males. These conditions should

result in higher incidence of clutch guarding, as well as in more frequent fights between males.

Variation in the prevalence of nest guarding behaviour between sites or between years has been reported for at least two gladiator frog species, suggesting behavioural plasticity in clutch guarding behaviour. In a study of a Costarican population of *H. rosenbergi* clutch guarding was found to be largely absent (HÖBEL 2000), while it was the norm in a Panamanian population (KLUGE 1981). Most of the time, males of the Smith Frog, *Hypsiboas faber*, do not guard their clutches (MARTINS & HADDAD 1988). But during one high density year, MARTINS et al. (1998) observed that some males returned to guard their nests the night following oviposition. KLUGE (1981) also observed that clutch guarding in Panamanian *H. rosenbergi* was more common during a high-density year. Because of these observations, variation in clutch guarding behaviour is generally attributed to local differences in male density. Male density, however, can not explain the lack of clutch guarding at the Costarican site (La Gamba). Chorus size at La Gamba was twice as high as in the high density year in the Panamanian population, and nearest neighbour distances were similar at both sites (KLUGE 1981, HÖBEL 2000). The environmental variable that did differ between the two sites was the relative abundance of basins that males could occupy. At the Panamanian site, males had to either built their own nest, or take over another males nest. At this site, re-use of nests was common, and 64% of all nests were used by more than one male (KLUGE 1981). Under conditions in which nests are a finite and highly prized resource, hostile take-overs were common and males could gain more by guarding an existing clutch and foregoing another mating opportunity than by calling to try and attract another female. At La Gamba, the low proportion of re-use of basins (only 15%), and the high availability of basins at the study site probably decreased the danger of clutch loss due to foreign male intrusion (HÖBEL 2000). Despite the high density of males, the adaptive value of clutch guarding was relatively low, and it was more advantageous for males to rest and feed, or to occupy a new basin and call to attract another female.

Finally, the abundance of unoccupied basins at La Gamba might not only explain the lack of clutch guarding, but also the absence of violent aggression between males. In Panama, fights were generally associated with defending or conquering a nest (KLUGE 1981). Thus, if there was no need for clutch guarding, which apparently was the case at the La Gamba site, there was also no opportunity for violent aggression.

Plasticity or genetic differences?

WELLS (1981), in his seminal treatment of parental behaviour in anurans suggested, that parental care should vary as ecological condition vary. The contrasting story of peaceful Costarican and rambunctious Panamanian gladiator frogs seems a good example illustrating this prediction. However, the two populations whose behaviour has been studied in detail (KLUGE 1981; HÖBEL 1999, 2000) represent not only populations living in sites with very different physical conditions (stream vs. cattle pasture), but also populations from different distribution ranges. Although *Hypsiboas rosenbergi* occurs from Costa Rica to Ecuador, its distribution is not continuous. There are three disjunct ranges: one in south-eastern Costa Rica, a very small one in south-central Panama, and a large one that stretches from the Panamanian canal zone over Colombia to Ecuador. The two populations discussed here (KLUGE 1981; HÖBEL 1999, 2000) come from different ranges that are separated by a gap of about 300 km, and they may therefore show substantial divergence. Thus, the observed behavioural differences may be due to behavioural plasticity in response to variation in ecological factors (availability of resources needed for reproduction) as suggested here. Alternatively, there may be a genetic component to the geographic variation in behaviour. Replicate studies looking at different populations throughout the range, or experiments manipulating resource availability at individual sites would provide fruitful avenues to further explore the behaviour of these fascinating anurans.

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