Short Notes

Interactions between the Balearic lizard *Podarcis lilfordi* and the plant *Dracunculus muscivorus*

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Islands are widely recognized as sites of peculiar interactions between plants and lizards (Traveset, 1999). Plants are used in several ways, from perching sites for basking to the consumption as food. Some of these interactions, as pollination and seed dispersal, are clearly mutualistic (see for example, Castilla, 1999; Traveset, 1999; Pérez-Mellado and Traveset, 1999 and references therein). Here we describe the interaction between the Balearic lizard, *Podarcis lilfordi* (Günther, 1874) (Squamata, Lacertidae) and the plant species *Dracunculus muscivorus* (L. fil., 1857), observed in Aire, a coastal islet of Menorca (Balearic Islands, Spain). This islet has a surface of 342500 m^2. It is situated at the southeastern corner of Menorca Island and probably is one of the oldest coastal islets (see Pérez-Mellado, 1989 for more details). The observations were made during the periods of blooming in early spring and fruiting in early summer.

Dracunculus muscivorus is a member of the family Araceae, confined to the islands of the Western Mediterranean basin, including Mallorca and Menorca islands (Rosselló and Sáez, 1997). It is sparsely distributed in Menorca island (Bonner, 1994), where the Balearic lizard is extinct (Mayol, 1985; Pérez-Mellado, 1998) and particularly abundant in two coastal islets, Colom and Aire, inhabited by *Podarcis lilfordi*.

Dracunculus muscivorus has a very specialized pollination system. The flowers are arranged in an inflorescence, the spadix, surrounded by a large spathe that has a long and narrow tube at its base, hiding the lower part of the spadix. Female flowers are localized in the lower part of the spadix and male flowers above them (Bogner and Nicolson, 1991). The plant produces a fetid odour of decomposed meat that attracts dipterans of different families. The flies land on the spadix or on the large surface of the spathe and normally enter into the spathe-tube where they pollinate female flowers with pollen from other individual plants previously visited. Insects are then trapped into the spathe-tube for some time by hairs from the inner walls of the spathe-tube. After this time, the maturation of male flowers takes place at the higher part of the spadix. When flies finally escape from the spathe-tube, they collect pollen from mature male flowers to pollinate the next plant visited. This asynchronous maturation of female and male flowers allows the cross-fertilization of the plant (Farràs, 1988). *Dracunculus muscivorus* produces fruits with rounded or pyriform seeds. Each fruit normally has two seeds (mean $\pm\ s_{\bar{x}} = 2.28 \pm 0.75$, range: 1-4, $n = 46$) and each plant can have several fruits (mean $\pm\ s_{\bar{x}} = 69.6 \pm 30.11$, range: 46-121, from a small sample of five individual plants from Aire islet).

During the months of April and June 1999 we made observations on foraging behaviour of the Balearic lizard in the islet of Aire. The islet is occupied by a dense population of the nominotypical subspecies of the Balearic lizard, *Podarcis lilfordi lilfordi*, characterized by a large body size and a melanistic coloration (Pérez-Mellado, 1998). Densities of lizards and plants were estimated with the line-transect method where an observer travels along a straight line of variable length recording the perpendicular distances of objects to this line (Burnham et al., 1980).

On 2nd April 1999 and during an interval of four hours (10.45 to 14.45 GMT) we randomly searched the southern area of the islet recording, in a surface of around 5000 m^2, 37 individual lizards perching on *D. muscivorus* spathes. During this period we observed the capture of one fly trapped in the spathe-tubes of the plant, four flies were captured from the flower spadix, and 18 unsuccessful capture bouts of flies by lizards perched on the spathes were also recorded. In addition, we registered nine lizards searching into the spathe-tubes of other individual plants. Once we observed the displacement of a lizard by another individual previously perched on the plant. Thus, it seems that *Dracunculus muscivorus* is commonly employed as a perch site to capture flies attracted by its particular odour. Apparently, lizards are also able to detect trapped flies in the spathe-tubes (one observation).

In June 1999 we again visited Aire islet, during the peak of the fruiting period of *Dracunculus muscivorus*. Several lizards were observed eating fruits of *D. muscivorus*. Thus, we tried to estimate the importance of this plant species as a food resource for lizards, as well as the lizards' role as potential seed dispersers. On 17th June 1999, in a random sample of 111 individual plants, we found 94 plants without seeds and only 17 with seeds ($\chi^2 = 53.41$, $P < 0.001$), indicating an intense consumption by lizards and/or other potential consumers. On the same day we obtained a sample of 99 faeces from Balearic lizards, in a surface of around 10.000 m^2, in the southern part of the islet. From this faecal sample we detected 70% of the faeces with one (64 cases), two (4 cases) or four (one case) seeds of *Dracunculus muscivorus*; 53% of the faeces were only composed of seeds of this plant species. Only 117 additional prey items were found in the sample, dominated by Formicidae (71%) and Coleoptera (13%). These results indicate that during the fruiting period of *D. muscivorus*, this plant is one of the most important food items for many individual lizards. In fact, in the southern part of Aire islet the density of *D. muscivorus* is extremely high; four line-transects of 25 m each gave an average density of mean $\pm$ $s_{\bar{x}} = 4800 \pm 1397$ individual plants per hectare. The lizard density is also very high in this islet. From a line-transect census made in April 1999, we recorded a density of mean $\pm$ $s_{\bar{x}} = 7641 \pm 905.3$ individuals/hectare (line length = 360.5 m, number of lizards detected = 174), even if the density can be very variable between years and/or seasons (Pérez-Mellado, 1989; Brown and Pérez-Mellado, 1994).

We also made a comparison of a sample of seeds from faeces and from plants and we found that seeds from faeces were significantly larger (maximum diameter) than those from plants (Student t-test of log-transformed values: $t = 2.82$; $P = 0.005$; from faeces: mean $\pm$ $s_{\bar{x}} = 5.07 \pm 0.069$ mm; range: 3.5-6.5; $n = 82$ and from plants: mean $\pm$ $s_{\bar{x}} = 4.83 \pm 0.516$ mm; range: 3.6-6.2; $n = 138$). This result could indicate an active selection of larger fruits by lizards. In addition, the seeds were apparently intact in faeces, suggesting that *Podarcis lilfordi* can be a legitimate seed disperser of *Dracunculus muscivorus* in Aire islet, even if that point has to be confirmed with future germination tests.

The capture of insects from plant perches was commonly observed in Balearic lizards (Salvador, 1986; Pérez-Mellado, unpub. obs.), but in the case reported here, the interest is that lizards' foraging behaviour clearly takes advantage of the particular pollination strategy of the plant. The spring interaction of *D. muscivorus* and *P. lilfordi* is thus considered a non-mutualistic interaction that probably only benefits lizards because of the capture of potential pollinators and the apparent lack of pollen transport by lizards (Pérez-Mellado, unpub. obs.). For other plant species, it has been demonstrated that flower visits of potential pollinators can be affected by the presence of predators of such pollinators (Wilkinson et al., 1991; Elliott and Elliott, 1994), but in our case, we do not have any evidence that the capture of flies by lizards can affect the reproductive success of *Dracunculus muscivorus*. As far as we know, this is the first record of this kind of foraging strategy in a lacertid lizard. However, we cannot discard that lizards can be also attracted to *Dracunculus* as a good site for basking, because of the raise of plant temperature during blooming (Bonner, 1994).

The apparently neutral or negative interaction of the plant species and lizards during spring is largely compensated by the role of Balearic lizards as seed dispersers during summer, which is probably an important factor to explain the high plant density observed in Aire islet. Seed dispersal of *D. muscivorus* by the Balearic lizard was previously recorded at Cabrera Island (Balearic Islands) by Traveset (1997, 1999). As it was observed in the seed dispersal of other plant species by *P. lilfordi* (Castilla, 1999), the consumption of fruits of *D. muscivorus* is an important part of the diet of *P. lilfordi* during June in Aire islet. As in the case of Cabrera island (Traveset, 1997), the Balearic lizard seems to be the principal seed disperser of *D. muscivorus*, as the most common terrestrial vertebrate of the islet.

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Dietary habits of *Boa constrictor occidentalis*, in the Cordoba Province, Argentina

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The Argentine boa constrictor or "lampalagua" is a subspecies found in Argentina in the semiarid plains of the phytogeographic provinces of Chaco, Monte and Espinal, where its populations are declining (Anónimo, 1994). In the Córdoba province, it is limited to the Chaco oriental, occidental and serrano, and to the NW of the Espinal (Di Fonzo de Abalos and Bucher, 1981, 1983; Reati, 1996; Chiaraviglio et al., 1998a). Due to intense farming, cattle raising and illegal hunting for the skin trade (Gruss, 1991), the species is endangered and has been included in Appendix I of CITES (1997). Therefore, studies to increase our understanding about its biology in its natural habitat are essential for recovering and preserving wild populations (Chiaraviglio et al., 1998b).

Identifying critical habitat and foraging requirements of endangered taxa is crucial to develop successful recovery plans (Chandler and Tolson, 1990). Most prey species of *Boa constrictor* that have been identified in its South American range are mammals, but they also include fish, other reptiles and birds (Luxmoore et al., 1988; Cei, 1993; Henderson et al., 1995). However, there is no quantitative analysis of the diet of *Boa constrictor occidentalis* nor a systematic report about the feeding habits of the subspecies in Argentina. Therefore, the aim of this study is to determine the specific composition and frequency of its diet in Northwestern Córdoba Province, in central Argentina.

The study area is a xerophytic forest of *Aspidosperma quebracho-blanco* and *Prosopis flexuosa*, and shrublands of *Larrea divaricata* and *Mimozyganthus carinatus* (Cabrera, 1976). The wet season spans from October to March, and the dry season from April to September. Annual average temperatures range from 18 to 23°C, with an average rainfall of 300 to 550 mm (Capitanelli, 1979).

The diet of 28 *B. c. occidentalis* (16 males and 12 females) was studied. Total length (TL) ranged between 68 and 290 cm ($\bar{x} = 189 \pm 44.7$ cm for males and 240 ± 34.2 cm for females), and weight ranged from 0.202 to 13.9 kg ($\bar{x} = 4.04 \pm 1.84$ kg and 7.94 ± 3.07 kg, for males and females, respectively) (the values following the means are standard deviations). Animals were captured alive by hand or, in a few cases ($n = 3$), were found dead in the Districts of Pocho, Río Seco, San Alberto and Sobremonte in NW Córdoba Province. A total of 7 males and 5 females were captured in the wet season, whereas 9 males and 7 females were captured in the dry season. No recapture was performed.

Gastrointestinal contents were obtained by stomach flushing or dissection techniques (Fitzgerald, 1989). Stomachs were flushed with variable amounts of water (from 0.5 l to 5 l) depending on the snakes' size. No remains were found by dissection in the gut of previously flushed boas. Food remains were preserved in 10% formalin. Their volume was measured by water displacement but due to the high degree of digestion, it was impossible to determine the biomass of each individual prey. All examined boas had at least some food remains in their digestive tract. Contents were identified to the lowest taxon possible. Hair was identified with microscopic analysis and compared to reference collections at the University of Buenos Aires. Feathers could be determined only for *Gallus sp.* Frequency and percentage of prey items were calculated for the 28 boas. A Cluster Analysis with the Average Linkage Method correlating the gastrointestinal contents data with the Simple Matching Technique was used to find potential dietary patterns. Individuals were grouped by sex, TL (female: small: ⩽ 220 cm, medium: 221-250 cm, or large: > 250 cm; male: small ⩽ 100 cm, medium: 101-180 cm or large: > 181 cm) and season (wet or dry).

Forty oral interviews with rural inhabitants of the area were conducted to obtain additional information about the feeding habits of the species. People were selected according to their closest contact with the animals in the field: most of them were loggers and farmers who have a good knowledge of the species' biology. Due to their daily activities in the field, they have direct contact with these snakes. Frequency and percentage of mention for each food item over the total oral surveys were calculated (Pérez-Emán and Paolillo, 1997).

According to the analysis of the gut contents and the taxa mentioned in the interviews, *B. c. occidentalis* feeds on at least 19 species of vertebrates, distributed as follows: 11 species of mammals belonging to 6 orders and 8 families; 7 species of birds (6 orders and 6 families) and 1 reptile (table 1).

Mammals were found in 71.4% of the contents and were mentioned in 75% of the interviews. Birds are the second most frequent group: their remains were found in 32.1% of the individuals and they were mentioned in 40% of the oral surveys. Both classes were recorded simultaneously in only one male of 68 cm TL (3.6%). Reptile remains were not found in the ingesta, but were mentioned in 12.5% of the interviews (table 1).

Lagostomus maximus is preyed upon by large male and female boas predominantly during the dry season (Group 1), while in the wet season they prey mostly on *Gallus sp.* (Group 2). Guinea pigs (*Microcavia australis*), mice (*Mus musculus* and other *Muridae*) and birds are consumed all year round by males and females of the three size categories (Group 3). With the available data, no predation preference is apparent for the remaining prey species (Group 4) (table 2).

The advanced degree of digestion of most of the remains made taxonomic classification difficult. In Burmese pythons, prey digestion time is directly proportional to meal size (Secor and Diamond, 1997a), and individuals feed sporadically and at unpredictable intervals (Secor and Diamond, 1997b). This pattern is likely to be found in *Boa* (Secor, pers. com.). Thus, the small volume of food remains found in most of the individuals could be due to the small size of the prey consumed, or to long time intervals from feeding to capture. Since not all food items could be identified to the same taxonomic level, and given the small sample size typical of species with the characteristics of *B. c. occidentalis*, diet indices were not applied (Pleguezuelos and Moreno, 1990).

There is a strong interspecific relationship between *B. c. occidentalis* and vizcacha, *Lagostomus maximus*: boas not only prey on this species of Chinchillidae but also take refuge in its burrows (Luxmoore et al., 1988; Rogel, 1998). Boas are used by local people as control agents against vizcacha (Chiaraviglio et al., 1998b), usually considered a harmful species by farmers (Kufner and Chambouleyron, 1993). Seven out of eight boas with vizcacha remains were captured in the dry season (fall/winter), which coincides

Table 1. Specific composition of the diet of *Boa constrictor occidentalis*. Number of gastrointestinal contents with each food item and its percentage (%) over the total ($n = 28$). Number of personal interviews with rural inhabitants in which each food item was reported and its percentage (%) over the total ($n = 40$).

Taxon	Number of gastrointestinal contents	%	Number of personal interviews	%
MAMMALIA				
Didelphis albiventris	1	3.6	1	2.5
Chaetophractus sp.			2	5.0
Lepus europaeus	1	3.6	1	2.5
Mus musculus	3	10.7		
Mice (undet. Sp)			5	12.5
Sygmodontinae	2	7.1		
Pediolagus salinicola	1	3.6	19	47.5
Microcavia australis	7	25.0	5	12.5
Lagostomus maximus	8	28.6	26	65.0
Lycalopex gymnocercus			7	17.5
Capra hircus			1	2.5
AVES				
Rhea americana			1	2.5
Tinamidae			4	10.0
Gallus sp.	4	14.3	11	27.5
Meleagris gallopavo			1	2.5
Columbidae			1	2.5
Myiopsitta monacha			1	2.5
Undetermined Passeriformes			3	7.5
Undetermined feathers	5	17.9		
REPTILIA				
Tupinambis sp.			5	12.5
TOTAL MAMMALIA	23	71.4	67	75.0
TOTAL AVES	9	32.1	22	40.0
TOTAL REPTILIA			5	12.5

seasonally with the accumulation of fat bodies in direct relationship with the process of vitellogenesis (Chiaraviglio et al., 1998b). *Pediolagus salinicola*, *Lepus europaeus* and *Didelphis albiventris* are less frequent prey of this boid. However, given the decline of vizcacha populations in the studied area (Chiaraviglio et al., 1998b), it is likely that these species may be preyed upon more regularly in the near future. Prey with small biomass such as Caviidae and Muridae are numerically important in both seasons.

It is apparent that *B. c. occidentalis* feeds on a wide range of prey sizes. One ontogenetic shift was recorded in its diet: only the largest boas (TL = 235 cm or longer) prey on *L. maximus*, while remains of small species like *Mus musculus*, Sygmodontinae or *Microcavia australis* were found both in young individuals (TL = 68 cm) as well as in large adults (TL up to 290 cm).

Table 2. Foraging categories in *Boa constrictor occidentalis*. M: male; F: female; D: dry season; W: wet season; body size: (1) small, (2) medium and (3) large. Categories: G1: *Lagostomus maximus*; G2: *Gallus* sp.; G3: *Microcavia australis*, *Mus musculus*, Muridae, Sigmodontidae and Aves; G4: *Lepus europeus*, *Didelphis albiventris* and *Pediolagus salinicola*.

	G1	G2	G3	G4
MD1	–	–	2	–
MD2	–	–	1	–
MD3	4	–	2	1
MW1	–	–	1	–
MW3	–	1	5	1
FD1	–	–	2	1
FD2	1	–	1	–
FD3	2	–	2	–
FW1	–	1	–	–
FW3	1	2	1	–
TOTAL	8	4	17	3

Remains of *Gallus* sp. were found in 14.3% of the contents while fowl were mentioned in 27.5% of the interviews. Attacks on chickens by boas are frequently observed by rural inhabitants due to their close contact with these domestic birds. Also, boas occasionally kill goats. For this reason, they are frequently hunted by local people to avoid these economic losses (Chiaraviglio et al., 1998b). Feathers of other species were difficult to identify in the gut contents. However, due to the terrestrial and arboreal habits of the boas, the results from interviews and the abundance of birds such as Passeriformes, Tinamidae and *Miopsitta monacha* (pers. obs.), it is possible that the collected remains belong to these bird species.

Although lizards are preyed upon by *B. c. occidentalis*, reptiles in general are not well represented in the adults' diet. Remains of an undetermined lizard were found in the gastrointestinal content of a female (TL = 165 cm) that was not included in this study because of its unknown locality. These ontogenetic shifts have already been mentioned by many authors in ophidian research (Pleguezuelos and Moreno, 1990; Wallace and Diller, 1990; Luiselli and Agrimi, 1991; Henderson, 1993; Luiselli, 1996; Shine et al., 1996).

Several species that were mentioned in the personal interviews were not found in the gut contents given the reduced sample size. As a result, a comparison between the results of both methods revealed low correlation (Spearman Correlation = 0.035) and similarity (Jaccard Coefficient = 0.30). However, it is important to remark the usefulness of the personal interviews carried out during this study. This methodology reveals the cultural traits and experience of rural people sharing the habitat with wildlife, and has been succesfully used in previous studies on feeding ecology of reptiles (Pérez-Emán and Paolillo, 1997).

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Dens and denning behavior of Morelet's crocodile (*Crocodylus moreletii*)

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The construction of subterranean burrows or dens has been documented in both tropical and subtropical species of crocodilians (Lang, 1987). Dens serve as overwintering sites (McIlhenny, 1935; Pooley, 1969; Chu-Chien, 1982; Hagan et al., 1983; Brisbin et al., 1992) and aestivation sites (Pooley, 1969; Kushlan, 1974; Whitaker and Whitaker, 1984; Varona, 1987; Walsh, 1989; Hayes-Odum and Jones, 1993; Christian et al., 1996), provide protection from predators (McIlhenny, 1935; Pooley, 1969) and dominant conspecifics (Taplin, 1988; Tucker et al., 1997), and serve as retreats for nesting females and neonates (McIlhenny, 1935; Dietz and Hines, 1980; Chu-Chien, 1982; Carboneau, 1987; Hayes-Odum and Jones, 1993; Rootes and Chabreck, 1993; Simmons and Ogden, 1998). The only reference to den use by Morelet's crocodile (*Crocodylus moreletii*) is a general account by Alvarez del Toro (1974) who stated that both males and females construct caves with submerged entrances in riverbanks. I herein describe den characteristics and observations of den use by Morelet's crocodile in northern Belize.

Data on dens were obtained from 1992 to 1997, incidental to studies on nesting ecology and population status of Morelet's crocodile in northern Belize (Platt, 1996; Platt and Thorbjarnarson, 1997). Northern Belize (Belize, Cayo, Corozal, and Orange Walk Districts) is a karstic plain characterized by alluvial floodplains, interfluvial swampy depressions, and sinkholes (Johnson, 1983); wetlands occupy 40% of the region (Alcala-Herrera et al., 1994). Surface and groundwater drainage are linked and consequently seasonal water-level fluctuations are dampened. However, periodic episodes of wetland desiccation are occasionally experienced during the annual dry season which extends from January to mid-June (Johnson, 1983).

Dens were located by walking or paddling a canoe along the shoreline of lagoons, creeks, rivers, and ponds, and searching for tunnel entrances. Searches were also conducted in the vicinity of crocodile nests. Villagers found one den while diving for turtles (*Dermatemys mawii* and *Trachemys scripta*), and former crocodile hunters identified four others. Additionally, two dens constructed by *C. moreletii* living in a semi-natural enclosure at the Belize Zoo were examined. Periodic inspections of previously identified dens were made throughout the study. The width and height of each den entrance were measured. Occupancy was determined by the presence of fresh tracks and tail drag marks. Attempts were made to measure burrow depth by feeding steel tapes or inserting poles into tunnels. Mean values are presented as ± 1 *s*. Habitat was classified as alluvial lagoons (located in floodplains of rivers and creeks; subject to overbank flooding; sparsely vegetated), non-alluvial lagoons or sinkholes (interfluvial wetlands not subject to overbank flooding; water-levels maintained by subsurface drainage and springs; typically heavily vegetated), rivers and creeks, or ponds (man-made; generally less than 1.0 ha; many dry completely during the dry season).

Twenty-five active dens were located during this study; nine (36%) in alluvial lagoons, ten (40%) in non-alluvial wetlands, four (16%) in rivers and creeks, and two (8%) in farm ponds. Dens proved difficult to locate, as entrances were often submerged or obscured by shoreline vegetation. Den entrances were most readily located when exposed by low water levels during a prolonged drought in 1994. Several dens in dense shoreline vegetation were found because faint plumes of suspended sediments were seen in the water near the entrance. At other sites, well-worn trails were noted leading to den entrances.

Den entrances were oval to half-moon shaped, averaging 43.9 ± 13.6 cm at the widest point (range = 20 to 65 cm), and 25.7 ± 10.4 cm at the apex (range = 13 to 50 cm). The entrances of 21 (84%) dens were partially flooded, and four (16%) were completely submerged at normal water-levels. The entrance to a den along the Sibun River was 250 cm below the surface. Other dens with submerged entrances were undoubtedly overlooked. One den had two entrances about 3.0 m apart, but others had only a single entrance. Both *C. acutus* (Varona, 1987; Thorbjarnarson, 1989) and *Alligator sinensis* (Chu-Chien, 1982) construct dens with multiple entrances. These species also reportedly excavate ventilation holes in tunnel roofs (Chu-Chien, 1982; Varona, 1987), a feature not observed at any *C. moreletii* dens.

Depth could be determined for only seven dens, and averaged 132 ± 28 cm (range = 100 to 180 cm); other dens were probably more extensive. A 360 cm pole thrust into one den failed to reach the end, and others extended 150 to 200 cm before tunnel curvature prevented further measurement. A den constructed by a large male (total length ca. 2.4 m) at the Belize Zoo collapsed allowing the tunnel system to be traced. This den followed a sinuous course extending 460 cm from the water to an enlarged terminal chamber measuring ca. 150 × 200 cm. In most cases no slope was associated with tunnels, although it is likely that deep burrows ascended to a terminal chamber as described for other species (McIlhenny, 1935; Chu-Chien, 1982; Varona, 1987; Chen et al., 1990). However, three shallow dens (115 to 150 cm deep) sloped downwards from the entrance at an angle of approximately 30°, ending in an enlarged chamber. The terminal chamber presumably allows crocodiles to turn around, as they were observed entering and leaving dens headfirst at the Belize Zoo.

Other crocodilians are known to construct extensive dens (McIlhenny, 1935; Whitaker and Whitaker, 1984; Brisbin et al., 1992). *Crocodylus acutus* dens up to 9 m long have been measured (Thorbjarnarson, 1989), *Alligator mississippiensis* dens are described as underground "labyrinths" (Mazzotti and Brandt, 1994), and *A. sinensis* dens often extend up to 50 m from water (Chu-Chien, 1982). The structural complexity of *A. sinensis* dens varies with age and sex, with those of adult females being the most complex (Chen et al., 1990).

Crocodylus moreletii dens were excavated in steeply sloping or vertical banks. Undercut banks were utilized in rivers, creeks, and farm ponds. Dens were excavated into the steep banks of islands at a non-alluvial lagoon where suitable sites were absent along the gradually sloping shoreline. Eleven dens (44%) were constructed among tree roots, and a single den was found in a mat of floating peat. With the exception of the latter, all dens were constructed in heavy clay soils. Factors influencing den construction remain largely unknown, but are probably related to the availability of suitable microsites. Alvarez del Toro (1974) stated that *C. moreletii* dens were often constructed among tree roots, and a similar association has been noted in other species (Kushlan, 1974; Whitaker and Whitaker, 1984; Thorbjarnarson, 1989; Walsh, 1989). Tree roots probably provide structural support and stabilize tunnels. In addition, soil type is likely important, with dens being constructed in heavy clay rather than sand (McIlhenny, 1935; Thorbjarnarson, 1989).

Active nests were associated with nine dens (36%), and these dens averaged 750 ± 731.5 cm from nests (range = 60 to 2,000 cm). The few available reports of *C. moreletii* reproduction make no reference to the presence of dens at nest sites (Campbell, 1972; Alvarez del Toro, 1974; Perez-Higareda, 1980; Casas-Andreu and Rogel-Bahena, 1986), and dens were not found at most *C. moreletii* nest sites in Belize (Platt, 1996). The proximity of dens to nests probably allows females to remain nearby and more effectively guard nests against predators. Dens may also serve as refugia for neonates. Neonates readily entered dens to escape my capture attempts, and at the Belize Zoo they were frequently observed with the female in the den. Den use by neonates has been reported for other crocodilians (McIlhenny, 1935; Dietz and Hines, 1980; Chu-Chien, 1982; Hayes-Odum and Jones, 1993; Rootes and Chabreck, 1993), and Pooley (1969) speculated that burrows offer especially good protection from avian predators.

Dens may also protect larger *C. moreletii* from terrestrial predators, particularly jaguars (*Panthera onca*), which are known to prey on other crocodilians (Alvarez del Toro, 1974; Emmons, 1989). Numerous jaguar tracks were found at the entrance to a den exposed by low water levels and inhabited by a subadult (TL ca. 100 cm) crocodile. Tracks and other sign indicated the jaguar had unsuccessfully attempted to reach into the den and extract the crocodile.

Drought or flooding may force temporary abandonment of dens. Abandonment occurred late in the dry season when water levels dropped and dens no longer contained water. Other dens containing water remained occupied even when isolated by falling water-levels; five dens were still in use despite being 5 to 6 m from open water. Den construction at the Belize Zoo also occurred in the dry season. Den use during the dry season may reduce body temperature and metabolic rate, thereby lowering energy consumption at a time when food resources are scarce (Walsh, 1989). In alluvial lagoons, rivers, and creeks, flooding forced crocodiles from dens during the wet season. However, in non-alluvial wetlands and sinkholes where water-level fluctuations are not as severe, dens were flooded for only 1 to 10 days, and remained occupied throughout the wet season.

Crocodylus moreletii dens appear to remain in continuous use for many years. This was difficult to demonstrate given the time constraints of the present study (1992 to 1997), but dens found in 1992 were still inhabited in 1997, and three active dens found in 1994 were located with the assistance of a hunter who had last removed crocodiles from them in 1982. Other hunters also claimed to have repeatedly killed crocodiles at specific dens over the years. These observations suggest that individuals replace former residents when a den becomes vacant. Similarly, hunters report that American alligators quickly reoccupy dens after the resident alligator is killed (Simmons and Ogden, 1998).

Apparently, only a small percentage of crocodiles in a given area occupy dens. Gold Button Lagoon, a 142 ha non-alluvial lagoon is estimated to contain 175 to 200 crocodiles (Platt, 1996), yet only six dens were found during five years of intensive searching. Likewise, when freshwater impoundments in coastal South Carolina are drained, the number of alligators is much greater than the number of dens present (Walt Rhodes, South Carolina Department of Natural Resources, pers. comm.).

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Unique structural pattern of the manicotto glandulare of *Hyla nana* tadpoles (Anura: Hylidae)

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The tadpole of *Hyla nana* was originally described by Lavilla (1990). A remarkable feature of this larva is the structure of its mouth, which has neither oral papillae nor keratodonts. It is formed by a small cylindrical and protrusible suctorial tube. The structure of the chondrocranium and the hyobranchial skeleton was studied by Fabrezi and Lavilla (1992), who characterized it as a macrophagous larvae.

While studying the diet of south Paraguay's tadpoles, we found a previously undescribed large structure on the digestive tract between the esophagus and foregut of the *Hyla nana* larvae.

Tadpoles were collected in a semi-permanent pond, near the city of Concepción (23°22′S; 57°18′W). Tadpoles at stage 31 (Gosner, 1960) were fixed in 3% glutaraldehyde, 3% formaldehyde, 1% picric acid in 0.1 M phosphate buffer, pH 7.4, dehydrated in acetone, embedded in Durcupan (FLUKA®), and sectioned at 0.8 μm with a Reichert Ultracut-S ultramicrotome. Cross sections were stained with Toluidine Blue and photographed with a BX50 Olympus Microscope. Tadpoles at stages 38 and 41 were fixed in 10% formaldehyde, embedded in paraffin and sectioned at 3 μm with a Reichert Jung Hn 40 microtome. Sagittal sections were stained with PAS-Indigo Picrocarmine to detect 1,2-glycol groups of the cellular mucous-polysaccharides and mucoproteins.

The analysis of the gastro-intestinal content was carried out on 20 gastro-intestinal tracts of *Hyla nana* larvae according with Lajmanovich (1994, 1997, 1998). The total number of each item was estimated following the Lackey Drop Microtransect Method (Lackey, 1938).

Hyla nana tadpoles have a large organ macroscopically similar to the manicotto glandulare of other anuran larvae (Griffiths, 1961; Terán and Michel de Cerasuolo, 1988;

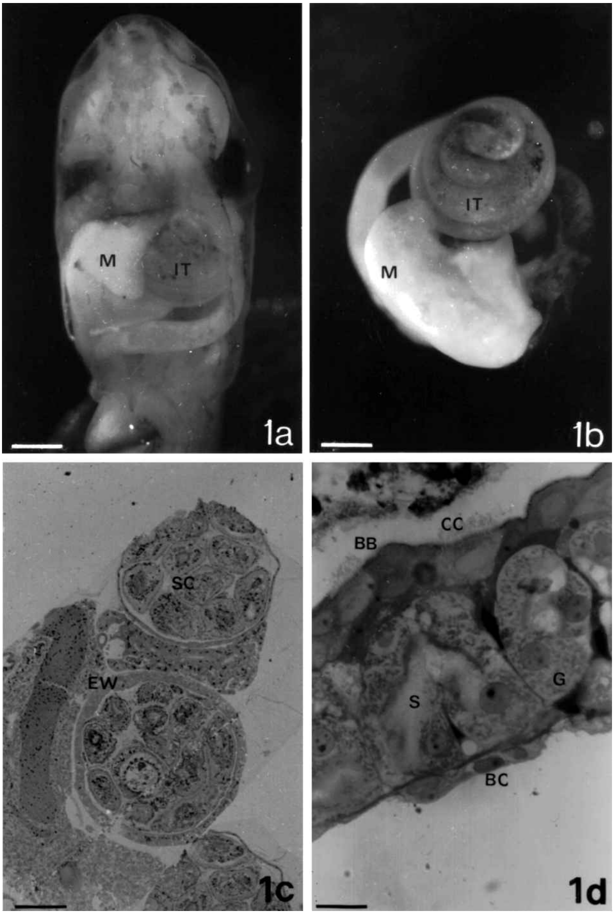


Figure 1. a: Ventral view of *Hyla nana* tadpole at stage 31, whose skin has been removed. The manicotto glandulare (**M**) is displaced toward to the right of the body axis. **IT**: intestinal tract (Bar, 0.55 mm). **b**: Macroscopic view of the manicotto glandulare **(M)** and intestinal tract **(IT)** dissected from a larvae at stage 31. Note the large size of the manicotto glandulare (Bar, 0.38 mm). **c**: Sagittal section of *Hyla nana* tadpole at stage 31 showing a cross view of the manicotto glandulare. Observe the external wall **(EW)** and the numerous internal secretory crypts **(SC)**, (Toluidine Blue) (Bar, 30 μm). **d**: Detail of the manicotto glandulare external wall of *Hyla nana* tadpole at stage 31. Note the surface cuboidal epithelium with two cellular types: ciliated **(CC)** and brush border cells **(BB)**. Beneath this epithelium there are acinous glands **(G)** with cuboidal cells and under these, elongated basal cells **(BC)** appeared. In the glands we observe secretory material (**S**) (Toluidine Blue) (Bar, 10 μm).

Rada de M. and Bello de L., 1988; Terán and Michel, 1996). This large organ is located between the esophagus and foregut, displaced toward to the right of the body axis (fig. 1a, b).

At stage 31, this structure is limited externally by a wall with a cuboidal epithelium consisting of two well-differentiated cellular types: ciliated and brush border cells (fig. 1c, d).

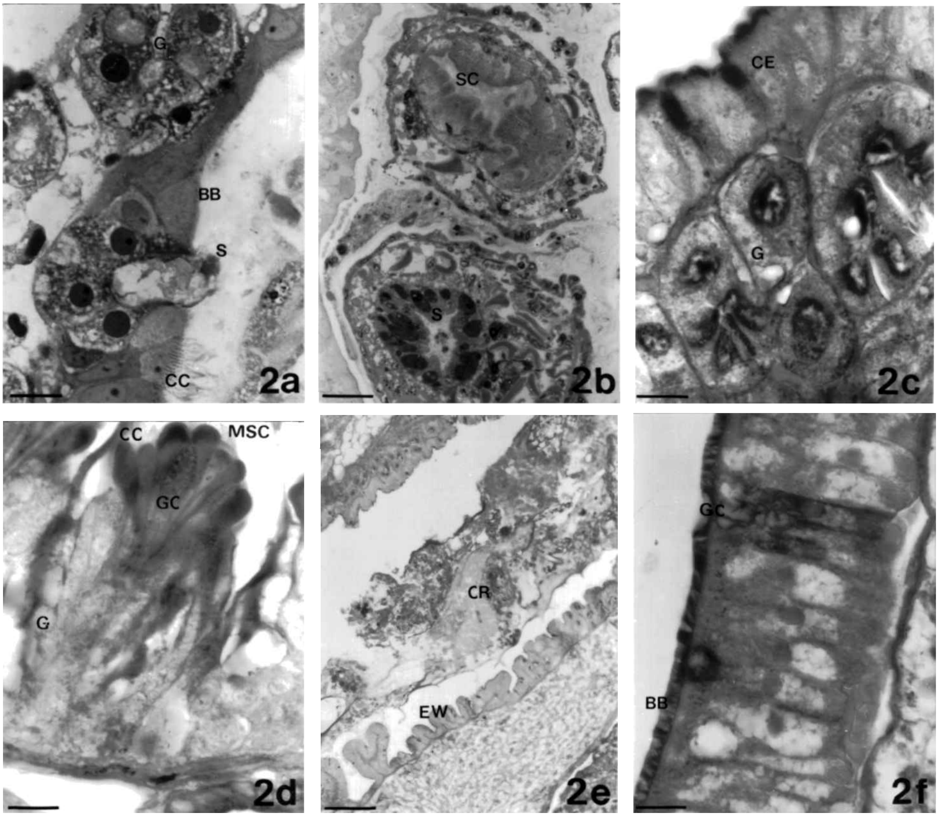


Figure 2. **a**: Detail of the manicotto glandulare external wall of *Hyla nana* tadpole at stage 31. Note the secretion released from the acinous gland and the vacuolated cytoplasm of cuboidal cells post-secretion. **CC**: ciliated cell, **BB**: brush border cell, **G**: gland, **S**: secretion (Toluidine Blue) (Bar, 10 μm). **b**: Detail of the manicotto glandulare internal secretory crypts of *Hyla nana* tadpole at stage 31. Note two stages of crypt secretory cycle: the upper empty pale crypt cells and the lower dark staining crypt cells full of secretory material cytoplasm. **SC**: secretory crypt, **S**: secretion (Toluidine Blue) (Bar, 30 μm). **c:** Stage 38 tadpole, detail of the manicotto glandulare external wall. The columnar cell epithelium **(CE)** containing PAS+ secretion apically. The glandular layer, more developed than that of the stage 31 tadpole, has PAS+ secretion inside of the glandular ducts **(G)** (PAS-Indigo Picrocarmine) (Bar, 10 μm). **d**: Detail of the manicotto glandulare external wall of a *Hyla nana* tadpole at stage 38 showing glands (PAS+) of the tubular type. Note the surface columnar cell epithelium with three cellular types: ciliated (PAS−) **(CC)**, mucus-secreting (PAS+) **(MSC)**, and goblet cells (PAS+) **(GC)** (PAS-Indigo Picrocarmine) (Bar, 10 μm). **e**: Detail of the intestinal tract and the manicotto glandulare of a *Hyla nana* tadpole at stage 38. Note that the manicotto glandulare is not organized in internal crypts but there are crypt vestiges **(CR)**. **EW**: external wall (PAS-Indigo Picrocarmine) (Bar, 30 μm). **f**: Detail of stage 38 *Hyla nana* tadpole intestinal tract. Note the columnar epithelium with brush border (PAS+) cells **(BB)**, and goblet cells (PAS+) **(GC)** (PAS-Indigo Picrocarmine) (Bar, 10 μm).

The connective tissue beneath the epithelium has acinous glands with cuboidal cells. These cells possess large nuclei and the cytoplasm is filled with secretory droplets. Beneath glands there are elongate basal cells (fig. 1d). The glands release their secretion into the

Table 1. Larval diet of gastro-intestinal tracts of *Hyla nana* ($n = 20$). (%N): Total number of each item estimated following the Lackey Drop Microtransect Counting Method (Lackey, 1938), (fo): Frequency of Occurrence percentage, (u): Non-quantifiable items.

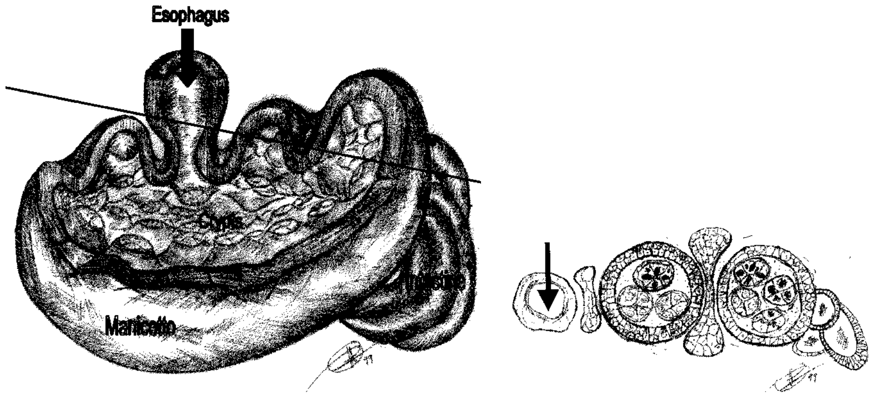
Item	%N	fo
Euglenophyceae	3.6	25
Bacillariophyceae	90	100
Chlorophyceae	6.4	40
Mineral remnants	(u)	100
Detritus	(u)	100

lumen of the organ (fig. 2a). Inside the manicotto glandulare, structures similar to secretory crypts in different stages of the secretory cycle were observed (figs. 2b, 3a, b). The lumen between the internal crypts had abundant quantity of algae, mineral remnants, and detritus (table 1). At stage 38, the external wall of this manicotto glandulare has a columnar epithelium consisting of three cellular types: ciliated cells (PAS−), mucus-secreting cells (PAS+), and goblet cells (PAS+) (fig. 2c, d). Interspersed with the ciliated cells, the mucus-secreting columnar cells characteristic of the vertebrate stomach commonly contain apically a variable amount of mucin and possess a free border in which striations are visible. The goblet cells have a granular cytoplasm. The glandular layer is better developed than at stage 31 (fig. 2c), and starts to change from acinous to tubular glands (fig. 2c, d). Inside the glandular ducts, there is mucous secretion (PAS+). Moreover, the internal crypts are lacking. However, an herbivorous-detritivorous trophic spectrum mainly composed by bacillariophyceae, green algae, mineral remnants and detritus was observed. These observations suggest a progressive change of this organ to a stomach structure when the metamorphic climax approaches.

The intestine has a typical columnar epithelium with brush border (PAS+) cells and intercalated goblet cells (PAS+) (fig. 2f). The PAS+ stain detects the presence of mucin.

The function of the larval stomach, called manicotto glandulare by Lambertini (1929), has been very controversial. Savage (1955) and Dodd and Dodd (1976) considered it as a storage organ. Barrington (1946) found no gastric digestion in *Rana temporaria* and suggested that the absence of a true stomach was correlated to the microphagous diet. Griffiths (1961) reported proteolytic activity in the manicotto glandulare but different from that of adult stomach. Griffiths (1961) suggested that the manicotto glandulare is part of a larval pancreatic complex and that a true stomach does not occur in any of the tadpoles examined. He described two principal types of manicotto glandulare: one embedded in the intestinal wall and the other as a discrete extra-intestinal organ.

In contrast with the structure found in *Hyla nana* larvae at stage 31, the manicotto glandulare found in species of other genera (e.g., *Gastrotheca, Rana, Ceratophrys, Pseudis, Xenopus*) has columnar cell layer and, underneath it, a glandular layer with cuboidal cells lacking internal secretory crypts (Griffiths, 1961; Terán and Michel de Cerasuolo, 1988; Rada de M. and Bello de L., 1988; Terán and Michel, 1996). Furthermore, the stomach of



(a) (b)

Figure 3. a: Schematic view of the manicotto glandulare of a stage 31 *Hyla nana* tadpole. **b**: diagrammatic cross section showing the internal crypts of the manicotto glandulare. The esophagus is indicated with arrows.

some carnivorous anuran larvae, e.g. *Lepidobatrachus laevis*, has a cuboidal epithelium with reduced number of ciliated cells and scattered goblet cells. In addition, there are submucosal multi-cellular tubular glands with cuboidal cells (Ruibal and Thomas, 1988).

The distinctive peculiarity of this organ found in *Hyla nana* larvae at stage 31 is the presence of internal secretory crypts (fig. 3). As it develops, this organ undergoes changes at the external mucosal epithelium and the submucosal glands which become very similar to the adult gastric mucosa at the stage 38; the internal secretory crypts begin to disappear. That process is completed at stage 41. It is possible that in *Hyla nana* the histological changes in the manicotto glandulare appear before those in other species. Histolytic and histogenetic changes have also been observed in the manicotto of *Gastrotheca gracilis* between stages 41-46 (Terán and Michel, 1996).

Taking in consideration the particular structure of the mouth, and the benthic habit of *Hyla nana* (Lajmanovich, 1998), we suggest that the specific structure of its digestive tract is related to a detritivorous diet, rich in organic matter in decomposition containing a great proportion of mineral remains. Consequently the manicotto glandulare would serve to coat these materials in mucous secretions during the digestion, especially the mineral remains, which could injure the walls of the whole digestive tube.

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Advertisement call of two Indian ranids, *Indirana beddomii* and *Tomopterna rufescens*

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A total of 85 ranid species are distributed all over India of which 46 species occur in Western Ghats (Daniels, 1991). Acoustic studies on Indian ranids have been done only for a few species (Kanamadi, 1996; Roy, 1996). In this paper we describe advertisement

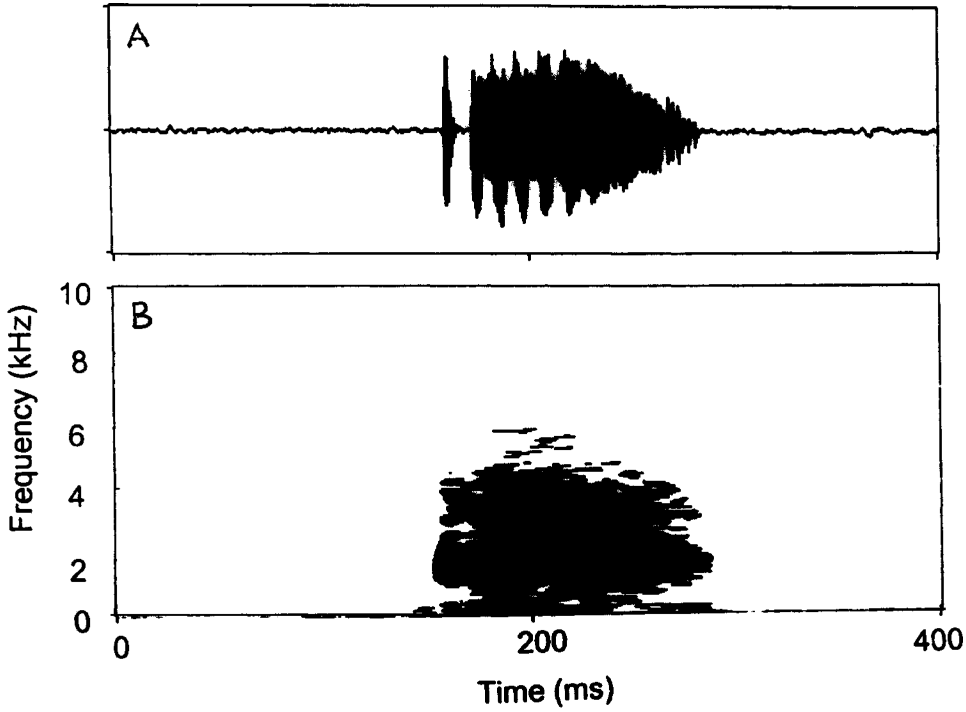

Figure 1. Oscillogram (A) and sonagram (B) of the advertisement call of *Indirana beddomii* (SVL 48 mm). Recorded at Agumbe. Air temperature 20°C.

Table 1. Acoustical features of the advertisement call of *Indirana beddomii* (Calls of 10 randomly selected individuals were used for statistical calculations).

Parameter	Sample size	Mean ± $s_{\bar{x}}$	Range
Pulse number	35	12.3 ± 0.16	10-14
Call duration (ms)	32	19.6 ± 1.23	109-134
Call interval (s)	13	14.38 ± 2.03	5.5-35
Call period (s)	13	14.50 ± 2.02	5.613-35.127

call of two ranids, *Indirana beddomii* and *Tomopterna rufescens*, from Western Ghats of India for the first time. Field observations were carried out from 1995-1997 around Agumbe (13°18′N, 75°04′E) and Jog (14°5′N, 74°9′E) towns. Calling frogs were collected and brought to the laboratory. Preliminary identifications were done (Boulenger, 1890; Daniel, 1975; Daniel and Sekar, 1989). Later they were confirmed by Zoological Survey of India, Chennai. The generic names have been updated (Dutta, 1992, 1997). Calls were recorded on Sony cassette tape using AKAI-AJ 490 FS tape recorder (4.8cm/s speed) with external unidirectional microphones (AKG D-707, C-190). Air temperature was measured by holding the digital thermometer 5-6 cm away from the frogs. Recorded calls

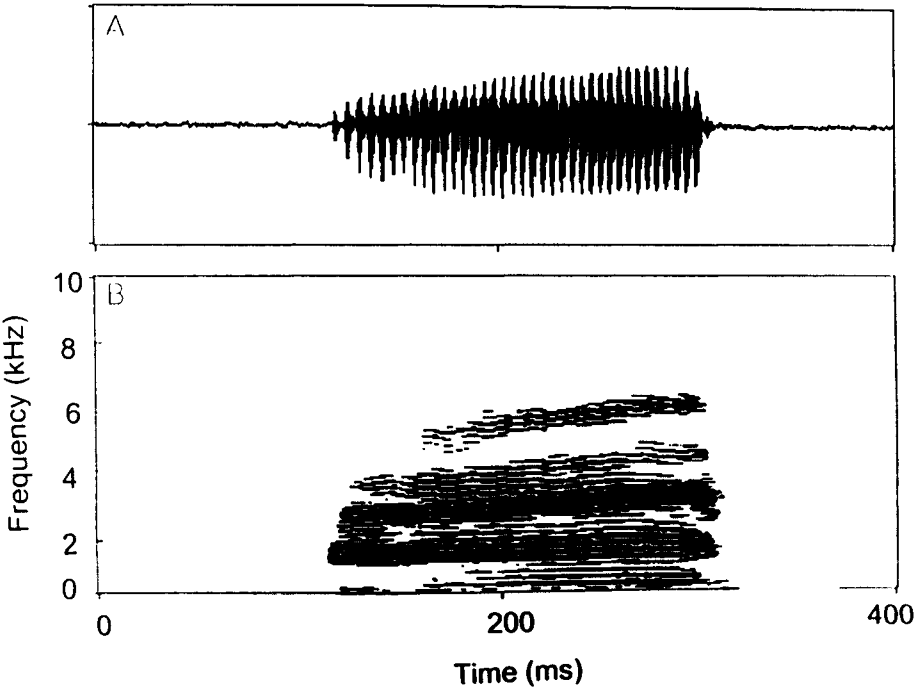

Figure 2. Oscillogram (A) and sonagram (B) of a pulse group of the advertisement call of *Tomopterna rufescens* (SVL 42 mm). Recorded at Jog. Air temperature 20°C.

Table 2. Acoustical features of the advertisement call of *Tomopterna rufescens* (Calls of 10 randomly selected individuals were used for statistical calculations).

Parameter	Sample size	Mean ± $s_{\bar{x}}$	Range
Pulse number	10	49.2 ± 2	39-58
Pulse groups/call	15	21.4 ± 0.19	19-25
Pulse group duration (ms)	20	241.9 ± 9	179-347
Pulse group interval (ms)	15	556 ± 132	186-889
Pulse group period (ms)	15	792 ± 136	391-2139
Call duration (s)	15	26.41 ± 1.12	2.8-49
Call interval (s)	15	1.8 ± 0.767	0.8-3.1

were processed at the Zoologisches Institut, Universität Bonn, Germany using acoustical analyzer computer programme MOSIP (R) Spectro analysis V6 8, 41/89 MEDAV GmbH. The statistical analysis was carried out with statgraphics program STSC Inc., Knoxville, USA.

Indirana beddomii is a medium sized frog (male SVL $\bar{x}$ = 49.3 mm, *n* = 10) commonly found on wet rocks in small and shallow water pools. Males possess an indistinct internal subgular vocal sac. During rainy days males emit advertisement calls from the rock surface under the grass. Calling begins with the onset of monsoon (June) and continues up to the end of the rainy season (September/October). Calls were recorded between June and August of 1995 and 1996. Calling frogs were well spaced, the distance between two nearest males being from 8 to 10 m (*n* = 10). Calls were antiphonal with a long call interval (table 1). Each call consists of 10 to 14 pulses (fig. 1A). The first pulse is always separated from the remaining pulses (fig. 1A). The amplitude of the first pulse is high, but it is lower in the next pulse. In subsequent pulses it rises slowly reaching a maximum in the middle of the call. Later on, the amplitude gradually decreases till the end of the call. The frequency spectra consist of indistinct harmonics with two energy bands (fig. 1B). The sound energy is concentrated between 37 and 6820 Hz. The fundamental frequency lies between 37 and 362 Hz and the dominant frequency between 862 and 1840 Hz. The air temperature during recordings varied between 20° and 22°C.

Tomopterna rufescens is a medium sized frog (male SVL $\bar{x}$ = 42.1 mm, *n* = 10) inhabiting the margins of streams between rock and hilly terrain and also grass patches on elevated places. Males possess a pair of external subgular vocal sacs. Frogs call from the ground on the edges of the bodies of water. Calls are emitted on rainy days only. Calling begins with the onset of monsoon (June) and continues till August. Advertisement calls were recorded during June and July in 1995 and 1996. The sunset during these days occurred between 18.20 and 18.30 hrs. Calls were heard from 20.30 to 04.00 on the following day. The distance between two nearest calling males was 10 to 15 m ($\bar{x}$ = 12.8, *n* = 10). Calls were antiphonal. Each call is composed of distinct pulse groups (fig. 2A). Pulse number in each pulse group varied between 39 and 58. Call parameters are summarized in table 2. The amplitude of the pulses in the beginning is low and gradually increases till the end except the last two pulses where it decreases and ends up with the lowest amplitude (fig. 2A). Advertisement call covers a broad frequency range from 100 to 7500 Hz having five energy bands with distinct harmonics and numerous side bands (fig. 2B). Fundamental frequency lies between 100 and 350 Hz and the dominant frequency lies in the third energy band between 2536 and 3520 Hz (fig. 2B). The air temperature during the recordings varied from 19° to 21°C.

The call interval of *I. beddomii* is high in contrast with *T. rufescens* and other Indian ranids described so far (Kanamadi, 1996). It is low compared to other Asian ranids, *Amolops larutensis* and *Amolops jerboa,* where the call interval is 22-37 s and 65-104 s respectively (Matsui et al., 1993). The frequency ranges of *I. beddomii* and *T. rufescens*, while differing from each other, are high in comparison with other Indian ranids (Kanamadi, 1996; Roy, 1996). The frequency range of *I. beddomii* beginning from 37 Hz is the lowest among Indian ranids studied so far. The maximum frequency range extending up to 7500 Hz of *T. rufescens* is high compared to *Tomopterna breviceps* having 4900 Hz (Kanamadi and Hiremath, 1990) and other Indian ranids (Kanamadi, 1996; Roy, 1996). However, it is low compared to *A. jerboa*, where the upper frequency range extends up to 11 000 Hz (Matsui et al., 1993). The long call intervals of *I. beddomii* and the high frequency range of *T. rufescens* are conspicuous features among Indian ranids described so far.

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Advertisement calls of seven species of hyperoliid frogs, from Equatorial Guinea

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The comparison of anuran advertisement calls is a powerful tool for the determination of the taxonomic position of specimens collected in less explored areas. In Africa, anuran faunas from the tropical rainforests are still poorly known. Most publications on anurans and their vocalizations are devoted to species from the forest belt of West Africa (i.e., Schiøtz, 1964, 1967). Many of those forest species were considered to have a broad African distribution, but further studies have demonstrated that, in some cases, they actually consist of two vicariant species, one living in West Africa and a second species occurring in central Africa. This often renders the species from the central African rainforest much less known that their occidental counterparts. Within the central African forest block lies the small country of Equatorial Guinea, which comprises a continental part, Río Muni, and some islands in the Gulf of Guinea, namely Bioko, Pagalu, Corisco and the Elobeyes. The anuran fauna of Río Muni includes a considerable array of species, which have only recently been described (De la Riva, 1994). However, its fauna remains among the least known even when compared to other countries in the area.

In this paper we contribute to the knowledge of the anuran fauna of Equatorial Guinea in particular, and central Africa in general, by providing a quantitative description of the calls and calling behavior of seven species in the family Hyperoliidae, some of which were previously undescribed quantitatively.

Recordings were obtained by the second author in 1993. Recording equipment included either a Sony WM D6C or a Sanyo M1120 tape recorder and a Sennheiser Me 80 directional microphone. We present a representative audiospectrogram and oscillogram for a selected 2.5 s recording segment for each species. A longer recording (10-90 s) was analyzed when available to generate numerical information (mean, s, range) on the spectral and temporal characteristics of the sounds. For each species calls from a single characteristic male were analyzed.

Recordings were processed with a digital signal analysis system based on an Apple Macintosh. The sounds were digitized and edited at a sampling frequency of 44.1 kHz and 16 bit resolution with Sound Tools hardware and software. Signalyze software was used to obtain numerical information and to generate audiospectrograms and oscillograms. Frequency information was obtained through fast Fourier transform (FFT) (width, 1024 points). The terminology used for the description of the advertisement calls follows Heyer et al. (1990). Unless specified, classification and nomenclature of the species follow Frost, 1985).

Eleven different call characteristics were recorded. The variables considered were: call duration, notes per call, note duration, number of pulses per note, pulse rate (pulses per second), pulse duration/pulse period (T/P), dominant frequency, other frequencies with substantial energy, change in dominant frequency (dominant frequency at the end of the note minus dominant frequency at the beginning of the note), frequency range (width of dominant frequency band at maximum amplitude), notes per minute (within call), and calls per minute. Collected individuals were deposited in the Centro de Estudios Tropicales, Sevilla, Spain. Unless specified, recordings were obtained at different sites of Monte Alén National Park, a protected area in the center of Río Muni. The area is mountainous and

Table 1. Numerical characteristics of the advertisement calls. Mean, standard deviation (in parenthesis) and range (in brackets). n = number of calls or notes of a single male.

Species	Air temperature (°C)	n	Call duration (ms)	Notes per call	Note duration (ms)	Pulses/ note	Pulses/ second	T/P
Afrixalus brevipalmatus Note A	23	2	832 (87) [741, 915]	1	166 (32) [143, 188]	20 (3.5) [18, 23]	123 (2) [122, 125]	0.605 (0.67) [0.557, 0.653]
Afrixalus brevipalmatus Note B	23	13	–	5 (1) [4-5]	39 (14) [22, 72]	5 (2) [4, 9]	141 (20) [117, 179]	0.589 (0.14) [0.284, 0.756]
Afrixalus paradorsalis	22	12	493 (146) [350, 731]	3 (1) [3, 5]	40 (13) [28, 77]	8 (1.5) [6, 10]	225 (32) [169, 261]	0.755 (0.118) [0.578, 0.885]
Alexteroon obstetricans	20	3	22 (6) [16, 28]	1	22 (6) [16, 28]	8 (1) [6, 9]	361 (71) [288, 431]	0.195 (0.31) [0.167, 0.227]
Hyperolius ocellatus	19	29	169 (20) [155, 213]	4 (0) [4, 5]	169 (20) [155, 213]	–	–	–
Hyperolius tuberculatus	19	13	1026 (508) [558, 1999]	12 (7) [7, 22]	20 (7) [10, 38]	–	–	–
Leptopelis aubryi	18	4	43 (8) [31, 50]	1	42 (8) [31, 50]	13 (2) [11, 14]	281 (31) [251, 312]	0.887 (0.03) [0.853, 0.926]
Phlyctymantis leonardi Note A	24	14	164 (35) [92, 197]	1	75 (12) [58, 94]	14 (1) [12, 15]	187 (20) [149, 209]	0.715 (0.129) [0.566, 0.914]
Phlyctymantis leonardi Note B	24	27	–	2 (1) [0, 4]	8 (7) [4, 40]	–	–	–

Table 1. (Continued)

Species	Dominant frequency (Hz)	Other frequencies (Hz)	Change in frequency (Hz)	Frequency range (Hz)	Notes/ minute	Calls/ minute
Afrixalus brevipalmatus Note A	3463 (271) [3271, 3655]	–	283 (57) [242, 323]	1646 (100) [1575, 1716]	289 (43) [259, 320]	–
Afrixalus brevipalmatus Note B	3642 (69) [3554, 3776]	–	– 3 (79) [– 161, 101]	1209 (219) [909, 1676]	401 (144) [287, 705]	–
Afrixalus paradorsalis	2894 (86) [2786, 3009]	–	126 (277) [– 141, 949]	1070 (289) [767, 1636]	347 (39) [318, 439]	25 (6) [20, 29]
Alexteroon obstetricans	3062 (12) [3049, 3069]	6037 (101) 5936-6138	20 (40) [– 20, 61]	828 (105) [707, 888]	17 (1) [16, 18]	17 (1) [16, 18]
Hyperolius ocellatus	3954 (192) [3026, 4079]	–	–	628 (99) [464, 909]	1201 (69) [1029, 1277]	20 (4) [15, 24]
Hyperolius tuberculatus	3228 (53) [3110, 3311]	6448 (98) 6239-6623	– 22 (99) [– 262, 101]	510 (103) [323, 686]	683 (66) [535, 855]	34 (9) [22, 50]
Leptopelis aubryi	2049 (461) [1454, 2423]	–	162 (225) [– 40, 404]	1540 (321) [1353, 2019]	19 (8) [12, 28]	19 (8) [13, 28]
Phlyctymantis leonardi Note A	2145 (305) [1413, 2484]	–	1269 (192) [868, 1575]	1209 (171) [787, 1373]	593 (99) [480, 755]	110 (75) [30, 256]
Phlyctymantis leonardi Note B	2471 (140) [2322, 2645]	–	–	691 (69) [585, 767]	1654 (327) [1210, 2429]	–

mostly covered with undisturbed rainforest. The study period comprised May to December 1993. The numerical parameters of the calls are shown in table 1.

Afrixalus brevipalmatus (Ahl) was common in the study area. Males called throughout the period of study at night, among the grass and other low vegetation (less than 1.5 m high), in open or disturbed areas, ponds, and overflowing streams, or areas of streams with calm waters. Recorded specimens were at a pond at the roadside. They were often heard with *Afrixalus paradorsalis* and *Hyperolius pardalis*. The call includes two notes (fig. 1A): the first one (note A) is a longer trill which is always included in the call. The dominant frequency of this note is high and increases (3.5-4 kHz). Note A is followed by four or five shorter trills (note B), higher in intensity. Both notes are pulsed, note A being composed of 18-23 pulses and note B of 4-9 pulses. All the B notes are similar except for slight differences in duration corresponding to different numbers of pulses. The power of the second note is concentrated in the 3.5-3.7 kHz range. Schiøtz (1999) provided a thorough discussion on the complicated and unsettled taxonomy of the *Afrixalus fulvovittatus* complex, which presents two types of morphologies and dorsal patterns, A and B. The specimens from Monte Alén [reported by De la Riva (1994) as *A. fulvovittatus*] belong to the type B. The proper name for the forest species of the type B from Cameroun southwards is *A. brevipalmatus* (Schiøtz, 1999; pers. com.). To the best of our knowledge, no description of the call of this species has been published.

Afrixalus paradorsalis Perret. This species was moderately common in the area. Individuals were recorded at a stream overflow near the Niegong-Evinayong road. Males called at night throughout the study period, from low vegetation (less than 1.5 m high), often together with *Afrixalus brevipalmatus*. The call is a sequence of three to five identical short pulsed notes with power in the 2.8-3 kHz range (fig. 1B). The total duration of the call is variable (range 350-730 ms). The call was repeated sporadically at irregular intervals. This species occurs in central Africa from Nigeria to Gabon (Schiøtz, 1999). Schiøtz (1967, 1999) described the call of *A. paradorsalis* (cited as *A. congicus paradorsalis* in Schiøtz, 1967) from Osomba (Nigeria). The overall structure of the call is similar to that reported by us, a sequence of short pulsed notes, with dominant frequency centered about 2.8-3 kHz. Schiøtz (1967, 1999) reports though that the call was composed typically of two notes and occasionally three, while we found the notes to be emitted in groups of three to five notes.

Alexteroon obstetricans (Ahl) is an uncommon species in the area. The recorded individual called on September 25, at night, perched in the vegetation more than 2 m above ground, near the Bilene river, in primary forest. Another frog species calling concomitantly nearby was *Nyctibates corrugatus*. The call is extremely short, pulsed, with most energy concentrated around 3 kHz, although some energy is present in the second harmonic (fig. 1C). The call is amplitude-modulated (not reaching 100%) and it is emitted at relatively long intervals (calling rate 15.7-17.8 calls/minute). Schiøtz (1999, p. 84) provides an audiospectrogram of the call of an undetermined locality in Cameroun, and describes it briefly as being “a metallic “toc”, repeated 5-6 times”. The frequency and duration of

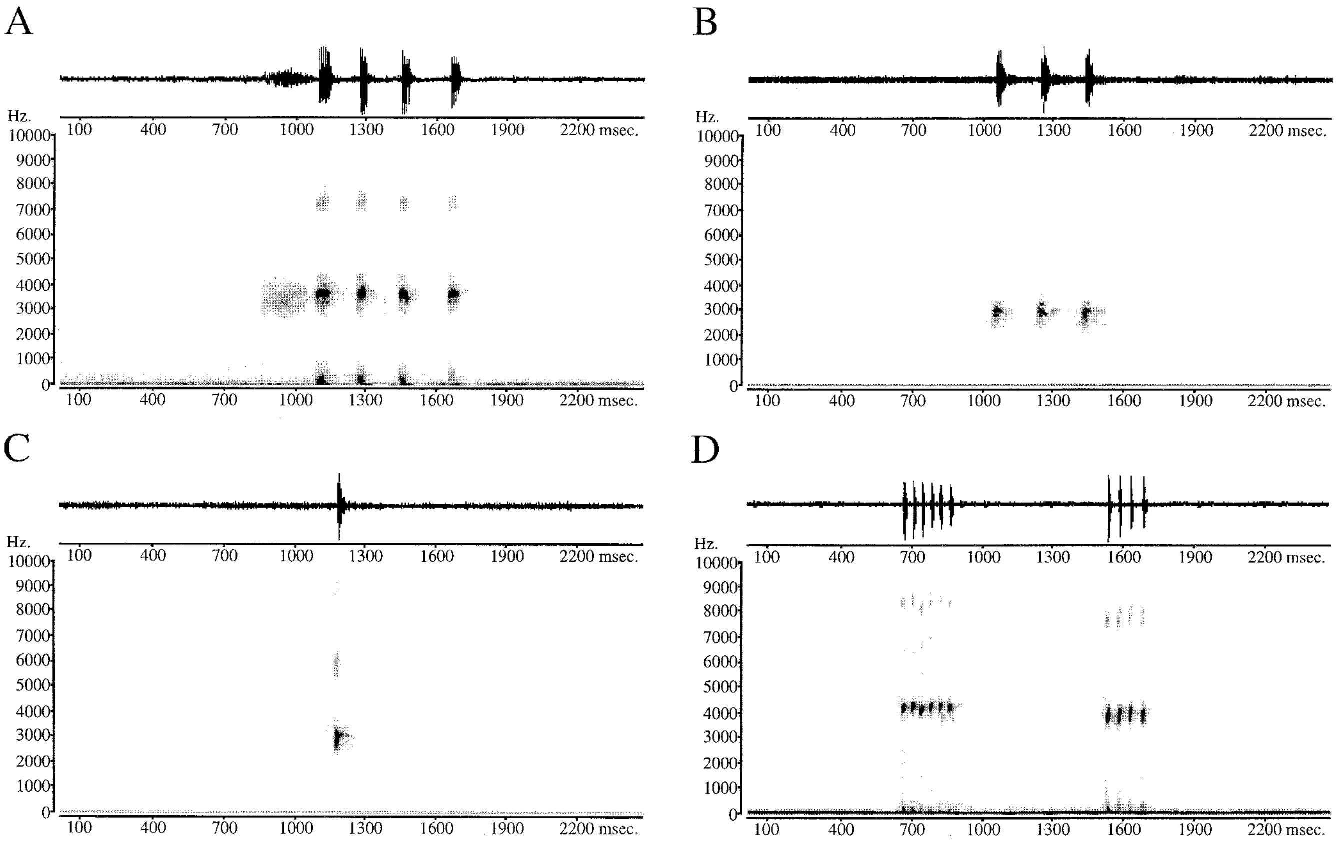

Figure 1. Characteristic audiospectrogram and oscillogram of an advertisement call of (A) *Afrixalus brevipalmatus* note A followed by four B notes, (B) *Afrixalus paradorsalis*, (C) *Alexteroon obstetricans*, (D) *Hyperolius ocellatus*, two calls emitted by the same male: one with six notes and one with four notes.

the call represented in Schiøtz (1999) coincides roughly with that of our recordings but no further quantitative information is provided.

Hyperolius ocellatus Günther was moderately common in the Park. Males called at night throughout the study period. They perched on vegetation (bushes, small trees, ferns) surrounding streams both in primary and secondary forest. Other species calling concomitantly were *Afrixalus brevipalmatus* and *Hyperolius tuberculatus*. The call is a brief sequence of four or five high frequency notes emitted at regular intervals (fig. 1D). The energy is concentrated between three and four kHz. Occasionally two isolated notes have been heard (not included in the statistics in table 1). This is a widespread species in Central Africa (Perret, 1975; Largen and Dowsett-Lemaire, 1991). Schiøtz (1999) provides an audiospectrogram of an advertisement call of *H. ocellatus* from Osomba (Nigeria) which is similar to our fig. 1D. He only provides an additional brief comment about its frequency "an indistinct frequency-intensity maximum at about 3800-4000 cps" which does not disagree with our description.

Hyperolius tuberculatus (Mocquard) is a moderately common species in the area studied, and seems to be more abundant during the dry seasons. Males called at night, perched on the branches of bushes and riparian vegetation in disturbed areas, but they were seen also in ponds in open areas with bushy vegetation outside the park, at the grassy coastal belt near Bome. Individuals were recorded at a stream crossing the road near Moka, in Monte Alén. The call is a sequence of 7-22 high frequency short notes. Most calls have seven to ten notes (fig. 2A). Largen and Dowsett-Lemaire (1991) describe the call of the species in the Republic of Congo as a rather quiet "chink-chink-chink." Although this description somewhat coincides with our recordings from Monte Alén, it is too limited to allow for quantitative comparisons. Schiøtz (1999) provided an audiospectrogram of a call of *H. tuberculatus* from Binguela (Cameroun) recorded by Amiet. He also stated that the individuals from this area differed "in many respects" from the sample treated by Largen & Dowsett-Lemaire (1991). The call shown in the audiospectrogram in Schiøtz (1999) has a note repetition rate of 12-13 notes/sec, a total of 21 notes per call, and the dominant frequency is approximately at two kHz. While the note repetition rate is similar to that found in our recordings, and the number of notes per call is also within the range found by us, the frequency found in our recordings from Monte Alén is substantially higher than that depicted in the audiospectrogram in Schiøtz (1999) which is about 2 kHz. This difference may just reflect a marked difference in size in the specimens or could be relevant taxonomically.

Leptopelis aubryi (Duméril) was moderately abundant in the park. Males called at night during September and October, from thick bushes on the sides of the road, at 1-1.5 m above the ground, occasionally near ponds. The advertisement call is a very sharp, rasping sound (fig. 2B). It is extremely brief (31.3-50 ms) and its energy is spread over a wide frequency band from two to four kHz and beyond. The call is amplitude-modulated, and it is emitted at relatively long, irregular intervals. Amiet and Schiøtz (1974) and Schiøtz (1999) describe two different vocalizations of *L. aubryi* from NíKongsamba (Cameroun).

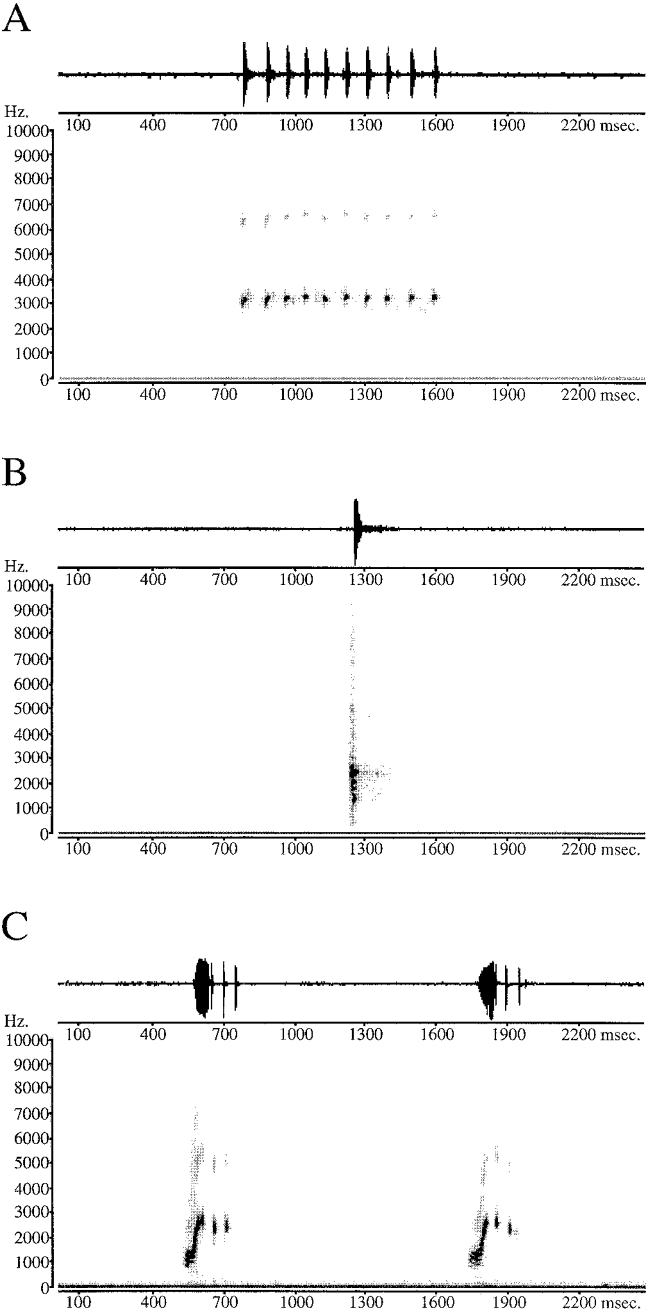

Figure 2. Characteristic audiospectrogram and oscillogram of an advertisement call of (A) *Hyperolius tuberculatus*, advertisement call with ten notes, (B) *Leptopelis aubryi*, (C) *Phlyctymantis leonardi*, two ABB calls from the same male.

The call identified by them as the mating call is similar to the call recorded by us, both in duration and in frequency. The second call type described in Cameroun (a fast sequence of groups of 2-3 clicks) was not recorded or heard in Equatorial Guinea.

Phlyctymantis leonardi (Boulenger) is a rare species in Monte Alén National Park, where only one individual was seen in a pond by the road, near Ayene. Contrarily, a notable aggregation of males was observed and recorded on November 8, calling from the ground around a pond near Bome, a locality outside the park, on the grassy prairies along the coast of Río Muni. The only other species observed concomitantly was *Hyperolius tuberculatus*. The call is extremely loud and is composed of two notes, a "woah" (note A) followed by a clicking sound or note B (fig. 2C). Note A can be emitted in isolation or followed by 1-4 notes B. Note A is a sequence of 12-15 pulses repeated at a irregular intervals. Note A is short with a long raise time peaking at the 11th pulse, and a faster fall time, followed by (1-4) isolated pulses emitted at relatively longer intervals (27.9 ms). The first pulses of the call have a much lower dominant frequency (about one kHz) than the last three or four pulses which reach 2.4 kHz. The resulting sound has therefore a marked upwards frequency change. An even higher dominant frequency is found in the B notes emitted after the A note which are extremely short. When more than one B notes are emitted it appears as if the dominant frequency and the intensity of consecutive notes decreased. The vocal sac of this species is remarkable as that of the rest of the Kassininae: it consists of a main, subgular chamber, with a lateroventral slit on each side. This slit is the opening to an invaginated, internal projection of the gular skin. Note A is produced using only the main sac, which is inflated for this purpose. When the air pressure within it rises, the two projections are evaginated and they vibrate, producing note B. The choruses of these frogs are extremely cacophonic and loud.

The recording obtained in Monte Alén (not shown in the figures) only included note A. The differences between the calls heard at Monte Alén and those from near Bome are probably due to the very different social context in which these recordings were obtained (a single, isolated male in Monte Alén versus a large chorus in Bome) although given the differences in frequency changes observed, we cannot reject the possibility that the individual recorded in Monte Alén may belong to a different taxon. Schiøtz (1967) described the "reproductive call" of *P. leonardi* from a site W of Danané (Côte d'Ivoire). The call described is 0.1 s long and shows upwards frequency change (from 0.9 to 2.9 kHz). This call is markedly different both in temporal and in spectral characteristics to the call recorded by us in Bome, supporting Schiøtz's more recent re-assessment, that considers that the species occurring in West Africa is *P. boulengeri* (Schiøtz, 1999). We can therefore suggest that the individuals recorded in Côte d'Ivoire and in Equatorial Guinea do not belong to the same species. On the other hand, the description of the recordings obtained by Largen and Dowsett-Lemaire (1991) in Tchissanga (Republic of Congo) suggest that the vocalizations are similar to those recorded in Bome and Monte Alén.

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Home range and shelter use in *Salamandra lanzai* (Caudata, Salamandridae)

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The spatial organization of salamanders results from environmental conditions (Ovaska, 1987; 1988; Mathis, 1990), the presence of congeners (Jaeger et al., 1995; Marvin, 1998a; Nishikawa, 1990), and of other species (Anthony et al., 1997; Marvin, 1998b; Nishikawa, 1990; Ovaska, 1993). The size and shape of home ranges are the basis for understanding spatial organization, yet the patterns of movements and home range definitions are often hardly discussed (Kenward, 1987; Rose, 1982; White and Garrot, 1990). Home range can be defined as the area over which an animal normally travels in pursuit of its routine activities (Jewell, 1966). Measurements of home range and movements of salamanders are poorly documented (Stebbins and Cohen, 1995), and this paucity of information is especially true for European salamanders. The large alpine salamander *Salamandra lanzai,* a completely terrestrial and viviparous species (Nascetti et al., 1988), is endemic to the area around Monviso Massif in the Cottian Alps (Gasc et al., 1997). This species exhibited shelter fidelity and short distances between recapture events (Andreone, 1992; Ribéron et al., 1996).

This study reports informations on activity, shelter use, and home range in radiotracked adult *S. lanzai.* Thirteen individuals were caught (8 males and 5 females) by hand on 15 and 16 July 1996 in the Natural Regional Park of Queyras (44°42′N, 7°03′W, French Alps), at an elevation of 2200 m along a morainal steep slope. They were measured (snout-vent-length) with a plastic ruler to the nearest mm. The study area is a typical alpine grassland with patches of dwarf juniper (*Juniperus nana*) and rhododendron (*Rhododendron ferrugineum*). Numerous boulders, crevices and small flows occur over the whole area. The climate is characterized by a long snow coverage period from October to May and the active period of salamanders is about 2 months each year in this population (Ribéron et al., 1996). The average rainfall during June to September is 65.5 mm. Annual temperatures range from – 6.6°C (mean January minimum) to 16.2°C (mean July maximum). Daily thermic amplitude may reach 30°C in summer. The transmitters (BD-2I, Holohil systems Ltd.) were surgically implanted in the peritoneal cavity of anesthetized salamanders. The muscle and skin were closed by continuous suture (Ethicon Ltd) with a taper needle. Transmitter mass (0.9 g) was a maximum of 7% of salamander mass (mean = 13.2 g, range = 10.9-16.3 g). The salamanders were released at their capture location 24 hours after surgery. The transmitters have about 4 weeks battery life and detection distance of around 100 m. Time intervals between locations were every hours during the three first days following release to 3 times each 24 h (6 a.m., 2 p.m. and 10 p.m.) for the rest of the radiotracking period. Individuals were recaptured and toe-clipped for age estimation via skeletochronological analysis at the end of the radiotracking study to prevent the possible impact of toe-clipping on movement patterns.

The snout-vent length of males (mean ± s = 85.0 ± 0.6 mm, range = 83-88 mm, $n = 8$) and females (85.0 ± 1.6 mm, range = 82-91 mm, $n = 5$), and the age of males (13.8 ± 1.7 yr, range = 9-24 yr, $n = 8$) and females (13.8 ± 2.4 yr, range = 8-19 yr, $n = 5$) did not differ significantly (Mann-Whitney U-test, $U = 10.5$, $P > 0.60$, $n = 13$ and $U = 15.8$, $P = 0.93$, $n = 13$, for size and age respectively). Five hundred and thirty-two locations were recorded during the monitoring of these 13 salamanders along 28 successive days, from 17 July to 13 August. Salamanders were active on the surface during the nights after recent rainfalls or dew (relative humidity > 80% on land). In the ground, they were detected in unoccupied rodent burrows, mainly of *Marmotta marmotta* (21%, $n = 14$), crevices (33%, $n = 21$) and rock complexes (46%, $n = 30$). Salamanders were more frequently located in shelter deeper than 0.30 m than in more shallow shelters ($\chi^2 = 5.27$, df = 3, $P = 0.02$, only one location in each shelter was used for this analysis). Distance

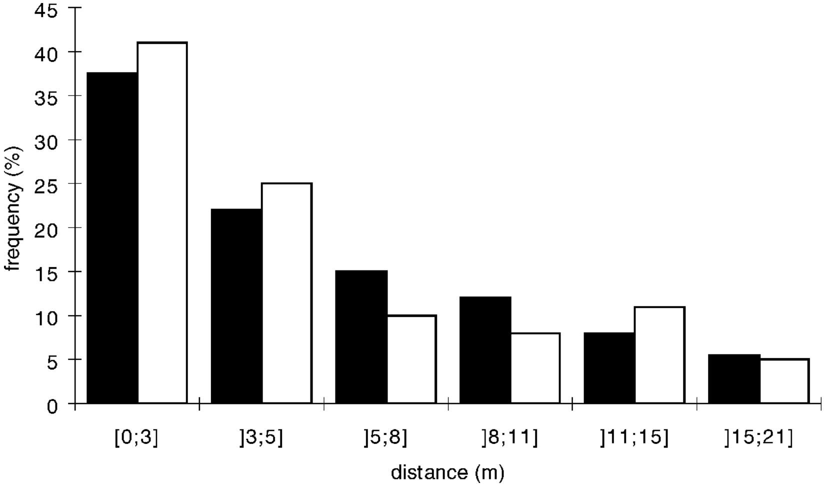

Figure 1. Distance moved on the surface between successive relocations in radiotracked *Salamandra lanzai* (Closed bars: 8 males, 91 locations, open bars: 5 females, 62 locations).

moved on the surface was similar between sexes (Kolmogorv-Smirnov-D test, $D = 0.33$, $P > 0.10$, $n = 153$) and ranged from 0.0 to 18.4 m for males and 0.0 to 21.0 m for females (fig. 1). Seven males and two females always stayed in the same shelter, returning to it after surface activity, while one male and three females occupied several different shelters during the period of study.

The concave polygon method was used to estimate home range (White and Garrott, 1990). The home ranges of males (46.8 ± 25.8 m^2, range = 16.6-97.3 m^2, $n = 8$) and females (51.4 ± 27.7 m^2, range 27.3-96.7 m^2, $n = 5$) did not differ between sexes (Mann-Whitney-U test, $U = 20.0$, $P = 1.0$, $n = 13$). These home ranges were not correlated with body size or age (Spearman-rank correlation, $r_s = -0.11$, $P > 0.05$ and $r_s = 0.17$, $P > 0.05$, respectively). The home ranges did not overlap. However, the initial distance between the first capture-release point of the individuals was larger than the range (distance between extreme locations) of these home ranges, so this observation cannot be interpreted in behavioural terms.

Only implantable radiotransmitters have been used in species of Caudata, in both aquatic and terrestrial habitats (Madison, 1997). None of these studies indicated signs of infection or rejection by the animal's immune system. The studied species have amazing regenerative abilities and the sutured wound was sealed rapidly except for one *Dicamptodon tenebrosus* that took six months to heal (Colberg et al., 1997). Field mortality was very low, Madison (1997) reported the death of nine salamanders during a snow storm. All these studies have shown no long term effects of the implant procedure on the survival of implanted salamanders. Ten of the *S. lanzai* implanted in 1996 were recaptured in 1997 and 1998. The suture was difficult to localise, and the weight of these individuals was similar to that of captured conspecifics. We make the assumption that such implantable transmitters did not alter the salamander behaviour.

The surface activity of terrestrial salamanders is generally limited by availability of suitably moist substrates (Duellman and Trueb, 1986). Increased moisture due to rainy weather or high ambient humidity is subsequently a major factor influencing foraging success of terrestrial salamanders. Several studies (review in Mathis et al., 1995) indicate the importance of shelter during dry periods and winter. *Salamandra lanzai* was active during twilight and nighttime, especially during or after rainfalls. During the day, they were found in former rodent burrows, crevices, and among fallen rocks. These shelters are similar to those used by the Alpine salamander *S. atra* in similar biotopes (Klewen, 1988). Terrestrial salamanders can use rodent burrows and mammal runway systems (*Ambystoma maculatum*, Madison, 1997) and sometimes show a commensal relationship with these small mammals (*A. californiense*, Loredo et al., 1996). In some plethodontids, competition has been observed among individuals for cover objects (Mathis, 1990), which can differ for foraging or mating resources (Mathis et al., 1995). In *S. lanzai*, individuals can stay long periods in underground shelters between successive rainy events and this could increase the trophic importance of such shelters. The relation between level of fidelity and trophic conditions in shelters remains however to be tested. Moreover, adult *Plethodon teyahalee* had at least one underground shelter within their territories and none were known to have been used by more than one individual (Nishikawa, 1990). We do not have quantitative data on the number of individuals in each shelter in *S. lanzai,* but we observed on several occasions more than one individual entering the same shelter.

The fire salamander *S. salamandra* has a definitive home range and always returns to the same hiding place even after a displacement (experimental transfer or spawning migration, Joly, 1963, 1968) and along several years (Joly, 1968; Feldmann, 1987; Himstedt, 1994). *Salamandra lanzai* also exhibit a long term shelter fidelity (Ribéron et al., 1996). *Salamandra salamandra* leave their shelter after sunset and walk about 10-30 m until they return home before sunrise (Plasa, 1979). A similar behaviour was observed in *S. lanzai.* The estimated *S. lanzai* home ranges were similar to these observed in *S. salamandra*, in lowland environment (68 m^2, Joly, 1968 and 55 m^2, Denoël, 1996). Home range size is considered to be a function of sex in many vertebrates (e.g. Rose, 1982 and Van Sluys, 1997 for lizards). In terrestrial salamanders, *P. glutinosus* males exhibited a larger home range than females (Merchant, 1972), while gender differences varied between populations in *P. jordani* (Merchant, 1972; Nishikawa, 1990). No difference between sexes was observed in *S. lanzai.* Home range size is also positively correlated with body size for many vertebrates (Harestat and Brunnell, 1979). Larger individuals may require larger foraging areas because of greater energetic requirements (McNab, 1963; Turner et al., 1969). However, in some species home range size is inversely correlated with body size (e.g. Mathis, 1991 for *P. cinereus*) indicating that larger individuals may gain higher-quality foraging areas.

Our study on *S. lanzai* confirms the sedentarity of other European terrestrial salamanders (*Salamandra* and *Mertensiella*). Researches would now be focused on function (e.g. relation with mating system and territoriality) and modalities (e.g. shelter recognition) of this behaviour.

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An estimate of maximum local population density of Red Hills salamanders (*Phaeognathus hubrichti*)

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The Red Hills salamander, *Phaeognathus hubrichti*, a species listed as threatened under the Endangered Species Act of 1973 (US Fish and Wildlife Service, 1976), has a narrow range restricted to southern Alabama between the Alabama and Conecuh Rivers (Jordan and Mount, 1975). Within this range, ideal Red Hills salamander habitat is narrowed further to areas in the Tallahatta and Hatchetigbee geological formations with the following characteristics: (1) north facing, steep to moderately steep mesic ravines, (2) outcrops of siltstone, (3) a mature hardwood overstory, (4) a rich forest-floor arthropod fauna, and (5) loamy, friable topsoil (Dodd, 1991).

Two studies have attempted to determine population densities of the Red Hills salamander. Jordan (1975) studied a selected population of animals which was described as “large”. He estimated the density of this population to be 43 individuals on a 2.6 ha site, but density at that site is thought to be greater than at most sites (US Fish and Wildlife Service, 1983). Dodd (1991) calculated densities of burrows, an index of salamander abundance, at several sites. Burrow densities ranged from 2.6 to 9.4 burrows per 100 m^2.

The distinctive burrows of Red Hills salamanders are relatively easy to sample and their abundance should correlate with salamander abundance. However, no data exist that document the proportion of burrows that are occupied by salamanders. Therefore, our objectives were to provide an estimate of population density from a second relatively pristine site and to relate this figure to the number of burrows present. The latter objective should allow interpretation of surveys of burrow abundance (Dodd, 1991).

Our study was performed along a single transect at Haines Island Park, a reserve operated by the US Army Corps of Engineers along the Alabama River in Monroe County, Alabama. The park has steep ravines covered by mature canopy trees, a shrub layer dominated by *Hydrangea quercifolia*, and a patchily distributed layer of mosses and liverworts interspersed with bare soil. The study site consisted of an 18 m transect oriented perpendicular to the slope and selected because burrows with salamanders were noted to be particularly abundant during preliminary surveys. Thus, our estimate of population density provides an upper bound to local population density for the Red Hills salamander. Animals were captured and recaptured during five collection efforts (15 and 21 Sept. 1995, 2 May 1996, 15 Oct. 1996, 26 April 1997 and 14 May 1997). Salamanders were collected using a #12 or 14 barbless hook baited with a cricket attached to a piece of wire that served as a handle. Animals either were lured from a burrow and grabbed, or bit the bait and hook and were pulled gently from their burrow. Captured salamanders were scanned for the presence of a passive integrated transponder (PIT) tag. If a tag was found, the ID and burrow number were recorded and the animal was released into that burrow. All unmarked salamanders were transported to Auburn University where PIT tags (see Donnelly et al., 1994) were implanted in the coelomic cavity. Because of the narrow diameter of each salamander’s body, a small surgical incision was required to implant the tag; individuals were anesthetized with MS-222 and the incision was sutured shut after a tag was implanted. Salamanders were kept in plastic boxes with mesh tops and damp paper towels during transportation and in captivity. Towels were replaced daily and crickets were provided ad libitum during a 2-4 week post-operative period. All animals were returned to the burrow from which they were captured.

A total of 24 individual Red Hills salamanders was captured during this study. Of these, eleven individuals were recaptured (table 1); one individual was recaptured twice and all others were recaptured once. To estimate abundance, a weighted mean method was used

Table 1. Capture-recapture data for Red Hills salamanders at Haines Island Park, Alabama. Capture periods are: (1) 15 and 21 Sept. 1995, (2) 2 May 1996, (3) 15 Oct. 1996, (4) 26 April 1997, and (5) 14 May 1997. New animals are unmarked individuals associated with each capture period. Salamanders recaptured during a capture period (column) are partitioned according to the capture period during which they were last recorded (rows).

		Capture period				
		1	2	3	4	5
New		14	0	0	6	4
Period of most recent capture	1	0	8	0	1	0
	2			1	1	0
	3				0	0
	4					0

(Begon, 1979) from which we estimated 26.5+ 7.4 ($s_{\bar{x}}$) salamanders along our transect. All animals were of adult size and appeared to be sedentary (Gunzburger and Guyer, 1998) and tags were unlikely to have been lost or failed; therefore, the assumptions of the weighted mean method (no recruitment through reproduction, no migration, no tag loss) are likely to have been met. Because all burrows were within 3 m above the transect, our estimate converts to a salamander density of 0.5 (+ 0.1 $s_{\bar{x}}$) animals per m^2, an estimate that is ca. 200 times greater than that presented by Jordan (1975). The disparity between these estimates results from the extreme aggregation of burrows within a slope. Our density figure documents abundance for a single deme and serves as an upper bound to local population density. Documentation of the distribution of demes within a slope is needed before a meaningful comparison of Jordan's (1975) estimate and ours can be made. An understanding of the distribution of such burrow clusters within slopes is likely to be important to understanding the genesis and maintenance of populations among slopes.

The 26 individuals estimated to occupy our transect were distributed among 33 burrow openings (Gunzburger and Guyer, 1998). Thus, the occupancy rate was 0.80 salamanders/burrow. Of 11 recaptures, 10 were of animals that occupied the same burrow from which they were captured originally; the other recapture was of an individual in a burrow immediately adjacent to the burrow from which it was initially captured. Two different animals were captured from one burrow, demonstrating overlap in burrow use, a feature also noted by Jordan (1975).

Burrows are known to branch underground and can be interconnected (Jordan, 1975). Coupled with our findings, we infer that, at sites maintaining characteristics of old-growth forest, salamanders (1) display burrow fidelity, (2) have occupancy rates that approach one salamander per burrow, and (3) show non-exclusive use of burrows. This pattern might be altered at sites where the habitat has been disturbed and salamander populations are declining. Additional samples from other habitats will be required to document the degree to which the proportion of burrows occupied by salamanders changes among sites. However, because half-lives of burrows are short (Gunzburger and Guyer, 1998), variance among sites in the proportion of burrows occupied should be reduced relative to other burrowing vertebrates that create holes that remain open long after the occupant has left (Burke, 1989).

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