

Natural and Cultural History of the Golfo Dulce Region, Costa Rica

Anton WEISSENHOFER, Werner HUBER,
Veronika MAYER, Susanne PAMPERL, Anton WEBER,
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HPSG.: Biologiezentrum der Oberösterreichischen Landesmuseen



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Impressum

- Katalog / Publication: Stapfia **88**, zugleich Kataloge der Oberösterreichischen Landesmuseen N.S. **80**
ISSN: 0252-192X
ISBN: 978-3-85474-195-4
- Erscheinungsdatum / Date of delivery: 9. Oktober 2008
- Medieninhaber und Herausgeber / Copyright: Land Oberösterreich, Oberösterreichische Landesmuseen, Museumstr.14, A-4020 Linz
Direktion: Mag. Dr. Peter Assmann
Leitung Biologiezentrum: Dr. Gerhard Aubrecht
Url: <http://www.biologiezentrum.at>
E-Mail: bio-linz@landesmuseum.at
In Kooperation mit dem Verein zur Förderung der Tropenstation La Gamba (www.lagamba.at).
- Wissenschaftliche Redaktion / Scientific editors: Anton Weissenhofer, Werner Huber, Veronika Mayer, Susanne Pamperl, Anton Weber, Gerhard Aubrecht
Redaktionsassistent / Assistant editor: Fritz Gusenleitner
Layout, Druckorganisation /
Layout, printing organisation: Eva Rührnößl
Druck / Printing: Plöchl-Druck, Werndlstraße 2, 4240 Freistadt, Austria
Bestellung / Ordering: <http://www.biologiezentrum.at/biophp/de/stapfia.php> oder / or bio.buch@landesmuseum.at
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- Umschlagfoto / Cover: Blattschneiderameisen. Photo: Alexander Schneider. Layout: E. Rührnößl.
- Zitiervorschlag für das Buch / The complete book may be referenced as follows: Weissenhofer, A., Huber W., Mayer V., Pamperl S., Weber A. & G. Aubrecht (Hrsg.; 2008): Natural and cultural history of the Golfo Dulce region, Costa Rica. — Stapfia 88: 768 pp.
- Zitiervorschlag für Einzelarbeiten / Single contributions may be referenced as follows: Weissenhofer A., Huber W. & M. Klingler (2008): Geography of the Golfo Dulce region. — Stapfia 88: #-#.
- Ausstellung / Exhibition: Der Pfad des Jaguars. Tropenstation La Gamba, Costa Rica
Ort / Address: Biologiezentrum der Oberösterreichischen Landesmuseen, J.-W.-Klein-Straße 73, 4040 Linz, Austria
Zeitraum / Period: 10. Oktober 2008 bis 22. März 2009
- Konzept, Organisation und Gestaltung /
Concept, organization, design: Mag. Stephan Weigl, Mag. Dr. Werner Huber, Mag. Dr. Anton Weissenhofer, Daniel Schaber
Ausstellungstechnik, Mitarbeit /
Exhibition techniques, collaboration: Jürgen Plass, Roland Rupp, Bruno Tumfart, Erwin Kapl, Josef Schmidt, Roland Zarre, Michaela Minich, Charlotte Füreder, Georg Proske, Franz Rammerstorfer
- Museumspädagogik / Museum education: Mag. Claudia Kiesenhofer
Leihgeber / Lenders: Naturhistorisches Museum Wien, Mag. Dr. Werner Huber, Mag. Dr. Anton Weissenhofer, Universität Wien; Mag. Felix Holzmann, Bischofshofen

Due to the orographic formation of its interior and its humid climate, the Golfo Dulce Region is rich with biodiversity, containing very dense flora and fauna. After HOLDRIDGE (1971), the region was subdivided into different zones, including the tropical rainforest, the tropical wetland forest, and tropical premontane rainforest. The biogeographical situation in this area shows many similarities to the flora and fauna in the Amazon and the Colombian Chocó Region and serves as a land bridge with a valuable genetic base between North and South America. After unregulated seizure of land by agricultural settlers, lumberjacks, and large landowners in the 1940s and 1950s, regulated, state-subsidised settlement reform intended to support agricultural exports in the 1960s, and intensification of the livestock industry in the 1970s, primary and secondary forest reserves have shrunk to a minimum. The constant expansion of monocultures on new land has far-reaching consequences for the local ecosystem.

The conservation and sustainable use of tropical forests is established in the Forest Declaration, Convention on Climate Protection, and Convention on the Protection of Species, which demonstrate worldwide concern for these issues. As a regional example, in the 4,304.80 km² drainage basin, the ACOSA (Área de Conservación OSA), which covers an area spanning the Cantons Osa, Golfito und Corredores, aims to protect species diversity within the 17 game preserves, which are 44.7% covered by forest, through integration and an alliance with the Parques Nacionales, Vida Silvestres y Forestales (Fig. 2). The main sector of the Corcovado National Park on the Osa Peninsula covers 424 km² and the Piedras Blancas National Park covers 148 km². The altitude ranges from sea level to 745 m on the Osa Peninsula (Cerro Rincón and Cerro Mueller in the Fila Matajambre) and to 579 m in the Esquinas forest (Cerro Nicuesa). The Golfo Dulce Forest Reserve (592 km²) was established between the two parks, thereby forming a natural forest corridor.

References

- CHINCHILLA V.E. (1987): Atlas cantonal de Costa Rica. — IFAM. San José.
- HARTSHORN, G.S. (1983): Plants: introduction. — In: JANZEN D.H. (ed.), Costa Rican natural history. Chicago: Univ. Chicago Press: 118-157.
- HERRERA-MACBRYDE O., MALDONADO V. JIMÉNEZ T.R. & K. THOMSEN (1997): Osa Peninsula and Corcovado National Park, Costa Rica. — In: DAVIS S.D., HEYWOOD V.H., HERRERA-MACBRYDE O., VILLA-LOBOS J. & A.C. HAMILTON (eds), Centres of plant diversity. A guide and strategy for their conservation. Vol. 3. WWF, IUCN.
- HERWITZ S.R. (1981): Regeneration of selected tropical tree species in Corcovado National Park, Costa Rica. — Univ. Calif. Publ. Geogr. 24.
- HOLDRIDGE L.R. (1971): Forest environments in tropical life zones. A pilot study. — Oxford.
- MALZER O. (2001): Geological History of Central America and the Golfo Dulce Region. — *Stapfia* 78: 34-46.
- MORA C.S. (1990): La Geología y sus procesos. — San José.
- TOSI J.A. Jr. (1975): The Corcovado Basin on the Osa Peninsula. — In: Tosi J.A. Jr. (ed.), Potential national parks, nature reserves, and wildlife sanctuary areas in Costa Rica: a survey of priorities. San José: Centro Científico Tropical. Separate pp. 12.

Addresses of authors:

Anton WEISSENHOFER
Werner HUBER

Department of Palynology and Structural Botany
Faculty Center of Botany
University of Vienna
Rennweg 14
A-1030 Vienna, Austria

E-mail: anton.weissenhofer@univie.ac.at
werner.huber@univie.ac.at

Michael KLINGLER
Workgroup Development Studies
and Sustainability Science
Institute of Geography
University of Innsbruck
Innrain 52

A-6020 Innsbruck, Austria
E-mail: michael.klingler@uibk.ac.at

The amphibians and reptiles of the Golfo Dulce region

Los anfibios y reptiles de la región del Golfo Dulce

Gerlinde HÖBEL

Abstract: The Golfo Dulce region is home to a sizeable subset of the rich herpetofauna of Costa Rica. In this chapter, I review the diversity of the amphibians and reptiles found in the Golfo Dulce region. I first give a brief description of the taxonomic groups and species found in the region. Then I examine aspects of the ecology, life history and behaviour of amphibians and reptiles, and use examples drawn from the Golfo Dulce region to illustrate the fascinating diversity of this group of animals. I describe the signal modalities by which amphibians and reptiles communicate, and show how different signal modalities dominate the communication behaviour of different taxonomic groups. I also review the reproductive modes of amphibians from the Golfo Dulce region, and contrast their fascinating diversity of reproductive modes to the relative paucity of reproductive modes found in reptiles. Finally, I close the chapter with suggestions for further research on the herpetofauna of the Golfo Dulce region.

Key words: activity patterns, diet, predation and anti-predator strategies, faunal communities, communication, reproductive ecology.

Resumen: La región del Golfo Dulce da hogar a una porción sustancial de la rica herpetofauna de Costa Rica. En este capítulo, hago una revisión de la diversidad de anfibios y reptiles que se encuentra en la región del Golfo Dulce. Empiezo con una descripción de los grupos taxonómicos y especies de la región. Luego examino algunos aspectos de la ecología, historia de vida, y comportamiento de los anfibios y reptiles, y uso ejemplos tomados de la región del Golfo Dulce para ilustrar la fascinante diversidad de este grupo de animales. Describo las modalidades de comunicación de los anfibios y reptiles, y muestro cómo diferentes modalidades predominan en diferentes grupos taxonómicos. También reviso las modalidades de reproducción de los anfibios de la región del Golfo Dulce, y contrasto su fascinante diversidad con la relativa pobreza de modalidades en los reptiles. Finalmente, cierro el capítulo con sugerencias para investigaciones futuras con la herpetofauna de la región del Golfo Dulce.

Palabras clave: patrón de actividad, hábitos alimenticios, depredación y estrategias contra la depredación, comunidades faunísticas, comunicación, ecología de reproducción.

Despite its small size, Costa Rica is blessed with a diverse fauna and flora. An important, albeit often overlooked, portion of this biodiversity is the herpetofauna, which includes the amphibians and reptiles. The high herpetological diversity is based in part on the geographic location between North and South America, which allowed faunal elements from both continents to invade the country, and also to its tropical climate and high variety of different landscapes. In his treatment of the reptiles and amphibians of Costa Rica, SAVAGE (2002) recognised 396 species of amphibians and reptiles in the country. In the Golfo Dulce region, there are 145 known species of amphibians and reptiles (Fig. 1). This remarkable species richness is comparable to or even exceeds that of other well studied Central American sites (Table 1) (DONNELLY 1994, GUYER 1994, GUYER & DONNELLY 2005), recommending the Golfo Dulce region as hotspot for anyone interested in studying amphibians and reptiles.

Diversity of the herpetofauna of the Golfo Dulce region

In the following section I give an overview of the amphibians and reptiles found in the Golfo Dulce region. I start the description of each taxonomic group by providing some general information pertaining to the group as a whole before focusing on the individual species that occur in the region.

Amphibians

Living amphibians comprise three groups, the limbless caecilians (*Gymniphiona*), the tailed salamanders (*Caudata*), and the tailless frogs and toads (*Anura*). Members of all three groups can be found in the Golfo Dulce Region, with anurans heavily dominating the amphibian species diversity (Fig. 2).

Fig. 1: Composition of the herpetofauna of the Golfo Dulce region. In terms of species numbers, the amphibian fauna is dominated by anurans, while the reptile fauna is dominated by snakes. The numbers of local species from each group is given in parenthesis.

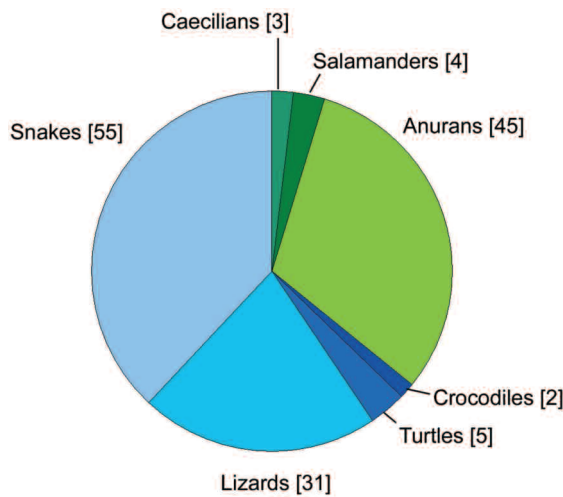


Fig. 2: Composition of the amphibian fauna of the Golfo Dulce region. Anurans dominate the amphibian fauna, with most species belonging to the families Leptodactylidae, Hylidae and Centrolenidae. The numbers of local species from each family are given in parenthesis.

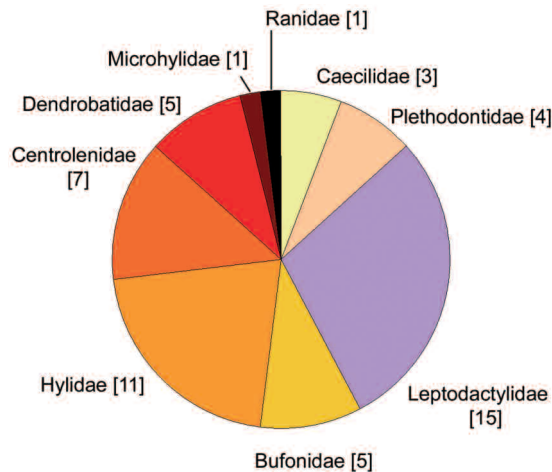


Table 1: Composition and diversity of the herpetofauna of four well studied Central American sites. La Selva and Tortuguero are situated in the Atlantic side of Costa Rica, while the Golfo Dulce Region is situated on the Pacific side of the country. Barro Colorado Island (BCI) is located in Gatun Lake, on the Atlantic side of Panama.

	Golfo Dulce	La Selva	Tortuguero	BCI
Gymnophiona	3	1	1	1
Caudata	4	3	2	2
Anura	45	44	30	30
Amphibians total	52	48	33	33
Crocodiles	2	2	2	2
Turtles	5	4	5	5
Lizards	31	25	22	21
Snakes	55	56	30	39
Reptiles total	93	87	59	67

Gymnophiona – Caecilians

The Gymnophiona are an order of limbless, worm-like amphibians. Due to their underground lifestyle, their eyes are small and covered by skin for protection. They possess sensory tentacles between the eyes and nostrils. They are extremely secretive and difficult to

find due to their burrowing lifestyle, and little is known about the life history of most species. The best chance of seeing one is after heavy rainfalls, when water has saturated the soil and they are forced to the surface. The Golfo Dulce region is home to three species from three different genera. This represents a substantial proportion of the diversity of caecilians in Costa Rica, because three of the four species found in the country also occur in the Golfo Dulce region. *Oscacaecilia osae* seems to be endemic to the Golfo Dulce and the adjacent Osa Peninsula.

Caudata – salamanders and newts

Of the tailed amphibians, only the lungless salamanders of the family Plethodontidae occur in Costa Rica. Plethodontids exchange respiratory gases across the skin lining the mouth, throat, and the outside of the body. They lay terrestrial eggs in which direct development of embryos occurs, by-passing the larval stage. In Costa Rica, salamander diversity is highest in the cordilleras (Central, Tilarán, and Talamanca, SAVAGE & VILLA 1986), so it is not surprising that only four species, i.e., just over 10% of the diversity found in the country, occur in the region of the Golfo Dulce. Salamanders are relatively uncommon and rarely seen. The two local members of the genus *Bolitoglossa*, *B. lignicolor* and *B. colonea*, are mostly arboreal and epiphyllous. They are typically found at night, perching on low vegetation, but hide during the day in bromeliads or under logs on the ground (BRUCE 1997). The two local worm salamanders (*Oedipina alleni*, *O. pacificensis*) are recognised by their slender body shape, small legs and very long tails. They are mostly fossorial, that is, they spend most of their lives burrowing underground. Sometimes they can be found under mats of wet moss or rotten logs. None of the four salamanders in the region has been studied in any detail, and very little is known about their ecology or behaviour.

Anura – frogs and toads

The faunas of lowland tropical forests are among the richest in anuran diversity (DUELLMAN 1988, DUELLMAN & TRUEB 1986). Anurans dominate the amphibian fauna in the number of individuals and species, and in the variety of habitats and reproductive modes that they use. Members of seven anuran families occur in the Golfo Dulce region, with Leptodactylidae, Hylidae and Centrolenidae accounting for almost 75% of the local anuran diversity.

Bufonidae – This globally widespread family comprises the animals commonly known as toads and their relatives. Typically, toads are easily recognised by their brownish coloration, dry, leathery and warty skin, and a pair of parotoid glands (lumps on either side of the back

of their head) that contain a poison which oozes out if the toad is attacked. Most species are terrestrial, but migrate to water for reproduction.

The variation in shape, size and coloration exhibited by bufonids is very well showcased by the five members of the family that occur in the Golfo Dulce region. Four of them are in the genus *Bufo*. Members of this group are generally nocturnal. The largest toad – and the largest amphibian – found in the region is the Cane toad, *Bufo marinus*, which can grow to an impressive length of up to 20 cm. Except for its exceptional size, it is a rather typical-looking toad. This ubiquitous, very adaptable toad is frequently encountered in disturbed habitats like pastures, fields or roadside ditches. Another quite typical brown toad is *B. melanochloris*. It is best distinguished from *B. marinus* by its smaller size overall and the much smaller parotoid glands. This species is unusual for breeding in the dry season, when it can be found in large choruses along rocky-bottomed streams. Although mainly brown in coloration, the smooth-skinned toad (*B. haematiticus*) is easily distinguished from other toads in the area by the smooth, almost velvety skin. This species lives in the forest, well camouflaged among the leaf litter. The last member of the genus is the green climbing toad (*B. coniferus*). This species is an excellent climber and can often be found a good distance up in the trees. It is easily recognised by its green coloration, sometimes accentuated by white and even pink spots. This species, too, breeds in the dry season. The fifth bufonid that used to be found in the Golfo Dulce region is the harlequin frog, *Atelopus varius*. This diurnal, brightly-coloured toad used to occur along many of the creeks and streams of the region. Sadly, many populations have recently gone extinct, although a few of these spectacular animals may still hang on.

Centrolenidae – This family is distributed throughout Central and South America and comprises a group of generally small, nocturnal, arboreal frogs. While the dorsal coloration of most glass frogs is lime green, the ventral skin of some members of this family is transparent, so that the internal organs, including the heart and digestive tract, can be seen through the translucent skin. This characteristic is the origin of their common name (glass frogs). Glass frogs are generally associated with small streams. Depending on the species, males call either from the top or the underside of leaves overhanging streams, and clutches are laid near the calling sites of the males, i.e. on vegetation overhanging streams. In some species, the males provide parental care by attending and guarding the clutches until the tadpoles hatch. When the tadpoles hatch they drop into the stream below, where they then finish their development.

Of the 13 glass frog species that occur in Costa Rica, seven species from three genera can be found in the Golfo Dulce region. The genus *Centrolenella* is represented by one species, *C. prosoblepon*. Adult males of this species are easily identified by having a bony hook on their upper arm. This glass frog calls from the surface of vegetation growing along the stream. Eggs are laid on the upper surfaces of leaves, and males do not provide parental care. The genus *Cochranella* is represented by three species (*C. albomaculata*, *C. granulosa*, *C. spinosa*). All Costa Rican species of this genus have green bones. The eggs are usually laid on the unshaded, upper side of leaves overhanging streams, and males do not provide parental care. The genus *Hyalinobatrachium* is also represented by three species (*H. colymbiophyllum*, *H. pulveratum*, *H. valerioi*). These little frogs are among the most commonly encountered streamside species. *H. pulveratum* lays the eggs on the upper surface of leaves, and it is not yet known whether they attend the eggs. Males of *H. colymbiophyllum* and *H. valerioi* call from the underside of leaves. Both are highly territorial species that call from the same site or nearby throughout the reproductive season (McDIARMID, 1978, McDIARMID & ADLER 1974, HAYES 1991). Eggs are laid on the underside of the leaf that also serves as the calling site. The males can accumulate several clutches from different females on the same leaf. Males of both species attend to the clutches, but they differ in the extent of parental care they provide. Males of *H. colymbiophyllum* attend to the egg masses only during the night, while males of *H. valerioi* remain with the eggs during both day and night.

Dendrobatidae – Poison dart frogs are a group of small, diurnal, and often brightly-coloured frogs native to Central and South America. These frogs received their common name from the numerous types of poisonous alkaloids found in the skin of many species. There is considerable evidence that toxicity in these frogs is derived from their diet: primarily ants, mites and beetles. These toxins are passed from the arthropod to the frog, then stored in glands on the amphibian's skin. Many poison dart frogs show spectacular aposematic (warning) coloration, although members of the most species-rich genus, *Colostethus*, are generally brown. They are all diurnal, and move on the ground or in lower vegetation in relatively exposed places, making them more easily observed than most frogs.

Five species from three genera occur in the Golfo Dulce region, and two species, *Dendrobates granuliferus* and *Phyllobates vittatus* have their centre of distribution here. Because of their bright, distinctive coloration, members of the genus *Dendrobates* and *Phyllobates* are easily recognised. There is the black and green *Dendrobates auratus*, the much smaller, reddish *D. granuliferus*, and *Phyllobates vittatus*, which has two bright orange or



Fig. 3: *Bolitoglossa lignicolor* is a relatively large lungless salamander.



Fig. 4: The green climbing toad, *Bufo coniferus*.



Fig. 5: Pair of *Bufo marinus* during oviposition

yellow lines running along both sides of this back. The two local members of the genus *Colostethus* are more drab in coloration. They are also diurnal, but do not possess the potent poison that is so characteristic for other members of the family. Most dendrobatids prefer habitats close to streams or pools, but particularly the two *Colostethus* species and *D. granuliferus* generally occur in close proximity to small creeks in the forest. All members of this family show complex reproductive behaviour and varying degrees of parental care.

Hylidae – This family of primarily arboreal frogs is widely distributed. The tree frogs, as they are also commonly called, are characterised by the enlargement of the tips of their fingers and toes into disc-shaped adhesive pads, enabling them to climb vertically. They are a large and diverse group of frogs, with substantial variation in size, body shape, coloration and lifestyle.

Much of the amazing diversity shown by hylid frogs can be observed in the 11 species that live in the Golfo Dulce region. They range in size from the small *Hyla microcephala*, that hardly reaches 30 mm in length to the gladiator frog, *Hypsiboas (Hyla) rosenbergi*, that can grow to 80 mm. All but two of the local species (*Smilisca sila*, *S. sordida*) breed during the rainy season. Some species breed along streams (*Smilisca sila*, *S. sordida*), some in ponds (*Agalychnis callidryas*, *Hyla ebraccata*, *Smilisca phaeota*), and some may even construct nests in which they lay their eggs (*H. rosenbergi*). Some are so called prolonged breeders, which reproduce throughout a period of several months (e.g. *Agalychnis callidryas*, *Hyla microcephala*), while others are so called explosive breeders, that mate only for a few nights after heavy rainfalls (*Agalychnis spurrelli*, *Scinax eleochoa*, *Phrynohyas venulosa*). Some species deposit surface film clutches (*Smilisca phaeota*, *Phrynohyas venulosa*), some deposit the eggs on vegetation over the water, either at low height (*H. ebraccata*), or 1.5 to 8 m above the water (*Agalychnis callidryas*, *A. spurrelli*), into which the tadpoles drop once they hatch.

Leptodactylidae – This is a large and diverse group of frogs with most of their diversity in South and Central America and the West Indies. Most leptodactylids are brownish or greyish in coloration. Variation in size is considerable, and there is also much diversity in appearance, habits and habitats used. With a total of 15 species from three genera (*Eleutherodactylus*, *Leptodactylus*, *Physalaemus*), this diverse group of frogs supplies the largest contingent to the anuran fauna of the Golfo Dulce region.

Nine local species are members of the genus *Eleutherodactylus*. These frogs are generally cryptically coloured, i.e. they show different shades of brown. All species of *Eleutherodactylus* are characterised by direct development, in which eggs hatch directly into small



Fig. 6: Harlequin toad, *Atelopus varius*.



Fig. 7: Venter of a glass frog.



Fig. 8: Male of the glass frog *Centrolenella prosoblepon*; note the characteristic hook on the upper arm.



Fig. 9: Male of the glass frog *Hyalinobatrachium valerioi* guarding his three clutches. (Photo: Walter Hödl)



Fig. 10: The poison-dart frog *Dendrobates auratus*.



Fig. 11: The poison-dart frog *Dendrobates granuliferus* has its centre of distribution around the Golfo Dulce.

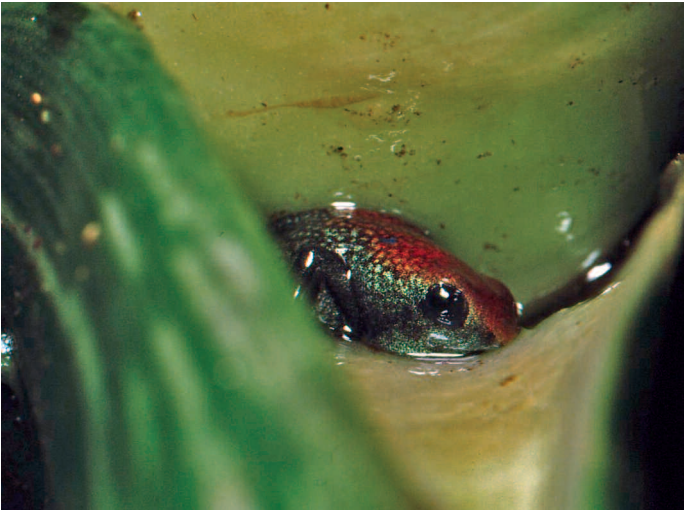


Fig. 12: Metamorph of *Dendrobates granuliferus*, raised in the leaf axilla of a *Diffenbachia* plant.



Fig. 15: *Smilisca sordida* is a stream-breeding tree frog.



Fig. 13: *Colosthetus* are non-poisonous member of the poison-dart frog family.



Fig. 16: The red-eyed tree frog *Agalychnis callidryas*.



Fig. 14: *Hyla ebraccata* is a small tree frog that breeds in ponds during the rainy season.

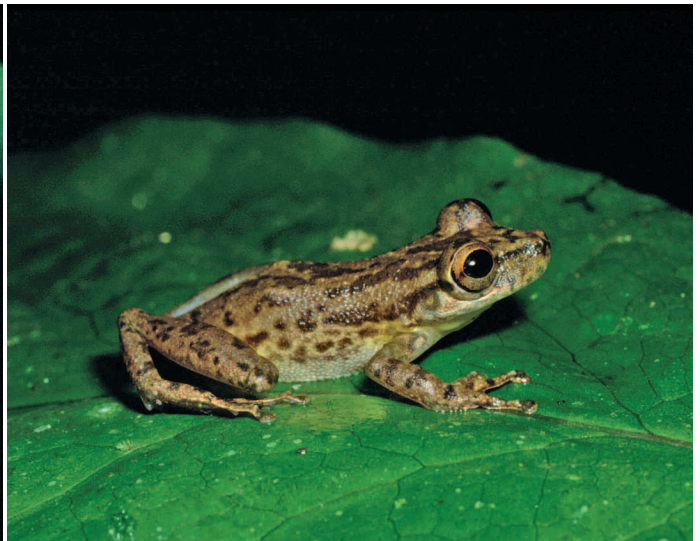


Fig. 17: *Scinax eleochoa* is an explosive breeder that only reproduces after heavy rainfalls.



Fig. 18: A female *Eleutherodactylus fitzingeri*



Fig. 21: *Rana warszewitschii* lives along creeks.



Fig. 19: *Leptodactylus pentadactylus* is one of the largest frogs found in the Golfo Dulce region.



Fig. 22: Example of the reproductive mode in which eggs are deposited as clutches in water (clutch of *Rana warszewitschii*).



Fig. 20: Pair of *Physalaemus pustulosus* building their foam nest in which they will lay their eggs. (Photo: Walter Hödl)

frogs, completely by-passing the tadpole stage. In our area of interest, these frogs range in size from the tiny *E. vocator* that hardly reaches 12 mm to *E. rugosus* or *E. taurus*, that can grow up to 80 mm. Some species are arboreal and spend most of their time up in the trees (*E. diastema*), others spend the day hidden in leaf litter and will climb up into the lower vegetation during the night (e.g. *E. fitzingeri*), and still others will spend most of the time hidden in leaf litter (e.g. *E. rugosus*). Some species are associated with running water, generally perched at night on boulders in the stream (e.g. *E. taurus*). All except *E. stejnegerianus* are nocturnal, but some species (e.g. *E. fitzingeri*) may become active during the day, especially during and after rainfall.

All five members of the genus *Leptodactylus* that occur in Costa Rica are found in the Golfo Dulce region. Superficially similar to ranid frogs, they can be distin-



Fig. 23: Caimans (*Caiman crocodilus*) inhabit nearly every body of water in the Golfo Dulce region.



Fig. 24: Mud turtles (*Kinosternon scorpioides*) are among the more frequently observed turtles in the region.

guished from them by the complete lack of webbing between the toes. They range in size from the relatively small *L. melanotus* (40 mm) to the large *L. pentadactylus* (185 mm). The latter species, which is also known as the South American bullfrog or “rana toro”, can be found in nearly every lowland rainforest. It is usually first spotted thanks to the bright red reflection of their eyes in the beam of a flashlight. All members of this genus lay their eggs in foam nests, which may be constructed in or near small water bodies or hidden under rocks and logs (*L. labialis*). The embryos start their development inside the foam nest that protects them from desiccation, but eventually they have to be washed into water bodies to finish their development.

Finally, the small *Physalaemus pustulosus* is commonly seen calling from puddles and roadside ditches. Despite their toad-like appearance (warty skin and promi-



Fig. 25: The helmeted iguana (*Corytophanes cristatus*) sits motionless, waiting for prey to approach.

nent parotoid glands) this small frog is also a member of the family Leptodactylidae, and they lay their eggs in small, white foam nests.

Microhylidae – This group has an almost worldwide distribution, but is not a very prominent component of the anuran diversity in Central America. Only three members of the family are present in Costa Rica, and only one species, *Nelsonophryne aterrima*, occurs in the Golfo Dulce Region. This is a nocturnal, secretive, rarely encountered inhabitant of the forest leaf litter.

Ranidae – Members of this globally distributed anuran family are often described as “typical” frogs. They are generally smooth, moist-skinned frogs, with large, powerful legs and extensively webbed feet. Many are aquatic or live close to water. Only one species of this family, the brilliant forest frog (*Rana warszewitschii*) is found in the Golfo Dulce region. This slender, agile species is commonly observed along slow-moving creeks and streams in the forest. It is easily recognised by the long pointy head and the yellow spots found on both the posterior surface of the thighs and the axillae.

Reptiles

Living reptiles comprise five groups, including tuataras, lizards, snakes, turtles and crocodylians. The latter four are represented in the Golfo Dulce Region of

Costa Rica. The composition of the local reptile fauna is heavily dominated by snakes and lizards (Fig 3).

Crocodylians

Both species of crocodylians found in Costa Rica occur in the Golfo Dulce Region (SAVAGE 2002). The crocodile (*Crocodylus acutus*) is restricted to larger rivers, while the smaller, highly adaptable caiman (*Caiman crocodilus*) can be found in a range of aquatic habitats.

Turtles

Of the 15 species of turtles and tortoises found in Costa Rica, five species from four genera are present in the Golfo Dulce region (SAVAGE 2002). One is a marine species (the olive ridley, *Chelonia olivacea*) which generally lives and feeds far offshore, but reaches the beaches of the Golfo Dulce to lay its eggs. The four other species are aquatic or semi-aquatic freshwater inhabitants. The snapping turtle (*Chelydra serpentina*) is easily identified by its comparatively large head with the powerful beak-like jaws. This species spends most of its time in the water and only goes on land to lay its eggs. The mud turtles (*Kinosternon leuostomum*, *K. scorpioides*) are recognised by the hinge on their plastron (the belly portion of the turtles shell). This allows them to not only withdraw the head and legs into the shell, but to completely close the shell. Mud turtles live near water, but may spend extended periods of time on land, travelling overland from one pond to the other. Finally, the pond turtle *Chrysemys ornata* can also be found in the region. This species is largely aquatic. Although it is frequently seen basking during the day, it is most active at night.

Lizards

Thirty one species of lizards from 23 genera in 9 families occur in the Golfo Dulce Region. Two microteiid lizards (*Bachia blairi*, *Neusticurus apodemus*) are endemic to the region – that is, they do not occur anywhere else in the world (SAVAGE 2002).

Anguidae – This family is widespread in the Americas, Europe and Asia. Limb reduction is apparent in many anguids, and some species are entirely limbless, resembling snakes more than lizards. Two species from two genera occur in the Golfo Dulce region (*Diploglossus bilobatus* and *Coloptychon rhombifer*). Both have only slightly reduced limbs, and with their smooth, shiny scales superficially resemble skinks. Both species are relatively uncommon and secretive.

Corytophanidae – This group of lizards is also called the casque head lizards, because males typically have well-developed head crests in the shape of a casque.

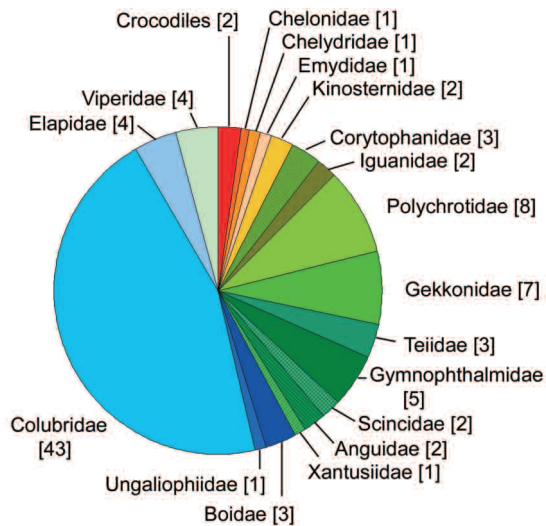


Fig. 26: Composition of the reptile fauna of the Golfo Dulce region. In terms of species numbers, snakes and lizards dominate the reptile fauna, with Colubridae being the dominant family of snakes, and Polychrotidae being the dominant family of lizards. The numbers of local species from each family are given in parenthesis.

Four species of this family occur in Costa Rica, and three species from two genera can be found in the Golfo Dulce region. In the helmeted iguana, *Corytophanes cristatus*, both sexes have large head crests. These lizards are highly arboreal, living in the forest canopy, but are occasionally found sitting on branches and trunks at lower levels. *Corytophanes* is a sit-and-wait predator, catching prey items infrequently, but regularly eating items half as long as its own body. In the highly sexually dimorphic *Basiliscus*, only the males have crests. In addition to the head crest, male basilisks also have large crests on the back and along the tail. The two members of the genus *Basiliscus* that occur in the Golfo Dulce region are generally associated with riparian habitats, i.e. vegetation along streams. The common name for lizards of the genus *Basiliscus*, Jesus Christ lizards, alludes to an escape behaviour in which they run on their hind feet on the surface of water. This is made possible by the presence of enlarged, fringed scales on their toes. These are rolled up when the animal walks on land, but when fleeing across water the flaps are opened and provide the increased surface area that allows them to run on water.

Gekkonidae – Geckos can vary in size and body shape, and they may be diurnal or nocturnal. Geckos are special among reptiles in that they not only produce noise when frightened, but many species use special calls to communicate.

Four species from four genera occur naturally in the Golfo Dulce region. The pretty yellow-headed gecko (*Gonatodes albogularis*) is diurnal and can often be observed perching on tree trunks. The species shows sexual dimorphism: only males show brilliant colours, while female coloration is a drab mottled grey. Another small, diurnal gecko found in the area is the orange-tailed gecko (*Lepidoblepharis xanthostigma*). It is an inhabitant of the forest floor, and is thus more often heard than seen as it scuttles through the leaf litter. By far the



Fig. 27: Green iguanas (*Iguana iguana*) are the largest lizards found in the Golfo Dulce region. Even large adults like to bask in the treetops.

Fig. 28: The nocturnal turnip-tailed gecko (*Thecadactylus rapicaudus*) is the largest gecko found in the Golfo Dulce region.



largest gecko in the Golfo Dulce region is the turnip-tailed gecko (“escorpión tobobo”, *Thecadactylus rapicaudus*), a nocturnal forest dweller. Although it is often found sitting on tree trunks at eye level, these geckos also forage up in the forest canopy.

The current list of species found in the Golfo Dulce region also includes three introduced geckos. *Hemidactylus frenatus*, *H. garnoti* and *Lepidodactylus lugubris* are Asian species that probably arrived as stowaways on freight ships, and are now slowly expanding their range. Because they often live in human habitations, they are among the most commonly observed geckos.

Gymnophthalmidae – This family is distributed throughout Central America and South America. Microteiids, as they are also referred to, are related to Teiidae, but with their smooth scales they look more like skinks. Most microteiids are diurnal, secretive leaf litter inhabitants. Many species show limb reduction, and often this is accompanied by body elongation.

Five species from five genera occur in the Golfo Dulce region. *Bachia blairi* and *Neusticurus apodemus* are endemic to the region, occurring nowhere else in the world. The leaf-litter inhabiting *Bachia blairi* is a small lizard with elongated body and limbs that are reduced to tiny flaps. It superficially looks more like a small black snake than a lizard. The rare *Neusticurus apodemus* is a small, semiaquatic lizard that is primarily active at dusk, hunting along the margins of small streams. *Leposoma southi* and *Ptychoglossus plicatus* are active but secretive diurnal lizards that forage in the leaf litter. *Gymnophthalmus speciosus* is a small, skink-like lizard with a bright red tail. These lizards are unusual among Costa Rican microteiids for preferring open, sunny situations. They can be locally abundant and are most active around midday.

Iguanidae – This family includes two of the largest lizards found in Costa Rica, the green iguana (*Iguana iguana*) and the black or spiny-tailed iguana (*Ctenosaura similis*). Both species are diurnal and herbivorous, feeding on leaves, flowers and fruit. They will only occasionally consume insects and other small animals, especially as juveniles. Despite their size, which can reach up to 2 metres, green iguanas are agile climbers that spend much time in the treetops. They prefer to live in trees near water, and if they are frightened, they will dive into the water and swim off. Green iguanas tend to live alone, but may be seen in groups occasionally in good sunny basking spots. Spiny-tailed iguanas, locally known as “garrobos”, are more terrestrial in lifestyle. Like most iguanids they are territorial, and male territorial displays, including push-up behaviours, may double as courtship displays.

Polychrotidae – This extremely species-rich group of lizards commonly known as anoles is widely distributed throughout South America, up into southern North America and the West Indies. Many of them are semi-arboreal, and show morphologies adapted for climbing. For example, many species have subdigital lamellae bearing setae (“sticky” toe pads similar to but less developed than that of geckos). They are diurnal and males are territorial. One of the most distinctive features of this group is that males have brightly-coloured dewlaps (subgular, extensible flaps of skin), which they use in defensive and courtship displays. Each species has a distinctive dewlap colour and a specific movement pattern.

Eight species from two genera can be found in the Golfo Dulce region, and the amazing diversity shown by lizards from this family is reflected in the selection of locally occurring species. There are species that live on boulders in and along streams (*N. aquaticus*), a variety of species that live in the understory of the forest or adjacent pastures (e.g. the ubiquitous *Norops polylepis*), as well as canopy-dwelling species (*N. pentaprion*, *Dactyloa insignis*). Dewlap size and coloration also vary substantially between species. The dewlap of *Norops capito* is relatively small and has a greenish-yellow colour, *N. polylepis* has a huge yellow-orange dewlap, and *N. biporcatus* has a medium-sized tricoloured one which combines a blue centre with red margins and a white basal colour.

Scincidae – This cosmopolitan group is characterised by smooth, shiny scales, a cylindrical body shape, a head that is not distinct from the neck, and short limbs. Two species from two genera occur in the Golfo Dulce region. The small, terrestrial *Sphenomorphus cherriei* is probably one of the most common lizards in the region, but due to its small size and secretive behaviour is seldom seen or captured. It is a leaf litter species that prefers forest edge situations or disturbed habitats. This species is oviparous, with females laying 1-3 eggs at a time. The larger *Mabuya unimarginata* occurs in a range of habitat types and is often very common. Although diurnal it is difficult to observe because of its shy and secretive behaviour. This species is viviparous, with females giving birth to up to 6 young at a time.

Teiidae – Teiids are an exclusively New World family, with numerous representatives in South and Central America. In general anatomy and ecology, they are most similar to the Old World family Lacertidae. Teiids have long pointed snouts, long tails, strong limbs with long claws and long, forked tongues.

Three species, all members of the genus *Ameiva*, are present in the Golfo Dulce region. They are small (*A. quadrimileata*) to medium-sized (*A. festiva*, *A. leptophrys*) active, diurnal lizards. They are often found in or around clearings, treefall gaps or along trails, where sun reaches the forest floor. This allows them to bask to attain the body temperature necessary for their active, searching foraging behaviour. Although often abundant and frequently encountered, they are wary and difficult to approach.

Xantusiidae – Night lizards are small and very secretive lizards. With their arboreal habits, large lidless eyes and granular skin, they are often confused with geckos. However, night lizards lack adhesive toe pads. Although small, night lizards are long lived. Contrary to the reproductive strategies of most small lizards, night lizards tend to have very low reproductive rates, giving birth to only

one or two offspring at a time. One species, *Lepidophyma reticulatum*, occurs in the Golfo Dulce region. The species consists entirely of females that reproduce by parthenogenesis. It is known that females give birth to live young, but otherwise little is known about the natural history of this interesting lizard.

Snakes

The Golfo Dulce region boasts a wealth of snake species: fifty-five species from 39 genera in five families (SAVAGE 2002, SOLÓRZANO 2004). Some species are exceedingly rare and seldom seen. The most frequently encountered snakes in the region are members of the families Colubridae and Viperidae.

Boidae – Boas are tropical or subtropical constricting snakes. They typically have a pair of reduced hind limbs that are partially visible as a pair of spurs on either side of the vent. The spurs are longer and more conspicuous in males than in females. Some species have special heat-sensitive organs called “labial pits” on their upper lips that help them track their warm-blooded prey. All boas give birth to living young. Boas are mostly nocturnal, but they may come out during the day to sunbathe.

Three species from three genera occur in the Golfo Dulce region. *Boa constrictor* is the largest snake found in the region, and can grow up to 4.5 m in length. This widespread, adaptable species feeds on a variety of prey items, from frogs and birds to rabbits and even small deer. They are very productive snakes, and females can give birth to up to 64 offspring (SOLÓRZANO 2004). The common tree boa, *Corallus hortulanus*, does not grow quite as large, and its habitat requirements are more restricted to relatively undisturbed forests. This species is easily distinguished from other snakes in the region by having deep labial pits. The third species, the rainbow boa *Epicrates cenchria* is the most terrestrial of the boids of the region. Its labial pits are less pronounced than those of *Corallus hortulanus*.

Colubridae – This is the largest, most diverse family of snakes, with a world-wide distribution. Colubrids are often called the “harmless” snakes, although some are rear-fanged (opisthoglyph) and venomous. But because of the location of the venom-delivering teeth (in the back of the mouth) they rarely present a danger to humans. Members of this family show an impressive diversity in size, colour, shape, and behaviour. They include snakes that are fossorial (live inside soil), terrestrial (live on the ground), arboreal (live on shrubs and trees) and aquatic (live in water).

With 43 species from 29 genera, colubrids represent the largest group of snakes found in the Golfo Dulce re-



Fig. 29: Male *Norops polylepis* use their large yellow-orange dewlaps to announce their presence to other territorial males.



Fig. 30: A cat-eyed snake, *Leptodeira septentrionalis*.



Fig. 31: The parrot snake (*Leptophis ahaetulla*) is easily distinguished by its bright green coloration and smooth scales.

gion (SAVAGE 2002, SOLÓRZANO 2004). The large number of species in this family precludes a detailed listing of every species. In the following account I will focus on some species that either merit special attention because they show some unusual feature, or because they are common and thus prone to be more frequently encountered by visitors to the region.

A common leaf-litter species is the brown debris snake, *Coniophanes fissidens*. This active terrestrial and diurnal snake hunts for frogs in the forest leaf litter. A terrestrial snake that is relatively uncommon but deserves special mention is the false coral snake, *Erythrolamprus mimus*. This is harmless snakes that mimics the colour pattern of venomous coral snakes, thus protecting itself against predators.

A range of medium-sized semi-arboreal snakes can be observed in the region. Among the commonly observed diurnal species are the parrot snake and the brown vine snake. The parrot snake (*Leptophis ahaetulla*) is easily distinguished by its bright green coloration and smooth scales. It forages in bushes and low trees for sleeping tree-frogs and arboreal lizards. The brown vine snake (*Oxybelis aeneus*) can be recognised by its elongated, pointed head. This species often remains stretched out and motionless, and is well camouflaged by resembling a small vine. It hunts small lizards, mainly *Norops* sp..

There are also some common semi-arboreal snakes that are most frequently encountered foraging during the night. The blunt-headed vine snake, *Imantodes cenchoa* is easily recognised by its long, thin, compressed body with a blunt, oversized head and large, bulging eyes. This species is an arboreal, nocturnal snake that preys mainly on frogs and anole lizards. It is very common in forested areas, secondary growth and even agricultural areas. Another common member of the Golfo Dulce herpetofauna is the cat-eyed snake, *Leptodeira septentrionalis*. Although this slender species is a slightly venomous, rear-fanged snake, its is not dangerous to humans. It is nocturnal and semi-arboreal, hunting for frogs and frog eggs. Members of two genera (*Dipsas* and *Sibon*) deserve mention because of their unusual dietary habits. These small- to moderate-sized snakes feed mainly on slugs and snails.

Finally, some relatively large snakes that are also commonly encountered in the area are the shiny whip-snake, *Chironius grandisquamis*, the bird-eating snake, *Pseustes poeciloichilus*, the tiger rat snake, *Spilotes pullatus*, and the speckled racer, *Drymobius margaritiferus*. All are active, diurnal snakes that can be found moving on the ground or forage in shrubs and low trees. Another common large snake is the mussurana, *Clelia clelia*. This terrestrial species is primarily nocturnal. Although it will

eat lizards and mammal, its main food are large poisonous pit vipers.

Elapidae – This group of venomous snakes is found in tropical and subtropical regions around the world. They are characterised by having a set of hollow, fixed fangs through which they inject venom.

Four members from two genera occur in the Golfo Dulce region (SAVAGE 2002, SOLÓRZANO 2004). The sea snake, *Pelamis platurus*, is easily recognised by its coloration (yellow belly and black dorsum), and the laterally compressed second half of the body. It normally lives offshore in the Golfo Dulce, but sometimes an individual can be washed onto the beach. This species is viviparous, and gives birth at sea. The other three species are coral snakes of the genus *Micrurus*. They are terrestrial or semi-fossorial snakes with cylindrical bodies. *Micrurus alleni*, *M. clarki*, and *M. nigrocinctus* all show the tri-coloured black, red and yellow banding pattern that is typical for many coral snakes. *M. alleni* also occurs in a bi-coloured, black and yellow form, but this pattern is usually only present dorsally, and the ventral sides do show the typical tri-coloured pattern. All coral snakes lay eggs.

Ungaliophiidae – The dwarf boas are a group of small to moderately-sized neotropical snakes, which are similar in morphology to the Boidae. They are viviparous and primarily nocturnal. One species, the southern bromeliad boa, *Ungaliophis panamensis*, can be found in the Golfo Dulce region. This rare snake is of moderate size (85 cm). It is mainly arboreal and nocturnal, and seems to prey mainly on frogs and lizards (SOLÓRZANO 2004).

Viperidae – All members of this family have comparatively large heads and stout, rather short bodies. They are characterised by the presence of a thermoreceptor organ called the loreal pit, located between the nostril and the eye, as well as large anterior fangs attached to the maxilla and a powerful venom with necrotic and haemolytic activity.

Four species from four genera occur in the Golfo Dulce region (SAVAGE 2002, SOLÓRZANO 2004). The terrestrial fer-de-lance (*Bothrops asper*) is a snake frequently encountered in the area. This adaptable snake is capable of surviving and even thriving in highly disturbed areas and human settlements (SOLÓRZANO 2004). The other large terrestrial pit viper occurring in the region is the bushmaster, *Lachesis melanocephala*. This beautiful snake is the largest poisonous snake in the region. The arboreal eyelash viper, *Bothriechis schlegelii*, comes in a variety of colour morphs, including yellow, reddish-brown to mottled-green, and siblings can show different colour morphs. Despite their gaudy



Fig. 32: The prawn snake (*Hydromorphus concolor*) is the only largely aquatic colubrid snake in the Golfo Dulce region.



Fig. 33: The hog-nose viper, *Porthidium nasutum* is the smallest pit viper in the Golfo Dulce region.

colours they can be surprisingly difficult to spot when they rest motionless on branches or bushes at a height of 1 to 1.5 m. At only 60 cm long, the hog-nose viper, *Porthidium nasutum* is the smallest pit viper in the region. Its coloration is also quite variable, but sombre grey or brown tones dominate.

All pit vipers are sit-and-wait predators that remain at one spot waiting for prey to come by. Except for the bushmaster, which lays eggs, all other pitvipers in the Golfo Dulce region give birth to live young.

Population ecology and habitat use

Activity patterns

The herpetofauna of the Golfo Dulce region includes diurnal and nocturnal species, as well as species that lack clearly defined daily activity patterns.

Few species of amphibians are diurnal. In the Golfo Dulce region, these species include the harlequin toad, *Atelopus varius* and the poison-dart Frogs (family Den-

drobatidae). Most of them show bright aposematic coloration, advertising their toxicity to potential predators. The possession of toxic skin secretions may have been the factor that first enabled this group of animals to shift to diurnal life. Among other anurans, members of the genus *Eleutherodactylus* have the greatest tendency to be at least partly diurnal. The leaf-litter specialist *E. stejnegerianus* seems to be a species that is mainly diurnal. While most other adult *Eleutherodactylus* frogs tend to be nocturnal, juveniles of several species have been observed during the day (MIYAMOTO 1982). Also, even adults of some species (e.g. *E. fitzingeri*) may become active during the day, especially during and after rainfall, when humidity levels are increased. In general, however, most amphibians are nocturnal. They hunt and breed at night, and spend the day resting. Terrestrial amphibians often spend the day hiding under logs or in the leaf litter. Arboreal salamanders (*Bolitoglossa*) and some arboreal leptodactylids (e.g. *Eleutherodactylus diastema*) spend the day in diurnal retreat sites, sites like treeholes or bromeliad tanks. Many tree frogs and glass frogs spend the day sleeping on more exposed sites like branches or large leaves. To conserve water, they tuck their arms and legs in tightly for maximum reduction of moisture loss.

Reptiles also show a range of activity patterns, but compared with amphibians, a much larger proportion of the reptile fauna is diurnal. The diurnal component contains mainly lizards, as well as many snakes. In the Golfo Dulce region, commonly encountered diurnal lizards include *Norops*, *Basiliscus*, *Gonatodes* geckos and species of *Ameiva*. *Ameiva festiva* and *A. quadrilineata* are active, heliotroph lizards that are often encountered basking in sunny spots in clearings or on trails. Various species of *Norops* are active in the understorey of the forest, males displaying their brightly-coloured dewlaps to announce their presence to other territory holders and to attract females. In addition, many skinks and microteiids are diurnal, but because of their secretive habits they are rarely encountered. More than half of the snake species occurring in the Golfo Dulce region are diurnal. Most of the diurnal snakes, like the parrot snakes (*Leptophis ahaetulla*) and the vine snake (*Oxybelis*), specialise in preying on sleeping frogs and lizards. The diet of the parrot snake consists primarily of tree frogs, found sleeping or resting during the day (SOLÓRZANO 2004), while the vine snake hunts anole lizards.

The nocturnal component of the reptile herpetofauna contains relatively few lizards, among them the gecko *Thecadactylus*, as well as the rare night lizard, *Lepidophyma reticulatum*. A larger portion of nocturnal reptiles is presented by snakes. Among them are some frog-eating snakes (*Leptodeira* sp., *Imantodes* sp.), the snail

eaters (*Dispas* sp., *Sibon* sp.), as well as several of the poisonous pit vipers and coral snakes. It seems that activity patterns, particularly those of snakes, is correlated to the activity pattern of their favourite prey items (GREENE 1988).

Turtles, crocodiles as well as several species of snakes do not have clearly defined activity patterns. Turtles and crocodiles may be found basking during the day, but they probably feed mainly during the night. The large *Boa constrictor*, as well as the fer-de-lance (*B. asper*) and some colubrid snakes, can be found active and hunting during the day as well as during the night (SOLÓRZANO 2004).

Faunal communities

Faunal communities are groups of species that typically share a given habitat. Generally, faunal communities are not discrete units, but rather integrate among each other in complex fashion. In the following account I give some general information on three faunal communities commonly found in the tropics, and list the amphibian and reptile species that are commonly associated with the respective community in the Golfo Dulce region.

Leaf litter communities

Despite the inconspicuous nature of their inhabitants, leaf litter communities have received considerable attention in many tropical sites (HEINEN 1992, SCOTT 1976, LIEBERMAN 1986). They are studied either by carefully shifting through leaf-litter collected in plots, or from pitfall traps distributed along transect lines. Studies of the faunal compositions of non-calling amphibians and reptiles are often hampered by the secretive habits of these species. Probably as a result of the random pattern of leaf litter sampling techniques, however, leaf litter assemblages are among the best known tropical communities. The amphibian component of the leaf litter herpetofauna is frequently quite diverse, and in the Neotropics, leaf litter communities are often dominated by rain frogs of the genus *Eleutherodactylus* (LIEBERMAN 1986). Many leaf litter species (Plethodontid salamanders, *Eleutherodactylus* frogs) are characterised by laying terrestrial eggs that undergo direct development, skipping the aquatic tadpole stage characteristic of most other amphibians. Thus, they remain in the leaf litter throughout all stages of their life history. The reptile component of the leaf litter herpetofauna is dominated by skinks (*Sphenomorphus cherriei*), *Ameiva* species, and ground-dwelling species of anole lizards (*Norops polylepis*, *N. limifrons*). Some small snakes (*Coniophanes fissidens*, *Enulius sclateri*, *Micrurus nigrocinctus*) are also associated with leaf litter. Often, leaf litter snakes show dietary specialisation for amphibians and

reptiles commonly found in the leaf litter. For example, the snake *Coniophanes* specialises in hunting small frogs (*Eleutherodactylus*) and lizards, while *Enulius sclateri* specialises in eating reptile eggs.

Riparian communities

Unlike pond communities (see below), riparian communities tend to be stable over time. Most species that breed in streams (generally during the dry season, when water currents are weaker), stay at the site throughout the year. Characteristic anuran members of a riparian community in the Golfo Dulce region are glass frogs (e.g. *Centrolene*, *Centrolenella*, *Hyalinobatrachius*), and some stream-breeding tree frogs (*Smilisca sila*, *S. sordida*). A few members of other frog families are also frequently found along creeks and streams. During the dry season, when the water levels are low, the brilliant forest frog *Rana warszewitschii* and the toad *Bufo melanochloris* breed in the calm pools along creeks. While most members of the large genus *Eleutherodactylus* are characteristic components of the leaf litter community, one species (*E. taurus*) is commonly associated with creeks in the Golfo Dulce region, and can be found at night sitting on boulders in the stream. Some poison-dart frogs, namely *Colostethus nubicola*, *Dendrobates granuliferus* and *Phyllobates vittatus*, are also commonly found alongside creeks. Except for members of the genus *Colostethus*, which will carry their tadpoles to the creek where they will finish their development, the other poison-dart frogs do not actually need the creek to reproduce, but probably benefit from the uniformly moist microclimate.

A range of reptiles in the Golfo Dulce region are associated with creeks and streams. All turtles found in the Golfo Dulce region have semi-aquatic lifestyles, and may be found in and around streams, especially in the quiet side pools. Few lizards are closely associated with streams. Among them are the stream anole (*Norops aquaticus*), which lives among the boulders and logs strewn in the streams and the rare gymnophthalmid *Neusticurus apodemus*, which hunts along the margins of small streams. However, several semi-arboreal or arboreal species can often be found in the vegetation along or above streams. Among them are the green iguana (*Iguana iguana*) and the several species of basilisk (*B. basiliscus*, *B. plumifrons*). Green iguanas tend to be more associated with larger streams and rivers, which create a considerable gap in the forest. There they climb the trees in the gallery forest to bask and feed on leaves. Basilisks will live along smaller creeks and streams. During the day, they can be found basking on open spots in the vegetation, and at night they are frequently encountered sleeping on lower branches along the creek. Among snakes, only the prawn snake (*Hydromorphus concolor*) is largely aquatic and may be encountered swimming in shallow

water in small streams. In addition, a variety of terrestrial and semi-arboreal snakes can also be found along streams, mainly because they find their favourite food there (frogs and lizards). Often encountered snakes include the whip snakes (*Chironius* sp.), blunt-heads (*Imantodes*) or cat-eye snakes (*Leptodeira*). The fer-de-lance (*B. asper*) is also commonly found along streams, often curled up and resting on logs or rocks.

Pond communities

Pond communities are, to a large extent, established when amphibian species gather at ponds and swamps during the breeding season. They are, as a consequence, often seasonal assemblages (AICHINGER 1987, DONNELLY 1994). Species diversity and composition may change over the course of the breeding season. Species diversity is often highest in the beginning of the breeding season, when both explosive breeders and prolonged breeders gather at the newly-filled breeding sites. As the breeding season progresses, the explosive breeders drop out and only the prolonged breeders remain (DONNELLY 1994).

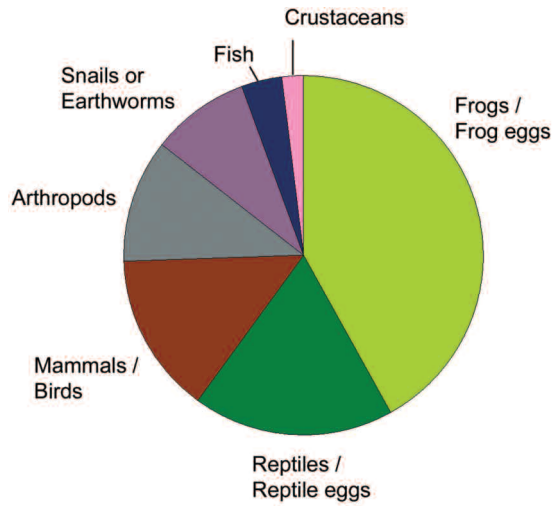
The anuran members of pond communities are often the best studied components of the herpetofauna of an area. Both sexes concentrate in the comparatively small area of the breeding pond, and male anurans attract attention by their loud advertisement calls. This greatly facilitates their study through acoustic and visual sampling. In the Golfo Dulce region, small hylid frogs like *Hyla ebraccata*, *H. microcephala* and *Scinax eleochoa* are typical anuran representatives of pond communities, as are the well-loved red-eyed tree frogs (*Agalychnis callidryas*).

Due to their secretive habits, the reptile component of pond communities are harder to sample and much less well known. Some reptiles can be found in and around ponds throughout the year. For example, all Costa Rican turtles are at least semi-aquatic, and consequently the snapping turtle (*Chelydra serpentina*), as well as the mud turtles (genus *Kinosternon*) and the pond turtle (*Chrysemys omata*) can be found in or near ponds. The same is true for caimans; juveniles are frequently encountered, even in small or temporary ponds. While lizards are rarely associated with pond habitats, many snakes of the frog-eating guild aggregate at ponds during the frog breeding season, attracted by the abundance of their favourite prey. Commonly observed snakes are cat-eye snakes (*Imantodes*), blunt-head snakes (*Leptodeira*) and parrot snakes (*Leptophys*). They climb through the vegetation around the ponds and gorge themselves on frogs or their eggs.

Diets

All adult amphibians, as well as the large majority of reptiles, are carnivorous. Amphibians will eat a range of invertebrate prey items, including crickets, beetles, ants,

Fig. 34: Dietary guilds in snakes. The predominant prey group taken by snakes occurring in the Golfo Dulce region is shown. Frogs and reptiles and their eggs make up a substantial portion of the snake diet, emphasising the importance that abundant populations of these groups have for the ecology of the forest.



spiders and worms. Most are opportunistic hunters that will eat whatever is small enough to swallow. Dietary specialisation has been reported for some species associated with leaf litter. For example, some small *Eleutherodactylus* frogs, as well as some dendrobatids, seem to eat mainly ants and termites (LIEBERMAN 1986). Some of the larger anurans, like the marine toad (*Bufo marinus*) or the South American bullfrog (*Leptodactylus pentadactylus*), are known to attack larger prey, including lizards, snakes or small mammals. Most anurans are sit-and-wait predators. They sit motionless until they detect a prey item visually, and then capture it by launching towards the prey. Typical examples of this foraging style include *Leptodactylus* and *Rana*. Other species, like many toads, have a more active foraging style, and move around in search of prey (SAVAGE 2002).

The trophic niche of tadpoles, the juvenile stage of anurans, is very different from that of the adults. Most tadpoles feed on plant material or detritus (decomposing animal and plant matter). To cope with this type of food, many tadpoles have horny beaks and teeth which they use to rasp organic material.

Compared with amphibians, reptiles show a larger variety of dietary habits, including herbivorous, omnivorous and carnivorous species. Reptiles also show a larger tendency towards dietary specialisation, particularly among snakes.

Among the species found in the Golfo Dulce region, adult iguanas (*Iguana iguana*, *Ctenosaurus similes*) are the only reptiles that are mainly herbivorous, consuming fruits, flowers and leaves. Juveniles of both species, however, will consume insects as well. Some turtles, like *Kinosternon leucostomum* are omnivores and will eat vegetable matter as well as insects, crustaceans and fish. The other turtles found in the Golfo Dulce region are generally carnivorous, eating fish, amphibians and worms. Most lizards, all snakes and all crocodylians are

carnivorous, and depending on their size take a large array of prey items ranging from insects over amphibians and reptiles to birds and mammals.

Carnivorous lizards show several types of foraging behaviour. Some species find their prey by taste. Skinks, anguils, and teiids (e.g. *Ameiva* sp.) typically move around and chemically track their prey. Most iguanids (e.g. *Norops* sp., *Basiliscus* sp.) and geckos on the other hand, are sit-and-wait predators that remain motionless while visually scanning the surroundings for approaching prey. Often the lizard then moves to the prey, captures and eats it, and then returns to its perch site to continue searching. Finally, the helmeted iguana (*Corytophanes cristatus*) is an extreme sit-and-wait predator that remains motionless and waits for the prey to approach its perch site (SAVAGE 2002).

The dietary habits of snakes as a group are the most varied, and many species show dietary specialisation (SOLÓRZANO 2004). A large range of this diversity can be observed in the species that occur in the Golfo Dulce region (Fig. 4). There are snakes that specialise in eating freshwater shrimp (*Hydromorphus concolor*) or small crabs (*Leptodeira rubricata*), snails and slugs (*Dipsas* sp., *Sibon* sp.), amphibians and/or their eggs (*Chironius* sp., *Leptodeira* sp.), lizards (*Oxybelis* sp.), reptile eggs (*Enulius sclateri*), other snakes (*Clelia clelia*; coral snakes), birds and their eggs (*Pseustes* sp.), and mammals (*Lachesis* sp.). Frogs and reptiles, and their eggs, make up a substantial portion of the snake diet in the Golfo Dulce region (Fig. 4), emphasising the importance that an abundant herpetofauna has for the ecology of the forest.

Depending on their size and the presence of venom, prey capture in snakes can vary substantially (SOLÓRZANO 2004). Some species, like the boas use muscular force (constriction) to subdue and kill their prey. Other large species, like the opisthoglyph colubrid snake *Clelia clelia* may use constriction in addition to venom to kill their prey. Some colubrid snakes that possess venom (opisthoglyphs) bite and hold on to their prey and allow the venom to terminate most resistance (e.g. *Imantodes*, *Leptodeira*, *Oxybelis*). Coral snakes and some vipers (e.g. *Bothriechis schlegelii*) use the same tactic of holding on while envenomation takes place. Other vipers (e.g. *Bothrops asper*) strike and release the prey immediately, locating it afterwards. Several colubrid species strike, bite and hold on to their prey with great force, dragging it until it succumbs and can be quickly swallowed (e.g. *Mastigodryas melanolomus*). The snail-eaters (e.g. *Dipsas*, *Sibon*) on the other hand patiently hold on to the body of the snails until they are able to extract them from their shell.

Predation and anti-predator strategies

Amphibians and reptiles play an important role in the food web of an ecosystem, both as predators as well as prey items. In all stages of their life, amphibians are hunted by a wide variety of carnivorous invertebrates and vertebrates that co-occur with them. Frogs and lizards make up a substantial portion of the diet of many snakes, and a large variety of both diurnal (e.g. birds, spiders) as well as nocturnal (e.g. spiders, bats, other mammals) animals prey upon amphibians and reptiles.

To avoid being eaten, amphibians and reptiles have evolved a range of morphological and behavioural predator-evasion strategies. Most amphibians are relatively defenceless, lacking claws and fangs to defend them. One of the most common strategies used against diurnal predators is cryptic coloration to blend in with the surroundings. Arboreal frogs like the red-eyed tree frogs (*Agalychnis* sp.) or glass frogs have green dorsal coloration, which helps them blend into the green surroundings of their diurnal sleeping sites. Terrestrial species that inhabit the leaf litter on the forest floor on the other hand often show brown coloration, as well as colour patterns or skin structures that disrupt the body outline that further help them blend in the surroundings. *Eleutherodactylus* frogs or the smooth-skinned toad *Bufo haematiticus* are good examples of this strategy. Among reptiles, the helmeted lizard (*Coryophanes cristatus*) is a good example of crypsis through motionlessness.

Another way to avoid being eaten is by being unpalatable or poisonous, and to advertise this to potential predators through aposematic (warning) coloration. The harlequin toad *Atelopus varius* and the poison-dart frogs of the genera *Dendrobates* and *Phylllobates* are examples that occur in the Golfo Dulce region. In this respect, it is interesting that the non-poisonous members of the family Dendrobatidae (*Colosthetus* sp.) show cryptic brown coloration that helps them to blend into the brown surroundings of their leaf-litter habitat. Warning colours can also be found among reptiles. The tricolour red- yellow-black coloration shown by the highly poisonous coral snakes is a colour combination often found in nature, and visually-orientated predators like birds quickly learn to avoid them. At least one non-venomous snake in the Golfo Dulce region, the false coral snake *Erythrolamprus mimus* shows red and black colour patterns, and is presumably protected by resembling a poisonous model.

Besides morphological adaptations for predator evasion, many animals have also evolved behavioural strategies. A common one is to simply hide in retreat sites or “day shelters” while resting. Little is known about these retreat sites, but at least for amphibians they function as protection against desiccation in addition to

hiding them from predators. Reptiles, too, frequently hide during the day under logs, rocks or in the leaf litter. Whether these are opportunistically taken advantage of each day, or whether animals have long-term shelters to which they return each day may vary between individuals and between species. The largely fossorial life style of caecilians and some salamanders, as well as several lizards, may also serve to avoid predators.

Even after the prey has been located by the predator, there are still ways of avoiding capture. One is to try and escape the predator. The jumping locomotion of anurans may function in this way, as a large jump quickly removes the prey from the direct reach of the predator (GLAW & VENCES 2003). Also, the erratic path traced by jumping frogs does not leave a continuous scent trail, which may throw off pursuing snakes. Even frog larvae still in their eggs may escape approaching predators. Red-eyed tree frogs (*Agalychnis callidryas*) deposit eggs on vegetation above water, and their developing larvae can sense the vibrations that are generated when an egg-eating snake approaches. They then have the ability to hatch very quickly, thus escaping the predator (WARKENTIN 1995). Many lizards and snakes will try to outrun a potential predator. When threatened, even the large green iguana and basilisk will simply jump off their perches in the trees. If their perches were above water, they will jump into the water and swim away from the perceived threat. Basilisks can try to escape by running across the water surface, thanks to the skin flaps between their toes.

Finally, threat displays, or loud or unusual vocalisations may be used as predator defences. Several reptiles as well as snakes show warning or threat displays. These include hissing, vibrating or rattling the tail, flattening the head and/or body to appear bigger and making fake attacks or striking movements towards the predator. Typical examples from the Golfo Dulce region include the impressive threat displays of the parrot snake (*Leptophis ahaetulla*) and the brown vine snake (*Oxybelis aeneus*). When frightened, both species raise the anterior part of their bodies, open their mouths that show contrasting red or black coloration. Sometimes they also hiss or pretend to strike. Many frogs will emit very loud cries, so-called distress calls, when captured (HÖDL & GOLLMANN 1986). Unlike other frog vocalisations, which are generally only produced by males during the breeding season, distress calls can be given by both sexes and even juveniles. These vocalisations may briefly frighten the predator so that it drops its prey to give them another chance to escape, or they may attract even larger predators that compete with or threaten the original predator – again giving the prey another chance of escape. Among the most impressive distress calls found in nature is that of a

species found in the Golfo Dulce region: when captured, the South American bullfrog (*Leptodactylus pentadactylus*) emits a series of loud, high pitched cries that resemble the cries of angry house-cats.

Communication

Although neither amphibians nor reptiles are particularly social animals, many of them do communicate with members of their own species and even other species. Most communication occurs in the context of reproduction.

There are four common signal modalities that animals use to communicate with each other: visual, chemical, acoustic and tactile. Visual signals used to transmit information are diverse, and can include colour, patterns or movements. Chemical signals can consist of plumes of odorous substances or chemical scent trails, and can thus involve both the sense of smell as well as the sense of taste. Acoustic communication involves the production and perception of sound waves. Finally, tactile communication occurs when one individual rubs, presses or hits a body part against another individual (BRADBURY & VEHCAMP 1998). Animals may use one or several modalities to communicate, but often communication is dominated by one modality. Although examples of all four signal modalities can be found in almost any animal group, there are taxonomic biases in the use of signal modalities. In the next segment, I will discuss in more detail how different groups of amphibians and reptiles communicate.

Amphibians

Very little is known about the social or communication behaviour of caecilians. Acoustic communication does not occur in caecilians, and their fossorial habits make visual communication unlikely (HIMSTEDT 2000). Communication in caecilians is thus probably dominated by chemical and tactile signals, but research confirming this notion is lacking. Salamanders and newts communicate mainly by chemical signals, although visual signals in form of colour patterns and body movements may also play an important role, especially in newts. Members of the salamander family Plethodontidae, to which all Costa Rican salamanders belong, probably communicate largely through chemical signals. All plethodontids have a nasolabial groove on the side of the head, running from the lower margin of the nostril to the edge of the upper lip. This structure picks up chemical cues from the substrate and carries them to the olfactory sac. It is used in prey and mate location, as well as intra- and interspecific communication (SAVAGE 2002). Adult male plethodontids have a circular mental gland under the chin, and during courtship, males rub the secretion from this gland onto the female's body.

In anurans, communication behaviour is heavily dominated by acoustic signals (GERHARDT & HUBER 2002). In the large majority of cases, it is the male that produces the calls. Advertisement calls, the most frequently used type of vocalisation in anurans, serves a dual function: it attracts females, but it also has a territorial function and facilitates the spacing between the males in the breeding chorus. In addition to the advertisement call, which is present in most species, many anurans have a larger repertoire of signals. At least four additional signal types are known. Courtship calls are produced by males when they perceive an approaching female in the vicinity. They serve to further attract and stimulate the female. Often, courtship calls are more attractive versions of advertisement calls, i.e. longer signals or signals produced at higher rates. Territorial calls, often also referred to as encounter calls, are given by males during antagonistic interactions when a rival male vocalises nearby or approaches closely. Unlike advertisement calls, territorial calls often show structural gradation that may reflect a male's level of aggression or willingness to escalate the encounter. Another signal found in many species is the release call, given by males as well as unreceptive females. Release calls are often combined with distinctive body vibrations. Distress calls may be produced by either sex as well as by juveniles. Distress calls are generally the only vocalisation given with the mouth open. Rarely, reciprocal calls are produced by females in response to advertisement calls of males (SCHLAEPFER & FIGEROA-SANDI 1998). Since females do not have vocal sacs, reciprocal vocalisations tend to be of much lower volume than those of males. Except for *Eleutherodactylus rugosus*, *E. cruentus* and *E. taurus*, all anuran species occurring in the Golfo Dulce region have advertisement calls (see SAVAGE 2002), and some also have courtship calls, territorial calls, release calls and distress calls (e.g. HÖBEL 2000, 2005).

A small number of species uses signal modalities other than airborne signals for communication. For example, the Puerto Rican frog *Leptodactylus albilabris* communicates at least partly through seismic signals, produced by rhythmic thumping of its vocal sac on the ground (LEWIS et al. 2001). Some species communicate at least partially by visual signals, that is by stereotyped flagging movements of the fore and/or hind limbs (HÖDL & AMEZQUITA 2001). Often, species with visual signals live in environments like waterfalls or along fast-flowing streams, where acoustic communication is hindered by the background noise created by the flowing water. Diurnal species like the poison-dart frogs (family Dendrobatidae) or the harlequin toads may communicate visually as well. Potential signals include body movements or skin coloration (WELLS 1977, SUMMERS et al. 1999). And some anurans may also use tactile sig-

nals, especially during the late stages of courtship, when male and female are close to each other. To date, visual or tactile displays have only been reported for one species living in the Golfo Dulce region. *Eleutherodactylus diastema* uses visual-tactile bumping displays during courtship (OVASKA & RAND 2001). However, only a fraction of the locally-occurring anuran species have been studied in any detail, and the rich anuran fauna may still have some surprises in store.

Reptiles

Visual communication plays the largest role in the social behaviour of lizards. Visual signals used to transmit information are diverse. Size alone can be a signal, and many species will puff up or position themselves in a way that makes them look bigger. Many male lizards also have brilliantly coloured dewlaps (e.g. *Norops* lizards) or patches of brilliant ventral coloration. They may also rapidly change colour or colour patterns. Males of some species will change or intensify their coloration during the breeding season (e.g. *Iguana iguana*, *Basiliscus plumifrons*), and females may signal receptivity by changing colour. Commonly used body movements include head bobs, push-ups, or waving motions of the arms or legs (see PIANKA & VITT 2003). Advertisement displays of iguanid and especially anoline lizards – dewlap extension in concert with head-bobbing – are among the best-studied forms of lizard communication, and several studies have shown that females prefer the displays of males of their own species to those of others (with different coloured dewlaps or rates of head-bobbing).

Chemical signals play a major role in communication among snakes and many lizards. These animals have three well-developed systems for detecting chemicals (SCHWENK 1995). In addition to a sense of smell (for airborne chemicals) and taste (non-airborne chemicals), they also have a vomeronasal system (also referred as Jacobson's organ). The vomeronasal system allows greater discrimination of less volatile compounds. Nearly all lizards use chemical cues in social behaviour, but the importance of this signal modality varies considerably. For example, geckos and skinks rely to a much greater extent on chemical signals than other reptiles. Chemical signals can consist of plumes of odorous substances or chemical scent trails (PIANKA & VITT 2003). Reptiles may use chemical cues to discriminate between species (COOPER & VITT 1986), and to determine the sex or the reproductive state of conspecifics (COOPER & VITT 1987). Some are able to recognise familiar and unfamiliar animals based on smell (COOPER 1996), and may even be able to recognise other individuals based on scent. Many of the reptiles found in the Golfo Dulce region communicate partly or primarily through chemi-

cal signals. These include all snakes, as well as many lizards, particularly members of the families Teiidae, Gymnophthamiidae, Scincidae, and Anguinae.

Among reptiles, acoustic communication is limited to crocodylians and some groups of lizards. Crocodylians are the most vocal of all the reptiles. They use bellows, barks and hisses in such diverse behavioral contexts as courtship, territoriality and mother-offspring communication. Both species of crocodylians found in the Golfo Dulce region (the crocodile, *Crocodylus acutus* and the caiman, *Caiman crocodilus*) vocalize. But compared to other crocodylians, particularly the American alligator, acoustic signals play a relatively minor role in their behaviour (see SAVAGE 2002). Among lizards, acoustic communications is primarily found in geckos, although some European lacertid lizards also produce sounds (BÖHME et al. 1985). Lizard sounds vary from barely inaudible squeaks to loud barks (BAUER et al. 1992), and are produced primarily during intraspecific interactions. In some species, females may also produce sounds when approached or called to by another animal, but generally it is the males that call to establish territories, maintain dominance hierarchies and attract females (e.g. MARCELLINI 1977). Of the lizards found in the Golfo Dulce region, only the two introduced Hemidactylus geckos and the turnip-tailed gecko *Thecadactylus rapicaudus* are known to use calls to communicate (MARCELLINI 1974, PIANKA & VITT 2003).

Tactile communication is common in turtles and snakes, but also occurs in many lizards (PIANKA & VITT 2003). During male-male interactions, tactile communication may follow after visual, acoustic or chemical contact has been established, and tactile interactions can escalate into ritualised combats or real fights. In male-female interactions, tactile communication often occurs late in courtship, when males try to copulate.

Finally, vibrational communication has been described for a chameleon (BARNETT et al. 1999). To date, few studies have been conducted that focused on vibrational communication in reptiles, and it still has to be determined how widespread this mode of communication is. So far, no reptile from the Golfo Dulce region has been shown to communicate through vibrational signals.

Reproductive ecology

The life cycles of amphibians and reptiles are very different. In amphibians, the most common life cycle involves three very different stages: a jelly-covered egg deposited in an aquatic habitat hatches into an aquatic tadpole that eventually metamorphoses into the adult form. There are variations to this theme, most commonly the loss of an independent tadpole phase. Here, em-

bryonic and larval development is completed within the egg, which is laid in a terrestrial nest (direct development; e.g. plethodontid salamanders, *Eleutherodactylus* frogs), or development takes place within the body of the mother (ovoviviparity; e.g. caecilians). Reproductive mode, as defined by SALTHER & DUELLMAN (1973) combines traits that include oviposition site, ovum and clutch characteristics, rate and duration of development, size and stage of hatchlings, and nature of parental care. Amphibians have evolved an amazing diversity of reproductive modes. Reptiles, in contrast, only show two reproductive modes: egg deposition (oviparity) or giving birth to young (viviparity).

Reproduction in amphibians

To date, 39 different reproductive modes have been described for anurans (HADDAD & PRADO 2005), seven for salamanders and four for caecilians (DUELLMAN & TRUEB 1986). The greatest diversity of reproductive modes is found in the Neotropics, where anurans have evolved 31 modes (HADDAD & PRADO 2005). Some reproductive modes are very rare, and are only described for a single species (e.g. eggs in floating bubble nests (HADDAD & HÖDL 1997), while others occur in a wide range of taxa (e.g. eggs and tadpoles in water).

Some trends in the evolution of reproductive modes are connected with life history (HADDAD & PRADO 2005). For example, tree frogs have adaptations for arboreal life, like adhesive discs and/or opposable thumbs and toes, and the main trend in tree frog reproductive modes is from oviposition in water on the floor to oviposition in arboreal sites. These include laying eggs in water-filled tree holes or aerial plants, laying eggs on vegetation above water or aerial foam nests. The reproductive modes of the much more terrestrial-orientated leptodactylids on the other hand, tend to be associated with the forest floor. These include foam nests on the edges of ponds or in subterranean chambers, or direct development of terrestrial eggs.

In the continental USA as well as in Europe, amphibians exhibit only four reproductive modes, and most species oviposit in water (DUELLMAN & TRUEB 1986). The amphibians in the Golfo Dulce Region exhibit 11 modes, ranging from eggs in water to viviparity.

Viviparity

Caecilians are the only live-bearing amphibians in Costa Rica. Because caecilians are secretive creatures, most of what is known about their reproductive behaviour comes from morphological studies. All caecilians are presumed to have internal fertilisation (DUELLMAN & TRUEB 1986). The posterior portion of the male cloaca is modified into an intromittent organ (called phalloseum),

which has a species specific morphology (WAKE 1977). The fertilised eggs are retained in the oviducts, and after the yolk supply is exhausted, the embryos hatch within the oviducts of the female. Upon hatching the embryos develop a special faetal dentition. Faetal caecilians feed on material produced by the oviductal glands of the female, a placental form of maternal nutrition.

Aquatic eggs and aquatic larvae

This is the most common reproductive strategy of amphibians in European and North America, and its is also very common among tropical amphibians. In the Golfo Dulce region, 16 species from four families (Microhylidae, Bufonidae, Hylidae, Ranidae) have aquatic eggs and larva. There are, however, variations in the type of aquatic habitat the eggs are deposited in, which allows for further sub-classification of this reproductive strategy. Eggs may be deposited in flowing water (e.g. *Smilisca sila*, *S. sordida*, *Rana warszewitchii*, *Bufo malanochloris*) or in still water. Egg deposition sites in still water can include ponds (e.g. *Bufo marinus*, *Scinax elaeochroa*, *Hyla microcephala*), puddles (e.g. *Smilisca phaeota*) or small, water-filled basins built by the male frogs along the edges of ponds or streams (*H. rosenbergi*).

Eggs in foam nest and aquatic larvae

To construct the foam nest, males kick semen, mucus, air, eggs and water into a foamy mass that resembles beaten egg white. The embryos start their development inside the foam nest, which protects them from predation and desiccation, but eventually they have to enter the water to finish their development. This reproductive mode is found in 6 species in the Golfo Dulce region, all of them members of the family Leptodactylidae. Foam nests are most often constructed in or near small bodies of water such as temporary pools and ponds (e.g. *L. pentadactylus*, *Physalaemus pustulosus*), but at least one species (*L. labialis*) hides its foam nest in small depressions under rocks and logs.

Terrestrial eggs and aquatic larvae

Many amphibians lay their eggs out of water. There are many variations of this mode of reproduction, which mainly differ in where the eggs are deposited and how the tadpoles end up in the water. Poison-dart frogs (family Dendrobatidae) lay terrestrial eggs in secluded sites in the leaf litter or under logs. Upon hatching, the tadpoles are transported to water. These aquatic rearing sites differ depending on species as well as local habitat conditions. In some species, the male will carry the tadpoles on his back to streams (*Colostethus* sp.), while other species transport the tadpoles to small bodies of water such as tank bromeliads, tree holes or water-filled crevices (*D. auratus*, *D. granuliferus*, *Phyllobates vittata*).

tus). Phytothelmata used by these frogs can be surprisingly small – along a stream in Golfo, tadpoles of *D. granuliferus* were raised in the leaf axils of *Diffenbachia* plants that were hardly large enough to accommodate the tadpole (MEYER 1996).

Arboreal eggs and aquatic larvae

Another variation of the theme of eggs outside the water, and tadpoles entering the aquatic habitat upon hatching, is by depositing eggs on vegetation overhanging ponds or streams. As the eggs hatch, the tadpoles drop into the water, where they will conclude their development as aquatic tadpoles. Ten species from the Golfo Dulce region show this reproductive strategy. All seven glass frog species (family Centrolenidae) lay their eggs on vegetation overhanging slow flowing streams. Their eggs are generally one to several metres above the water level. A number of local tree frogs also lay their eggs on vegetation, but they do so over lentic water like pools and ponds. *Hyla ebraccata* deposits eggs on vegetation relatively close to the water surface, while the oviposition sites used by the red-eyed tree frog, *Agalychnis callidryas*, and the parachuting frog, *A. spurrelli*, tend to be higher in the vegetation.

Terrestrial eggs and direct development

This is a surprisingly common mode of reproduction in the neotropics, mainly because it is practised by two of the most species-rich groups of amphibians, the pletodontid salamanders and rain frogs of the genus *Eleutherodactylus*. Clutch size is small, but the eggs contain substantial amounts of yolk, which is not surprising given that all the nutrition for the complete development of the embryo has to be contained within the egg. Oviposition occurs in moist, secluded sites, and clutch attendance has been described for several species. It has been suggested that direct development has been important in the radiation of both groups in the new world tropics (DUELLMAN & TRUEB 1986, WAKE & LYNCH 1976).

Parental care by amphibians

Examples of parental care can be found in all three groups of amphibians (CRUMP 1996). However, parental care is particularly common among amphibians that breed on land because the terrestrial environment is rather inhospitable to the permeable eggs of amphibians. In caecilians and salamanders, the only type of parental care provided is egg attendance, that is, one of the parents remains with the eggs for part of all of their development. Often, the parent sits on the eggs, or has its body curled around the clutch. The benefits of this behaviour include defence of eggs against parasites, small predators and some pathogens. The attending par-

ent may also modify moisture condition to be more suitable for egg development. It seems that world-wide, all or almost all oviparous caecilians attend eggs, while about 20% of all salamander species stay with their eggs (CRUMP 1996). There are no examples of parental care in caecilians in the Golfo Dulce region, because all local species are viviparous. Members of the genus *Bolitoglossa* seem to practice egg attendance, while the worm salamanders, genus *Oedipina*, apparently have no parental care (SAVAGE 2002).

Compared to caecilians and salamanders, parental care is relatively infrequent in anurans (CRUMP 1996). Egg attendance is the most common form of parental care practised by this group of amphibians. Several species from three anuran families (Dendrobatidae, Centrolenidae, Leptodactylidae) found in the Golfo Dulce Region show this type of parental care. In *E. fitzingeri* and *E. crassidigitus* it is the female that stays with the clutch (RYAN 2005), while in the glass frogs *Hyalinobatrachium colymbiophyllum* and *H. valerioi* it is the male that stays near the clutch (MCDIARMID 1978; DRAKE & RANVESTEL 2005). Male *H. colymbiophyllum* attend the eggs only during the night, while male *H. valerioi* stay with the eggs the whole time. MCDIARMID (1978) showed that egg survival is higher in the species that provide more intense egg attendance (*H. valerioi*). For other species that breed terrestrially, parental duties do not stop once the tadpoles hatch. In all five species of poison-dart frogs living in the Golfo Dulce region, tadpoles from terrestrially laid eggs have to be transported to aquatic sites to complete their development. In most species, it is the father that carries the tadpoles to streams (*Colosthetus* sp.) or phytothelms (*D. auratus*, *Phyllobates vittatus*) where the tadpoles are then left to fend for themselves. In *Dendrobates granuliferus*, parental care is taken one step further. Here it is the female who carries each tadpole to its own small phytothelm, and she will come back every couple of days to feed the tadpole with unfertilised nutritional eggs (MEYER 1996). Female *Leptodactylus bolivianus* have been observed to lead their densely-packed aggregations of tadpoles around in the water (WELLS & BARD 1988). The significance of this behaviour is not yet clear.

Reproduction in reptiles

Reproductive modes in reptiles are much less diverse than in amphibians. Oviparity (egg laying) and viviparity (giving birth to live young) are the two main reproductive modes.

Oviparity

Most reptiles lay eggs, which can be flexible-shelled or with a rigid, calcareous shell (PACKARD et al. 1982). Most lizards and all oviparous snakes have flexible eggs either without a calcareous layer or a very thin one. As a

consequence, these eggs are highly affected by the moisture content of the environment, and have higher hatching success when adequate moisture is available. The eggs of many turtles, a few lizards (e.g. Gekkonidae) and crocodylians have a well developed calcareous layer, similar to birds. These eggs are rather independent of the hydric environment in which they develop. Eggs with hard, calcified shells are often deposited in open, relatively dry places and abandoned, while eggs with more leathery shell that allow transport of water into the developing embryo are often deposited in carefully constructed nests chambers. For example, female green iguanas dig nest burrows that are typically 1-2 metres long and 30-60 cm deep, but can sometimes reach 20 m and more. These burrows may be complex, branched structures with several tunnels, caves and entrances. Normally, each female builds her own nest, but communal breeding sites in which several females share a large burrow are also regularly found. Average clutch size vary between different species of lizards from one to over 50 eggs (FITCH 1970). *Norops* lizards lay only one egg at a time, but eggs can be produced in rapid succession (as little as 7 days apart) (ANDREWS 1979, VITT & ZANI 2005). Geckos generally produce two eggs, but some, like the turnip-tailed gecko *Thecadactylus rapidauda* lay only a single egg (VITT & ZANI 1997). Female green iguanas (*Iguana iguana*) can lay up to 50 eggs at a time.

Oviposition sites in oviparous snakes vary considerably. Depending on the species, females deposit their eggs buried or semi-buried in sand or soil, in terrestrial or arboreal vegetation, between the roots of trees or shrubs, under logs, or in animal burrows (SOLÓRZANO 2004). The bushmaster (*Lachesis melanocephala*), for example, uses rodent burrow to lay its eggs. Clutch size can vary considerably between species. For smaller snakes like *Dipsas* sp., *Imantodes* sp. or *Leptodeira* sp., clutch sizes of two to eight eggs seem to be the norm (SOLÓRZANO 2004). Larger snakes like *Pseustes* sp. or *Spilotes* also lay about eight eggs. Large bushmaster snakes can lay up to 16 eggs; the development of the eggs lasts 45-130 days (SOLÓRZANO 2004).

Viviparity

Although most reptiles are oviparous, the evolutionary shift from oviparity to viviparity has taken place independently in at least 100 lineages of lizards and snakes, but never in turtles or crocodiles (LEE & SHINE 1998). In viviparous species, the oviduct does not secrete the outer shell around the egg as in oviparous forms. In addition, a variety of placental connections are established between the uterine wall of the female and the structures of the developing embryo (STEWART & BLACKBURN 1988). It is believed that maternal selection of high body temperatures may provide the major

selective advantage for the evolution of viviparity from oviparity in reptiles. Eggs that are laid in a nest in a cool climate will develop only slowly or not at all, while eggs retained within a sun-basking female's uterus will be kept warmer and thus can complete development faster (SHINE 2005 and references therein). Uterine retention also keep the eggs moist as well as warm (SHINE 2005).

Three viviparous lizards (*Corytophanes cristatus*, *Mabuya unimarginata* and *Lepidophyma reticulatum*) occur in the Golfo Dulce region. The natural history and reproduction of *Lepidophyma reticulatum* is particularly interesting. This nocturnal species consists entirely of females. Females produce eggs that, without requiring fertilisation, develop into new lizards. This phenomenon is called parthenogenesis. Moreover, the developing eggs are maintained within the mother's body for the duration of their development (SAVAGE 2002). Viviparity in snakes is more common in Costa Rica. Sixteen percent of all Costa Rican snakes are viviparous, including all boas, most pit vipers and the sea snake *Pelamis platurus* (SOLÓRZANO 2004). Eight viviparous snakes occur in the Golfo Dulce region. Gestation in viviparous Costa Rican snakes lasts 4-8 months. Litter size in smaller species like *Epicrates cenchria* or *Bothriechis schlegelii* is about 10-20 young, while larger snakes like *Boa constrictor* or *Bothrops asper* can have litters of 65-90 offspring (SOLÓRZANO 2004).

Parental care by reptiles

Parental care is distributed unevenly among the major reptilian groups. Parental care is essentially non-existent in turtles, rare in lizards and snakes and apparently universal in crocodylians (GANS 1996).

Egg attendance is the most common form of parental care in lizards and snakes, and it is generally limited to eggs. Few species extend care to hatchlings. Among the very few species from the Golfo Dulce region that seem to provide egg attendance is *Diploligossus bilobates* (SAVAGE 2002). Females stay with their egg clutches, which are hidden under logs.

Parental care by crocodylians is generally performed by the female. Females typically remain near the nest after oviposition and defend the nest against predators. As they get close to hatching, the young inside the nest will start to call and attract the female to the nest, where she may open the nest and help the young to hatch and get to the water. The young often stay together for an extended period of time in the territory of the mother, who will continue to defend them. Young crocodylians produce special distress calls when threatened or captured, which elicit defensive behaviour by the adults.

Suggestions for future research

Despite the richness of the herpetofauna and the relatively easy accessibility of many sites in the Golfo Dulce region, very few species have been studied in any detail. Among the amphibians, very little is known about the ecology and behaviour of caecilians and salamanders. Among anurans, some groups are better studied than others. The most glaring lack of information concerns the life history of rain frogs of the genus *Eleutherodactylus*. Although they are generally abundant, and despite the fact that almost every time a species is studied in detail some amazing behaviour is reported, very few species have been studied so far. Even among relatively well-studied groups like tree frogs and poison-dart frogs, in depth studies on any aspect of communication or reproductive behaviour is lacking for all but a handful of species (SCHWARTZ & WELLS 1985, WELLS & BARD 1987, WARKENTIN 1995, MEYER 1996, HÖBEL 2000). The same is true for reptiles, where studies have mainly focused on some species of *Norops* lizards (e.g. ANDREWS 1979, VITT & ZANI 2005). Consequently, detailed studies of any species in the area are needed and are bound to yield new and interesting results. Also, many species have a larger range of distribution, yet most of them have been studied at only one locality. Comparative studies carried out in the Golfo Dulce region may reveal geographic variation, and yield new insights in the ecological factors influencing morphology or behaviour.

References

- AICHINGER M. (1987): Annual activity pattern of anurans in a seasonal Neotropical environment. — *Oecologia* **71**: 583-592.
- ANDREWS R.M. (1979): Reproductive efforts of female *Anolis limifrons* (Sauria: Iguanidae). — *Copeia* 1979(4): 620-626.
- BARNETT K.E., COCROFT R.B. & L.J. FLEISHMAN (1999): Possible communication by substrate vibration in a chameleon. — *Copeia* 1999: 225-228.
- BAUER A.M., DOUGHERTY J. & A.P. RUSSEL (1992): Vocalizations of the New Caledonian giant gecko, *Rhacodactylus leachianus*. — *Amphibia-Reptilia* **13**: 412-417.
- BÖHME W., HUTTERER R. & W. BINGS (1985): Die Stimme der Lacertidae, speziell der Kanareneidechse (Reptilia: Sauria). — *Bonn. Zool. Beitr.* **36**: 377-354.
- BRADBURY J.W. & S.L. VEHCAMP (1998): Principles of Animal Communication. — Sinauer Associates, Sunderland, Massachusetts.
- BRUCE R.C. (1997): Life history attributes of the salamander *Bolitoglossa colonneae*. — *J. Herp.* **31**(4): 592-594.
- COOPER W.E., Jr. (1996): Chemosensory recognition of familiar and unfamiliar conspecifics by the scincid lizard *Eumeces laticeps*. — *Ethology* **102**: 1-11.
- COOPER W.E., Jr. & L.J. VITT (1986): Interspecific odour discrimination among syntopic congeners in scincid lizards (genus *Eumeces*). — *Behaviour* **97**: 1-9.
- COOPER W.E., Jr. & L.J. VITT (1987): Intraspecific and interspecific aggression in lizards of the scincid genus *Eumeces*: chemical detection of conspecific sexual competitors. — *Herpetologica* **43**: 7-14.
- CRUMP M. (1996): Parental care among the amphibian. — *Advances in the Study of Behavior* **25**: 109-144.
- DONNELLY M.A. (1994): Amphibian Diversity and Natural History. — In: McDADE L.A. et al. (eds), *La Selva: Ecology and Natural History of a Neotropical Rainforest*. The University of Chicago Press, Chicago, 199-209.
- DRAKE D.L. & A.W. RANVESTEL (2005): *Hyalinobatrachium colymbi-phyllum* Egg mass defense. — *Herpetological Review*. **36** (4): 434.
- DUELLMAN W.E. (1988): Patterns of species diversity in anuran amphibians in the American tropics. — *Ann. Mo. Bot. Gard.* **75**(1): 79-104.
- DUELLMAN W.E. & L. TRUEB (1986): *Biology of Amphibians*. — McGraw-Hill, New York.
- FITCH H.S. (1970): Reproductive cycles in lizards and snakes. — *Mis. Publ. Univ. Kansas Nat. Hist.* **52**: 1-247.
- GANS C. (1996): An overview of parental care among the Reptilia. — *Advances in the Study of Behavior* **25**: 145-157.
- GERHARDT H.C. & F. HUBER (2002): *Acoustic Communication in Insects and Anuran*. — University of Chicago Press, Chicago.
- GLAW F. & M. VENCES (2003): Amphibians. — In: GOODMAN S.M. & J.P. BENSTEAD (eds), *The Natural History of Madagascar*. The University of Chicago Press, Chicago: 883-898.
- GREENE H.W. (1988): Species richness in tropical predators. — In: ALMEDA F. & C.M. PRINGLE (eds), *Diversity and Conservation of Tropical Rainforests*. California Academy of Science, San Francisco: 259-280.
- GUYER C. (1994): The reptile fauna: diversity and ecology. — In: McDADE L.A. et al. (eds), *La Selva: Ecology and Natural History of a Neotropical Rainforest*. The University of Chicago Press, Chicago: 210-216.
- GUYER C. & M.A. DONNELLY (2005): Amphibians and Reptiles of La Selva, Costa Rica, and the Caribbean slope. — University of California Press, Berkeley.
- HADDAD C.F.B. & C.P.A. PRADO (2005): Reproductive modes in frogs and their unexpected diversity in the atlantic forest of Brazil. — *BioScience* **55**(3): 207-217.
- HADDAD C.F.B. & W. HÖDL (1997): New reproductive mode in anurans: Bubble nests in *Chiasmodeis leucosticta* (Microhylidae). — *Copeia* 1997: 585-588.
- HAYES M.P. (1991): A study of clutch attendance in the Neotropical frog *Centrolenella fleischmanni* (Anura: Centrolenidae). — Ph.D. thesis, University of Miami, USA.
- HEINEN J.T. (1992): Comparisons of community characteristics of the herpetofauna of leaf litter in abandoned cacao plantation and primary forest in a lowland tropical rainforest: Some implications for faunal renaissance. — *Biotropica* **24**: 420-430.
- HIMSTEDT W. (2000): Reproductive biology in Gymnophiona. — In: HOFRICHTER R. (ed.), *Amphibians*. Firefly Books: 154-157.
- HÖBEL G. (2000): Reproductive ecology of *Hyla rosenbergi* in Costa Rica. — *Herpetologica* **56**(4): 446-454.
- HÖBEL G. (2005): On the acoustic communication system of *Eleutherodactylus fitzingeri* (Anura: Leptodactylidae). — *Herpetological Review* **36**(3): 242-244.

- HÖDL W. & A. AMEZQUITA (2001): Visual signaling in anuran amphibians. — In: RYAN M. (ed.), *Anuran Communication*. Smithsonian Inst. Press, Washington, DC.: 121-141.
- HÖDL W. & G. GOLLMANN (1986): Distress calls in neotropical frogs. — *Amphibia-Reptilia* **7**: 11-21.
- LEWIS E.R., NARINS P.M., CORTOPASSI K.A., YAMADA W.M., POINAR E.H., MOORE S.W. & X.-L. YU (2001): Do male white-lipped frogs use seismic signals for intraspecific communication? — *Amer. Zool.* **41**(5): 1185-1199.
- LEE M.S.Y. & R. SHINE (1998): Reptilian viviparity and Dollo's law. — *Evolution* **52**: 1441-1450.
- LIEBERMAN S.S. (1986): Ecology of the leaf litter herpetofauna of a Neotropical rainforest: La Selva, Costa Rica. — *Acta Zool. Mex.* **15**: 1-72.
- MARCELLINI D. (1974): Acoustic behavior of the gekkonid lizard *Hemidactylus frenatus*. — *Herpetologica* **30**: 44-52.
- MARCELLINI D. (1977): Acoustic and visual display behavior of gekkonid lizards. — *Amer. Zool.* **17**: 251-260.
- MCDIARMID R.W. (1978): Evolution of parental care in frogs. — In: BURGHARDT G.M. & M. BEKOFF (eds), *The development of behavior: comparative and evolutionary aspects*. Garland STMP press, New York: 127-147.
- MCDIARMID R.W. & C ADLER (1974): Notes on territorial and vocal behavior of Neotropical frogs of the genus *Centrolenella*. — *Herpetologica* **30**(1): 75-78.
- MEYER E. (1996): Ökologie und Biogeographie des zentralamerikanischen Pfeilgiftfrosches *Dendrobates granuliferus* TAYLOR. — Unpublished PhD thesis, University of Ulm, Ulm, Germany.
- MIYAMOTO M.M. (1982): Vertical habitat use by *Eleutherodactylus* frogs (Leptodactylidae) at two Costa Rican localities. — *Biotropica* **14**: 141-144.
- OVASKA K. & A.S. RAND (2001): Courtship and reproductive behavior of the frog *Eleutherodactylus diastema* (Anura: Leptodactylidae) in Gamboa, Panama. — *J. Herp.* **35**(1): 44-50.
- PACKARD M.J., PACKARD G.C. & T.J. BOARDMAN (1982): Structure of eggshells and water relations of reptilian eggs. — *Herpetologica* **38**(1): 136-155.
- PIANKA E.R. & L.J. VITT (2003): Lizards: windows to the evolution of diversity. — University of California Press, Berkeley.
- RYAN M.J. (2005): Egg attendance by female frogs in two species of *Eleutherodactylus* from Costa Rica. — *Herpetological Review*. **36** (3): 234-236.
- SAVAGE J.M. (2002): *The amphibians and reptiles of Costa Rica*. — The University of Chicago Press, Chicago.
- SAVAGE J.M. & J.D. VILLA (1986): Introduction to the herpetofauna of Costa Rica, *Contribution to Herpetology* **5**. — Oxford, Ohio, Society for the Study of Amphibians and Reptiles.
- SALTHE S.N. & W.E. DUELLMAN (1973): Quantitative constraints associated with reproductive mode in anurans. — In: VIAL J.L. (ed.), *Evolutionary Biology of the Anurans*. University of Missouri Press, Columbia: 229-249.
- SCHLAEPFER M.A. & R. FIGEROA-SANDI (1998): Female reciprocal calling in a Costa Rican leaf-litter frog, *Eleutherodactylus podiciferus*. — *Copeia* **1998**: 1076-1080.
- SUMMERS K., SYMULA R., CLOUGH M. & T. CRONIN (1999): Visual mate choice in poison frogs. — *Proc. R. Soc. Lond. B* **266**: 2141-2145.
- SCOTT N.J., Jr. (1976): The abundance and diversity of the herpetofauna of tropical forest litter. — *Biotropica* **8**: 41-58.
- SOLÓRZANO A. (2004): *Snakes of Costa Rica*. — Editorial INBio, Santo Domingo de Heredia, Costa Rica.
- SCHWENK K. (1995): Of tongues and noses: chemoreception in lizards and snakes. — *Trends Ecol. Evol.* **10**: 7-12.
- STEWART J.R. & D.G. BLACKBURN (1988): Reptilian placentation: structural diversity and terminology. — *Copeia* **1988**(4): 839-852.
- SHINE R. (2005): Life-history evolution in reptiles. — *Annu. Rev. Ecol. Evol. Syst.* **36**: 23-46.
- SCHWARTZ J.J. & K.D. WELLS (1985): Intra- and interspecific vocal behavior of the Neotropical tree frog *Hyla microcephala*. — *Copeia* **1985**(1): 27-38.
- VITT L.J. & P.A. ZANI (1997): Ecology of the nocturnal lizard *Thecadactylus rapicauda* (Sauria: Gekkonidae) in the Amazon Region. — *Herpetologica* **53**: 165-179.
- VITT L.J. & P.A. ZANI (2005): Ecology and reproduction of *Anolis capito* in rainforest of Southeastern Nicaragua. — *J. Herp.* **39**(1): 36-42.
- WAKE D.B. & J.F. LYNCH (1976): The distribution, ecology and evolutionary history of plethodontid salamanders in tropical America. — *Sci. Bull. Nat. Hist. Mus. Los Angeles Co.* **25**: 1-65.
- WAKE M.H. (1977): The reproductive biology of caecilians: an evolutionary perspective. — In: TAYLOR D.H. & S.I. GUTTMAN (eds), *The reproductive biology of amphibians*. Plenum Press, New York: 73-101.
- WARKENTIN K.M. (1995): Adaptive plasticity in hatching age: a response to predation risk trade-offs. — *Proc. Natl. Acad. Sci. USA* **92**: 3507-3510.
- WELLS K.D. (1977): The courtship of frogs. — In: TAYLOR D.H. & S.I. GUTTMAN (eds), *The reproductive biology of amphibians*. Plenum Press, New York: 233-262.
- WELLS K.D. & K.M. BARD (1987): Vocal communication in a neotropical tree frog, *Hyla ebraccata*: responses of females to advertisement and aggressive calls. — *Behaviour* **101**: 200-210.
- WELLS K.D. & K.M. BARD (1988): Parental behavior of an aquatic-breeding neotropical frog, *Leptodactylus bolivianus*. — *J. Herp.* **22**: 361-364.

Address of author:

Gerlinde HÖBEL
 Department of Biological Sciences,
 Lapham Hall
 3209 N. Maryland Ave.
 University of Wisconsin-Milwaukee
 Milwaukee, WI 53201, USA.
 E-mail: hoebel@uwm.edu

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