# THE LIFE HISTORY OF THE GREEN ANACONDA (*EUNECTES MURINUS*),
## WITH EMPHASIS ON ITS REPRODUCTIVE BIOLOGY

A Dissertation

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"…Federmann…[….]..wandered out into the Llanos to the banks of a mighty river. Since there were various signs that the region at other times had been densely populated, Federmann wished to ascertain the cause of its present desolation. He learned from the several captured Indians that in the river there lived an animal so carnivorous and voracious that it had eaten many of the inhabitants. The rest had abandoned the site and fled to a remoter [sic] section to escape the ferocity of so deadly an enemy. Federmann and his soldiers considered this statement true because by night they had heard the formidable bellows of the wild beast. Some even said they had seen it and affirmed that it was a species of serpent of terrifying corpulence."

From The conquest and settlement of Venezuela. Don José de Oviedo y Baños. 1723; (p: 56).

# DEDICATION

This dissertation is dedicated to

Renée Y. Owens,

my wife, who has been not only important help in the field but also an endless source of inspiration and support

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It is hard to give proper credit to all the people that have in one way or another helped me in during all this time. I will start, because it is easiest, by mentioning my sponsors. The Venezuela Council for Science and Technology (CONICIT) and the Banco Interamericano de Desarrollo (BID) partially sponsored my attendance to the University of Tennessee. My field research was sponsored by grants from The Wildlife Conservation Society, The National Geographic Society, The Convention for the International Trade of Endangered Species (CITES), The Venezuelan Fish and Wildlife Service (Profauna), and CONICIT.

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# ABSTRACT

Many species of a secretive nature that inhabit remote areas are largely unknown to science and have the potential to provide the diversity of life styles and factual information that is needed to unravel important questions regarding behavioral ecology. In this contribution I present some of the relevant information regarding the reproductive biology and general natural history of the green anaconda (*Eunectes murinus*, Familiy Boidae) gathered during 7 years of data collection in the Venezuelan llanos.

Due to the novelty of the study animal I had to design methods to collect much of my data. I developed new methods for subduing and measuring the animals. I also document the efficacy of force feeding transmitters as a way to radio-tag the animals. Although the emphasis is on reproductive biology, I also present information on many other aspects of the anaconda's life history collected both systematically and opportunistically. Anacondas use relatively small home ranges in wet and dry seasons but they perform relatively long migrations from one season to the other. Anacondas seem to be generalist ambush predators that feed on wading birds at early ages, but switch to larger prey as they grow older. They risk being injured or even killed by their prey when attacking large, dangerous prey items. Anacondas experience relatively high mortality in early ages that decreases as they grow larger. Adult males always face relatively high risk of predation by caimans, which seems to be specially dense in the breeding season. Other causes of mortality are overheating, parasites and diseases.

The determinants of breeding output were analyzed in detail using data collected from wild animals. Larger females produce large clutches of large individuals, but breed less often than smaller females, incurring a smaller reproductive investment in every breeding event, as well as on an annual basis. The maximum size of females seems to be optimized to maximize their breeding output. The maximum expected size for anacondas, as well as the maximum recorded in this study, are well below the maximum reported in the literature. I discuss this contradiction in light of my findings and possible environmental differences.

The mating system of the species was analyzed using data collected from the field and from captive observations. Anacondas show a striking female biased Sexual Size Dimorphism (SSD), larger than the SSD reported for any other terrestrial vertebrate. This is especially surprising because males mate in multiple-male breeding aggregations, where larger males seem to benefit from their large size. Anacondas breed in large breeding aggregations composed of one female and 1 to 13 males. These aggregations last up to four weeks and are scattered in the landscape fairly unpredictably. Larger males seem to be selective in their mating, selecting larger females, and larger females are courted by a higher number of males. Males spend a considerable amount of time and energy in courtship and the mating season is relatively short. Hence, factual polyandry is proposed as the main mating system in the species. Multiple mating increases the breeding success of the females. Large variance in the female's breeding success related to male preference sets the scenario for the action of sexual selection on female size. The possibility of a runaway process acting on female size is proposed. I also review the mating system of other species of snakes as well as the evolutionary environment of the group and conclude that polyandry might be more widespread among snakes than formerly believed

Finally, I use my findings to review the possibilities of sustained management of the species. Due to their secretive nature, low commercial value of the skin, female biased sexual size dimorphism, reproductive biology, and slow growth rate, I conclude that harvesting wild populations is not a likely possibility.  Ecotourism is a recommended way to incorporate the anacondas into the local economic activities.

# PREFACE

I started this project as an applied research effort that was intended to be used to develop the methods to use anacondas sustainably. During my research I discovered a fascinating world far more interesting than the demographic data. To the present I have gathered eight years worth of data on this species and in this dissertation I have included a sizable part of the information gathered. The focus of this volume is the reproductive biology of the anaconda; issues not covered in this volume in detail are demography, habitat use and mobility, and diet. I have included basic information of these topics needed to understand the main aspects of the dissertation but the reader will find frequent citations to my unpublished work. This dissertation was written in several chapters designed to be published independently. Even though there are abundant cross references, some information is repeated in different chapters.

Due the minimal knowledge that many readers have of the study site, I have written an extensive chapter describing the area. Also, due to the newness of anacondas as a research subject, I had to come up with my own way of finding the animals and gathering much of the data. Listening to tales and anecdotes from local inhabitants of the llanos was a key element to learning the basic elements that allowed me to develop the study methods. Studying anacondas presents a challenge even in activities as basic as measuring the animals and capturing them. Chapter two includes detailed information on the way the data were collected plus anecdotal information that could help future researchers trying to study this species.

Chapter three contains general information about the natural history of the species oriented to facilitate the understanding of the rest of this dissertation. Again, abundant accounts of anecdotes and general information are provided to assist future researchers.

Chapters four, five, and six are the main body of the text where all the information about reproductive biology is presented and the results analyzed in light of the ecological theories. Lastly, chapter 7 provides information about the conservation status of the anaconda and the perspectives of commercial use of the species. In this chapter I discuss the prospect of commercial harvest based on the information presented and also alternatives uses of the anaconda. Here I provide personal perspectives about sustainable use of natural resources in the neotropics developed over many years of dealing with these issues in Venezuela. After having worked in the Venezuelan fish and wildlife service I also include the “inside scoop” of the management programs and possible future directions.

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# CHAPTER 1 INTRODUCTION

The green anaconda (*Eunectes murinus*) considered to be one of the longest species of snakes, and is clearly the heaviest (Minton and Minton 1973). Anacondas are semi-aquatic and many morphological traits are adaptations for such a lifestyle. These include having eyes and nostrils on the top of the head and having a dark olive coloration with black spots with lighter blotches inside that blend perfectly with aquatic vegetation. It is distributed in all the lowlands of tropical South America to the east of the Andes (Beebe 1946). Within the family Boidae, anacondas are considered to be a primitive (basal) species (Greene 1997). Evidence for this includes their possession of spurs reminiscent of the thighbone on either side of the cloaca (Mole 1924). Regardless of how famous the anaconda is among herpetologists, very little is known about its life history. No field research has been carried out on this species. The available information is limited to casual encounters with animals in the field and notes on captive specimens (Beebe 1946; Belluomini and Hoge 1957/58; Belluomini et al. 1959; Belluomini et al. 1971; Blomberg 1956; Holmstrom 1980; 1982; Holmstrom and Behler 1981; Mole 1924).

Anacondas have a number of traits that make them an excellent subject for the study of snake ecology. First, it is a very primitive snake and an excellent representative of the South American boids that can provide insight regarding the evolution of the group (Minton and Minton, 1973). Second, anacondas are ectothermic top predators that experience an incredible change in body size from birth (200 g; Belluomini and Hoge 1957/58) to adulthood (104.4 Kg; Mole 1924), compared to other snakes. Third, their large size make them an excellent model to study the ecology of snakes in the field, since they are easier to equip with transmitters than other smaller species; this is true even for juveniles and newborns. Fourth, they are possible to find and catch during the dry season in the Venezuelan Llanos. Gathering baseline information on the life history of this animal will enrich future research addressing diverse questions in snake ecology and evolution and in the ecology of large-sized reptiles.

Reproduction is clearly one of the key traits in the life history of any species. The total number of healthy, viable offspring that an individual can produce is what will determine its fitness. Lifetime Reproductive Success (LRS) refers to the reproductive value of an individual. Individuals tend to reproduce in a way that maximizes their LRS (Daan and Tinbergen 1997). How an organism will administer its resources and what strategy it will use to breed are most relevant questions in the study of any animal. Williams (1966) argued that any investment in reproduction at any given time is at the expense of future reproduction. Once an animal reaches maturity it is faced with the decision of whether it should spend energy in breeding in a given year, and secure some offspring, or use that energy to grow larger where it can make a larger reproductive investment. If the animal breeds there is still another decision that it has to make. how to breed? The female can produce a relatively small Reproductive Effort (RE) and save part of her energy to continue growing or make a very large RE that would forfeit growth in the near future and handicap future breeding events. A female can also have a few offspring of large size or several offspring of smaller size. In species with indeterminate growth, these two decisions (whether and how) keep appearing and overlapping throughout life. The way an organism faces these decisions is often under strong phylogenetic influence. However, several environmental and developmental variables can produce important variation (Stearns 1992).

While the questions about clutch size and investment per offspring are often referred to in regard to females, the male's investment and reproductive strategy is also of interest. The amount of energy that each sex invests in reproduction is not necessarily equal. Males produce smaller gametes than females (anisogamy). The subsequent investment and behavior of the individual is influenced by this first premise (Bateman, 1948). In general terms, males will benefit most by achieving many matings while the females will benefit most from "good" matings. Mating with the wrong individual represents a low cost for the males and a high one for the female. Males are, therefore, generally polygynous while females are "choosy." However, if the male has few possibilities for obtaining other mates, or if he invests a lot of energy in every mating, it pays for him to be "choosy" as well (Arnold and Duvall 1994; Reynolds and Harvey 1994; Trivers 1972).

Sexual selection is based on the differential reproduction of members of each sex. Some individuals leave more offspring than others; hence, following generations will have a higher proportion of the genes of those individuals. Sexual selection typically is produced by differential mating success whether it results from the exclusion of rivals, female choice, or from the ability to locate receptive females. However, sperm competition (Parker 1970) has the potential to decrease the benefit of large size in siring success (Andersson, 1994). Mating systems are characterized by the relationship between fecundity and mating success (Sexual Selection Gradient: SSG). If one sex produces more offspring from more matings, it will have increased SSG and will be under sexual selection. The sex that has the higher SSG will be under stronger sexual selection than the other and therefore be more likely to seek multiple mating (Arnold and Duvall 1994).

Large size in females is supposedly a benefit in species that grow throughout life with little or no parental care. Large animals can produce large numbers of eggs and can store large amounts of fat for their development. Natural selection should therefore favor large size in females (Andersson 1994). The development of large size in males can occasionally be regarded as a handicap since they are more conspicuous to predators, but it may give an advantage in male-male combat and in fighting off predators. Larger males can win more combats, drive away more rivals, and thus monopolize more females (Darwin 1871; Trivers 1972). For example, large size enables males to outcompete other males and obtain more mates in several mammals (Le Boeuf and Reiter 1988; Packer et al. 1988), lizards (Dugan 1982; Rodda 1992; Stamps 1983), and spectacled caimans (Thorbjarnarson 1990). In some male lizards, large body size can help males to force copulation with smaller females (Dugan, 1982). However, in snakes males are apparently unable to forcibly copulate with females (Shine 1993). Shine (1994*a*) reviewed sexual dimorphism in snakes related to male-male combat and provided a revised theoretical model. He found that males were generally larger compared to conspecific females in those species that have male-male combat, but the relationship is not universal. Shine (1993) argues that the determinant for Sexual Size Dimorphism (hereafter SSD) is the Operational Sex Ratio (OSR). If the probability of encounter of two or more males with a female is low, then male-male combat is not likely to occur. Hence, there is no selection pressure for the evolution of large body size. Rather, sexual selection in this case is shunted to the development of refined abilities to locate the female (scramble competition; Andersson, 1994). Shine (1993) speculated that this should occur when species are in low densities, live in aquatic or arboreal habitats, or utilize locomotive methods that do not leave a continuous track, such as side-winding.

In addition to the scientific knowledge gained from studying the biology of a species as exceptional as the anaconda, it is also important to study this species because of its value as an economic resource. Anacondas can be used rationally due to their potential value in the skin trade, pet trade, and for nature-tourism. Anaconda skin has been used for luxury articles such as bags, purses, and boots in the past. Currently, the trade of anaconda products is forbidden by Venezuelan laws and is regulated internationally by the Convention for the International Trade of Endangered Species (CITES). In Venezuela, some species has been used commercially for relatively long time. Capybara (*Hydrochaeris hydrochaeris*) has been harvested commercially since 1968 (Ojasti, 1991) and the spectacled caiman (*Caiman crocodilus*) since 1983 (Thorbjarnarson, 1991). Other species of reptiles that are being considered for commercial harvest due to their population status and economic value include the tegu (*Tupinambis teguixin*), the green iguana (*Iguana iguana*), and the green anaconda (*Eunectes murinus*). Thus, managing anacondas is not an isolated use of natural resources. The use of all these animals does not involve any kind of habitat destruction or degradation since they occur at high densities in the Llanos. Furthermore, managing these resources offers a sustainable use with no net losses to the ecosystem and has the potential to encourage habitat preservation on the economic sector that benefits from the management (Thorbjarnarson 1999). At this time, however, due to the lack of detailed information on the natural history of these species, it is not possible to implement a management plan. In 1992, Profauna, CITES, and the Wildlife Conservation Society sponsored the first study of the ecology of anaconda. This study aimed to find out the basic ecology of anacondas in order to implement sustainable management. I carried out the initial investigation and continued it over the following 7 years. I have tried to fill to some degree the gap of knowledge on natural history that is needed for the conservation of this species (Greene 1986; 1993; Rivas 1997). Here I present the basic aspects of reproductive ecology, mating system, determinant of reproduction, substantial information about natural history, and how this information can be used for management and conservation of the anaconda.

# CHAPTER 2 METHODS

## 2.1 STUDY AREA

Venezuela is located in the northern part of South America between 25° 46' and 0° 43' north latitude and 59° 38' and 73°23' wait longitude. It is bordered on the north by the Caribbean sea, on the west by Colombia, on the east by the Atlantic ocean and British Guyana and on the south by Colombia and Brazil (Figure 2-1). This research was done on several cattle ranches in the Venezuelan Llanos: Puerto Miranda (4,000 ha) in the state of Guárico, Santa Luisa (25,000 ha), El Frío (80,000 ha), and El Cedral (54,000 ha) in the state of Apure. The owners of these ranches are keen to protect wildlife and also combine their cattle ranching activities with tourism.

### Climate

The data were obtained from the field station in Mantecal (30 Km from the study sites) managed by Ministerio del Ambiente. The average temperature in the lower Llanos is 26.6 C°, the mean diurnal fluctuation is 9.5 C°, and the mean seasonal fluctuation is 3.0C°. The area receives an average of 1,575 mm of rainfall a year with over 90% of the rain falling between April and November. The period between January and April is acknowledged as a dry season when all the water bodies shrink to minimum size and only the surfaces that hold water are large depressions called esteros (see below) and lagoons. From July to October there is a distinct wet season when the savanna floods and there is abundant standing water due to rainfall and overflowing of the rivers. The two months between each season are considered transitional (Figure 2-2). During this study, I encountered marked droughts as well as very wet years (Figure 2-3) in which I gathered data on the population, behavior and reproductive activities.

### Landscape and vegetation

The following description of llanos was taken from Berroterán (1985), Lopez-Hernández (1995), Ojasti (1978), Ramia (1967), Rivero-Blanco and Dixon (1979), Sarmiento (1983), Thorbjarnarson (1990), Troth (1979), Vila (1960) and personal observation of the study area.

The llanos is a large geosyncline (252,530 km$^2$) tilted to the East and located in the intersection of the Andes ridge and the Caribbean ridge in the northern part of South America. The most flooded area is located at the eastern part and drains into the Orinoco river; it is transected by its tributaries west to east. Situated over pre-Cambrian basement rocks, the llanos is composed primarily of alluvial deposits from the Tertiary and Quaternary periods. Sediments are quite recent, associated with the upper Pleistocene uplift of the llanos region and deposition due to erosion from the Andes and Caribbean Cordilleras after the last glacial period.

The Llanos includes several topographic areas, but the gen[1]eral profile is flat with a slope of 0.02% to the east. It can be divided by four basic subregions: piedmont region adjacent to the Andes, the high plains, the alluvial overflow region, and the aeollian plains (Sarmiento 1983). The alluvial overflow plains, where this study was carried out, are situated in a central tectonic depression in the middle of the Llanos. The relief is especially flat with high elevations below 80 meters above sea level. The dominant vegetation associated with this region is a hyper-seasonal savanna with a few trees or palms. Gallery forest bordering the rivers and patches of dry forest

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[1] All figures and tables appear and the end of the corresponding chapter.

adjacent to them interrupt the otherwise continuous plain. In the wet season, the rivers overflow and flood most of the savanna due to a combination of heavy rainfall, poor surface drainage, and poor permeability. There are three different physiographic positions in the overflow plains: banco, bajío and estero. These differ from each other in relative elevation, drainage soils, and vegetation.

Bancos are the most elevated regions, composed of the riparian areas that run along the river banks and cover 29% of the area. They are elongated in shape, 1 to 2 meters higher than the surrounding areas. The bancos are sandy loams, poor in organic matter, acidic (pH 4.5 to 5.5), and have moderate to good internal and external drainage. The soils of the bancos are classified as Aquultic Haplustalf and Aeric Tropaqualf. The dominant vegetation is a gallery forest with dominant tree species including palms (*Copernicia tectorum*), saman (*Pithecelobium saman*) masaguaros (*Pithecelobium guachapale*), fig (*Ficus* spp.), caruta (*Genipa* ssp.), palo de agua (*Cordia collococa*), and Camoruco (S*terculia apetala*).

Bajíos are lower regions more distant from the rivers where sedimentation of finer particles takes place. It covers 44% of the total surface of the overflow plains. These regions have poorer drainage and most soils contain a high proportion of expandable clay (2:1) and stilt (Vertic Tropaqualf and Udorthentic Pellusterts). The bajíos soil is acidic pH (4.5 to 5.0) and is richer in organic matter than the bancos. In the rainy season, the bajío is partially covered by water, but it dries out completely in November or December. The only trees that occur in the bajío are the palm (*Copernicia tectorum*) and caujaro (*Cordia* sp.). The area is dominated by spiny scrubs called barinas (*Cassia aculeata*), guaica (*Rocherfortia spinosa*), *Mimosa pigra, Mimosa dormiens* and *Hydrolea spinosa*, and by grasses including T*rachypogon* spp., *Paspalum* spp., *Paratheria prostata, Eleocharis spp., Leersia hexandra,* and *Hymenachne amplexicaulis*.

Esteros are the third and lowest region of the low overflow plains and cover 19% of the surface. They are characterized by poorly drained soils with very fine texture (> 60% clays) where the main route of water loss is evaporation. As the dry season progresses, the esteros hold water for longer than any other areas; they dry up only at the end of the dry season (March or April). The soils are heavy, composed 2:1 clays (Udorthentic Pellusterst, Entic Pellusterst and Vertic Tropaqualfs). Deep cracks in the soil are often observed in the peak of the dry season in the dry esteros. Since the esteros are flooded most of the year and have soil with heavy texture, tree growth is inhibited, with the exception of the occasional palms. Instead the esteros are dominated by floating vegetation of which *Eichhornia crassipes* and *E. azurea* occupy a large percentage. Other common elements are *Salvinia* sp., *Pistia stratiodes*, and *Ludwigia* sp.. Some rooted vegetation also occurs: *Thalia geniculata*, *Ipomoea crassicaulis, I. fistulosa, Eleocharis* spp. and *Cyperus* sp.. Even though there is a continuum among these three physiographic units, it is easy to identify them by the amount of time they remain flooded and the vegetation that grows on them (Berroterán 1985; Ramia 1967).

## Fauna

The fauna in the llanos is both abundant and diverse. More than two hundred species of birds form a large group of both residents and migrants that gather in the dry season to feed in the drying waters. Important groups are: herons, (*Ardea cocoi, A. herodias, Nycticorax nycticorax*), ibises (*Bubulcus ibis, Eudocimus ruber, E. albus, Butorides striatus*), egrets (*Egretta tula, Casmerodius albus*), storks (*Ciconia maguari, Jabiru mycteria,* and *Mycteria americana*), ducks (*Amazonetta brasiliensis, Anas discor, Cairina moschata, Dendrocygna* *viduata, D. Autumnalis, Neochen jubata*) shorebirds (*Jacana jacana, Actitis macularia, Himantopus himantopus, Rynchops niger, Chloroceryle amazona, C. americana*), and many birds of prey (*Heterospizias meridionalis, H. nigricollis, Buteo magnirosris, Parabuteo unicintus, Rostrhamus sociabilis, Pandion haliaetus , Falco femoralis F. sparverius,* and *Caracara plancus* among others). There are other also species of more terrestrial birds such as: *Ortalis ruficauda, Colinus cristatus, Columba ssp, Zenaida auriculata, Piaya cayana, Crotophaga ani, C. major, C. sulcirostris* and many passerines among the large diversity of species that either live or migrate to this areas (Phelps and De Schauensee 1978).

Among non-volant mammals, the most abundant are Capybaras (*Hydrochaeris hydrochaeris*), followed in abundance by white tailed deer (*Odocoileus virginianus*). Other mammals to be found in the savanna include giant ant eaters (*Myrmecophaga tridactyla*), crab eating foxes (*Cerdocyon thous*), lesser anteaters, (*Tamandua tetradactyla),* armadillos (*Dasypus sabanicola*) raccoons, (*Procyon cancrivorus*), giant river otters (*Pteronura brasiliensis*), opossums (*Didelphis marsupialis*), agouti (*Dasyprocta fuliginosa*), pacas (*Agouti paca*), porcupines (*Coendou prehensilis*), and several small rodents (*Holochilus sciureus, Sigmodon asltoni*, and *Zygodontomys brevicauda* among others). Howler monkeys (*Alouatta seniculus*) are common in the tree tops. The least common mammals also present are fresh water otters (*Lontra longicaudis*), pink fresh water dolphins (*Inia geoffrensis*), peccaries (*Tayasu pecari and Pecari tajacu*), skunks (C*onepatus semistriatus*), tapir (*Tapirus terrestris*), and felids such as ocelots (*Leopardus pardalis*), pumas (*Puma concolor*), and Jaguars (*Panthera onca*).

Reptiles are very abundant in the llanos. Other than anacondas, we find large numbers of spectacled caimans (C*aiman crocodilus*), side-neck turtles (*Podocnemis vogli*), green iguanas (*Iguana iguana*), and tegu lizards (*Tupinambis teguixin*). These reptiles constitute a great percentage of the biomass of the area. Other reptiles found in much lesser abundance include mata-mata turtles (*Chelus fimbriatus*), hinged turtles (*Kinosternon scorpioides*), river turtles (*Podocnemis unifilis* and *P. expansa*), Orinoco crocodiles (*Crocodylus intermedius*), and dwarf caiman (*Paleosuchus palpebrosus*). We can also find smaller species of lizards such as *Cnemidophorus* spp., *Ameiva* spp., and snakes, including: *Crotalus durissus, Liophis lineatus, Helicops angulatus, Corallus hortulanus, Spilotes pullatus, Chironius carinatus,* and *Epicrates cenchria*.

Amphibians are very abundant and ubiquitous in the wet season. The most common species include *Bufo marinus, Hyla crepitans, H. microcephala, H minuscula, Leptodacylus bolivianus, Scinax rostrata, Pleurodema brachyops* and *Pseudis paradoxus* among others. Fishes are also very abundant and diverse in the llanos; when the rivers flood the savanna they invade the new wet land foraging and breeding. In the dry season some return to the rivers but a large number of them cannot find their way back and become isolated in temporal ponds where the density of fish increases as the dry season progresses.

### 2.2 MAIN STUDY SITE: EL CEDRAL

El Cedral is where most of the study was performed and where the project was carried out for longest time (most of 1992 to 1997). It is a 54,000 ha cattle ranch located in Apure state, Muñoz district (7º 30’ N and 69º 18” W). This location was chosen due to its abundant population of anacondas, the active vigilance of the owners to discourage poaching on the ranch, and by its good internal roads for traveling during wet season.

El Cedral is a good representative of the alluvial flood plain described above. A series of human-made dikes have created more permanently flooded habitats (Módulos) where the impact of the dry season is diminished. The gates of the dikes are closed at the end of the wet season to hold the water for pastures and cattle. Each módulo has an approximate extension of 7,000 h. Due to the natural slope, the water gathers at the east of the módulo leaving the higher western surface dry and available for cattle ranching. As the dry season progresses, the cattle move toward the new land that is exposed by the drought, thereby allowing the growth of new buds in these areas.

As a result of this water management, the lower lands suffer a premature drought due to the water sequestered in the upper módulos. During the middle of the dry season, the gates are opened for a short period of time (one or two days) and the lower módulos flood again stimulating the growth of the plants there. The decrease in water on the surface flooded in the upper módulo exposes a large area where the soil is moist and grass growth begins. This management continues throughout the dry season to provide green pasture for cattle despite the lack of rain. When the wet season begins, the gates are opened again to let the water out and prevent overflowing and breaking of the dikes.

The dikes provide good and reliable roads to move around the ranch even in the heights of the wet season. The construction of dikes (and roads) produced another kind of habitat that is used by the anacondas and was advantageous for the study: borrow pits. Borrow pits are large holes left over from where dirt was taken to build the uplifted road. Accordingly, borrow pits are found along the roads and their variable size and depth determines how long into the dry season they hold water. Different arrays of aquatic vegetation grow in them as the season changes

## 2.3 SAMPLING EFFORT

Data were collected from the beginning in 1992 through 1998, sampling was concentrated in the dry season of each year, but the years 1992 and 1996 were sampled completely. See Table 2-1 for a summary of the sampling effort along the study period.

## 2.4 FINDING THE ANIMALS

### Intensive searches

Despite their size, anacondas are anything but conspicuous. Their secretive nature in an aquatic habitat with murky water and dense vegetation, and cryptic coloration, combine to make finding these animals a real problem. Early in the study I gathered all the pieces of folk wisdom that I could from local residents, and by testing them in the field I discovered a successful method for finding the animals. The dry season provides the best time for this activity because all the snakes that live in the flooded savanna gather in the few depressions that hold water during that time.

I systematically searched all the water bodies (esteros, borrow pits, lagoons and rivers) of the study area where water depths were less than 50 cm (searches in deeper water proved to be unsuccessful due to problems caused by restricted mobility of the researchers combined with the increased ease of escape by the snake). Searches were conducted by wading, shuffling in the water under aquatic vegetation, and poking poles into the drying mud. Other places that I found animals were in the caves on the river banks, large cracks on the ground of dry esteros (vertisoils), and spots protected from the sun under bushes neighboring the water bodies. These areas maintain a relatively low temperature even at the height of the dry season.

Early experience indicated that anacondas do not move much in the early hours of the day and their activity levels are also very low during the peaks of the heat of the day. Searching for animals began in the morning (around 0800 hr.) and continued until the afternoon, depending on the success of captures. On some days, by 1000 h I had already caught more animals than I could process during the rest of the day. However, on other days the search went on for several hours without much success. On these days I would stop around 1300 h and resume searches around 1530 h until the end of the day.

Intensive searches were conducted during the height of the dry season in the areas where the water was low enough to successfully catch the snakes. Due to the dikes of the módulos, some areas would dry fairly early, allowing us to make thorough searches in all areas even relatively early in the season. Later in the season the gates flooded the lowest módulos, creating a drop in the water levels in the upper ones and making them available for searching.

### Cruising

Another method for finding the animals was conducted by systematically patrolling the area looking for moving animals. This was done either by riding on top of a truck, horseback riding, or by motor boat, depending upon flooding conditions. This method proved useful in the areas that had more water and when the intensive search (wading in the water) was not feasible

## 2.5 CATCHING AND RESTRAINING THE ANIMALS

The search and capture of snakes was always in teams of 2 to 7 people since I needed a lot of help to catch and subdue the large animals. At first several people needed to be involved in the process of finding the snakes as well as in preventing the large animals from coiling around the person that was holding the head. Volunteers and keepers from the Bronx Zoo or others zoos around the United States came to help at different times.

Submerged snakes were located by detecting them with feet or poles followed by confirmation of their presence by gently touching them with the hand. Wading through a swamp looking for snakes, we often stepped on spectacled caimans that were under the haycinth. Caimans were surprisingly oblivious to being stepped on. They were often confused with logs for their tough texture and immobility. The most reactive animals shook violently, sometimes throwing a person on his or her back, but these animals never made any attempt to bite (in no less than a hundred encounters). In a similar incident with a 4-meter long Orinoco Crocodile in 1998, the crocodile behaved in a similar way. Perhaps the animals under the hyacinth are in some sort of seasonal sopor or estivation that significantly decreases their aggressiveness.

Once the presence of a snake was confirmed, the animal was captured by seizing the head and exhausting it through physical struggle. When the water level was too high to control an animal, we dragged it to shallower water or to the shore where it was slower and more easily subdued. Although strong, anacondas are bulky and heavy, and move slowly on land. When the animals became defensive and started to try to bite the handlers, due to its slow movements, it was always possible to recognize the intentions of the snakes by carefully watching their behavior. This way we could move out of reach, and avoid being injured. When the snakes were in caves, where the head could not be seized, the animals were gently poked with a stick encouraging them to leave the hole. After a short time the animals would move to the water where they were subdued as described

Once the snake had been controlled, it was put in a large sack or in a 200 l. metallic drum, depending on the size of the animal. At first many people were needed to subdue and process each snake, but as the project advanced I was able to subdue and restrain the snakes with fewer people. A most important procedural advance was the discovery that, once the head had been seized, the snake's defensive mechanism is to form a powerful loop with the first part of the body (the basis of the constriction movements). This loop forces the hand of the holder forward (from neck to nose), making the holder lose his grip. Then the snake proceeds to wrap the hand of the holder with its body, leading to many complicated situations because, at that point, the snake was loose and the “holder” held! I discovered that by keeping the first fifth of the animal’s body stretched, I could prevent the animal from developing the loop in first place. This change in procedure made handling of the animals much easier and safer. After making this discovery, I could control all the animals with only the help of my wife (47.7 kilos and 160.7 cm).

Another problem was keeping an animal restrained while it was being processed. Restraining large and potentially dangerous reptiles for field studies without using anesthesia can pose a risk to the researcher as well as the subject. Several techniques developed for safely handling crocodilians and venomous snakes are reviewed by Flower (1978), Almandarz (1986) and Gregory, et al. (1989), but passive restraint of large boids has not been addressed, possibly because few field investigations into their natural history have been undertaken.

Sometimes when handling a large specimen the handler held the snake’s mouth closed by applying strong pressure on the snake’s head and jaws. On some occasions this resulted in the teeth of one gum cutting into the opposing gum. This was a minor injury for the animal, but it was a circumstance I tried to avoid. In order to reduce stress on the specimen, and to minimize risk during the captures, the number of handlers needed, and the time required to take data from each animal, I developed the following method for safely working with anacondas (Rivas et al. 1995).

While holding the anaconda’s jaws closed, a cotton sock of appropriate size was pulled over the snake's head. Once the snake’s snout contacted the terminal end of the sock, several loops of plastic electrician's tape were firmly, but not tightly, secured over the sock around the snake's neck (directly behind the quadrate bone) securing the sock on the anaconda’s head. Taking care to keep the mouth closed, a second length of tape was secured over the sock and around the snake's snout (midway between eyes and nostrils) to secure the jaws. At this point the anaconda could be released for measuring, scale counting, scale clipping, parasite collection, and blood sampling without risk to the investigators.

This technique for rendering anacondas safe to work with proved quite reliable. No health problems were attributed to the use of this technique. Anacondas treated in this manner frequently struck with great accuracy, but they were unable to inflict injury and usually settled down after a short period. Sometimes the snake managed to bite the sock at the moment of muzzling so some teeth stuck out of the sock enabling it to snag the handlers during processing, but no important wounds occurred. Some small animals that had relatively loose fitting tape managed to remove the sock during the processing, but this did not create much of a problem either. On some occasions, the sock on the muzzle became wet and produced breathing problems for the animal. Luckily we detected it early on and prevented any damage to the animal as a result of this restricted breathing, wet socks should be avoided when using this technique. Releasing the snakes into cloth bags or steel barrels for transportation may be accomplished by removing the tape and the sock while the animal is restrained. This passive restraint method could be used effectively on many species of large, non-venomous snakes in both field and captive situations.

## 2.6 PROCESSING THE ANIMALS

### Data collected

For each animal captured, I recorded the following data: total length, tail length (to the nearest 0.5 cm in large animals and to the nearest 0.1 cm in snakes smaller than 1 m long), mass (to the nearest 100 g in large animals, to the nearest 5 g in small ones), and sex. Since snake's length is critical data in the analyses I used here and throughout herpetology, a separated section (see below) is devoted to the methods I used. In this report, unless it is clearly explicit, all lengths are given in centimeters and all masses are given in grams or kilograms.

To identify the sex of a squamate reptile a metallic probe may be in introduced into the cloacal pouch of the animal. Males have deeper pouches than females; if the animal is a male the probe would go in a longer distance than if it is a female (Rivas and Ávila 1996). At the beginning of this study, all animals were probed to identify sex until I learned to identify the sex by external characters (see below). For sub-sample of 56 individuals (18 females and 38 males), I also measured the left spurs to compare sizes between sexes. From a sub-sample of 56 males and 38 females, I recorded the injuries and scars present on the animals. I classified the scars and wounds based on the estimated length. Scars smaller than 2 cm were recorded as small, scars larger than 2 cm and smaller then 5 were recorded as medium, and scars larger than 5 cm were recorded as large.

### Marking and identification

Snakes were marked by scale clipping at both sides of the spurs. Each animal was identified by a unique combination of clipped scales that allowed for future recognition. Even though scales do regenerate, regenerated scales have a darker color than the original ones, so it is possible even after several years to reliably identify the animal. A backup method for identification of individuals was to copy the pattern of spots the snakes have in the first 15 subcaudal scales. Every animal I recaptured was identified by the clipped scales and confirmed by the pattern of the spots.

Each animal captured was released within 24 hours at the same place of capture unless it showed evidence of having fed recently, in which case the animal was kept in a drum with water until it defecated (usually within 7 days). Feces samples from these animals were analyzed immediately. Items found in these samples that could not be identified to the species level were labeled and preserved in formaldehyde for future identification. Some animals were radio-tagged by force-feeding the transmitters to them. Since this technique revealed important traits of the snakes ecology they are described in a different section (see bellow). All animals were assigned with a number for identification. Some individuals that where radio implanted or that were captured in several occasions were also assign with a name for easy of reference.

### 2.7 WHAT IS THE LENGTH OF A SNAKE?

#### Introduction

The way that herpetologists have traditionally measured snakes is by stretching them on a ruler and recording the total length (TL). However, due to the thin constitution and slim muscular mass of most snakes it is easier to stretch a snake more than it is to stretch any other vertebrate. The result of this is that the length we record of a snake is influenced by how much we stretch the animal. Stretching the animal as much as we can is perhaps a precise way to measure the length of a specimen but it might not correspond to the actual length of a live animal. Furthermore, it may seriously injure a live snake. Other methods consist of placing the snakes in a clear plexiglass box and pressing the snake with a soft material (e. g. rubber foam) against a clear surface. Measuring the length of it may be done by following the snake's body with a string (Frye 1991). This method, though, is restricted to small animals that can be placed in a box. In this contribution I propose an alternative way of measuring snakes that is more accurate than stretching the animals on a ruler. I further analyze the precision of this method by using a sample with a large range of sizes.

#### Methods

To record a more naturalistic measure of the length of the animal we followed a middle line of the body from head to tail with a string and then measured the length of the string by laying it loosely on a ruler (Figure 2-4). This allowed us to record the actual length of the animal regardless of its position and without having to stretch it. I used newborn anacondas born from 14 females that had been kept in captivity during gestation for a study of female's reproductive output (Chapter 5). A total of 82 newborn live babies and 42 stillborn were measured for this study. Repeated measures of the same animal with the string were slightly different due to the errors caused by the snake struggling and moving from under the string. Thus each measure was taken three times and the average of the three measures was calculated.

I also recorded the TL of each snake in the sample using the conventional method of stretching them on a ruler. I used a sign test to compare both measures of each animal. I divided the measurements obtained by the stretching method by the measurements obtained by the string method in order to calculate a relationship between the two measures. In order to analyze the changes of this relationship in respect to size, I used the mass as an independent measure of the size of the animal. I performed a Spearman correlation test between the variables. The use of stillborn in this study was to remove the effect of the error introduced by the struggle of the animal. By removing this I attempted to determine the actual TL of the animal.

Another sample of 81 animals from a wild population (ranging from 84.7 cm to 494.7 cm TL) was measured by three different people without allowing any of them to know the value recorded by the other people. All of the animals were measured by one of two researchers who had three years of experience performing the procedure, and by two people well instructed in the technique but without much previous experience.

In order to assess the accuracy of the measurements collected from 60 animals by different researchers, I used a sign test to compare the values collected by an experienced researcher with the values obtained by one of the inexperienced researchers. A t-test was used to compare the means of both sets of measures. I also compared the measurements taken by the two researchers that had experience, using a sign test on 13 animals that were measured by both.

I calculated the coefficient of variation (CV) on the three measures collected on animals from the wild to study the changes on the precision of the measurement of snakes of different sizes. The CV was calculated by dividing the mean by the standard deviation (see formula in Sokal and Braumanm 1980) and provides a measurement of the variance that is not dependent on the absolute value of the variable measured. This is especially important when dealing with variables that vary in a wide range of values. All statistical analysis were made with SSPS 8.0.

## Results and discussion

The string technique described here is comparable to using it with the squeeze box except that it can be used on larger animals that cannot fit in a box or that cannot be pinned and restrained. Thus it has a larger applicability. Measurements taken with the string were consistently shorter than when measured with the ruler ($Z= 6.82$; $p < 0.000$; Table 2-2). The quotient among the measurements is smaller in larger animals ($r = –0.362$; $p< 0.001$; Figure 2-5). This suggests that smaller animals are being significantly stretched when measured on a ruler.

All the measurements estimate a unique parameter: "the size of the neonate". However, measurements from the two methods of measuring using stillborn snakes had a higher discrepancy between them than measurements on live individuals (Table 2-2). Measurements of stillborn snakes with the ruler were the largest of all and the measurements of stillborn with the string were the shortest of all (Table 2-2). An ANOVA shows significant difference between the measurements of all the groups ($F = 70.47$; $df = 3$; $p<0.0001$I used in the analysis only stillborn animals that were completely formed and whose cause of death was most likely due to dystocia of the female or other problems at the end of the gestation (Ross and Marzec 1990). I believe that the size of the stillborns was not significantly different than the size of live neonates, supported by the fact that there was no significant difference in mass ($t= 1.252$; $df = 120$; $p = 0.21$; Table 2-2). Thus the difference in the measurements of the live babies and the stillborns are most likely due the struggling of live animals.

If we assume that the "real" length of the animal is the length when it is relaxed, and not struggling or being over-stretched (as is usually the case when most other vertebrates are measured), then the length of the stillborn measured with the string should be the closest estimate. This is the most accurate way to measure a live animal, but the data suggest that this method is not error-free.

Repeated measurements collected with the string on the same animals showed a relatively high variance. The average variance in animals around 80 cm was 0.514 cm and the maximum was up to 2.35 cm. It was clear while processing calmer animals that the repeated measures on them were more similar than measures of more active animals. In animals that the struggled a lot, the first measurement tended to be the most different. After the process was done once on the individual, it tended to calm down more.

The struggle of the animal during the measurement can potentially influence the repeatability of the measure. The data collected by experienced researchers and by the newer ones were significantly different (Z= -3.13; p< 0.002), where inexperienced researchers consistently obtained shorter measurements than experienced ones. The data collected by the two experienced researchers were consistent between each other and were not significantly different in a Wilcoxon sign test (z= -0.27; p< 0.79).

The variance of the measurements changed with the size of the animal being measured (Figure 2-5). Notice that between the size of 2 to 3 meters the variance is particularly high, mostly due to a few animals that had a very high CV. This might be a consequence of the higher level of struggling found in some smaller animals. The smallest animals can be easily subdued during the process and the measures are more consistent with each other (but see below). Beyond a certain size the snakes are stronger and some of them are able to put up more of a struggle, which decreases the precision of the measurements. Larger animals are calmer and although they could make the measuring much harder they tend to be easier to measure consistently (Figure 2-7). Notice, however that the CV is high in all the early sizes and goes down after three meters. Thus the lower variance found in figure 2 for smaller sizes is probably an artifact of smaller values. I noticed that the first measurement of each animal tended to be more different than the following two; this was especially true in medium-sized animals. Larger animals are only females and the medium-sized ones are mostly males so some differences in the behavior of each sex could be involved in this trend. However, these two effects can not be disentangled easily because adult males are always smaller and females are typically larger (Chapter 6).

Stretching a snake apparently has a considerable effect on the measurements collected on the length of the snake. Smaller animals seem to provide less resistance to being stretched than larger ones, thus studies involving measuring animals among several size classes must consider this issue. This method is not different in theory from the method of the squeeze box (Frye 1991) but this has a much broader application to larger sizes. The size of newborn anacondas is within what is considered a small snake. Herpetologists have traditionally considered that this size range can be reliably measured by stretching it on a ruler, yet I have shown that this is not the case. This trend must be particularly critical on larger animals (e.g. exceeding 130 cm) as they would present more resistance to be stretched. Stretching the animal on a ruler is less time consuming and in some situations it might seem appropriate. However, the degree that the animal is stretched can be influenced by the size and behavior of the animal, or even the mood of the researcher! Measuring the animals with a string is a more reliable method especially if it is done by people properly trained in the technique. Research involving mark and recapture, or growth studies must consider these issues.

## 2.8 FORCE FEEDING TRANSMITTERS: A TECHINQUE TO STUDY SNAKE'S REPROUCTIVE BIOLOGY IN THE FIELD

### Introduction

The secretive nature of the snakes imposes a serious challenge for field studies. Snake's mating systems, for instance, have been hard to study by direct observations unless in exceptionally large aggregations (Gardner 1955, 1957). These exceptional events may bias the observations to particular situations that do not necessarily reflect the typical mating system of the species.

Radiotelemetry has been used in studies of snake biology typically oriented for research of home range and habitat use (Reinert 1992), and thermoregulation (Peterson et al. 1993). Telemetry also has been used to study mating systems and reproduction of squamate reptiles (Bock et al. 1985, 1989; Duvall et al. 1992; Duvall and Schuett 1997). However, to surgically implant radiotransmitters requires a higher degree of invasive manipulation than is desirable if we do not want to perturb the natural behavior of the animals. Force-feeding transmitters to the snakes to be studied can be done much faster and with less perturbation. It has been used in the past to study ecology of snakes (Madsen and Shine 1994); however, we do not know details of the duration of the transmitters and how effective the technique was to study the biology of the animals. In this chapter I document the efficiency of a force-feeding radio transmitters to study the mating system in anacondas (*Eunectes murinus*).

## Methods

The transmitters used were model 15A2 built by Advanced Telemetry System Inc. containing the antenna coiled inside the unit, and covered with a waterproof resin. The dimensions of the units were 15 cm long by 2 cm radius and 91 g; with two batteries in series, of 3.6 volts each. The frequency of these units was in the range of 164-165 MHz range**.** These units were set to last for 8 months. I lubricated the transmitter with vegetable cooking oil and, holding the snake vertically below the head, forced it down the digestive track of the animal by palping it down to the stomach, or as far down as possible (Figure 2-9). In larger females, the muscles of individuals tended to prevent the maneuver too far down, but I always could push it far enough to prevent the animal from regurgitating it. Due to their small size, in males (Chapter 6), I could push it all the way to the stomach or even palp it out later and recover the transmitter if I needed to implant it in another animal.

Over a four year period, I gathered males before and during the mating season that were actively searching for females, and or females that were involved in breeding aggregations (Chapter 6). I equipped 16 males and 15 females with transmitters and monitored the snakes' behavior during the mating season and throughout pregnancy. On several instances, when a male found a female, I removed the transmitter from the male by palping it out. I also palped out the transmitter of all the males at the end of the breeding season of each year to recover them for future use. Retrieving the transmitter from females was not possible due to their more muscular body, which prevented me from feeling or pushing the transmitter by palping.

## Results and discussion

The method of force feeding transmitters proved to be an effective means of studying the mating system of anacondas. No animal died or showed any ill effect as a consequence of either the force-feeding or the extraction of the transmitter. In fact, after the procedure all the females continued with the mating and all the males continued with their trailing activities. In no instances was the transmitter regurgitated after the implantation and all animals were followed for at least a week. The transmitters were 0.3% of the average females size and 1.3% the average size of the males (Chapter 6). Perhaps due to its small size, the transmitter was not perceived as a meal or an obstacle to the animal's movements.

I removed transmitters from 13 males. In two cases, after 21 and 23 days respectively, the transmitter had to be palped out through the cloaca. In eleven cases the transmitter was still in the stomach, even after more then 30 days, and was extracted through the mouth. In three males I allowed the transmitter to pass naturally, which took 21, 43, and 45 days, respectively. Notice, however, the large variance in the time that the transmitter remained in the animals (Figure 2-10). Even though I extracted most radios before they came out naturaly, it must be noted that the transmitters did stay in the male's tract for long enough to follow them during the courtship and mating. Most females (9 of 13) kept the units until delivery, as they do not feed during pregnancy. Only four females defecated the transmitter before parturition (in 12, 14, 24, and 36 days). The extreme difference between these females and the others suggest that they might have had food in their digestive tracts at the time of the procedure so the transmitter might have passed along with the stomach contents. Two females were not captured after mating and I could not record the exact time that they kept the transmitters. These animals had not defecated the transmitter after 61 and 68 days respectively when the rainy season started, and presumably they kept it until the parturition since they do not fit the pattern of the animals that defecated soon. The retention times found in females that defecate early are not conspicuously different from those of males (Figure 2-9). There does not seem to be a correlation between the passage time and the size of the animals. The variation in retention time in females seems to be strongly influenced by the effect of pregnancy on feeding. Thus, the time that the transmitter is retained is highly variable, and perhaps it is most related to whether the animals were digesting or not. Breeding females do not eat during pregnancy or breeding (Chapter 5), and courting males seem not to eat during the mating season either, judging for the long time that most transmitters lasted in many animals.

I implanted transmitters in 16 males of which 8 found breeding females (the time and distance traveled will be published elsewhere). This is not necessarily an accurate reflection of males success in finding females, because in three cases I removed the transmitter before the end of the season. Thus 50% might be a minimum estimate of the actual success rate.

Due to their particular feeding morphology, it is easy to force feed a transmitter to a snake to study its biology. This technique proved to be reliable for short-term follow-ups, since none of individuals implanted regurgitated the transmitter. The procedure did not seem to interfere with the animal's natural behavior, as suggested by the large number of males that found females and all the females whose mating was studied. This technique can be used quite successfully for studies of mating systems, or even reproductive biology, if care is taken in not implanting the transmitters in animals that have recently fed. Even though force feeding transmitters to snakes to study their behavior has been done in the past the duration of the transmitters in anacondas makes this technique specially useful in anacondas. The presence of the transmitters in the anaconda's tract does not prevent it to feed due to its relatively small size. The long time that the transmitter last on the animals is a consequence of the low feeding rate of the individuals especially in mating season. I believe that this method can be used successfully with other species, however, it might be less effective in smaller species with shorter passage times and higher feeding frequency.

Table 2-1. Field time spent in the study along with the name of the individual performing the work. MM= María Muñoz, CC= Carlos Chávez, RA = Rafael Ascanio, CM= Cesar Molina, JR = Jesús Rivas.

| | 1992 | 1993 | 1994 | 1995 | 1996 | 1997 | 1998 |
|---|---|---|---|---|---|---|---|
| January | JR | JR | | | JR | JR | |
| February | JR | JR | | | JR | JR | |
| March | JR | MM | MM | JR | JR | JR | JR |
| April | JR | MM | MM | JR | JR | JR | |
| May | JR | MM | JR | JR | JR | JR | |
| June | JR | | | | CM | | |
| July | JR | CC | RA | | CM | | |
| August | JR | CC | RA | | JR | | |
| September | JR | CC | RA | | JR | | |
| October | JR | | RA | | JR | | |
| November | JR | | RA | | JR | | |
| December | JR | | RA | | JR | | |

Table 2-2 Total length of neonate green anacondas measured by stretching them on a ruler and by following their midbody line with a string. Lengths are the mean of the three measures of each snake.

| | Length Ruler (cm) | Length String (cm) | Mass (g) | N |
|---|---|---|---|---|
| Live | 79.72 | 77.57 | 228.11 | 82 |
| Stillborn | 85.12 | 76.0 | 225.54 | 42 |

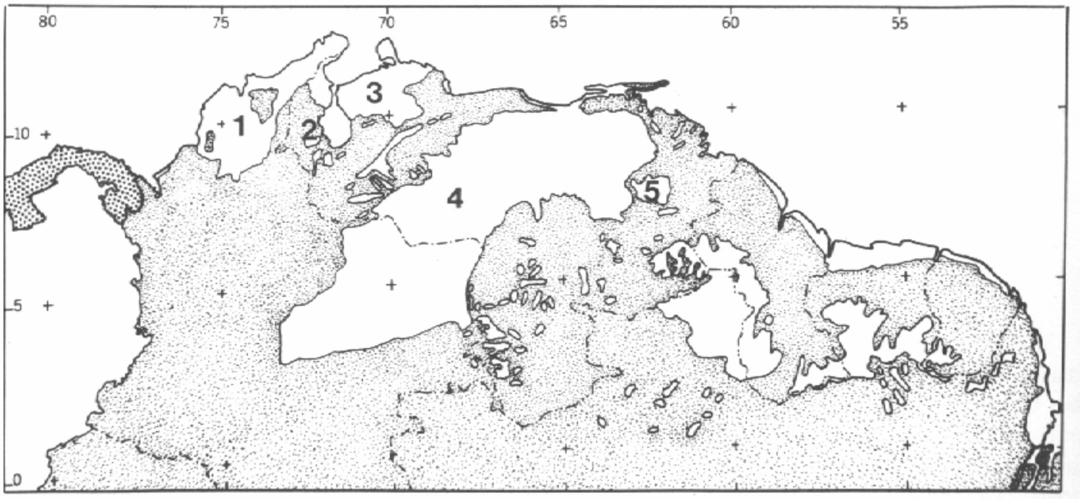


Figure 2-1 Map of Northern South America. The area of the llanos is marked with the number 4 (from Rivero-Blanco and Dixon 1979).

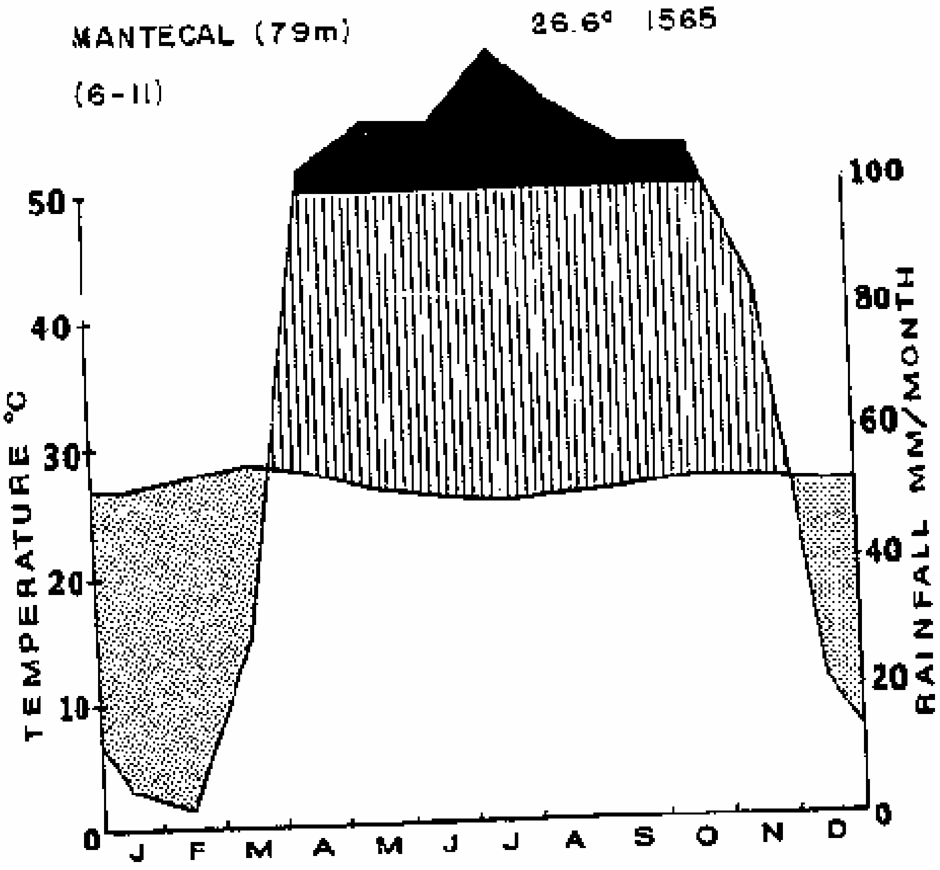


Figure 2-2. Holdridge’s representation of climate of Mantecal (from Ojasti 1978). Located aproximatedly 30 Km from the study site.

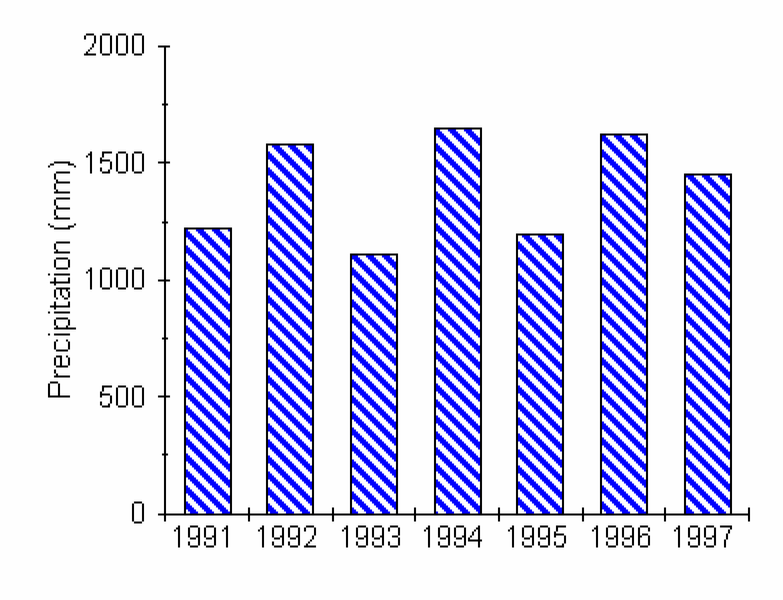


Figure 2-3. Annual precipitation during the years of the study from the Estación meteorológica de Mantecal (Ministerio del Ambiente y de los Recurson Naturales Renovables) located aproximatedly 30 km from the study area.

Figure 2-4 Measuring technique streching the string over the back of the anaconda to asses its length.

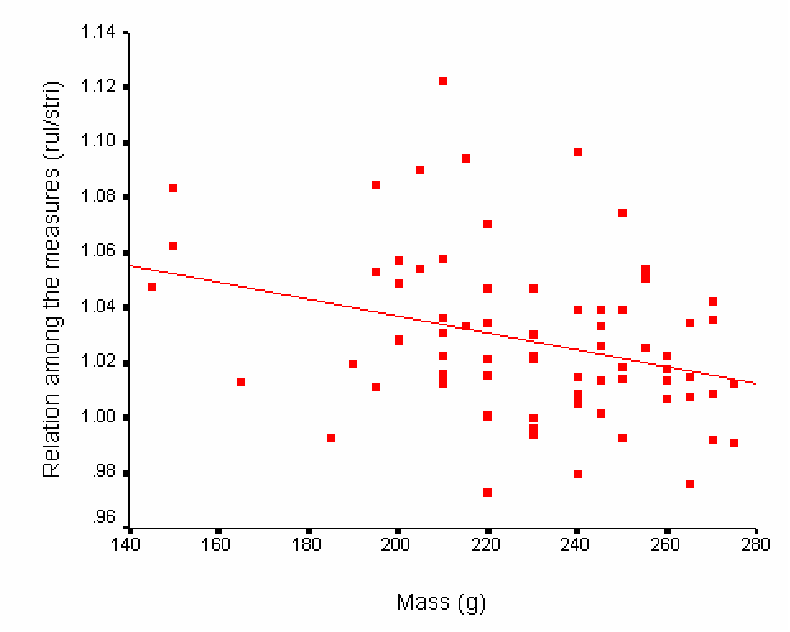


Figure 2-5. Scatter plot of ontogenetic change of the quotient between the measures of neonate anacondas obtained stretching them on a ruler and follwing the midline of the body with a string. Notice how the relationship between the two measures changes with the size (r = –0.362 p< 0.001; n= 124).

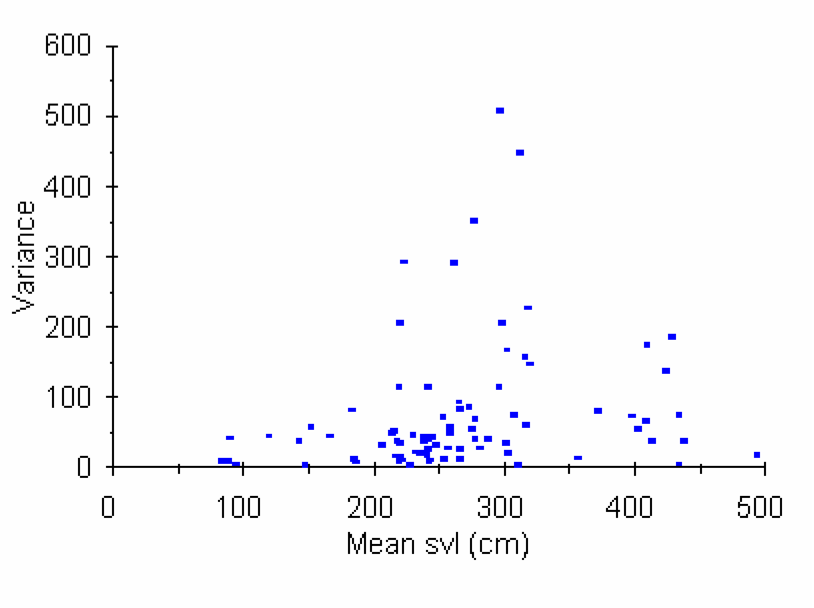


Figure 2-6. Size related change of variance of three measurements of SVL obtained from each anaconda using a string to follow the midle line of the body.

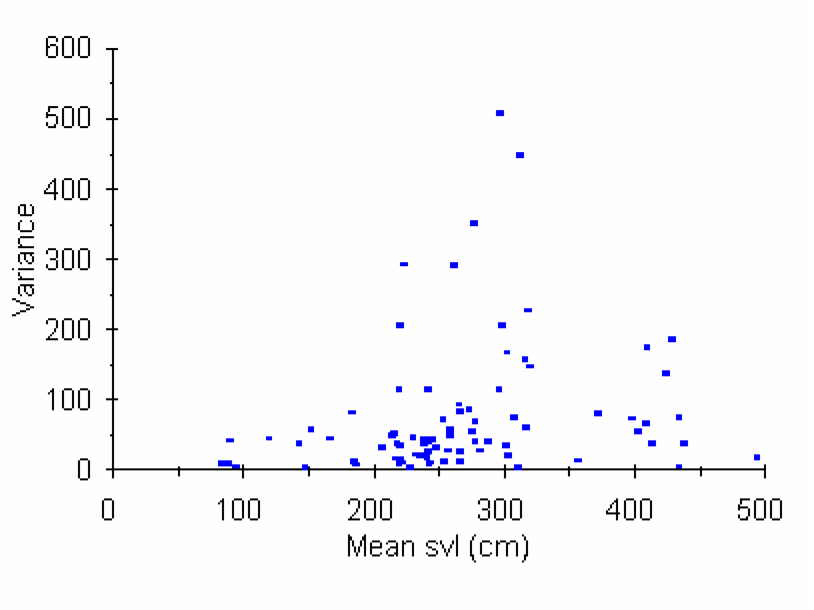


Figure 2-7. Size related change of variance of three measurements of SVL obtained from each anaconda using a string to follow the midle line of the body.

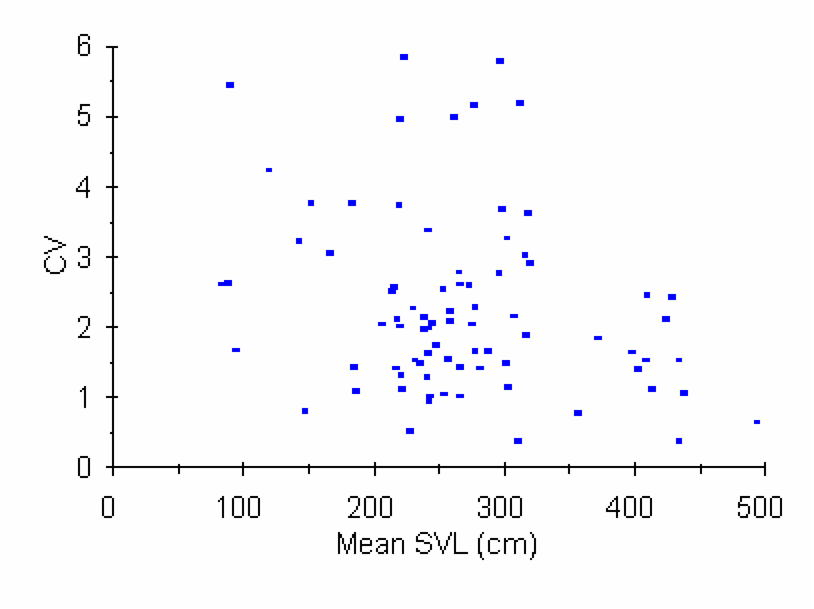


Figure 2-8 Relationship on the coefficient of variantion from three measurements on the same individual anaconda measured with the string. Notice the decrease in larger sizes.

Figure 2-9. Force feeding the transmitter to an adult male anaconda. The unit is oiled and pushed gently down the snake's throat. Photo Phillips Bourseiller

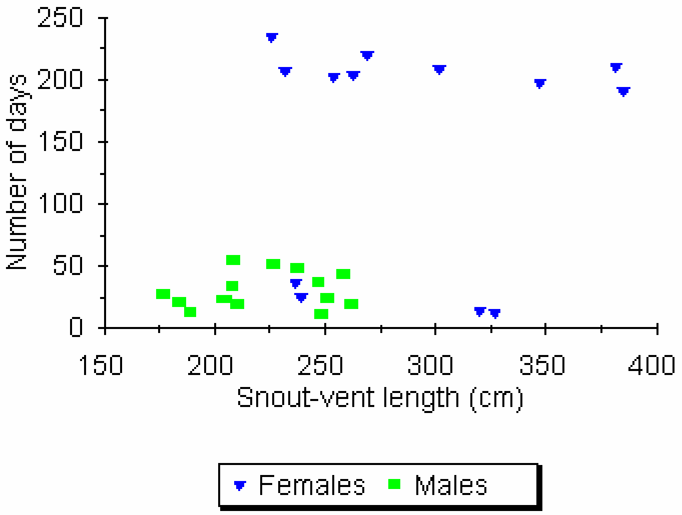


Figure 2-10. Time that the transmitter stayed in the tract of anacondas that had recevied a forced unit. All the females passed the transmitter naturally. Most males had the transmitter removed artificially at the end of the breeding season or when they found a female. Thus, the duration time for males is a minimum estimate.

# CHAPTER 3 NATURAL HISTORY AND GENERAL RESULTS

Since this is the first intensive study of this species, I have collected much novel information over the years through systematic data collection (telemetry or mark and recapture) as well as in a more casual manner. Although the aim of this contribution is on the reproductive biology, in this chapter I give some general results, as well as some basic information needed to understand the reproductive biology that will eventually be published elsewhere. These details also provide base-line information to understand the major parts of my research presented here as well as methodological tools for future researchers conducting field investigation on this or related species.

## 3.1 HABITAT USE AND MOBILITY

The information on habitat use and mobility comes from four years of radio telemetry studies involving 26 females and 22 males as well as information from mark and recapture over the 7 years of the study. Anacondas occur in the South American lowlands and are always associated with water; I found them either in the water (86% of the times) or at the water edges (14%). They primarily use shallow, still water covered by aquatic vegetation (92% of the time). They are found also in bushes (*Mimosa* spp.; *Cassia aculeata*) next to the water's edge, in caves along the river bank, in crevices that are formed in the soil during the peaks of the dry season, or even under the hardened dry mud. Rivers bordered by gallery forest often have caves with walls supported by the roots of the trees. Anacondas reliably use these caves during the dry season. Where the gallery forest has been cut there are fewer caves (perhaps destroyed by erosion) and anacondas are much less abundant. In wet season, anacondas stay in or near shallow tributaries and pools created by the overflow of the river beds, towards the upper parts of the savanna, or in the higher ground of the módulos always using shallow (less than 50 cm deep) water (more than 80% of the locations). Even though they are good swimmers and occasionally pass streams of moving water, they seem to avoid currents and use mostly areas of still water where there is medium to dense aquatic vegetation (Rivas unpublished).

Anacondas seem to have very well defined home ranges as indicated both by repeated recaptures of the same animals in the same areas and by radio telemetric studies. During the dry season they have well-defined and relatively small home ranges (25.2 ha). When the savanna floods (approximately late May to early June) non-breeding females and males move towards higher elevations, as the areas that retain water in the dry season become much deeper in the wet season and are apparently unsuitable for the anacondas and/or their prey. After a migratory movement averaging 1.3 km, the anacondas settle again and uses a relatively larger home range (37.4 ha). When the dry season resumes and the water level starts subsiding (November to December) the anacondas return to their original home ranges with a very high degree of philopatry (Rivas unpublished). Breeding females on the other hand, have a much smaller home range using in average 0.01 ha throughout their pregnancy and remain in the same areas near the river bank, elevated roads, or other high areas basking regularly during the entire wet season. In the swamp and esteros, where elevated areas are lacking it is possible to see female anacondas basking on top of the aquatic vegetation or on top of termite mounds. Occasionally they also use semi-submerged logs or even the tops of short bushy trees at the water's edge (Rivas unpublished). After giving birth, they move back to the flooded savanna, presumably to foraging grounds. Non-breeding animals are seldom seen basking. Males move frequently during the mating season and it is common to see them crawling on dry land, often crossing the road, tongue flicking thoroughly both to the air and to the substrate (Rivas unpublished).

## 3.2 ACTIVITY PATTERNS

Anacondas have been reported to be nocturnal (Lancini 1986), however, I did not find much evidence of this. If anything anacondas seem to be more crepuscular animals; showing higher activity at the end of the day and early in the evening. However, I found snakes moving, stalking prey, constricting prey, and mating at all times of the day as well as during the night. In the morning, once some heat has been gathered, it is possible to see the animals moving around. Females that are going to breed can also be seen basking. At the hottest time of the day animals seek refuge and are not as easy to see. They tend to appear again towards the end of the day and become active; times of captures of animals by road cruising shows a bimodal pattern consistent with it (Figure 3-1).

Anacondas seem to live on a different time scale than other smaller predators. Their large size allows them to fast for long periods, and to wait until their prey comes to them. Being an ambush hunter, they attack prey whenever it gets into range regardless of the time of the day. After a meal an animal can go for several weeks without any activity at all. Mating goes on for several days in a row without showing any diurnal pattern of activity (Chapter 6). However, for local migrations as well as for female-searching performed by males, there does seem to be a pattern where the animals do it preferentially at the end of the day, after the peak of the heat has passed. This was apparent to me on

cloudy days when snakes are more active throughout all hours of the day. Even though my sampling at night was not as well represented as in the day, I radio tracked animals for continuous periods of 24 hours and did not find any enhanced activity during this time period. Prior to the mating season males are more active than during the rest of the year and can be seen even in the times of the day when other animals do not move.

## 3.3 POPULATION BIOLOGY

### Population sample

I caught 780 animals in the seven years of the study. Figure 3-2 shows the animals caught each year with the different methods of searching. Notice that intensive searches produced most of the captures in all years. Despite the longer duration of field work in 1992 (Table 2-1) the number of animals caught was low compared with the other years (Figure 3-2). This is due to the fact that in the beginning I had not yet refined my searching methods and a considerable amount of time was spent looking in places with too much water or without the appropriate vegetation. After this first year I improved searching methods producing an increase in captures in later years. The smaller number of animals caught during 1998 was due to the shorter sampling season. Still, there were striking variations in the number of animals caught from year to year, even after the first one. This was due to differences in the amount of water that the llanos had received the year earlier, the handling of the water in the módulos by the ranchers, and the time I spent in the field for a given year (Figure 2-3; Figure 3-2; Table 2-1). In dry years animals were easier to find and catch, and there were more places on the ranch where intensive searches were possible. However, none of the methods were effective in detecting small anacondas (Figure 3-3). The cryptic nature of the small animals makes them hard to see when road cruising, and their small size prevents them from being detected with the feet or poles in intensive searches. Small anacondas greatly resemble the roots of the water hyacinths when felt with feet or poles while shuffling through the mud; this contributed to the poor representation of this size class in the sample. Intensive searches are much more effective during in the height of the dry season whereas road cruising is a better method during the wet season and transitional periods. Figure 3-4 shows the total average number caught with each method throughout the year. The higher number of animals found during the height of the wet season corresponds to pregnant females that are easy to find basking during this time of the year (Chapter 5).

### Consideration for handling large animals

None of the 780 animals I caught showed any signs of injury or any ill effect due to the catching and handling. Recapture of 170 healthy animals suggests that the procedure did not adversely affect individuals. On two occasions I caught large females that had recently eaten large meals. To prevent potential injury, the snakes were not intentionally induced to vomit; however, both animals regurgitated anyway, simply due to being handled. These two animals had eaten white-tailed deer and both died after vomiting. The necropsies did not show any wound or injury of the digestive system that could account for the deaths. After these two unfortunate events I stopped collecting any large animal that had evidence of a recent large meal. Instead, I would keep track of the animal for two or three weeks (in general they do not move more than 20 or 30 meters from the place of the kill). I would then proceed to capture the animal and keep it in a drum to identify the meal by fecal analysis. Sometimes I did not realize that the snake had eaten a recent meal until it was too late and I had initiated the capture. In these cases, if the animal regurgitated relatively large prey, I kept the snake in outdoor enclosures. These animals did not show any ill effects. At present, the best explanation for the death of the first animals is that death was due to toxicity of some of the gasses from the decomposing regurgitated prey in the confinement in the drums. The capture of very large animals with very large meals must thus be avoided, for two reasons: the animals are at risk and large prey are costly for large snakes that probably feed very few times in a year.

On several occasions during catching and handling of animals the catchers were bitten by the snake. The wounds inflicted by the animals could be fairly severe if the person reflexively withdrew the arm or leg while being bitten. The curved shape of anaconda teeth prevents an easy release, and often the teeth tore flesh and muscles. If, however, the person bitten avoided the natural reaction of withdrawing and instead seized the neck with the other hand, injuries were reduced. The normal reaction of the animal is to open the mouth and try to bite the gripping hand, thus releasing the bitten member and leaving only the painful print of the teeth in the skin, but no serious wound.

Throughout the study I found a very consistent trend in the aggressiveness of the animals. Smaller animals are much more aggressive and disposed to bite than larger ones. This is probably due to the lack of enemies of large snakes that produces no advantage in having an overly active response. A similar trend of lowered aggressiveness in larger sizes was found in other species of snakes (Herzog et al. 1989). Metabolic constraints on larger animals due to temperature could also explain this trend, since larger animals need more heat to activate their metabolism. However, in preliminary studies of temperature and thermoregulation I found that both large and small animals did not differ greatly in temperature and all snakes had a body temperature near the temperatures of water they were in (Rivas unpublished). I caught 125 individuals larger than 3.5 meters long and none of them ever tried to bite at initial capture. They simply tried to flee up to the moment when one of us seized the neck, or after many unsuccessful attempts to escape and been pulled to land by the tail or mid-body. Animals that had been caught before, however, behaved very differently. As soon as they were seized they turned around and fought aggressively, posing a greater danger to people. In many cases I could tell whether the animal had been caught before based on its behavior during the capture prior to identification.

## Population dynamics and density

Throughout the 6 years, when I could collect data for the whole dry season, I caught males and females in varying proportions. Males were better represented than females in the sample during most years (Figure 3-5). This is perhaps a consequence of the higher activity of males and the fact that many were captured in breeding aggregations where there were several males per females (Chapter 6).

The difference in size between both sexes is striking: females are remarkably larger than males (Figure 3-3, Table 3-1; see Chapter 6 for adults only). Sex identification by cloacal probing was easy but problems did occur at the beginning. Due to the muscular strength of anacondas, it is easy to judge a male as a female because they can strongly resist introduction of the probe. Thus an unskillful person can easily make a mistake. The easiest way to identify the sex of adult anacondas is by looking at the spurs, which are much larger in males than in female (Figure 3-6). Males have absolute longer spurs (7.47 mm) than females (5.13 mm) regardless of the larger female size ($t= 8.49$; $p<0.000$; $df= 51$).

Growth rate varies among individuals regardless of the size of the animals. Preliminary analysis of the recapture data shows that some animals grew considerably over one year, while others experienced very little growth (Figure 3-7). It is expected that larger animals grow less than smaller ones as supported by some studies with captive animals (Holmstrom 1982), but some very small animals (newborn size) experienced no growth at all over an entire year; thus this trend is not universal. The growth rate of larger animals was highly variable, and does not show a clear relationship with the size of the specimen. The most reliable trend found was that breeding females experienced no growth at all during the year they bred, but grew much more in the later years. Some adult animals, both males and females, did not grow at all in as much as five years (Rivas unpublished). More detailed analysis of the data of mark and recapture is needed to fully understand the population dynamic and recruitment to the different sizes.

Most captures were in the hyper-seasonal savanna of the area and very few in the neighboring rivers. An important locality difference in sizes was found with some animals caught in a nearby river, Caño Macanillal, Hato El Frío. In Macanillal I caught three males, two of which were larger than any of the 433 males I had caught in the neighboring savanna, and the other one was only slightly smaller than the largest male caught in the savanna. This strongly suggests an important size difference among the animals in the river and in the savanna (Chapter 5).

I captured a large number of animals in relatively small areas. In El Cedral I caught over 550 animals in an area of approximately 1,500 ha. This is a very high density (0.36/ha), particularly considering that anacondas are a top carnivore and I caught only a fraction of the population, lower than 30%, as suggested by the recapture rate of the last years. Starin and Burghardt (1992) estimated that in an area of 33.5 ha they observed at least 20-25 African rock pythons (*Python sebae*) in Gambia. Although this density (0.6 -0.75/ha) looks higher than the density of anacondas that I found, *P. sebae* lives in the dry forest and uses the water less often than anacondas so, the detection of *P. sebae* is probably higher. Thus, the densities found in this study are probably comparable to the densities of rock python in Gambia

## Predation

Anacondas seem to suffer high mortality in their first year. I implanted transmitters in four neonates, and two of them were predated within the first month. I found one of the transmitters at the bottom of the tree that held an active crested caracara (*Polyborus plancus*) nest. The other transmitter was found among some bushes with the antenna chewed up, but no other hint as to identity of the predator. The transmitters lasted only one month so there are no data regarding mortality in later ages. I also saw a tegu lizard (*Tupinambis teguixin*) carrying a baby anaconda in its mouth, but I did not see the actual capture. The snake did not have any bite marks or evidence of having been killed by the tegu so it was not possible for me to assess whether the tegu killed it or had found it dead and was simply scavenging, but tegus are probably predators of neonates.

Large animals seem to suffer lower predation, since there are few animals that dare to attack a full grown female anaconda; however, juveniles or smaller adults are prey to various predators. On April 25 of 1995 I observed a female (187 cm TL and 3.25 Kg) being harassed by a crab-eating fox (*Cerdocyon thous*). The snake had been surprised while crawling on dry land, and had adopted a defensive position. The fox repeatedly tried to reach at it, but jerked back each time the snake snapped defensively. I interrupted the actions and caught the snake, which had numerous ticks (evidence of having been on dry land for a while). If I had not interrupted the situation, the snake would have probably been eaten since she would have been exhausted in a short time and, not having any water nearby she was not likely to escape successfully.

Caimans seem to be an important predator of anacondas as the following events reported by Rivas et al. (1999) suggest. On May 25 1996, I discovered a large caiman (>180 cm TL) firmly gripping the head of a radio-implanted female anaconda (Olivia, 494 cm TL, Table 3-2), who in turn had wrapped herself around the caiman's head and neck. After approximately 15 min the snake relaxed her coils, apparently losing the struggle. I interrupted the event to recover the transmitter when the snake stopped struggling. This was a large snake that I had seen eating caimans of comparable size to this one. Since I had found this snake severely wounded 2 and a half months previous to this event, it is likely that she was not in top physical shape and this may have played some role in the outcome of the event.

I observed another instance that took place April 29 1996 in a roadside channel covered partially by water hyacinth (*Eichhornia* ssp.). The caiman (> 180 cm TL) was on the left side of the anaconda (approximately 2.5 m long), gripping it by the anterior 1/5 of its body. The snake had thrown a loop of its body over the dorsal surface of the caiman and wrapped its posterior body and tail around the caiman's left hind leg. The snake, although much smaller than the caiman, was wrapped so tightly around the hind leg that the head of the caiman was pulled towards its hindquarters. The snake was observed to periodically tighten its loop, causing the caiman to flip over to the right and under the water. The caiman repeatedly attempted to drag the snake out of the water, but each time the anaconda managed to flip the caiman and pull it back under water. The wrestling match continued for five hours, often punctuated by both animals disappearing under the water for periods of ten to fifteen minutes. Finally, at 1900 h, as the light faded, I saw an unidentified caiman of similar size leaving the area with no snake in its mouth

Five days later (04 of May) I found a dead male anaconda (247 cm total length, 5.5 kg), with wounds from a caiman bite on the anterior 1/5 of its body. The wounds matched the position of the teeth of a caiman skull 29.5 cm long, with an estimated total length of 226 cm and mass of 43 k (Thorbjarnarson, unpublished). The snake showed no signs of decomposition, indicating a recent death. I surmise that the snake escaped from the caiman but subsequently died from his wounds. Judging by the size relationship, I believe that it was the caiman trying to eat the snake and not vice-versa.

Another observation, on March 19 1997, also involved a large caiman attacking a small female anaconda (152 cm total length, 1.7 kg). The caiman (> 180 cm TL) was in a small borrow-pit with the snake in its mouth when I found it. Upon my approach, the caiman dropped the seriously wounded female anaconda. Although the snake survived, I consider this a predation event since it was not struggling when I arrived and thus would not have survived without my intervention.

During the two years when I made systematic observations on predation (1996 and 1997) I found twelve dead anacondas (six males and six females). Based on my observations and examination of the animals (presence of deep circular bite marks matching the size and position of caiman teeth), I determined that all six males and two of the females had been killed by spectacled caimans (Table 3-2 and Table 3-3).

Males found dead and not eaten were slightly larger (mean 270.7 SVL) than the average size of the population of adult males (mean 263.2 SVL), suggesting a bias toward larger males in the sample that were killed. It is likely that the animals that I found dead but not eaten escaped the caiman attack but died afterwards (like the reported event). Of course, I would not have found any evidence of the attacks on smaller males that did not escape and were eaten. Hence actual predation pressure is probably higher than my data indicate.

Male and female anacondas seem to suffer different predation pressure by caimans. Adult females, being larger, seem to be at lower risk than adult males of being attacked and killed by caimans. Larger, healthy anacondas must have a better chance of wrestling their way free from caimans and surviving the wounds. Support for this interpretation is found in my data which show that females are less likely than males to be attacked and killed.

There were two instances where relatively larger anacondas were, however, eaten: number 178 (Table 3-3) had a throat infection since the year before the event, so its physical strength may have been compromised. The other animal, Olivia (Table 3-2) had given birth the year before the encounter. After delivery, she lost 24 kg and was extremely weak. During the time I followed the animal with radio telemetry I saw her killing and eating caimans of comparable size as the one that ended up killing her. Increased risk of predation in postpartum animals has been reported as an important part of the reproductive cost in viviparous snakes (Madsen and Shine, 1993*a*).

Caimans appear to exert a high predation pressure on male anacondas during the dry season. Most predation events occurred in close proximity to breeding balls, suggesting that males are particularly vulnerable to caiman attacks during this time (Table 3-3). Hence, searching for females in dry season can be considered a costly activity, more so because of the very high density of caimans in the dry season (Thorbjarnarson, 1991). The risk of being eaten while tracking females might be a selection pressure toward delayed maturation and large size in males (Bell, 1980; Shine and Schwarzkopf, 1992).

The risk for the males does not end with the risk of being eaten by caimans or other predators. Large females can cannibalize males near the breeding aggregations as well. The following evidences reported by Rivas and Owens (In press) suggests this. One of the observations of this involved a large female (434.7 cm TL and 40 kg) that was caught on April 27 1995 next to a breeding aggregation, but not participating in it. The snake had an engorged stomach that indicated a recent meal. After putting her in a cage, she regurgitated a male anaconda (42 cm tail length, 283 cm estimated TL; 5.7 kg, Figure 3-8). On May 28 1996, at the end of the breeding season, I discovered another female constricting a medium-sized male (230 cm TL; 5kg). The male was dead by the time I found it, and the female (370 cm estimated TL) managed to escape when I tried to capture her. Judging by the girth and overall condition of the snake (Chapter 4), she was most likely breeding, and probably had just recently finished her mating activity. Lastly, on March 18 1997 I collected a feces sample that contained anaconda scales. The sample was from a female anaconda (300 cm. TL, 14.8 kg) that was breeding that season.

All the records of cannibalism in green anacondas involve cannibalistic females, and for the instances when the sex of the cannibalized individual was been known it was a male. This asymmetry is probably a consequence of the strong sexual size dimorphism found in the species where females are much larger than males. Green anacondas become concentrated around more permanent water sources during the dry season, and at this time breeding occurs. Male anacondas looking for water and/or females appear to be especially vulnerable to cannibalism by larger females. After mating, pregnant females do not eat for seven months (Chapter 5). It is possible that some breeding females eat their mating partners in order to help them survive the long fast associated with pregnancy.

My data suggest that searching for females, and even mating itself, may be a highly risky task for male anacondas. This could explain the enhanced aggressiveness found in adult males. Therefore, the risk of predation while searching for mates and mating could be a major part of male reproductive investment. This could shape the mating strategies of the males, constraining philandering, since the effort invested per mating is relatively higher. High risk of mating might lead males to select for mate quality over quantity (Chapter 6).

### Parasites and diseases

Anacondas sometimes suffer from various diseases and infections. Here I summarize some relevant accounts of some specific animals that were found with either infections or diseases, and the outcome of their condition. On March 14, 1992 I caught Maria Eugenia (female 356 cm TL, 20.5 Kg) in which I implanted a transmitter. Maria Eugenia had an ocular and maxillary abscess due to a twig that was stuck in the roof of the mouth. The swelling produced by the abscess had affected one of the eyes and rendered it useless. I drained the abscess and cleaned it with peroxide and iodine. I also gave preventive antibiotic treatment (enrofloxacine) as part of the surgical protocol for the implantation of the transmitter. In the next two weeks I saw the swelling return, indicating that the abscess was probably still present. I followed Maria Eugenia throughout an entire year in which she survived and reproduced. One year later the swelling of the eye continued, but to a lesser degree than at the time of the capture or after the implantation. Just before the transmitter expired Maria Eugenia was seen with a recent meal.

I caught #178 (male, 308 cm TL 8900 gr) on April 14, 1995 and the snake showed some swelling in the throat and abundant secretion that caused the animal to make a noise when in breathed. On March 13, 1996 I caught it again with the same kind of infection. It had lost 500 g of mass but otherwise seemed to be in similar condition. One month later I found it predates by a caiman (Table 3-3).

Anacondas were frequently discovered with wounds and infectious processes associated with them. Sometimes they lose teeth during predation events and the alveolus is often exposed to a relatively common bacterial infection called stomatitis (Ross and Marzec 1990).

Anacondas may face other causes of mortality, such as disease and parasitic infestation. Sometimes leeches were found in recent wounds or in places where the scales were not covering the skin. Animals that were on dry land commonly were found to have ticks (*Amblyomma dissimile*). Blood analysis and health assessment conducted by a veterinarian collaborating from Bronx Zoo (Paul Calle) revealed that all 24 snakes studied had malaria (*Hemoproteus* sp). Analysis of two dead animals revealed abundant cestodes and trematodes in the jejunum and also duodenum in one of the specimens. In both animals, the tapeworm *Crepidobothrium* sp. was identified. Several apparently healthy anacondas also had subcutaneous nematodes (*Draunculus* sp.) (Calle et al. 1994).

Anacondas seem to withstand diverse parasitic loads and still appear healthy. Some animals that were infested by several endo- and hemoparasites lived for at least five years after the infestation was detected. During this time I observed them hunting, putting on weight and even mate and breed. It is possible that the parasites and the hosts have reached a stable point of virulence where they live on the hosts without harming them too much (Brooks 1979).

In some cases I found dead animals for which I could not assess a clear cause of death. In the necropsies I noticed dark spots (1mm square) in the fat tissue and other parts of the body. One of these instances was on April 12, 1997 I found Sue (Female, 420 cm TL 44,5 Kg); alive but not moving. Later in the day I returned to find her dead in the same place. Upon preliminary examination she looked perfectly healthy other than having several old, small wounds on the tail inflicted by a small capybara that could not have killed an animal of that size. Histo-pathologic analysis of her tissue revealed that the animal had some type of lymphatic cancer (Lymphosarcoma; Figure 3-9), which probably was the caused of death. I had caught Sue every year from 1992 when she was detected to have malaria. However, she looked healthy and very active; she even bred in to of the former years. Even in the necropsy I detected that she had large amounts of body fat and was preparing for breeding that year as evidenced by eggs in early stage of development.

## 3.4 DIET

### Dietary Composition

Over the years, I gathered data on diet from over 100 animals. Data were collected via observations of predaceous events, feces, or stomach contents. Although many of these data are still in process of identification, some partial results are given below. To date, 26 prey species have been identified (Table 3-4). Most of the stomach contents contained only one specimen and about half of the animals encountered were birds. The other half was evenly distributed between large mammals and large reptiles (Table 3-4). There is only one record of a fish and the consumption of this item is questionable due to the fact that the snake did not actually swallow the animal (see below). I believe that fish are too fast for this sit-and–wait predator to catch in the water. Indeed, this one fish prey item observed was a bottom dweller that the snake perhaps caught in a crevice.

Newborn animals seem to feed on birds at very early ages. On November 10, 1996 one of the females gave birth in an outdoor cage. I tried to collect all the offspring but I failed to find one. On the 30th of the same month I found the neonate still in the enclosure where it had eaten a small passerine (*Phacellodomus rufifrons*). Other animal of the size of neonates were found preying on jacanas (70 g) and other small wading birds. Judging by the habitat newborn snake use, and the timing of their birth, it is very likely that they also feed on newborn caimans (approximately 40 to 50 g). Theoretically they also could catch amphibians (which would not be easy to identify in the feces) but the neonates are born at the end of the wet season when the numbers of amphibians decline. Amphibian numbers do not recover until 6 months later, so newborn anacondas probably do not rely on them for survival.

Smaller anaconda feed heavily on birds, and gradually include reptiles and mammals in their diet as they grow larger. Large anacondas feed almost exclusively on large prey (mammal and reptiles). Anacondas seem to be opportunistic predators that will take any prey they can kill and swallow. In some cases they go after prey of considerably large size. In one event on December 22, 1992, I found Olivia next to recently killed full grown white-tailed deer that she was apparently unable to swallow due to the deer's antlers. I saw the marks of her teeth on the face of the deer all the way up to the antlers. Olivia laid in the water close to it for several days and eventually vultures ate the deer.

On several occasions I was told by locals and some collaborators that they had seen anacondas eating animals that were in process of decomposition. I did not document it myself, but in one case I caught a snake with a very recent meal and the snake's body smelled like rotten meat. It is possible that the snake found the animal dead and acquired the scent of the carcass while swallowing it. In any event it is not surprising, since anacondas should be able to digest rotten meat. When a large animal swallows a large prey, the prey starts decomposing from inside out before the digestive enzymes of the snake can reach the digestive tract and inner parts of the prey. So anacondas that consume large prey will always have to deal with some degree of decomposition of the flesh they are digesting. Once the anaconda has the physiological mechanism, it is possible for the animal to take advantage of some carrion and ingest food that is already at some level of decomposition. Yellow anacondas (*Eunectes notaeus*) has been reported to feed on carrion (Strussman 1997)

### Predatory strategy

Anacondas seem to be able to eat a wide variety of prey, perhaps depending on the prey's abundance in the system. The innate prey preferences of newborn snakes can be tested by presenting a cotton swab impregnated with the scent of the potential prey to naive animals and recording the number of tongue flicks that snakes directs toward the cotton swab (Burghardt 1970). Some preliminary experiments of prey choice were conducted using different potential prey: a bird (a domestic chick), a mammal (a lab mouse), a reptile (newborn caiman), fishes (assorted caracids), and an amphibian (marine toad). Newborn anacondas showed high level of response to of all the prey except the fish. In this preliminary test the sample was not very large and while rubbing the swabs on the toads the parotids gland were avoided, however, the generalist nature of the anaconda's diet is clearly suggested.

Large constrictor snakes are potentially dangerous to people due to their size and strength (Branch and Haacke 1980). However, there are no documented attacks by green anacondas (*Eunectes murinus*) on humans. Lack of documentation may be due to low human population density in areas where anacondas are common, and to the nature of their behavior and the habitat where they live. Here I document predatory strikes by green anacondas on two of my field assistants (Rivas 1998).

The first attempt was by a large female (Lina; 54 kg, 5.04 m total length) that had had a serious mouth infection at the time I captured it and implanted a radiotransmitter. Two months after implantation, my assistant (female, 1.56 m and 56 kg) followed the transmitter signal with the intention of assessing the status of the snake's infection. The snake was in a shallow channel, approximately 80 cm deep, which was partly covered by emergent aquatic vegetation (*Eleocharis* sp.)**.** Without being seen, the snake emerged from the water striking, and grabbing her by the knee. Fortunately, the pants tore, and the snake did not get a firm hold by which to drag my helper into the water. The snake immediately struck again with her mouth open to about 180 degrees, this time at a height level with my helper's waist. However, her prompt retreat resulted in an unsuccessful attack.

The other event was on another of my helpers (male, 1.74m 57 kg) while we were looking for snakes in a river covered by aquatic hyacinth (*Eichhornia* ssp.). After we walked past the snake without detecting it, the snake followed my helper, tongue flicking at him for approximately 2.5 m, while raising itself up to 25 cm above the aquatic vegetation. The event was seen and filmed on a video camera by a photographer behind us who warned us about the snake. I managed to grab the snake by mid-body just as it struck at my helper, who in turn jumped backwards. By both events, I pulling the snake backwards and my helper jumping out of reach, making the snake fail and snap into the air (Figure 3-10 a to f). Upon catching and subduing the animal (Penelope), she measured 445 cm in total length and 39 Kg in mass. The overall appearance of the snake was healthy but very thin.

I believe that both attacks were predatory attempts by the snakes on my helpers. In the first instance, the following evidence suggests that the snake must have been foraging when she attacked the researcher: First, Lina had not eaten during the two months she had been radio-tracked, and probably longer, due to an oral infection. Second, eight days before the incident the snake thoroughly tongue flicked at me (male, 1.77 cm, 83 kg) in a similar situation but lost interest after approximately 5 min (perhaps estimating that I was above her prey-size range). Finally, four days after the incident I saw Lina with a distended midsection indicating a recent meal. Lina's attack is unlikely to have been defensive. In my experience of catching hundreds of anacondas of all sizes, I have found that large individuals are very unlikely to attack when disturbed (see above). Large individuals in water tend to swim away. Recaptured animals are, if anything, even more skittish than naive ones (before handling) and try to escape as soon as they detect the proximity of the researchers. Thus, the proximity of the researcher is unlikely to have induced a defensive strike.

Anacondas can capture prey as large as adult capybaras (40-55 kg), adult white tailed deer (55-70 Kg), and full grown spectacled caiman (35-55 Kg); consequently, a prey as heavy as 55 kg (the mass of the first target) is within the range of prey sizes that a snake as large as Lina could take. Thus, I consider this event to be a predatory the strike. Lina was being followed by telemetry, thus enhancing the number of times she encountered a human being. This artificially high encounter rate with people might have exceeded the threshold of abundance that makes a potential prey item profitable (Stephen and Krebs 1986), despite the high risk of attacking a large potentially dangerous prey.

The second event was performed by large animal that was fairly thin for her size (Chapter 4). Penelope was observed performing predatory tongue-flicks directed towards the person; she was following in an obvious stalking fashion. Given the time of year (March) and the snake's thin condition, it is likely the snake had given birth the year before (November to December) and was hence in need of a large meal to recover from her reproductive investment. She was probably in a large energetic deficit, and taking the risk of attacking a large prey was warranted. The prey/predator mass ratio of this event (1.46), while impressive, falls within the reported prey/predator ratios for other snakes (Greene 1992).

Both attacks were on people that were looking for anacondas in places that people often do not walk. We had been staying in these places for longer than locals normally do, when they use these areas, if they use them at all. In light of this, both predatory strikes occurred after especially high exposure. Although anacondas are not "man-eaters" by nature, they are generalists and will take any prey they can subdue and swallow, including human.

### Meal size

Smaller anacondas eat mostly birds while larger animals switch to mammals and reptiles as they grow larger. Larger animals seem to take rather risky meals and often are wounded by their prey. Here I relate several events where the animals were wounded or even killed by their prey. The first event was on 26 April 1992 following a female (Susana, 455 cm total length, 46,000 g) that had a transmitter. I discover her floating in the middle of the pond at 0600 h. By 0800 h the animal had not moved, and I touched it confirming that it was dead. The head of the snake was missing but no other injury was apparent upon the physical examination and necropsy. The next day a young capybara (*Hydrochaeris hydrochaeris*) of approximately 2.5 kg was found floating on the pond. The capybara had been dead for approximately 24 h, and showed clear scratches and anacondas tooth marks in the middle of the body; also, the spine was dislocated at the cervical level. I surmise that Susana attacked it and then she was attacked by the relatives of the prey that bit her in the neck, killing her. Piranhas and other scavenger fishes might have eaten Susana's head. Capybaras are heavy-bodied rodents whose incisor teeth are razor sharp and capable of inflicting fatal wounds. Attacks of capybaras on anacondas are relatively common as evidenced by scars and wounds on several female anacondas that uniquely matched the size and shape of capybara teeth (Figure 3-11).

I once came close to witnessing one of these defensive attacks, but my presence probably altered the outcome of the event. On January 24, 1993, I was wading in a river looking for snakes and I heard the squealing of a baby capybara. As I ran to the source of the noise, I saw a herd of capybaras on the river bank running in disorder in all directions; however a female remained standing, looking in the direction of some bushes at the water's edge. The female looked at me as I approached and looked again down at the bushes. She repeated the movement several more times as the distance between us shortened. When I was apparently too close for her to stay there any longer, she jumped into the water and reunited with the rest of the herd. In the bushes where she was pearing, I found Zuca (Female, 504.7 cm; 40.5 Kg) constricting a juvenile capybara (estimated mass 15 kg). I did not capture her so as not to interrupt her feeding, but I could identify Zuca by the location, size and distinctive marking and scars that she has next to her neck. Another predatory event that brought complications to the predator was on February 4, 1993 I was informed that a large anaconda was seen eating a large turtle (*Podocnemis sp.*). On February 16, 1993 I saw a large snake (Francis, 485 cm total length; 61.3 Kg) in that same spot with very lose skin around mouth and neck. After capture, I saw that the skin and flesh was torn more than 20 cm from the mouth to the neck (Figure 3-12). I collected measurements of the animal and put her back in the field. I monitored the animal regularly and saw her basking often in the same place. On February 18 1993 Francis died. In the necropsy I found epidermal scutes of *Podocnemis vogli* that matched the scutes of a turtle shell 20.3 cm long. The only explanation that I can think of is that the turtle was too large for the snake, and it perhaps was in the wrong position, tearing the esophagus and skin of the snake as she was swallowing it. It is surprising, though, that the snake did not stop the swallowing process when her skin first ripped. Francis's skin was deposited in the herpetological collection of Universidad Nacional Experimental de los Llanos Ezequiel Zamora (UNELLEZ; Guanare, Protuguesa state; Catalog # MCNG-R 1474).

A third event was recorded on February 12, 1997 in the river bank of Caño Guaritico (7 45' 48'' and 69 02' 57''). I found a male anaconda (268 cm total length and 10.7 Kg) swallowing a catfish (*Pseudopimelodus apurensis*, 29 cm total length and 425 g). This fish is characterized by a wide head bordered by long sharp spines. These spines had punctured a large hole through the snake's esophagus wall, muscle, and outer skin. The fish, still alive, was biting the snake's esophagus and was held in place by some of its spikes that were stuck in the snake's skin (Figure 3-13). I caught the snake, and extracted the catfish with very little effort. The snake was kept in captivity with no treatment until it healed completely; two months later the injury was completely healed and the snake even ate an iguana that was put in the cage. Anacondas had been reported to eat spiny catfish in other localities (Beebe 1946) but it definitely not the a common prey in the llanos.

### Cost of predation: How much is supper?

Many animals displayed a large numbers of scars on the skin, apparently a result of attacks from potential predators or the defensive efforts of prey. Females had scars more frequently (35 of 38 animals) than males (25 of 56 animals), and the numbers of scars found on females was higher than those found on males (Figure 3-14). This seems to be correlated to the larger size that females reach (Figure 3-15). I believe that the animals accumulate more scars as they grow older; thus, larger animals have more scars both because they have endured more predaceous events and because they attack larger prey. The lower number of scars that males typically have is due to the fact that they attack smaller and less dangerous prey. An alternative explanation is that males face a higher mortality than females while tracking females during courtship and mating and they do not live long enough to gather a large number of scars in the skin. However, this second scenario would involve a female biased sex ratio that is not supported by the data.

Anacondas take relatively high risks when feeding on certain large or specific prey items, sometimes even leading to death of the predator. Predators should avoid prey that can injure them since recovering from wounds can be so costly that the benefit of the meal is largely expended on it. Little is known, however, of the way reptiles deal with infections and recover from wounds. The high incidence of wounds that anacondas receive and recover from suggests that such injuries may not be as costly as an equivalent wound would be for mammals. Why do anacondas attack prey that can, and do, inflict serious injuries on them is a question that is very relevant in the ecology of the species. Do they not have other prey available? The abundance of waterfowl and other relatively "safe" birds in the llanos does not seem to support this hypothesis. However, birds are a fairly lean prey item since they have constraints of weight for flying; and they might not pay for the metabolic cost of digestion (see Chapter 5). Furthermore, it might prevent the animals from catching another more profitable prey. Hence, a testable hypothesis is that larger anacondas switch from birds to mammals and reptiles because these prey item has more fat reserves and are energetically more profitable despite the risk that they involve.

### 3.5 OTHER CAUSES OF MORTALITY

Another cause of mortality is accidental overheating. Sometimes animals are caught by the dry season in small ponds. In most cases they lay under the mud and stay there until the wet season resumes. However, if they are perturbed or move out in search of a deeper pond there is a chance they will be caught by the strong sun of the day and overheat before they can find water or shade (Figure 3-16**).** On one occasion, I found 34 anacondas in a mud hole that was approximately 20 by 10 meters. These animals were in the last place with moisture in the neighborhood.

The human management of the water in the savanna affects the water level in a manner that increases the duration of the water during the dry season, increasing effectively the size of the esteros at the expenses of the bajíos (see Ramia 1972, Morales and Pacheco 1986**,** for discussion on the effects of módulos in the landscape). Thus, although no new habitat created, the dynamic of the water in it may change from the natural dynamic of the savanna and negatively affects the anacondas. When the water of the módulos is released for the lower módulos the level in the upper modulo drops a few feet in a matter of 24 or 48 hours. In the flat landscape of the llanos that drop in water results in a large extension of land that is uncovered. When it happened there were anacondas in the shallow side of the módulo that were left over night on dry land. In some occasions the snakes could not move towards the new water line before the heat of the day killed them. Dying of overheating is a risk that most animals suffer in the llanos and anacondas, being legless, and depending on water so much, are probably at a particular risk of it.

Table 3-1. Summary of the measures of 780 anacondas caught over 7 years. TL = Total length, SVL = Snout-vent length. All the measures of length are given in cm and all the masses are given in kilograms.

| | Females | | | | Males | | | |
|---|---|---|---|---|---|---|---|---|
| | Mean | STD | Min | Max | Mean | STD | Min | Max |
| TL | 311.0 | 110.5 | 64.5 | 521 | 242.6 | 50.5 | 78.7 | 339.0 |
| SVL | 275.1 | 99.7 | 54.7 | 477 | 208.8 | 44.2 | 66.7 | 331.8 |
| Mass | 20.3 | 18.5 | 0.107 | 97.5 | 5.9 | 2.9 | 0.2 | 17.0 |

Table 3-2. Female anacondas found dead during 1996 and 1997 with the likely causes for their death.

| **Individual** | **TL** | **Mass** | **Date** | **Reason of death** |
|---|---|---|---|---|
| **Ada** | 368 | 34 | 04/22/96 | Unknown, pregnancy related |
| **Olivia** | 494 | 29 | 04/25/96 | Caiman attack |
| **752** | 340 | 20.3 | 04/27/96 | Unknown, likely overheated |
| **Courtney** | 441 | 61.5 | 05/05/96 | Unknown, pregnancy related |
| **Seen event** | 152 | 1.7 | 03/19/97 | Caiman attack |
| **Sue** | 422 | 44.5 | 04/12/97 | Lymphosarcoma |

Table 3-3. Male anaconda killed by caimans during two seasons. Males were considered involved in a breeding aggregation if they were found 25 meters or less from it (Chapter 6). The length marked by an asterisk was visually estimated.

| **Individual** | **TL** | **Mass (Kg)** | **In breeding ball** | **Date** | **Successful predation** |
|---|---|---|---|---|---|
| **Unidentified** | 250* | | Yes | 04/23/96 | Yes |
| **Seen event** | 247 | 5.5 | Yes | 05/04/96 | No |
| **Gary** | 297 | 8.5 | Yes | 05/08/96 | No |
| **178** | 304 | 8.75 | No | 05/10/96 | Yes |
| **803** | 290 | | Yes | 05/01/97 | No |
| **889** | 286 | 11.0 | Yes | 05/04/97 | No |

Table 3-4 Species found to the present to be eaten by anacondas.

| **Latin Names** | **Common Names** | **Number of events** |
|---|---|---|
| **Fishes** | | |
| *Pseudopimelodus apurensis* | Catfish | 1 |
| **Reptiles** | | |
| *Caiman crocodilus* | Spetacled caiman | 5 |
| *Eunectes murinus* | Green anacondas | 3 |
| *Iguana iguana* | Green iguana | 2 |
| *Podocnemis expansa* | Side-necked turtles | 1 |
| *Podocnemis vogli* | Side-necked turtles | 10 |
| *Tupinambis teguixin* | Tegu | 2 |
| **Birds** | | |
| *Anas discor* | Blue-winged tile | 1 |
| *Botaurus pinnatus* | Pinnated bittern | 1 |
| *Casmerodius albus* | Great egret | 1 |
| *Colinus cristatus* | Crested bobwhite | 1 |
| *Crotophaga ani* | Smoothed-billed ani | 1 |
| *Dendrocygna sp* | Whistling duck | 5 |
| *Eudocimus ruber* | Scarlet ibis | 1 |
| *Jacana jacana* | Jacana | 7 |
| *Mesembrinibis cayennenesis* | Green ibis | 2 |
| *Neochen jubata* | Orinoco goose | 1 |
| *Nycticorax nicticorax* | Black-crowned night-heron | 1 |
| *Phacellodomus rufifrons* | Plain-fronted thornbird | 1 |
| *Phalacrocorax olivaceus* | Olivaceous cormorans | 1 |
| *Phimosus infuscatus* | Bare-faced ibis | 1 |
| *Plegadis falcinellus* | Glossy ibis | 1 |
| *Scardafella squamata* | Scaled dove | 1 |
| *Zenaida auriculata* | Eared dove | 1 |
| **Mammals** | | |
| *Hydrochaeris hydrochaeris* | Capybara | 5 |
| *Odocoileus Virginianus* | White-tailed deer | 5 |
| Unidentified small rodent | Unidentified small rodent | 1 |

Figure 3-1 Activity period of anacondas assessed by the cruising technique.

Figure 3-2 Number of anacondas caught each year using the different methods of searching.

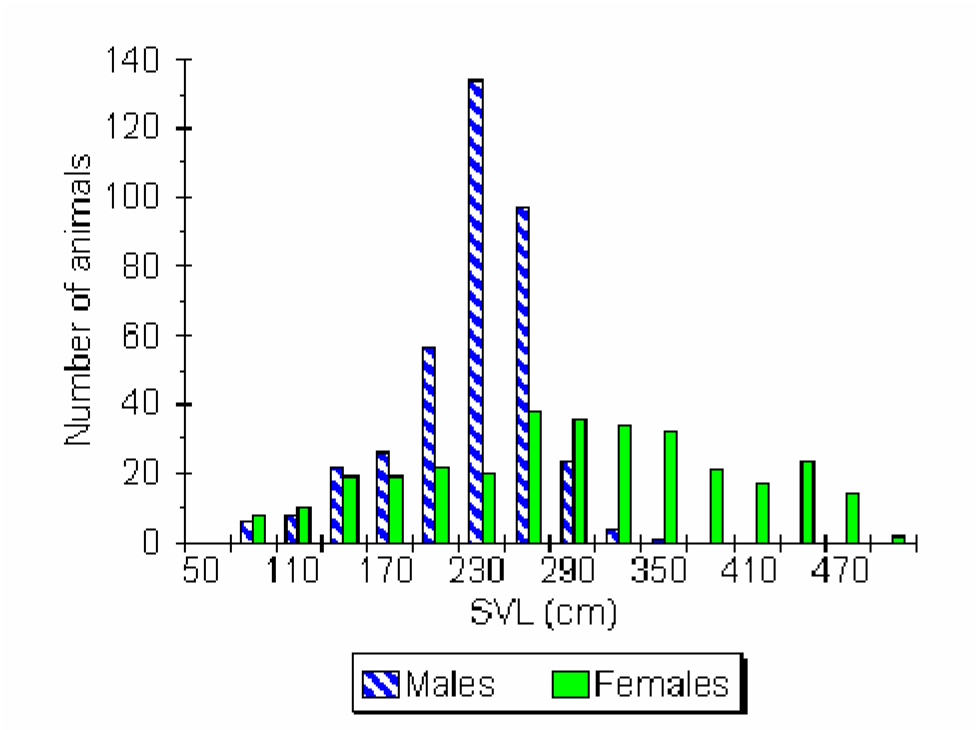


Figure 3-3. Size distribution of the anaconda population. Notice the strong differences in size among the sexes

Figure 3-4. Efficiency of the different searching methods for anacondas used along the year.

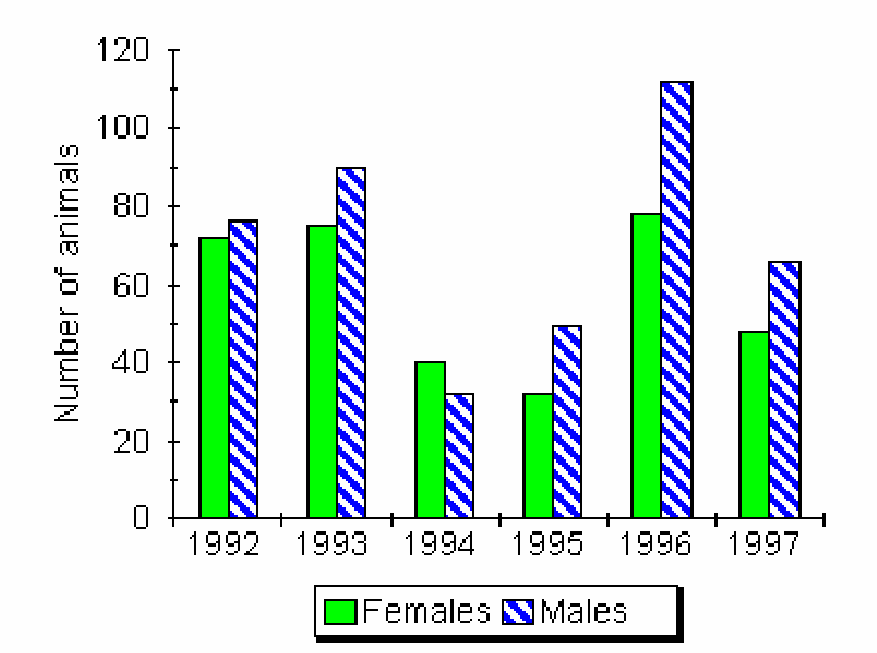


Figure 3-5. Sex distribution of anaconda caught during the study.

Figure 3-6. Spur length (mm) and snout-vent length (cm) of males (empty squares) and females (full squares), in a sample (51) of adult anacondas caught in the Venezuelan Llanos.

Figure 3-7.  Growth rate of adult female anacondas.

Figure 3-8  Female anaconda (Laura, 434.7 cm TL; 40 Kg) disgorging a male anaconda that she had eaten near a breeding ball. Photo Tony Rattin.

Figure 3-9  Tissue found in the necropsy of a female anaconda (Sue, 420 TL; 44,5 Kg) Pathologic analysis revealed a lymphatic tumor, lymphosarcoma.

Figure 3-10  Sequence of the anaconda following and tongue flicking to my helper for about 2.5 meters.  The letter “P” indicates Penelope’s head.  Notice in 1f, right before the strike, the curvature of the neck adopting the S-shaped position typical of the readiness to strike.

Figure 3-11. Bite marks of caiman (a) and Capybara (b and c).

Figure 3-12. Green anaconda (Francis, 485; 61.3 Kg) showing the injury produced while swallowing a turtle (see text for details).

Figure 3-13. Wound inflicted in a male anaconda after unsuccessfully trying to eat a catfish. The snake healed from the wound and survived without any treatment

Figure 3-14. Scars classified by relative size found in the anacondas in the sampling.

Figure 3-15. Changes in the number of scars with length in both sexes of anaconda.

Figure 3-16  Carcass of anaconda found on the dried savanna.  Anacondas move in the dry season looking for water bodies.  In ocassions they cannot reach a safe, cool refuge before the peak heat of the day.

# CHAPTER 4 DEVELOPMENT OF A CONDITION INDEX FOR STUDYING REPRODUCTIVE BIOLOGY OF SNAKES.

## 4.1 INTRODUCTION

March to May is the period that corresponds to the anaconda's breeding season (Chapter 6). The variance in body condition of the adult females was remarkably high, with some animals fat and heavy while other individuals were emaciated. These differences in body condition were independent of the length of the adult females. Anacondas form breeding aggregations of one female with 1 to 13 males during the late dry season (Chapter 6). I observed that the animals that were involved in these breeding groups were the heaviest while the thinner females were solitary and were never found in mating balls. Based on these observations, I hypothesized that body condition could be used to predict the breeding status of female anacondas.

Assessment of the well-being of animals based on body measures has been widely discussed in the literature. Many indexes have been developed to study the mass-length relationship (condition) of the individuals of different species (Bolger and Connoly 1989; Cone 1989, 1990; Harvey 1982; Setzler-Hamilton and Cowan 1993; Smith 1980;). The literature regarding snake reproduction has been inconsistent over the use of such condition estimators (Barron 1997; Bonnet and Nauleau 1995, 1996*a*; King 1993; Madsen and Shine 1992, 1996; Ramo et al. 1992; Shine 1992; Shine and Madsen 1997; Whittier and Crews 1990; Weatherhead & Brown 1996). A major problem has been that a specific index may only be valid for a particular situation, a particular species, or even a particular size range. I will review the kinds of measures most commonly employed (Table 4-1 provides a summary of the equations) and present an improved condition index (CI) that seems to be more broadly applicable and easier to interpret than other proposed measures.

One of the simplest CI methods is to use the mass of the animal divided by snout-vent length (Madsen and Shine 1996). However, the untransformed data can only be used in limited situations and range of sizes because mass does not change linearly with the length (Andrews 1982; Huxley 1932; Appendix A).

Transforming length and mass data using the logarithm makes the relationship between the variables linear and the condition can be estimated by the residual of the regression among the variables (Huxley 1932). However, this method does not take into account that the average condition might change with the size of the individuals; hence, the estimated condition will be dependent on an average condition of the animals of that size (Weatherhead and Brown 1996). To use a standard to measure condition (condition index) that is not independent of the condition is equivalent to measuring length with an elastic ruler! It is inaccurate, gives a poor estimate of condition, and is likely to mask important ecological trends. Furthermore, the log transformation does not have any relation with the nature of the data and is a completely artificial (Smith, 1980), its calculation is not straight forward and does not meet the criteria of simplicity and ease of interpretation that Bolger and Connolly (1989) request from a condition index. Moreover, changing the scale to a logarithmic one makes it harder to analyze and interpret the data (Smith 1980). Transforming data to a log-log scale can be used to analyze allometric relationships within a species. If the slope of the log-log regression is 3.0, the species does not change in shape with body size. If the slope is different from 3.0, however, the species experiences ontogenetic changes that must be studied. For example, consider a species that has a slope of 2.85. As the slope is smaller than 3.0 one might claim that the species changed ontogenetically in shape by becoming more slender. In species that develop particular morphological structures like turtles, some lizards, and certain fishes, it is probably valid to consider a legitimate change in shape by the animal. However, in snakes, all the major differences in shape throughout the life are probably due to changes in mass due to food intake, hence to assume major a change in shape is inappropriate. The question I am raising here is: Does the species really change in shape or is it just getting thinner (or fatter)? In other words: Is it a legitimate change in shape or is all the difference found only due to changes in food intake resulting in the animals becoming leaner or more obese? For instance, the described case of log/log coefficient less than 3 could be due to lack of food; perhaps larger animals cannot gather the energy they need to both maintain themselves and breed. This was found to be the case in *Liasis fuscus* and *Nerodia sipedon* (Madsen and Shine 1996; Weatherhead and Brown 1996). A coefficient larger than 3 could represent a bias in the sample, say, toward pregnant females that in general are fatter than non-breeding animals, or toward animals that have recently eaten a meal (and perhaps are basking and are easier to find and catch). Assuming that the animals grow isometrically, the shape (as understood for the relationship between length and girth) of the animal does not change, provides us with a rigid yardstick of comparison that allows detection of any trend of this kind and compare conditions throughout a wide variety of sizes

Mass is a dependent variable of the length (Bolger and Connolly 1989) and in a snake it varies based on its cubic power (Appendix A). Therefore, the only legitimate transformation of the data is a cubic one. Cubic transformation has been used heavily by fisheries scientists (Bolger and Connolly 1989, 1989; Cone 1989, 1990, for a review) and also applied to snakes by Bonnet and Naulleau (1995, 1996*a*). The indexes used involve dividing the mass by the cubic power of the length, resulting in a linear relationship of the data. However this conversion involves bringing the independent variable to the scale of the dependent variable (Table 4-1). Thus, it makes more sense to transform the cubic dependent variable to the linear scale of the independent variable. Bonnet and Naulleau (1995, 1996*a*) also include in their calculation the ratio of length by average neonate length. This brings up further complications that limit the applicability of the index, such as data that are not always available (e.g. measurement on neonates), and the ratio of two variables that are likely to have different sources of errors, since smaller snakes are easier to manipulate and measure accurately than larger ones (Chapter 3).

In this chapter I present an index based on a simple transformation that is unbiased, and size-independent fulfilling the requirements of simplicity, appropriateness to the particular data set, and statistical correctness requested by Bolger and Connolly (1989) and Cone (1989). I propose a simple transformation that is derived from the equation of the cylinder (the best geometrical model to apply to a snake). Analyzing the equation of the cylinder, it is evident that the volume (and thus the mass) is a cubic function of the length (Appendix A). Thus, calculating the cubic root of the mass and dividing it by the length, we can obtain an index that reflects how “fat” the cylinder is. For the sake of representation this index can be multiplied by 100 (see Table 4-1). This condition index assumes that larger animals have the same shape as smaller ones (isometry). In other words, there is not an ontogenetic change in shape other than those we want to measure with the condition index. Mathematically speaking this index is no different from that of Fulton (Table 4-1), but transforming the data to the units of the independent variable makes the index easier to interpret and analyze. Furthermore, the mass can change abruptly if the animals has a large meal or decrease after long time without a meal so the snout-vent length (SVL) is a more stable measure of size; and thus, should be preferred for the analysis.

## 4.2 METHODS

I used data from 660 animals from the population to analyze the mathematical appropriateness of the index. I also collected information on the breeding status of 87 adult females (44 breeding and 43 non-breeding) during the annual dry season (from March to May). The criteria used to assess breeding condition were: 1) observing the female in a mating aggregation, 2) maintaining the female in captivity until she gave birth, 3) recording presence or absence of eggs or embryos by ultrasound analysis, and 4) dissecting road-killed animals. A fifth criterion to assess breeding condition was developed from the long-term following of individuals. Since breeding involves a very large energy expenditure that the female cannot afford two years in a row, those animals that had bred one year where considered as non-breeders the year before. This is a common pattern in relatively large snakes (Madsen and Shine 1996; Martin 1992; Sazima 1992; Shine et al. 1999a; 1999b). From those animals that I have data from in both conditions, I assigned them a priori to a group (breeding or non-breeding) to balance the number of individuals of both conditions. Each animal was used only once in the database. I calculated a discriminant analysis to separate the groups and assess membership. I also calculated the condition index of both categories and evaluated the distribution of the data graphically.

## 4.3 RESULTS

The relationship between mass and SVL of 660 animals is an exponential relationship (Figure 4-1). By calculating the cubic root of the mass, this relationship becomes linear (Figure 4-2). Finally by dividing the mass's cubic root by the SVL it is possible to obtain an unbiased and size-independent estimator of how fat the animal is (Figure 4-3). For the sake of representation this index may be multiplied by ten in order to obtain an index that is easier to handle.

The condition index proved to be size independent and an unbiased tool to assess obesity in a large range of sizes (Intercept = 0.87; slope = -.000; $R^2$= 0.0009) and normally distributed around the mean in a probability plot (D'Agostino et al. 1990). Using this index in a population of free-ranging adult green anacondas I was able to predict breeding condition using body measures. There was a significant difference between the mean CIs (t= 12.1; Table 4-2) in pregnant (9.40) and non pregnant females (8.11) (Figure 4-4). Furthermore, the midpoint between the means (8.75) was considered an appropriate cut-off point to classify new observations. Notice that most observations (82 out of 87; 94.3%) are classified properly using this criterion (Figure 4-4).

A second method used to classify the body condition of the anacondas was a discriminant analysis using both the length and the cubic root of the mass. Both groups were efficiently separated by the analysis (generalized square distance = 6.3202). Membership assessment based on body measures turned out to be highly reliable in a jackknife test and consistent with the assignment done with the condition index (94.3%). In

I give the values of the Fisher's linear discriminant function (Morrison 1990) and show an example of the functioning of the model to assess membership of new individuals with the measures of length and mass.

### 4.4 DISCUSSION

Both methods of assessing breeding status of wild caught females proved to be effective and mutually consistent. Four out of five of the mistakes were non-breeding females that were improperly classified as breeding. Even though I dropped from the analyses any animal that appeared to have had a recent meal, some animals may have had some partially digested prey that went undetected and might have inflated their mass thus biasing the results of the condition analysis.

The fact that it is possible to predict pregnancy by only using the condition index indicates that the main determinant for breeding in an adult female is whether she has enough fat reserves to do so. Thus acquiring sufficient food supply is the main requirement for an adult female to breed. Food availability and its determinants should be a focus of any study attempting to understand the population dynamics of the species. Seasonal fluctuations in the food availability as well as geographical variability in prey abundance are expected to create important differences in the reproductive rate of individual females and therefore in the population as a whole.

The validity of the condition index to assess pregnancy in anacondas has been proven and its applicability in other species is suggested. Species with thinner constitutions may have different averages, and the cut-offs to determine pregnancy may have different values in different species; however, the potential for a condition index to study the breeding status of snakes is strongly suggested and deserves more attention in inter-specific studies.

While the Fisher's linear discriminant function provides a confidence interval for the prediction using information for the two data sets, the condition index is easier to calculate and, being size independent, it is potentially useful for other taxa. Indeed, the condition index correctly predicted the breeding status of two *Boa constrictors* found dead in the highway, of a *Helicops angulatus* that later laid eggs in captivity, and another *H. angulatus* found dead on the road. On the other hand, using Fisher's discriminating coefficient the boas were properly ranked but not the *Helicops* (Table 4-4).

Assessment of breeding condition of a snake is important for population studies. In large boids, breeding condition cannot be assessed by palping, as it is done in other less muscular snakes (Tolson et al. 1984). Both the discriminant analysis and the condition index provide reliable tools to assess breeding condition. The use of this method only requires basic measurements that are commonly taken in mark and recapture studies. The decision of breeding or not is one of the most important, and least understood, traits in the life history of snakes (Seigel and Ford 1987; Shine and Madsen 1997). My result suggest that the single most important criteria in the breeding decision of an adult female is whether she is fat enough to do so. The condition index I propose has proven to be a useful tool in predicting such an important biological parameter. Being size independent, it offers the potential to be used in a broad range of sizes and perhaps of species. The index also presents some added benefits which are: to be in an intuitive linear scale, to be meaningful (higher = fatter = better condition; lower = thinner = worse condition), and to be easy to calculate.

Table 4-1 The most common condition indexes. M = mass; SVL= snout-vent length.

| Statistic | Formula | Reference |
|---|---|---|
| Relationship mass- length | $= M/SVL$ | Madsen and Shine 1996 |
| Residuals from: | $\text{Log}(M) = \text{Log}(a) + b\,\text{Log}(SVL)$ | Cone 1989 |
| Fulton index | $= M/(SVL)^3$ | Bolger and Connolly 1989 |
| BCI | $M / TM$ where;<br>$TM = (SVL_{adult} / SVL_{newborn})^3 \times M_{newborn}$ | Bonnet & Naulleau 1996*a* |
| Condition Index | $(M^{1/3} / SVL) \times 100$ | This contribution |

Table 4-2. Means of the condition index of breeding and non-breeding female anacondas. A two tailed t-test found significant differences at $p < 0.0001$.

|  | Non-breeding | Breeding |
|---|---|---|
| Means | 8.105 | 9.398 |
| Standard deviation | 0.4293 | 0.5572 |
| Number | 44 | 43 |

Table 4-3 Summary coefficient of the Fisher's discriminant linear function. To assess membership of a given animal one has to multiply the measure of the animal (entries are snout-vant length in cm and cubic root of the mass in grams) by the corresponding coefficient and add the results to the constant. The set of coefficients that produces the highest values would be the group to which the animal belongs.

| | Breeding | Non- Breeding |
|---|---|---|
| Constant | -13.11382 | -11.31538 |
| Length | -0.06520 | 0.06342 |
| Mass Cubic root | 1.59722 | 0.05441 |

So if the measures of an animals are 385 cm length and 29500 gr. (cubic root = 30.90) the calculation would be :

Breeding: -13.11382+ 385(-0.06520)+ 30.90 (1.59722) = 11.1387

Non-breeding: -11.31538+ 385(0.06342)+ 30.90(0.05441) = 14.782589

This animal would be ranked as non-breeding since the formula led to a higher result using the non-breeding coefficients.

Table 4-4 Data from other species testing the generality of the method to assess pregnancy using the condition index and the coefficient of the discriminant analysys (see text for details). One of the boas and both of the *Helicops* were found to actually be breeding. The condition index correctly ranks all the females (as determined by whether or not their condition index exceeds 8.75; see text for details). Membership assignment can also be with the Fisher's linear discriminant function. The individual must be classified as the category which coefficient is higher. See for explanation to use the coefficients of the discriminant analysis.

| Species | Svl (cm) | Mass's cubic root | Condition Index | Breeding coefficient | Non-breeding coefficient | Breeding prediction with Fisher's coefficient | Breeding status |
|---|---|---|---|---|---|---|---|
| Boa constrictor | 150 | 12.806 | 8.57 | -2.4398 | -1.1056 | Non-breeding | Non-breeding |
| Boa constrictor | 162.5 | 15.037 | 9.25 | 0.30858 | -0.1915 | Breeding | Breeding |
| Helicops angulatus | 71 | 6.694 | 9.43 | -7.051 | -6.448 | Non-Breeding | Breeding |
| Helicops angulatus | 57.5 | 5.313 | 9.24 | -8.3767 | -7.3797 | Non-Breeding | Breeding |

Figure 4-1. Relationship of mass and snout-vent length in 660 wild caught anacondas over a 6-year period.

Figure 4-2. Data from Figure 4-1 after calculating the cubic root of the mass (Intercept = -0.26; slope = 0.087; $R^2 = 0.93$;)

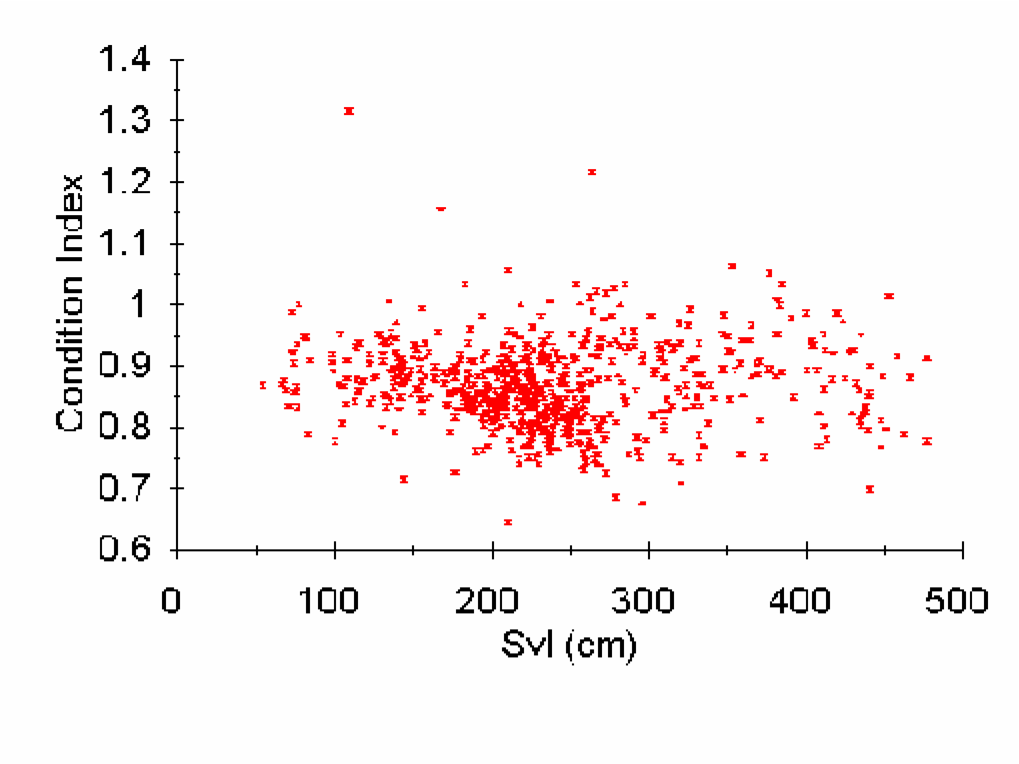


Figure 4-3. Condition index (CI) of the data from 660 anacondas from the wild population (Intercept: 0.87 Slope = 0.000; $R^2$ = 0.0009). The CI proved to be normal in a normal probability plot (D'Agostino et al. 1990).

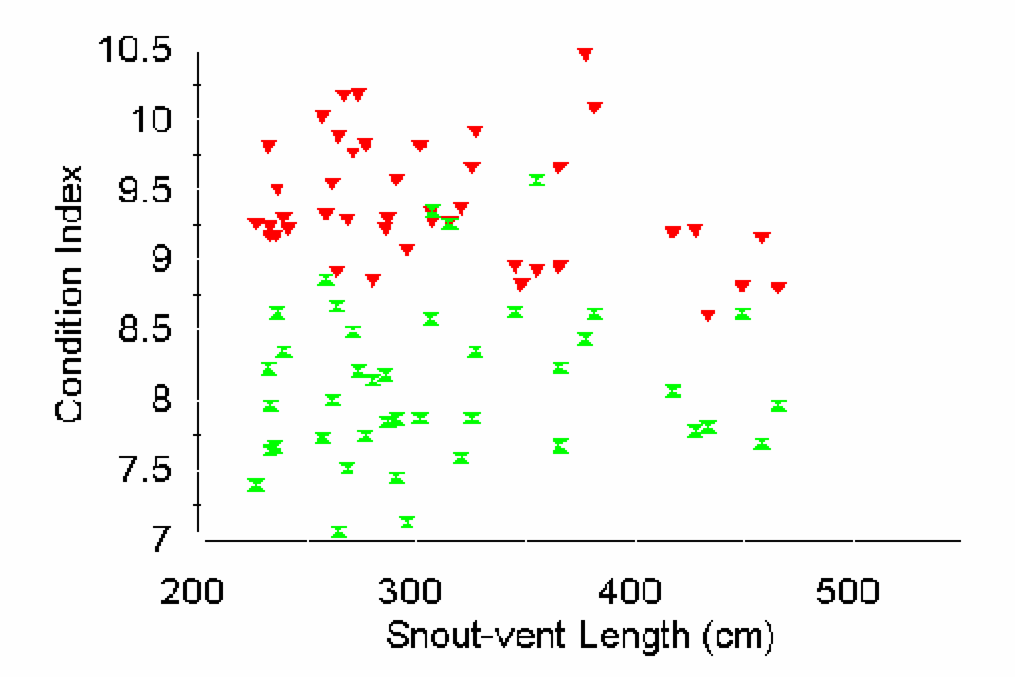


Figure 4-4 Condition index of breeding and non-breeding female anacondas. Notice that most non-breeding females had a CI below 8.75, while this breeding females were above this cutoff.

# APPENDIX A

Here I will demonstrate that the mass is related to the third power of the length. Let the volume of a cylinder (a good model for the snake's body) be:

$V = l\,\pi r^2$

Where the l is the length and the r is the radius. The volume and the mass are directly proportional so there is a constant c such that

$m = c\,l\,\pi r^2$

In an isometric growth any increase in length will be followed by a proportional increase in radius. In other words, if the cylinder does not have change in shape, regardless of the size of the cylinder, there is a constant "k" such that

$l = rk$

then:

$r = l/k$.

If we replace r using the former equation

$m = cl\,\pi\,(l/k)^2$

Re-grouping

$m = l^3 c\pi/k^2$

and there is a constant $C = c\pi/k^2$ such as

$m = l^3\,C$.

At this point it is clear that the mass is a cubic function of the length. Therefore the logical transformation of the data is to take the cubic root of the mass which makes the relationship between them linear

# CHAPTER 5 DETERMINANTS OF THE REPRODUCTIVE OUTPUT IN GREEN ANACONDAS.

## 5.1 INTRODUCTION

Reproductive value or lifetime reproductive success (LRS) is the number of potential offspring that an individual can leave in the population over its lifetime. Natural selection should maximize it since it is a true measure of fitness (Williams 1966; Daan and Tinbergen 1997). In animals with undetermined growth, clutch size increases with female size due to an increase in the coelomic cavity. An adult female that has enough fat reserves can either breed in that year and secure some offspring or skip reproduction and breed the following year when she can produce a larger clutch. The decision to breed, including the age of first reproduction, depends largely on the increase of fertility of the animals due to the growth attained by delaying reproduction an extra-year, and the likelihood of dying during that year. If the female can increase significantly the number of offspring by increasing her size during one year, selection should favor skipping reproduction that year. If the increase in fertility is not large and the female faces a high mortality during that year, selection should favor breeding and securing some offspring in the current year (Bell 1980; Kozlowski and Weigert 1986).

Once the female makes the decision to breed another question arises: How to invest her breeding resources? She can produce a large number of neonates of small size or a few offspring of very large size. Large offspring may reach larger size more quickly and should suffer less predation. Larger individuals can also kill and subdue larger and more diverse prey than small ones, an additional benefit of having larger offspring size (Arnold 1993; Shine 1978*a*, 1989). On the other hand, it would also benefit a female to have as many offspring as possible. Thus a trade-off appears between the size of the neonates and the number of them in every clutch (Ford and Seigel 1989*a*; Sinervo and Licht 1991; Stearns 1992). Generally, if the animals have a high mortality early in life it would benefit the mother to have many offspring (r-selected strategy); on the other hand if there is a relatively secure environment it is best for her to have few very well endowed offspring (Wiewandt 1982). Thus, the female should optimize clutch size in order to have the largest number of offspring that have a good chance of survival (Kozlowski and Weigert 1986**;** Lack 1968).

Williams (1966) established the relationship between growth and reproduction. In animals that grow throughout life the amount energy that is invested in reproduction is at the expense of future growth, since the energy used in reproduction will not be available for growth. Any increment in size of the animal will eventually be reflected in larger clutches; thus, any investment in reproduction at any given time is at the expenses of future reproduction. Williams also introduced the idea of the Residual Reproductive Success (RRS), which is the reproductive value of the animal left at any given time of its life. Thus animals with a long life-span, that can produce many clutches in the future should invest proportionally less per individual reproduction. This model predicts changes in the reproductive investment: younger individuals are expected to have a smaller reproductive investment per clutch as a consequence of their small size and their allocation of the energy surplus into growth and reproduction. Older individuals, on the other hand, have less to lose, since they do not forfeit much growth by breeding, and are expected to incurr in larger reproductive investments.

For snakes, this topic has been studied both in the field (King 1993; Madsen and Shine 1993*a*, 1996; Plummer 1992) as well as in captivity (Ford and Killebrew 1983; Ford and Seigel 1994; Seigel and Ford 1992). The available information deals with only a few taxa and limited geographic distributions (Slip and Shine 1988; Shine & Fitzgerald 1995**;** Seigel & Ford 1987; Madsen and Shine 1996; Shine et al. 1998*a*, 1998*b*). This may be the first reproductive study in any mainland neotropical snake where selection pressures leading to size at first reproduction, clutch size, reproductive investment, and the ontogenetic changes are evaluated by using data collected from reproduction of wild animals.

## 5.2 METHODS

### Data collection

Forty-two live animals were collected in the savanna either during the dry season immediately after the conclusion of mating or during the wet season when the animals frequently bask at the river bank and elevated areas (Chapter 3; Figure 5-1). When the animals were not seen mating, the pregnancy was determined by the condition indexes of the animal (Chapter 4). The animals were put in outdoor enclosures each of which contained a pool with enough water so they could dive in and be covered. Smaller animals were put in circular cages, 4-m in diameter with a pool in the middle, and larger ones were placed in 5 m x 4 m cages. Aquatic vegetation (*Eichhornia* spp.) was provided as well a refuge on the land where the snake could hide from the sun and still stay dry. All the cages were leftover from a caiman farming program and were located in the same area where the anacondas where caught. Parallel to this work, a mark and recaptures study of 780 individuals was being carried out. The measurements of 234 adult females from the population were used to calculate the breeding frequency of the population at discrete

Measurements

I took the following measures of all females at the time of the capture: total length (TL), tail length (to calculate the snout-vent length, SVL), and mass (M). After parturition, I weighed the animal again before the next meal. A sub-sample of 5 animals was weighed three times during the pregnancy in order to monitor mass changes during gestation. The sample of animals from which I took weigh throughout the pregnancy was kept small due to the stress and disturbance that the handling meant for the female. Within the first 48 hours of birth I collected the same data from the neonates and determined sex by cloacal analysis. Due to the large number of neonates and time constraints, from 5 of the females I processed only a representative sample (10 individuals).

### Parturition and gestation

The date of the delivery was converted to the day of the year in order to have an ordinal variable. I calculated the gestation time by subtracting the date of mating from the date of parturition in a sub sample of 14 individuals from which I had the exact date of both, mating and birth.

### Reproductive investment

I calculated the Relative Clutch Mass (RCM) of the animals by dividing the mass after birth by the total mass of the clutch. This measure estimates the proportional amount of energy that the female invests in reproduction. The Relative Investment per Offspring (RIO) was calculated by dividing the mean neonate mass by the female's mass and multiplying it by 100 to estimate the percentage of her mass that she invests per individual offspring.

Some of the females had many infertile eggs. This was perhaps influenced by the handling of some animals during pregnancy, although the occurrence of some infertile eggs is not uncommon (see below). I consider that the infertile egg size may be used as an estimator of the size of the eggs at the time that they are fertilized. Thus the difference in mass of the average baby size and the average infertile egg size can be used as an estimate of the increase in size of the embryo during the gestation. In this calculation I labeled "embryo" both actual embryo and the yolk associated to it; no further attempt to separate the development of any of this units is made. I estimated the growth rate of the embryo within the womb by subtracting the average egg mass from the average neonate mass of every clutch, and dividing it by the gestation period.

### Path analysis

Path analysis is a method for partitioning the correlation among the variables in an attempt to identify the relationships among them. It assumes a causal relationship among the variables based on an "*a priori*" knowledge of the system (Kingsolver and Schemske 1991). For instance, if it is possible to identify a temporal relationship among the variables and label them as "earlier" or "later"; and thus draw predictions among them. This way it is possible to represent them in a diagram with arrows that shows their relationship. Furthermore, it is possible to include in the diagram the standardized partial-regression coefficient on the arrows to show quantitatively the relationship among them. The correlation among the variables can be due to direct effect or to indirect effects. An indirect effect is the product of the path coefficients representing multiple direct effects. The total effect of one variable on another is the sum of the direct and indirect effects of the different paths. The unexplained variance of each regression is calculated by the square root of $1-R^2$, where $R^2$ represents the proportion of the variance of the dependent variable that is explained by the regressors included in the model, and varies from 0 to 1. It is represented as U in the diagram.

The relationships in the path coefficients were derived from multiple regression models that included all the variables that had a significant contribution to the dependent variable predicted in each model. To build each model I used all possible regressions among the variables that were relevant, and selected the best model based on the one that produced a higher $R^2$ and used fewer variables. I made sure to include all the regressors whose contribution was significant to the calculation of the regression coefficient and that did not have important miulticollinearity effects with the other regressors (Neter et al. 1996).

### Breeding frequency

During the first six year of the study I collected females of all sizes and by calculating the condition index I could determine the breeding status of the animals. Two methods were used to assess the breeding frequency. One was by determining the condition index of all the animals caught during each year and then calculating the proportion of animals that bred in that year. This method offers a large sample size but is sensitive to detection bias. Breeding females were more conspicuous than non-breeding ones and thus the estimation of frequency based on it is likely to be biased towards breeding females (Bonnet and Naulleau 1996*b*). The other estimator was based in those animals that I caught in consecutive years so I could estimate a breeding frequency of each animal by dividing the number of years that it was breeding by the total number of years that I caught the animal. In the collection of data during 1994 I relied heavily on Rafael Ascanio; some of these data will be published in collaboration with him.

## 5.3 RESULTS

### Measurements

The sample was a representative of all the sizes of the population (Figure 5-2). Notice, however, that there seem to be a pattern that does not match the shape of the size distribution of the total population (Chapter 3; Figure 3-3). A Kolmorow-Smirnov test comparing the distribution of pregnant females (n = 43) with the adult females from the population (n = 167) show significant difference (Z = 2.14; p = 0.000) suggesting that the pattern found in the Figure 5-2 involves a legitimate biological trend.

Analyzing the CI of the breeding females I found another inconsistency with my former finding. The CI of the pregnant females before delivery tends to decrease on larger sizes (Figure 5-3; r= -0.42 p = 0.007; n = 41; CI = 1.04 – 2.75 x$10^{-4}$x SVL) but the CI after delivery does not show such tendency (Figure 5-7; r= -0.12 p = 0.54; n= 28). The CI of the females after birth was strongly correlated to the CI before birth (r= 0.66; p < 0.000; n =27).

Pregnant females moved very little using only 0.001 ha during pregnancy (Rivas unpublished). They spent approximately 70% of their time basking next to the water or inside the refuges that were provided. Initially I provided several species of fowl for feeding the animals, but they refused to eat. Once the females gave birth, however, they resumed feeding immediately, ingesting in one event as many as 8 chickens in a row. Surprisingly, despite the long fast female anacondas lose little mass during pregnancy (Figure 5-4).

### Parturition

Parturition occurred at the end of the wet season from October to late December (Figure 5-5). Gestation lasted on average 202.6 days (sd 14.71), however, the time that the female was fertilized is uncertain due to the long time that the mating lasts (Chapter 6). I could collect information of the place where 19 births occurred either by witnessing them or by the place where the remains of the births were found; they were both on the land (12) and on the water (7). For 16 animals I managed to record the time of birth. Most births were in the evening after the peak of heat had passed (Figure 5-6). Most births lasted between 20 to 40 minutes, but some animals took much longer (min =10; max = 145). In 3 cases that lasted a long time, the females expelled some neonates, or feces and then gave clear signs of distress, such as moving restlessly throughout the enclosure and spinning their bodies on the land or water. On two occasions when this happened there was a large number of stillborns, and I found that the females had some stillborns stuck in the duct. The time of a normal birth is probably between 20 and 30 minutes.

Some of the females had a large number of stillborn young that could to be related to having been handled during pregnancy and mating. Some animals were very shy in the enclosures and remained in the water most of the time without coming out to the land to bask like most of the others. These individuals had a very poor breeding success and large numbers of stillborn offspring. In one case, the skin of the female developed a surprising level of fragility, getting to the point of breaking at the very contact with the hand during handling. This animal died after having a completely unsuccessful clutch.

### Relation between the reproductive variables

The path analysis shows the relationship among the variables (Figure 5-8). Notice that SVL and condition, followed by the clutch size, are the most important predictors of the rest of the variables. To understand the interrelationship of the other variables the effect of size and condition must be considered in order to eliminate the influence of these variables and possible trade-offs.

### Clutch size

Clutch size was calculated as the sum of all the live and stillborn neonates plus the infertile eggs. The average clutch size of the anacondas was 29.4 but it was strongly correlated with the mass of the female (Figure5-9; $r= 0.83$ $p < 0.000$; $n = 36$). The single variable that best predicts clutch size is the mass ($Y = 8.98 \times 10^{-4}(\text{Mass}) + 3.14$; $R^2 = 0.82$; $F = 168.8$; $p< 0.000$), but it can be predicted well also by the combination of SVL and condition ($Y= 0.26 (\text{SVL}) + 113.4 (\text{CI}) -160.6$; $R^2 = 0.81$; $F= 70.2$ $p < 0.000$).

### Relative Clutch Mass

The RCM mass was fairly high of average (Figure 5-10) but it showed high variation in the population (Table 5-1). The RCM can be predicted by including clutch size, SVL and CI in the model ($Y = -2.8 \times 10^{-3} (\text{SVL}) + 0.6 (\text{condition}) + 1.19 \times 10^{-2} (\text{Clutch size}) + 1.48$; $F = 7,66$; $p= 0.001$. There was no clear relationship between RCM and SVL other than the fact that RCM was more variable in the smaller females, than in larger ones. However, if we remove the effect of the other variables, it is clear that the RCM decreases with the SVL of the female (Figure 5-11; $r= -0.71$; $p <0.000$; $n = 20$) and with the female condition (Figure 5-12; -0.27; $p = 0.23$; $n=20$), but this trend is not significant. Not surprisingly, the RCM increases with the clutch size (Figure 5-12; $r= 0.7$; $p < 0,000$; $n=20$).

### Relative Investment per Offspring

The neonates are on average 1 % the mass of the female (Table 5-1); although there is considerable variation depending on the female size. The snout-vent length of the female was strongly correlated to the RIO ($r=-0.9$ $p <0.000$; $n = 30$; Figure 5-14 ) and was best predicted in the model by using the clutch size and the relative clutch mass ($Y = -2.48 \times 10^{-2} \times (\text{clutch}) + 2.03 \times (\text{RCM}) + 0.95$; $R^2 = 0.77$; $F=38.5$ $p< 0.000$).

### Predictors on neonates size

Neonates are relatively large at birth compared with the size of other snakes (Table 5-1). There was no significant relationship between the females length and the length of her neonates ($r = 0.25$ $p= 0.20$; $n = 27$) but the mean mass of the neonates was strongly correlated with the females SVL ($r = 0.60$ $p< 0.000$; $n = 30$; Figure 5-15). The neonate mass can be predicted by using RCM, SVL, clutch size and condition in the model ($Y= 0.94 \times (\text{svl}) – 2.95 \times (\text{Clutch}) + 222.6 \times (\text{condition}) + 202.2 \times (\text{RCM}) – 285.3$; $R^2 = 0.64$; $F = 8.9$ $p < 0.000$). The sex ratio at birth calculated from all the newborns obtained in the study was even (1.12 females: males; $n= 437$; two-tailed Binomial $p = 0.25$). However, the average sex ratio from individual females is

1.25 (SD 0.59; n = 21) which is a greater difference from 1 (t-test = 1.89; df = 20) than it would be expected by chance (Figure 5-16). So, while the total sex ratio of the newborns that are entering the population is close to 1.0, the average sex ratio of the individual clutches is not (Table 5-1). Smaller females seem to have female-biased sex ratios while larger females show a more even distribution. However, this trend is not apparent in Figure 5-16, perhaps due to the small sample size.

Neonates anacondas did not show any sexual size dimorphism (two-tailed t-tests performed on mass; t = -0.28; p = 0.20; df = 331) or snout-vent length (t= -0.23 p = 0.82; df = 315) comparing all the newborns. I also did a Mann-Whitney U test comparing the mass of the males and the females within the same clutch and found no significant difference among them (Z= -1.32; p = 0.189; n= 22). The tail length seems to be different at birth between males and females (t= -1.98; p= 0.05; df = 277). However this difference is not confirmed in a Mann-Whitney U test comparing the tail length of the males and the females within the same clutch (Z= -1.23; p = 0.22; n = 20). Due to the small size of the spurs in neonates, I did not measure them regularly because it was too time consuming to do it accurately.

### Stillborn animals and infertile eggs

Normal clutches seem to have from none to two stillborn or infertile eggs. Most births (27 out of 34) had some stillborn and some a few infertile eggs (11 out of 34). Some eggs did not show any development, but during dissection some structures (resembling a small embryo) were identified suggesting that some of the eggs were fertile but did not develop for some reason (see Chapter 6).

Some females showed a high number of stillborns, but this might be related to my interfering with her mating activities or handling during pregnancy. Stillborn mass (avg 214.68) was not significantly different than that of live ones (217.39; t= 0.76; p = 0.51; df = 575), they looked fully formed physically, and did not show any deformity or physical problem other that being dead. It was possible to observe in some individuals infiltration of the bladder content out side of it, perhaps evidence that the animals died a few hours before delivery. The largest animals seem to have slightly higher likelihood of having proportionally lower reproductive success (Figure 5-17), but this trend is not clear. One female was not seen mating at all and she had the most unfertilized eggs (See Chapter 6).

At least 8 of the females studied ate or attempted to eat either stillborn or infertile eggs. Right after birth the female pushes her snout across the mass of neonates, which encourages movement in those animals that did not crawl away right after birth. As she does it, she grabs and eats both stillborn and eggs. Several times a female grabbed a live neonate that was not moving, releasing it hastily when it moved.

### Growth of the embryos

Surprisingly, the average size of the eggs (124.6 g) had no relationship to the female's mass (r = 0.14; p =0.69; n = 11; Figure 5-18) but the growth rate of the eggs (mean 0.44 g/day) was correlated with female's mass (r = 0.67 p = 0. 023; n= 11; Figure 5-19).

### Breeding frequency

The proportion of captured females that were pregnant during the mark and recapture efforts was 0.57. It seems to be lower in longer animals (Figure 5-20) but a similar pattern than that present on Figure 5-2 seems to appear. The proportion of females pregnant in every year varied across the years and was probably influenced by the areas where the sampling was concentrated in a given year. For instance, in 1997 much of the sampling was done in the upper part of the módulos looking for breeding balls, investing less time in searching other areas where the non-breeding females are more abundant (Figure 5-21; Chapter 5). The proportion of females that breed in a given year may be related to the precipitation of the area in the two former years (Figure 5-22; $r = 0.66$; $p = 0.16$; $n = 6$).

The ratio (0.57) suggests that more than half of the female anacondas breed in a given year but the detection of animals is probably biased toward pregnant females. Thus it is possible that it overestimates the actual number of pregnant females in the population. I calculated the frequency in which each animal bred, from a sample of 28 females that were recaptured in successive years (17, 6, 3, 1, and 1 in 2, 3, 4, 5 and 6 consecutive years Table 5-2). The average of all the animals turned out to be 0.379. This seems to be a combination of some animals in a biannual cycle and some that breed at a lower frequency (Table 5-2).

I used the animals that were recaptured in more than three consecutive years and bred in at least one of them (to rule out animals that did not breed for some particular reason such as wounds or disease) to calculate the relationship between breeding frequency and size. I found a declining tendency when I graphed the breeding frequency against the SVL (Figure 5-23; $r = -0.81$; $p = 0.005$; $n = 10$). The breeding frequency can be predicted by Frequency = $0.863 – 1.34x\ 10^{-3}$ SVL.

### 5.4 DISCUSSION

Up to the present all the studies of reproductive biology with large snakes have been using data from harvesting of wild animals (Shine et al 1998*a, b;* 1999*a, b*). This is the first study of the reproductive biology of any giant snake in the wild using naturalistic methods which allows followup of animals over several years.

The lack of activity by the pregnant females is probably due to the large bulk of the animal and the fact that, thanks to their fat reserves, the females do not seem to need to forage. This is consistent with the behavior found in some radio-implanted individuals (Chapter 3). It is surprising, though, that anacondas do not eat during pregnancy despite the expected metabolic investment that gestation involves. A possible explanation for this is the fact that anacondas often are wounded by their prey while subduing them (Chapter 3); and the body and womb of the snake is exposed during the process. To receive a wound in the body cavity holding the embryos might be very dangerous and perhaps compromise the health and success of the clutch. Indeed, long term captive animals at Bronx Zoo, that are regularly fed with euthanized animals, ate throughout pregnancy until just one or to months before delivery (Holmstrom, personal communication) and lost only 22 to 30 % of their mass (Holmstrom and Behler 1981). This supports the idea that wild females are “playing it safe” when they stop feeding. Despite a very large breeding investment, female anacondas still have fat reserves after reproduction as assessed in a few animals found road-killed after the delivery season, and the relatively high CI of some females after birth. Thus, the risk of a wound compromising the survival of the clutch is probably too high considering that the anacondas have enough reserves to survive. A similar behavior of little movement and no foraging during pregnancy has been reported in one other instance in a wild anaconda (Belluomini and Hoge 1957/8) and also in other viviparous (Sazima 1992; Martin 1992) and oviparous snakes (Harlow and Grigg 1984; Hutchinson et al. 1966).

It is surprising that the mass of the anacondas does not change during the pregnancy. There must be losses of energy due to respiration and the metabolism of the female and her embryos. A possible explanation for this is that the losses in metabolism are balanced out by adding water in the conversion of fat tissue and yolk into flesh and live tissue of the neonates.

Is it possible that anacondas reduce their basal metabolism to some sort of lethargy during pregnancy (hence the lack of activity and foraging) and, thus, behave like living incubation chambers for their brood? I do not have any data on the physiological state of the female, but the lethargic behavior of the animal suggests that it is a plausible hypothesis. The closest related species that has been studied are pythons and they use a completely different strategy. They provide heat to the eggs by producing continuous muscular contractions in a type of twitching that generates the heat needed for the incubation of the eggs (Ellis and Chappel 1987; Harlow and Grigg 1984; Hutchinson et al. 1966). Future studies on the physiology of the pregnant anacondas should address this question.

### Parturition

Duration of pregnancy was relatively variable, perhaps due to uncertainty in assessing the actual time that animals were inseminated and the uncertainty in assessing when embryonic development begins. Anacondas mate for a whole month, in some cases, (Chapter 6) and it is unlikely that the development of the embryos starts as soon as the mating occurs, since it would mean a developmental difference of several weeks within the same clutch. It is likely that the sperm is stored during the mating and it is used after the mating finishes. Short-term sperm storage seems to be relatively common among snakes; some pitvipers regularly exhibit short-term sperm storage from fall to spring (Schuett 1982, 1992).

Females gave birth mostly in the evening or afternoon (Figure 5-6). This might be driven by two non-mutually exclusive reasons. One, a proximate explanation is that the females need the high temperature of the day to trigger the energetic demands involved in the delivery, and another, ultimate, reason that the neonates have a better chance of survival at night time when flying predators are not as abundant and the odds of dispersing safely are higher.

The feeding of the females on the stillborn and unfertilized eggs has been reported before (Holmstrom and Behler 1981). A likely explanation for the observed phenomena is that the females are recovering part of the energy invested in the offspring after the long fast and energy expenditure that being pregnant entails.

Relatively similar number of animals gave birth on land and in water. Neonates tend to go into the water and very seldom use dry land (Rivas, unpublished data). The most likely scenario is that the females give birth in shallow water or at the water's edge from which the neonates disperse.

Pregnancy tends to be a very critical moment for the health of the female. Four of the animals I had in captivity died during pregnancy without any apparent reason other than minor wounds present at the moment of the capture, wounds which would have not killed a healthy non-breeding animal. After parturition, the females often look very weak and thin, and may be more likely to be predated (Chapter 3; Rivas et al. 1999). Animals in this condition may attack larger, more dangerous prey in order to overcome their energetic deficit, taking the risk of been injured or even killed by their prey (Chapter 3; Rivas 1998).

Anacondas give birth at the end of the wet season. This seasonality is not surprising given the great influence that the two extreme seasons (wet and dry) have in the life of most organisms that occur in the llanos. Just after birth, the neonates have little time to grow before the onset of the dry season. The peak of the dry season is the least favorable for the survival of the neonates, since there is less water and the newborns have fewer refuges to hide from aerial predators. Furthermore, other predatory animals such as caimans, foxes, storks, herons, and tegus concentrate around the bodies of water. It seems that it would be more convenient for the anacondas to give birth at the beginning of the wet season so that the newborns would have a longer time to grow and reach a size such that they more easily can fight off predators. On other hand, due to the low growth rate of the neonates (Chapter 3), it is possible that any increase in survival derived from being born a few months early is not enough to produce an important selection pressure. Thus, the survival of the newborn may have less influence on it, as compared to the survival of the female. After a large reproductive investment it is on her best interest to find food and recover from the breeding investment. The beginning of the dry season is a very good time for the female to find food due to the above mentioned concentration of animals around the water bodies. Predators of newborn anacondas are potential prey for adult females.

Anacondas are not the only large reptile of the llanos whose offspring are born at this time of the year. Spectacled caimans have a similar reproductive timing. In fact, it is a possible that the timing of the newborn caimans might be a selection pressure leading to the reported timing for anacondas. Newborn caimans use a habitat very similar to that of newborn anacondas and do not overlap in trophic niche. A newborn caiman (from 40 to 50 g) represents between 20 to 25% of the mass of a newborn anaconda, and this is a very common prey size relationship for young snakes. I have not found any newborn caiman among the diet of baby anacondas; however, the representation of this size class of snakes in my sampling is very small. Newborn anacondas seemed very interested in the cotton swabs rubbed on newborn caimans in the predation trials done in captivity (Chapter 3).

Another possible explanation for the seemingly inconvenient time for being born from the offspring's perspective, is that it is simply a consequence of the timing when the mating season occurs and the incubation time. Considering this level of analysis mating season occurs in the dry season as a consequence of the high encounter rate between males and females (Chapter 6) and the neonates are born at the end of the wet season as a consequence of the gestation time needed to develop the embryos.

### Clutch size

Not surprisingly, clutch size is strongly correlated with female's size (Figure 5-9). This trend is expected in animals with indeterminate growth and has been previously reported in other snakes (Ford and Karges 1987; Ford and Siegel 1989*a*; Madsen and Shine 1996; Seigel and Ford 1987; Shine 1994*a*, Shine et al 1998*a*, 1999*a*, *b*). Larger animals have larger coelomic cavities and more room for the production and development of larger clutches (Shine 1992). Not only the size but also the condition index is important in determining clutch size. This is expected since animals with more fat reserves are expected to have a larger surplus of energy to invest in reproduction. A similar trend where the condition is important in the clutch size has been found to occur in studies from the wild (Madsen and Shine 1996) and in captivity (Ford and Seigel 1989*a*, 1992).

### Relative Clutch Mass

The relative clutch mass was lower, but close, to the average value (0.57) found for other species of snake (Seigel and Fitch 1984), and within the value found for other large-sized snakes (Slip and Shine 1988; Shine et al. 1998*a*). The RCM is expected to be lower in viviparous aquatic species due to physical limitations for swimming if the rear is bulky and heavy; as happens with a large clutch (Siegel and Fitch 1984; Shine 1988). Furthermore, animals that have a longer life span are expected to have lower reproductive investments per clutch since the animals have a larger residual reproductive success (RRS) after every single breeding event (Williams 1966).

The average RCM in anacondas seems to decrease with the size of the snake (Figure 5-11). This does not support the idea that young individuals partition their energy investment into one part for maintenance and growth, and another part for reproduction; such a strategy should have resulted in an increase in the RCM with the size. If the larger animals do not forfeit future growth or breeding they are expected to have a relatively larger reproductive output (Williams 1966). The reproductive investment in young (smaller) animals is more variable than that of larger animals (above approximately 330 cm SVL). This is not expected for animals that do not have much benefit of saving energy for growth. On the other hand, if smaller anacondas have a larger risk of being predated (Chapter 3; Rivas et al. 1999) then saving energy for future growth would not be adaptive and the best strategy would be to make very large breeding efforts when possible. The CI of the animals is inversely correlated with the RCM (Figure 5-12). This is counterintuitive since animals with higher condition are supposed to have surplus energy to make a larger investment than animals in lower condition. A possible explanation is that part of that higher condition of the animal is not due to fat storage or yolk only, but to flesh and muscles that increase the mass of the females and are not available directly for reproduction (Madsen and Shine 1996). Notice that the females with higher CIs also have higher CIs condition after the breeding event (Figure 5-7), so the amount of energy used in the reproduction is not dependent on the condition, but it is based in other variables. The fact that the CI after birth is correlated to the CI before birth further suggests that the relative investment of energy for reproduction is not dependent on the condition of the animal; this is similar to the findings of Ford and Seigel (1989*b*).

### Condition index

Contrary to the trend found in the general population of anacondas (Chapter 4), the condition index (CI) of the population of pregnant females decreases with their size (Figure 5-3). This indicates that larger animals are breeding at a lower CI (relatively thinner) than the smaller animals. This is not a trend of larger sizes alone since in the graphs with animals from the all sizes classes this trend is not present (Figure 4-3). It is possible that the larger female are constrained by their mass. A very heavy snake might be constrained in crawling on dry land, which anacondas must often do in the seasonal savanna. Thus, as the female grows in length she is constrained by the maximum mass that her body can carry on land. I believe that not having a rib cage (for the lack of a sternum) there may be a mass limit where the mass of the body might constrain breathing while the animals is on land. This consideration might set an upper mass limit that forces the females to grow thinner as she grows longer. Another possible explanation is that larger animals only need to gather the energy they need to breed and need not reserves for growth and, thus they can breed as soon as they have the minimum surplus of energy to do so. However, they would benefit of breeding with higher CI, since the could produce larger clutches (Figure 5-8).

The lower condition of larger females may also be related to the lower breeding frequency found. Another explanation in a different level is that larger females might take longer to gather the energy they need and thus, they need a longer time to recover from a breeding event and also to attain a high CI. Larger females might also have a harder time coming across the amount of energy needed for reproduction. Larger *Liasis fuscus* have been found to have problems gathering the amount of energy they need to be able to breed with the result that the larger individuals do not breed as often as the younger ones and the largest might not breed at all (Madsen and Shine 1996). Due to the large amount of potential prey found in the llanos (capybara, caiman, turtles and wading birds) in the very areas where the anacondas occur, it is hard to believe that food availability might be limited.

Larger animals have a different diet than smaller ones. The latter feed primarily on birds and the larger snakes feed mostly on mammals and reptiles (Chapter 3). In anacondas there is the added cost of healing from the wounds that larger snakes are more likely to experience (Chapter 3). It is also possible that larger animals cannot catch birds quite as easily as smaller ones as the female have become much heavier. To feed on larger prey might involve a lower rate of feeding, since it takes longer to catch, to process, and to digest them. Larger prey are less common than smaller ones, and the processing of them must take longer simple by virtue of the larger mass to be digested, and the scaling of the digestive process (Calder 1996); this could explain both the lower CI and the lower breeding frequency. Alternatively the amount of food and energy in a bird might no longer compensate for the metabolic investment of digestion for larger females. Large snakes that practice a sit-and-wait strategy of feeding and regularly go for long time without a meal, have developed certain adaptations to that kind of feeding strategy. Side-winder rattlesnake (*Crotalus cerastes*) can undergo atrophy of the intestine and digestive organs in order to lower the metabolic expenses of an idle digestive system. Upon feeding there is a tremendous metabolic expenditure in regenerating the atrophied organs in order to trigger digestion (Secor et al. 1994). Burmese pythons (*Python molurus*) can experience an increase of 44 times its standard metabolic rate while digesting a large meal (Secor and Diamond 1997). It is a testable hypothesis that the energy contained in small birds does not pay for the expenditures of triggering reproduction. Birds are a very lean prey item that maintains low body fats due to the constraints that flying imposes to the body mass. Thus, although abundant in the llanos, birds might not be very profitable for a large snake, and feeding on a bird might forfeit the chance of feeding on a more profitable prey item. This may explain the reported apparent switch in diet (Chapter 3). Although, larger snakes have a lower relative energy expenditure per unit of body mass, their absolute metabolic expenditures are considerably larger than those for smaller ones (Secor and Diamond 1997). Shine et al (1998*b*) found a similar switch in the diet of reticulated python (*Python reticulatus*) in approximately the same size classes. They also found a decrease in the feeding and breeding frequency of larger females (Shine et al. 1999*b*).

If takes longer for a large female to reach a very heavy condition; it is possible that as soon as she is fat enough to breed, she is found by males who start courting her. The courtship and mating itself can play and important role in inducing ovogenesis (Whittier and Crews 1989; Whittier et al. 1987). This phenomenon might happen more with larger females than with smaller ones, since larger females are more sought out by the males (Chapter 6), and smaller females may need less food to reach a high condition. Support for this idea is that Olivia (a very large female) mated in 1995 with a lower condition than the threshold for reproduction (8.5 short of 8.75). Olivia was found the following year extremely weak, with many capybara wounds. Shortly afterwards, she was attacked and killed by a caiman no larger than other caiman that I had seen her eating (Chapter 3; Rivas et al. 1999). If the ovulation is induced by the male's courtship or mating, then it is possible that a female being marginal enough to breed can be induced into an inconvenient breeding event. Olivia was a very large female, with her skin all covered by scars. She did not grow at all in the five years that I followed her and was, perhaps, a very old individual. She gave birth in the wild so I could not collect reproductive information such as RCM or clutch size. The question remains as to whether she made an extremely large breeding investment (perhaps suicidal since her RRS was low at her old age) that produced her weak state, or whether she was simply too thin to breed (as suggested by the condition index) and mating in that year was a wrong decision.

The idea of a maladaptive mating induced by courting males contradicts the conventional wisdom that female snakes emit pheromones to attract the males (Ford and O'Bleness 1986; Ford and Low 1984). However, it is a working hypothesis for a species that is probably not fully adapted to the llanos and might have evolved in different environments (see below).

There are some fertility-independent costs of reproduction such as the long fast of the females, the weakness associated with the postpartum activities, and complications giving birth (see below), among others (Madsen and Shine 1993*a*). If females skip reproduction for a year they would be able to produce an even larger clutch due to their higher CI (Figure 5-8). To produce a larger number of offspring would reduce the fertility-independent cost of reproduction for the female making the breeding investment more profitable. Why are the larger females going into reproduction as soon as they reach breeding condition instead of gathering resources for the following year, when they could have larger clutches? It is possible that the females breed as soon as they meet minimal conditions in order to avoid the risk of dying while foraging on dangerous prey. To die at that point without breeding in that year would involve losing a clutch that was already large, and the increase of clutch size for having a higher condition might not be high enough to compensate for the risk. It is likely that the females are playing it safe when they breed in a relatively thin condition.

The lower condition found in larger females could be related to the apparent decrease of the breeding investment in larger animals (Figure 5-11). The switch in biomass makes the snake switch to a different temporal scale in which they need more time to gather the surplus of energy needed. The reproductive effort (RE) must be measured considering three aspects: 1) the potential cost of fecundity (which RCM measures), 2) the time needed to gather the energy, and 3) the reduction in the survival rate that the female suffers by reproduction (Shine and Schwarzkopf 1992). In light of this interpretation larger females could have a comparable RE than smaller females despite the apparent difference in RCM.

### Relative Investment per Offspring and size at maturation.

Neonate anacondas are relatively small in mass compared to the size of the females. This RIO is comparable to the RIO reported in other large-sized species (Madsen and Shine 1996; Shine et al. 1998*a*). However, they are at birth the size of adult of many species of snakes. The female would get most benefit from making as many neonates as possible. Why is she not producing many more smaller animals? One explanation is that the neonates need at least a minimum size in order in order to gather the food they need in the llanos. Data that I have collected show that they prey on small birds, such as *Jacana jacana* (approximately 70 g), and small passerines associated with the water bodies (Table 3-4; Chapter 3). The snakes also could catch neonate caimans (from 40 to 50 g). The mass of a neonate anaconda is 200 g at birth so a prey of 40 to 70 g is a relatively convenient size for it to eat (Secor and Diamond 1997). Neonates might not be able to catch fish due to the fast movements of this prey item (Chapter 3). Another possible prey item that I have not found in the diet, but are very abundant in the areas is juvenile turtle (*Podocnemis vogli*). *Podocnemis vogli* are small prey items but with a particular shape that make them very difficult or even dangerous to swallow it the snake is not large enough (Chapter 3). I believe that if the neonate anacondas were smaller they would have a very hard time coming across the food they need and probably they would have a very high mortality. Thus the minimum size of the neonates might be a selection pressure influencing the RIO that the female exhibits, and the minimum size at maturity. The fact that smaller females have a higher RIO than larger ones could be a consequence of the minimum size that the neonates require in order to be viable.

There is another possible explanation that is on a different level of analysis: phylogenetic correlation. The selection for large size on some sector or stages of the population produce changes on other traits that are not the actual target of selection (Halliday and Arnold 1987). Females may be very large for several selected reasons and the large size of the neonates is thus simply a consequence being born to a very large female.

Larger females, with larger oviducts, should be able to produce larger eggs. However, RIO decreases with female's size. The females could produce larger offspring that have a better chance of survival instead, they produced larger clutches. Perhaps the females "choose" to make smaller neonates and produce larger number of them turning into a more r-strategy (Lemen and Voris 1982). The decrease in RIO does not seem to jeopardize the theoretical chances of survival of the offspring; its larger size allows the female to incur in a smaller investment per offspring while still producing larger offspring than the smaller females. This is a similar trend to that found in *Thamnophis butleri* (Ford and Killebrew 1983), several marine snakes (Lemen and Voris 1981) and in Australian elapids (Shine 1978*b*). Smaller females need to produce comparatively larger offspring which produces an apparent ontogenetic switch in RIO. Thus the minimum size of neonates might be a selection pressure pushing upwards the age (and size) of the females at maturity. This decrease in RIO suggests that the females are optimizing the clutch size producing as many offspring as possible that have a good chance of survival (Lack 1968).

### Stillborn animals

Stillborn animals were fully developed and their size did not differ from live ones. The reasons these individuals died before birth are not clear. It is likely that the female had problems expelling embryos and they are asphyxiated in the womb. Animals that give birth late seem to have a higher likelihood of having many stillborn offspring. This suggests that such females have some problems delivering.

Belluomini and Hoge (1957/58) report on a wild caught female anaconda that had problems giving birth in captivity. They performed a cesarean surgery and found many stillborn in similar conditions to the ones I found; they also found a few individuals that were alive. Ford (1980) found that animals that had clutches larger than average were at a higher risk of having stillborn or developmental anomalies. The relatively larger proportion of large females that had lower reproductive success (Figure 5-17) could be attributed to this problem. In some cases I believe that the handling of the animals might have influenced in the production of many stillborn. Some of the females acted very shy during pregnancy, spending much time under the water, and might not have basked as much as needed to develop the clutch. This problem has been reported to lead to dystocia, the death of the clutch, or even the female (Ross and Marzec 1990).

### Egg size and embryo's growth

Egg size is surprisingly similar among the females of varying sizes. There does not seem to be any clear tendency. If anything, we seem to appreciate the same pattern that we see in the RCM where smaller females have a larger variance than larger ones (Figure 5-18). While the neonates from larger females are larger than those from smaller ones, this trend is not present in the eggs. This involves a differential growth rate in embryos of females of the different sizes. Indeed, the growth rate of the embryos from larger females was faster than the embryos from smaller ones (Figure 5-18). The different in size of neonates that developed from eggs of equivalent size suggests that the females transfer nutrient differentialy to the neonate in the embryos through some sort of placenta (Stewart et al. 1990).

Why do larger females produce relatively smaller eggs than small females? Allometric growth of the reproductive organs would predict that the embryos from large females would be proportionally larger (Huxley 1932). Furthermore, production of a placenta for the development of eggs and additional provisioning of it means an extra investment of energy and structures. It is possible that the females do not invest in larger eggs in order to not have too many resources committed in some eggs that might not be fertilized, since the females do not seem to be able to reabsorb the energy invested in the unfertilized eggs. The fact that some eggs where fertilized but did not develop could involve two different phenomena. The first could be incompatibility between the sperm and the egg (Zeh and Zeh 1996), and the second, the possibility that the females might exert control on the paternity of her clutch by developing selectively some eggs (see Chapter 6). Both of these are fascinating possibilities that deserve further attention.

### .Breeding frequency

It is not easy to answer the question of how often an anaconda breeds. It seems certain that they do not breed every year. The only two cases where that situation was suggested by the condition index were in very young individuals that perhaps skipped reproduction in the first year (Table 5-2). The fact that parturition is at the end of the year (Figure 5-5) and the mating is early in the year (Chapter 6; Figure 6-4) gives very little time for a female to find, process and assimilate enough food to engage in a new breeding event. Furthermore, it has not been possible to breed animals in captivity that eat *ad libitum* in two successive years (Holmstrom personal communication and Strimple personal communication). Although some animals do breed every other year, it is not the rule. Some other individuals seem to take a longer time to recover and engage in a new reproductive event. Some animals skipped reproduction for three years and bred in the fourth (Olivia) and some other animals did not attained breeding condition for four straight years (Chinga) (Table 3). Chinga was missing the tip of the snout which was an open wound. This probably affected her foraging efficiency and she might not have been able to gather the energy needed to breed. A biennial pattern in reproduction of other snakes have been suggested or found in several species (Madsen and Shine 1992, 1996; Martin 1992; Sazima 1992). Decrease in breeding frequency with the size also has been reported (Madsen and Shine 1996; Shine at al 1998*a*, 1999*a*, *b*) and it even seems to be the rule in large-sized species.

Younger individuals that benefit by growing more might be expected to breed less often than larger ones, but this is not supported by the data. Smaller individuals breed more often than larger ones (Figure 5-20). This might be related to the lower CI found in larger females and perhaps due to a lower feeding frequency (see above). Furthermore, the fact that smaller females end up with larger condition indexes after birth than larger females suggests that they might need less time to recover to optimal breeding condition.

The sample of the population illustrated in Figure 5-2 shows two peaks, where females of snout-vent length of approximately 3 and a half meters are not very abundant. This is consistent with the decrease in the proportion of pregnant females found in the total sample at this size interval (Figure 5-20). Here I summarize four possible non-exclusive explanation for this findings. First, it might be a consequence of their development. Thus, the first peak one sees is when females just reach adulthood and initial breeding size. The next gap in breeding females corresponds to the year (or years) after breeding while the animals are recovering and also growing until they reach the next size class. The difference in the heights of both peaks does not support this idea since the number of females in the older peak is much lower than the former one. This would necessitate high mortality between both peaks which is not supported by the data. The growth rate of the animals in general is not fast enough for the females to move from one peak to the other (in one year or a few; Figure 3-7).

As second reason for the bimodal distribution is that there may be a switch in strategy, whereby smaller females breed as often as they can until they reach a size when the growth they can achieve in one year increases their reproductive output sufficiently to make it worthwhile to skip reproduction (Figure 5-1; Bell 1980; Kozloswki and Weigert 1986). However, at this point, not enough is known about growth rate of every size class to evaluate this hypothesis. However, Figure5-9 does not suggest a change in strategy or any particular increase in fertility that could be related to it.

The third possibility is that females start breeding when they are large enough to produce viable offspring; it would not pay for her to skip reproduction to grow to a larger size because of the risk of being eaten by caiman or other predator (Chapter 3). Healthy females larger than 3.3 meters are not likely to be eaten by any predator; thus, after the females reaches this size it would pay for them to skip reproduction for a few years to reach a much larger size and have larger clutches.

Finally, the fourth possibility is that, the gap of breeding females between 3.3 to 3.8 m could be a byproduct of energy intake, since larger animals feed on more dangerous prey than smaller animals. The switch in diet from birds to mammals and reptiles seems to coincide with this gap in reproductive females. At the body size at which an anaconda switches her diet for energetic, foraging, of other reasons, a females might go through a period when she cannot find the right amount of food due to her lack of experience in finding, subduing, or ingesting it. Consistent with this gap in reproductive females and the decrease in breeding condition is the finding that after 3.3 meters the snakes seem to have more wounds than before (Figure 3-15). A detailed study on the diet of anacondas as well as the energetic benefit of different prey items is needed to shed light on whether the gap is due to the switch in the diet. These four hypotheses are not mutually exclusive and some of them could be acting simultaneously. The idea that the first peak is due to some animals that breed early to ensure some offspring due to the risk of predation, and the hypothesis that the gap is due to a dietary transition are fully compatible and deserve future attention.

The proportion of females that breed in a given year seems to be related to the preccipitation of the two former years. It is probably related to an increase in the density of prey that benefit by abundant water such as capybara, caimans, wading birds, and the fish that the wading birds feed on. The reason that the relationship is with the amount of precipitation for the two former years is because the female might need to forage for two years to gather the energy needed for reproduction. Furthermore, the increase in biomass that benefits the anacondas might be delayed due to the time needed for the prey population to increase.

## 5.5 GENERAL DISCUSSION

### Selection for large size

Large size is normally constrained by high mass, high cost of mobility, and a conspicuousness that both constrains stalking prey and increases detection by predators. The aquatic environment, where anacondas live, diminishes all those problems. The rich fauna found in the area provides abundant food to sustain a large biomass of predators. In the case of anacondas, larger size offers more advantages besides the above mentioned benefits of increased fertility, such as larger number of prey available and resistance to times of shortage. Furthermore, the fact that anacondas are live bearers confers a stronger selection pressure for a large coelomic capacity (Shine 1994*b*).

The following scenario might explain the large sizes obtained by anacondas, especially females. Females need to produce relatively large offspring in order to enhance the offspring's survival by escaping predators and subduing sized prey items. This pushes upwards the size of the female at first reproduction, and might be an important reason leading to large size in anacondas. Skipping reproduction to increase future reproductive output has been found in other species such as *Elaphe guttata* (Ford and Seigel 1994). They found that animals that skip reproduction and thereby increased growth have a higher reproductive output after the third year than animals that breed at an earlier age. This strategy of delaying reproduction increases the LRS only if the survival to older age is high. If, on the other hand, the female suffers high mortality during the main growing period she is better-off by breeding as soon as she reaches the minimal size to breed. Several fertility-independent costs of breeding such as risk of death for dystocia, long-term fasting and weakness after birth; along with the minimum size needed for the neonates to survive, may lead the size of first reproduction upwards.

Larger females produce larger clutches of larger individuals at a lower relative total reproductive investment (RCM) and investment per offspring (RIO) than smaller animals. This benefit for large size might contribute to selection for large body size in females. Notice that fertility of the females does not plateau at the larger sizes (Figure 5-9). This suggests that females would benefit by reaching even larger sizes. However, the breeding frequency decreases with the size of the female so a point might be reached where the benefit of larger clutches might be balanced out by the decrease in frequency. The optimum size for the females would be to have a large size so they can have larger clutches, but remain small enough to find their food supply, locomote easily, and breed regularly. Are the females growing too large for their own good? I calculated the reproductive value of a female at any given time and labeled it Current Reproductive Value (CRV). I calculated it by multiplying the expected breeding frequency for her size by the expected clutch size for her mass**.** The CRV of females increases with body size despite the decrease in breeding frequency and the relative decrease in clutch size due to the lower CI (Figure 5-24). Not only would females benefit from being larger by increasing the number of offspring they can produce, but larger animals would perhaps also be able to eat larger prey and subdue them easier and with less risk. If an anaconda grows sufficiently large, she would also benefit from increase availability of prey such as pecaries (*Pecari tajacu, Tayassu pecari*) tapirs (*Tapirus terrestris*), *Podocnemis expansa*, and *Crocodilus intermedius*. The two latter species were surprisingly abundant historically (Humboldt 1799-1804/1985).

So, why are not the females even larger? The following reasons support for an even larger size in female anacondas: First, the high abundance of prey and their concentration in dry season, which suggests that yearly food supply may not be a problem. Second, due to their aquatic habitats and crypsis, the problems of conspicuousness to their prey, that other predators have, do not seem to apply either. Third, really large size animals might be predator-free, so being detected by predators is not a selection against large size. I have discussed how parasites can affect the animals, and as the time passes, the individuals is expected to reach a larger load of them just as a consequence of the longer time that she is exposed; however, to date there are no field data to document this. One possible limitation to a larger size is the long time that it takes for them to reach it. If animals suffer some size-independent mortality over the years (such as that produced by parasites or accidental injuries by their prey) its life expectancy decreases as it grows older, so the upper range of sizes found is perhaps a direct consequence of their ages. Another possible limit may derive from the seasonal availability of their food supply. Although there is abundant prey item in a given part of the year, the strong seasonality may prevent the females to feed regularly thus imposing on the animals an intermittent feeding schedule that may decrease they growth rate, and also make less profitable the prey consumed (Seccor and Diamond 1997).

### How large can an anaconda be?

The maximum size that anacondas can reach has been subject of longstanding debate among herpetologists. There are many accounts of snakes around 9 to 11 meters (Gilmore and Murphy 1993; Beebe 1946; Blomberg 1956, Pope 1961, among others). A lot of the controversy concerns the credibility of the records, the confusion created by the fact that the skins stretch when the snakes are skinned, and animals whose length was merely estimated or measured with unreliable methods. I do not intend to revisit that discussion, but it is striking that the largest snake that I have caught, out of 780 animals, is only a little more than 5 m. What is the reason for such a difference? Why have I not found any animal anywhere near 9-11 m? The slow growth rate of the anaconda (Chapter 3) requires a long time to reach a large size. My study area is a cattle ranch where the protection of wildlife is a recent practice (last 15 years). Presumably the really large animals might have been killed off earlier and the animals that occur now in the areas where I studied (relatively close to human activities) might have not had enough time to grow to really large sizes. One important gap in the knowledge needed to address this issue is the longevity of the species. There are no good records of longevity and no field data to document it. In captivity it has been reported that the can live more than 20 years but this record was from an animal obtained as an adult (Snider and Bowler 1992). I will address the questions regarding maximum size in the rest of this section using the information that I have gathered.

### *Measurement errors*

I discussed in chapter 3 the problems of measuring a large snake and how the reliability of the measure is low if the animal struggles and when the measure it taken by people without the proper experience. Doing it following a tight methodology I found that the measuring error could be as high as 5% of the length of the animal which translates into 45 cm in a snake 9 meters long. This could be even higher when measuring a very large snake that is not muzzled by people who are struggling with the animal as they try to stretch it. However, I doubt that this can account for the large difference found.

### *Constraints on large body size*

The condition index of larger females decreases with body size. I have argued that mass can be a problem for animals when crawling on dry land, so larger animals might be constrained by their mass. Larger females might alternatively have problem coming across the energy they need to reach the breeding condition (see above). It would not pay for the females to grow to a size where she cannot find enough food to breed. It would not pay for her either to be so large that her mass would be unbearable (and risky). Regardless of the reasons, extrapolating the decrease in condition index I found that a female with 600 cm snout-vent length (approximately 670 cm total length) would have a condition index of 0.875, which is the cutoff below which females do not breed. In other words, if this trend holds for larger animals, a female larger than 6.7 meter would never reach breeding condition. Thus, there would not be any reason for the female to reach this size. However the theoretic limit (670 cm TL) and the actual maximum (521 cm TL) are still far apart.

Assuming that larger females do attain breeding condition, I also calculated the decrease of the expected breeding frequency with size using the regressions presented above. The expected breeding frequency of a female of 8.46 m total length is zero; this size is reasonably closer to the reported values; and the difference could be explained by the measuring error. However, does it really pay for the female to be that large? I calculated the CRV of the animals extrapolating the breeding frequency and the clutch size from the data collected (Figure 5-25) Notice that the CRV peaks slightly before 5 meters of SVL. Natural selection would not favor any increase in size beyond that point. This is about the largest SVL that I found (477 in the total population; Table 3-1). Thus largest range of sizes is optimized to increase the number of offspring than the female bares. Figure 5-25 summarizes the selection pressures affecting female size.

A five meters limit for female size is consistent with the calculation that Pritchard (1994) made about the maximum size of the snakes. In a revision of the size at maturity and maximum size of several North American snakes, he found that the maximum size of the snakes was about 1.5 to

2.5 the size at maturity. The minimum size of a breeding anacondas that I found was 210 cm SVL (Table 6-2) so the expected maximum size of the anacondas following this pattern would be 525 cm.

### ***Explaining the records in the literature***

How does one explain all the records of much larger animals documented in the literature? The above analysis suggests two limits on the development of larger size. One is the decrease in the condition index that sets a 6.7 m limit above which the females does not reach breeding condition. The other is the decrease in breeding frequency as the female grows larger that makes it unprofitable for the female to grow beyond 5 meters. Both limits are probably dependent on the environment and are likely to be less important when the females live in more permanent water or in an area without a long dry season. For instance if the anaconda lives in a river or deeper lagoon, or in the aseasonal rainforest, she would not face the constraints of gravity and hence the limitations of mass to crawl on dry land would not exist. Both the decrease in CI and breeding frequency might well be related to a decrease in the feeding frequency or a lower supply of highly profitable prey items due to seasonality. Will a very large female have enough food intake in the new habitat to reach breeding condition and a relatively higher reproductive frequency in more permanent water bodies? I have shown that the amount of water during the previous two years has an influence on the breeding frequency of the anacondas (Figure 5-22), so that the hypothesis that breeding frequency is higher in more wet areas is plausible.

In the savanna, a large female might face some limitation due to the strong seasonality. Early in the arrival of the dry season there is a period of high prey encounter rates as the water level drops over a period of 1 or 2 months. During this time the female might be able to take one or two good meals, but shortly after this, the peak of the dry season arrives and conditions turn overly hot and dry, forcing the female to seek refuge from the heat to places where she is perhaps unlikely to find food. After the wet season starts, the prey encounter rate drops dramatically. With all the savanna flooded the anacondas might not encounter many prey during the wet season either. So the prey availability of the llanos provides some food intake, but this might not be constant. This restricts females to a relatively small number of prey every year, and also imposes the high metabolic expenditures that their switch in metabolism involves (Secor and Diamond 1997, 1998; Secor et al. 1994).

Although predators are not a problem for large females, living in more permanent water body might be safer for large anacondas too. They would not be exposed to overheating, since they do not have to crawl on dry land (Chapter 3). If an anaconda attacks prey in, or near, a river, she can drag it down to the water with less risk of being attacked by the relatives of the prey (e. g. capybara). The risk of being wounded during predation is relatively high for anacondas in the savanna, (chapter 3). Bringing the prey to an unfamiliar environment where the mobility of the prey is constrained may be a further strategy to increase the efficiency of the subduing behavior (Rivas and Andreadis, in prep.). Thus, in a river habitat (or neighboring oxbows and lagoons) a large female might be able to locate their food in a safer manner, allowing her to use her energy and skills in a more efficient way, since there would be less risk of injury.

There are other selection pressures for the female to grow larger in the rivers as well. A 5 m long anaconda can kill and subdue all the native animals occurring in the savanna so there would not be any advantage in the food intake for the female to grow larger. However, in the rivers and associated gallery forest live larger and more diverse prey items such as pecaries, tapirs, crocodiles, and Arrau turtles that can be important food sources. A larger size would benefit the females by enabling them to capture those prey. Also other less dangerous (non-social) rodents such as agoutis (*Dasyprocta* spp) and pacas (*Agouti paca*) become available on a more regular basis than in the savanna. An animal living in rivers cannot take advantage of a season of high concentration of prey when the female anaconda, an ambush hunter, has a high probability of encountering some prey. Instead, animals living in the more stable but prey-unpredictable environment probably must take advantage of more diverse prey (size and species). So, larger body size would benefit females by increasing their range of potential prey. Also, in more wet places where smaller anacondas might have less predation due to the lower encounter rate with predators, the females would have less mortality at early ages. Thus females in more permanent water bodies would be selected to grow large and also would have the food supply and added safety enabling them to grow to larger sizes and live longer. Due to the search method I used, I could not catch or find animals that used deeper waters, so the decrease in the condition index and breeding frequency could be particular traits of the animals that live in the hyper-seasonal savanna.

If these assumptions are correct I can make the following predictions. First, females in wetter habitats would start breeding at a larger size due to the lower encounter rate with predators in the dry season, which would make it more profitable for an “adolescent” female to keep growing in order to produce larger clutches. Indeed, a female that was born in captivity and fed *ad libitum* throughout her life started breeding at 3.1 meters svl (3 years of age; Holmstrom 1982), much closer to the second peak of Figure 5-20. Second, females would produce larger offspring at maturity, since the neonates would need a larger size to cope with the unpredictable food supply. Again this new selection pressure can increase the size at reproductive maturity. Third, females would have a more uniform condition index across different sizes of reproductive females; alternatively, the decrease in condition with size would be less steep, since they are not constrained by gravity. Fourth, females would maintain a higher breeding frequency as they grow since they can forage throughout the year. The breeding frequency would probably still decrease, since the amount of food needed for larger animals increases with the size, and the time to gather it should increase proportionally. As a consequence of all these predictions, I expect the females to reach larger size. In fact, the model described in Figure 5-25 is very sensitive to changes in the breeding frequency so the optimum size can easily shift upwards if the snakes live in different environments. Indeed, most of the records of very large snakes come from rivers (Gilmore and Murphy 1993). Furthermore, the opportunistic capture of a female anaconda in the Tiputini river (Ecuatorian rainforest, Napo province) supports these ideas. The individual caught (Silvia) was 522.8 cm in TL and 459.8 cm SVL. This is the second largest individual in SVL in the 8 years I have been studying them. The one animal caught in the rain forest was larger than 779 of the individuals caught in the seasonal savanna. Furthermore Silvia presented only 13 scars total which is remarkably lower then the expected for an animal of its size (Figure 3-15) supporting the hypothesis that animals in more aseasonal habitats face less risk of wounds from their preys.

Notice that human activities would preclude the meeting of the conditions that would favor the development of very large size in a snake. Larger prey items (tapirs, capybara, pecaries, crocodiles and Arrau turtles) are decreased by human presence and human activities; indeed, most of these species are themselves endangered. Human presence also would prevent the anacondas from growing to large sizes due to the propensity of people to kill snakes (Chapter 7). Thus, truly large snakes are probably restricted to permanent waters with little or no human intervention.

### Two different strategies

To this point I have assumed that size and ages are perfectly related and this is not necessarily the case. Old individuals that have had a low energy income can retain a relatively small size, while young animals that eat well can grow to larger sizes in short time. Thus differences in the behavior of animals associated with their individual metabolic activities can produce confusion in these trends (Ford and Seigel 1989*a*, 1992, 1994). Additionally, differences in how the animals invest their energy can produce even more confusion. There might be some animals that invest a lot of energy in reproduction or that breed very often and might not have a lot of energy left to grow. Thus, these might well be older individuals that have not grown much due to the fact that they invest all the energy in reproduction and very little in growth. These animals would be playing optimum strategy for smaller sizes. Thus, the animals that breed less often acquire larger size because they devote a larger part of their resources into growth. These explanations would account for the high variance found in smaller sizes since smaller individuals could be young animals with a Small-RCM-Grow-Large (SRGL) strategy or older animals with a Large-RCM-Grow-Small (LRGS) strategy. The difficulty in assessing the ages of reptiles prevents an easy solution to this question. The presence of some relatively small animals that did not grow over several years suggests that individual differences in growth do exist. A more detail analysis of growth rates of the population is needed. The presence of two different tactics co-existing with similar conditions has been documented before. Ford and Seigel (1994) found that some captive reared *Elaphe guttata* fed with high energy diet breed at 20 months of ages while other individuals grown in the same conditions did not breed until 32 months of ages. The earlier breeders had a lower LRS than the later breeders.

### Why would two strategies exist?

Two alternative strategies may coexist if both are in equally efficient. I calculated the contribution to the population of individuals below 340 cm of svl (first peak) and of individuals larger than 340 cm (second peak) by adding up the estimated clutch size of all the breeding females of those two size-groups. The second peak, despite the lower number of females, is responsible for 59.5% of the offspring born in a given year. Furthermore, the offspring of larger females have a higher expectancy of survival due to their larger size so their contribution to the recruitment in the population must be even higher. If SRGL females produce more offspring than the LRGS ones, they are expected to replace them in the population. However, the smaller animals are less conspicuous, and use water with more vegetation; so the possibility exist that this group might be under represented in the sample; so the competitiveness of each strategy in the local environment can only be hypothesized.

Animals with a slow growth rate (LRGS) might produce higher contributions to the population than SRGL individuals in times of prolonged shortage (several strong dry seasons or relatively dry wet seasons) when the larger animals have problems finding food and are more constrained by the drought and SRGL individuals might do better in wetter periods. Changes in the efficiency of these strategies between the years might prevent them from replacing each other in the population.

Assortative mating may prevent individuals with different strategies from interbreeding (see Chapter 6).

Alternatively, the genetic flow from other areas might prevent adaptation to local conditions. The savanna (bajío) is adjacent to the river banks, and the seasonal overflowing of them is part of the water supply of the savanna. There may be gene flow between these populations, however, the habitats are quite different and the selection pressures are expected to be different too. Animals with a SRGL strategy are probably adapted to the river and animals with a LRGS strategy may be fitter for the savanna. The shape of the Figure 5-10 may result from two strategies adapted to two different habitats. Is it really likely that in the same population two alternative strategies coexist? Anacondas in the savanna live right next to the gallery forest and the river. The sample (collected in the savanna) is probably composed by some LRGS individuals (first peak) and SRGL individuals as well, which are fittest in the neighboring river. The constant migration of animals from one side to the other prevents the population to fully adapt to the conditions they are on. This lack of adaptation to the local conditions due to genetic flow from neighboring population has been reported to occur in other species (Riechert 1993*a*, 1993*b*). Genetic studies are needed to test these hypotheses.

This is the first naturalistic study of the reproductive biology of any large snake. The ability to follow up animals for several years gives new information about their natural history. The natural history of the anacondas presents unexpected challenges for the conventional wisdom regarding life-history traits. The condition and size of the females seem to play important roles in the reproductive output of the species, where larger animals produce more and larger offspring. However, larger animals seem to breed less often and perform smaller reproductive investment than smaller ones. Ecological constraints regarding the interaction with predators at different ages and prey availability can be responsible of the trends found. Further studies on the population dynamics, mobility, and genetic structure of the populations are needed to understand better the trade-offs and the selection pressures that are affecting the population.

Table 5-1. Body measures of the anacondas caught and some statistics of the reproductive output calcualted from the parturition. TL = Total Length, SVL= Snout-vent length, M = Mass, RCM = Relative Clutch Mass (see text for formula), RIO= Relative investment per offspring (%); CL = clutch size, NTL= Neonate total length, NSVL = Neonate Snout-Vent length, NM= Neonate Mass, N= sample number. The sex ratio was calculated over the 21 clutches from which I have full data.

| | **Mean** | **SD** | **Min** | **Max** | **N** |
|---|---|---|---|---|---|
| **TL (cm)** | 365.5 | 77.5 | 242.7 | 521.3 | 45 |
| **SVL (cm)** | 318.8 | 71.37 | 210.7 | 466 | 42 |
| **M (Kg)** | 30.82 | 18.22 | 9.25 | 70.00 | 45 |
| **RCM** | 0.39 | 0.095 | 0.17 | 0.52 | 27 |
| **RIO** | 1.03 | 0.43 | 0.32 | 2.15 | 32 |
| **CL** | 29.4 | 18.4 | 5 | 74 | 39 |
| **NTL** | 78.77 | 4.21 | 63.9 | 91.43 | 504 |
| **NSVL** | 68.42 | 4.01 | 54.7 | 80.93 | 492 |
| **NM** | 216.8 | 35.6 | 145 | 330 | 578 |
| **Sex Ratio** | 1.25 | 0.59 | 0.38 | 2.6 | 21 |

Table 5-2. The breeding frequency of the adult female anacondas that were caught in several years. Y and N stand for Yes and No indicating whether they bred in a given year.

| Year | 1992 | 1993 | 1994 | 1995 | 1996 | 1997 | 1998 |
|---|---|---|---|---|---|---|---|
| E101C | Y | -- | Y | -- | -- | | |
| Lina | N | Y | -- | -- | -- | -- | |
| Kathalina | N | Y | -- | -- | -- | -- | |
| E145C | Y | N | -- | -- | -- | -- | |
| E155C | Y | -- | Y | | | | |
| E161C | N | Y | -- | -- | -- | -- | |
| Hermelinda | Y | N | -- | -- | -- | -- | |
| Sarah | Y | -- | -- | N | | | |
| Laura | -- | Y | -- | Y | -- | -- | |
| Araine | -- | Y | N | -- | -- | -- | |
| E200C | -- | N | -- | N | -- | -- | |
| E223C | -- | N | Y | -- | -- | -- | |
| Renée | -- | -- | Y | -- | N | -- | |
| Diega | -- | Y | -- | -- | -- | Y | |
| E436C | -- | N | N | -- | -- | -- | |
| E486C | -- | -- | Y | -- | Y | -- | |
| Guaratarita | -- | -- | Y | -- | N | -- | |
| E78C | N | Y | -- | -- | -- | -- | |
| Julia | -- | -- | -- | -- | Y | Y | |
| Mary-Jo | -- | -- | -- | -- | N | Y | |
| Alice | -- | -- | -- | N | Y | -- | |
| Courtney | -- | -- | -- | N | Y | -- | |
| E90C | Y | -- | N | -- | -- | -- | |
| Yuang-Ly | -- | -- | -- | N | N | Y | |
| E204C | -- | N | Y | Y | -- | -- | |
| Zuca | N | N | -- | -- | Y | -- | |
| Musiua | N | N | -- | -- | Y | -- | |
| Mirna | Y | N | N | -- | -- | -- | |
| Mónica | Y | N | -- | -- | Y | -- | |
| Antonieta | -- | Y | -- | Y | N | -- | |
| Andrea | -- | Y | -- | Y | N | N | |
| Marion | N | N | Y | -- | Y | | |
| E437C | -- | Y | -- | N | N | Y | |
| Chinga | N | N | N | N | -- | -- | |
| Joan | -- | -- | N | Y | N | N | |
| Olivia | N | N | N | Y | N | -- | |
| Madonna | Y | N | -- | N | N | Y | N |
| Sue | Y | N | N | Y | N | Y | |

Figure 5-1. Anacondas basking on termite mounds (Judy-Lee) during the wet season. Photo Bob Caputo.

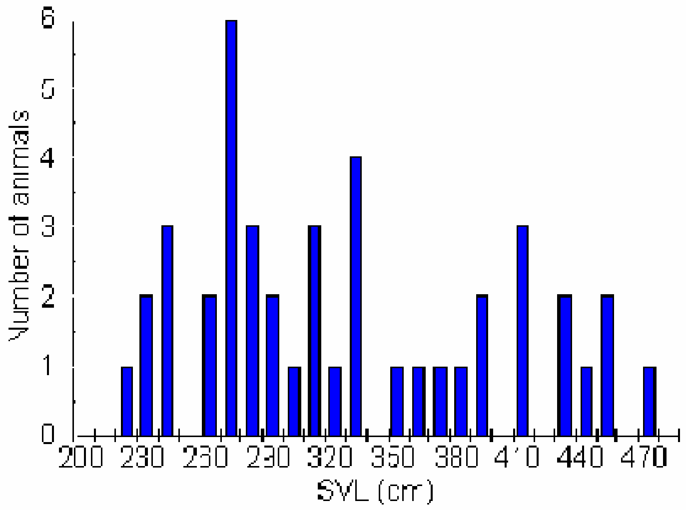


Figure 5-2. Size distribution of the breeding 42 female anacondas.

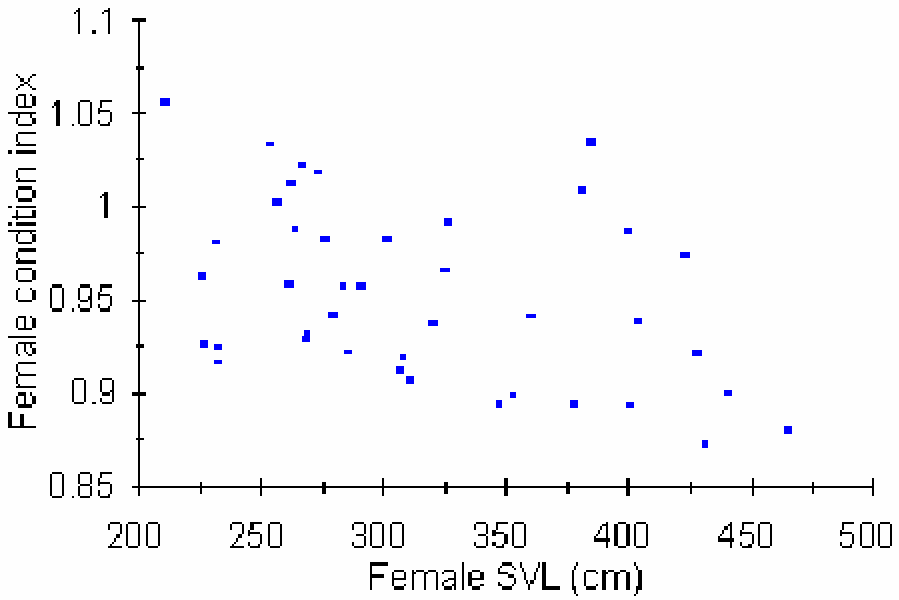


Figure 5-3. Size related changes on the condition index before birth of pregnant female anacondas in relation to female snout-vent length (r= -0.42; p=0.007; n = 41).

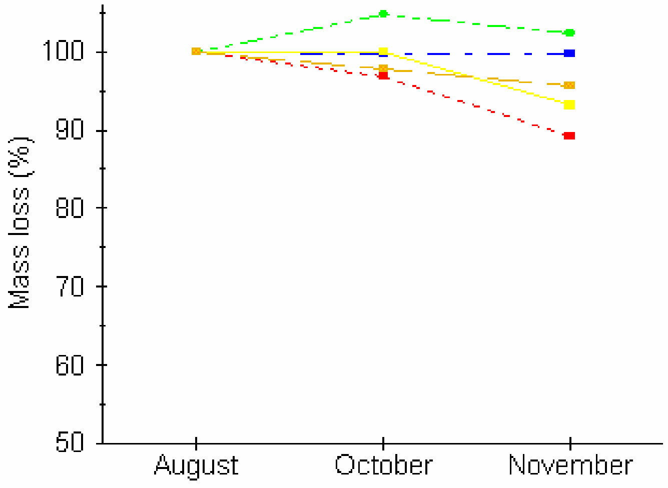


Figure 5-4. Mass loss during pregnancy of a sample of five female anacondas.

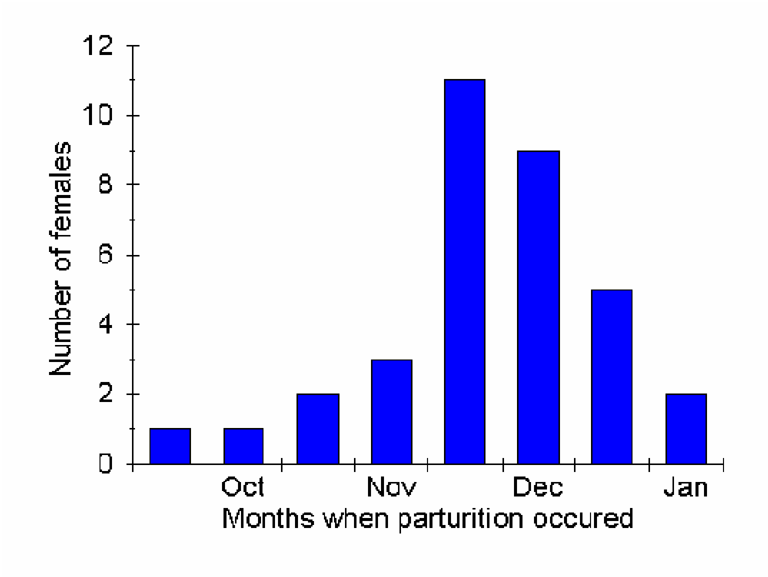


Figure 5-5. Timing of parturition of anacondas during the year.

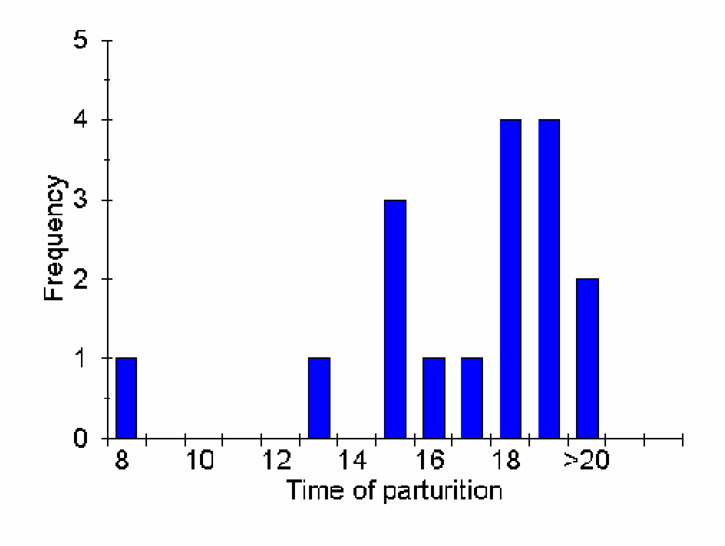


Figure 5-6. Time of the day when the anaconda parturition occurred. All the births that occurred after 19:30 were scored as > 2000.

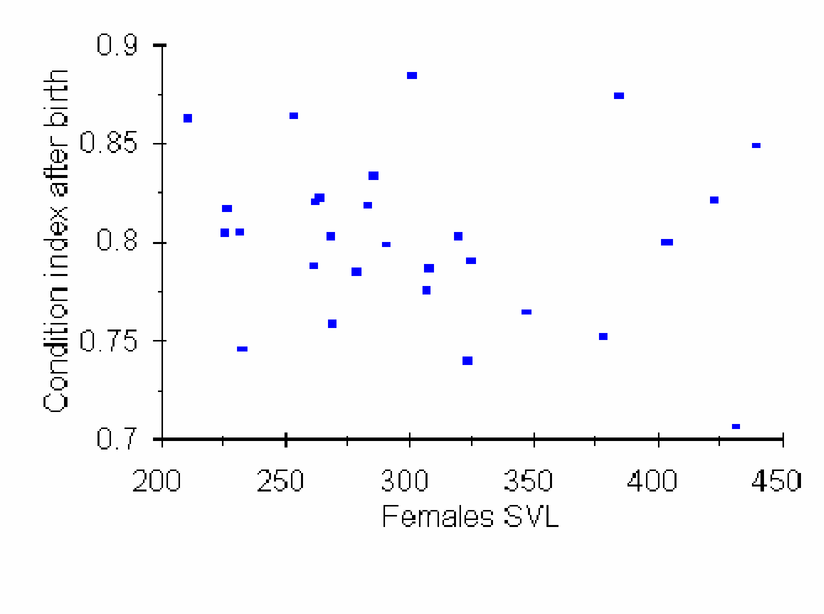
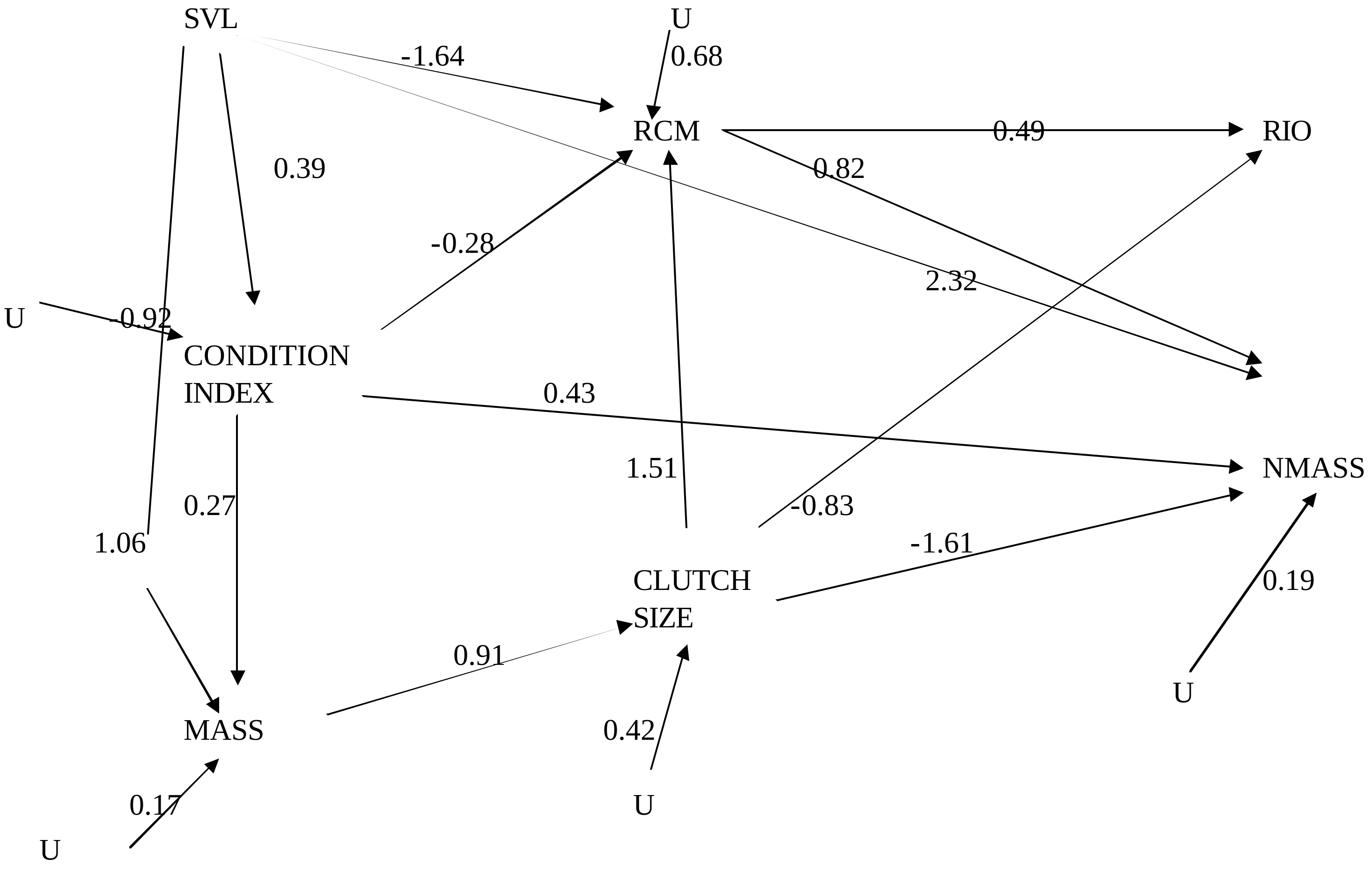


Figure 5-7. Condition Index of female anacondas after birth vs female snout-vent length (r = -0.12; p= 0.49; n= 28).

Figure 5-8. Path diagram of the reproductive variables of anacondas. The number over the lines is the standarized regression coefficients of the model that predicts each dependent variable. SVL snout-vent length, RCM = relative clutch mass, RIO = relative investment per offspring, NMASS= neonate mass. U = represents the unexplained part of the variance. See text for details



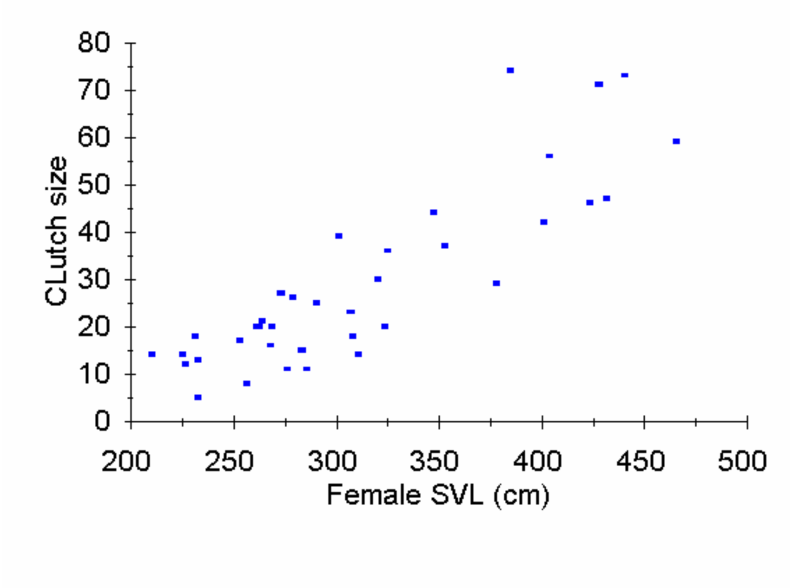


Figure 5-9. Relation between the clutch size of female are anacondas and their snout-vent length (r=0.83; p< 0.000; n= 36).

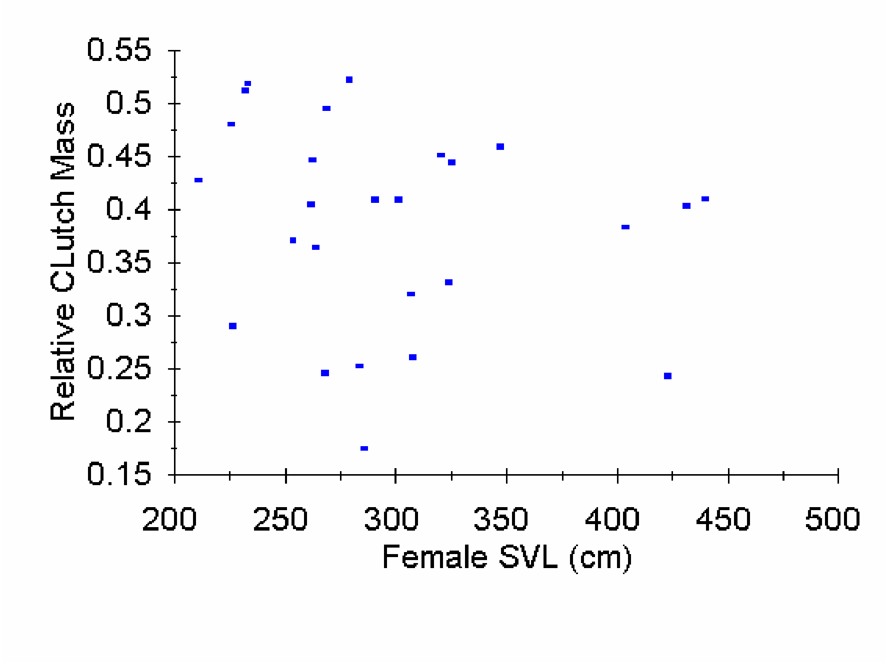


Figure 5-10. Relation between Relative Clutch Mass and female Snout-Vent-length (r= 0.23; p< 0.28; n = 25). The Relative Clutch Mass is calculated by dividing the mass of the clutch by the mass of the females after birth.

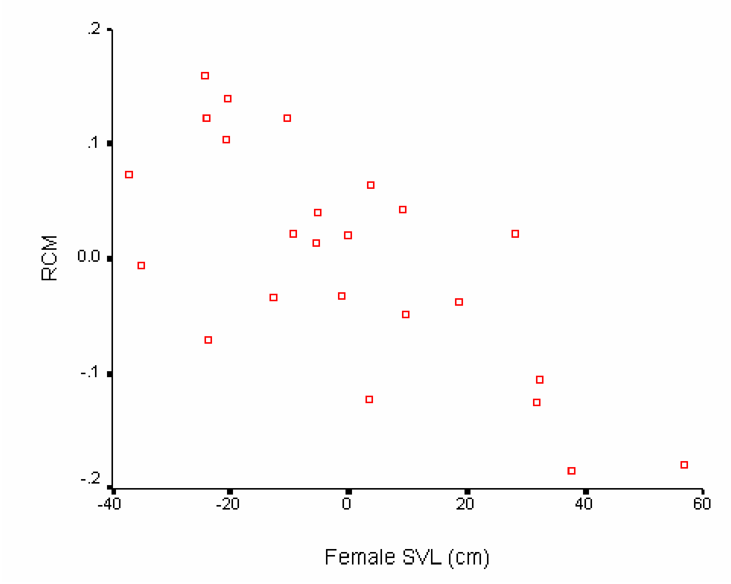


Figure 5-11. Partial correlation plot of anaconda relative clutch mass and SVL holding clutch size and condition index constant (r= 0.71; p = 0.000; n = 20)

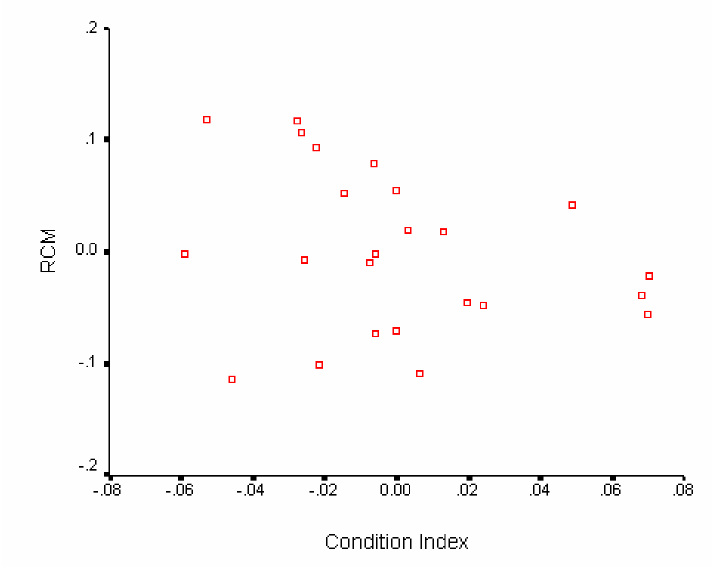


Figure 5-12. Partial correlation plot of anaconda relative clutch mass and condition holding SVL and clutch size constant (r= -0.27; p = 0.23; n = 20)

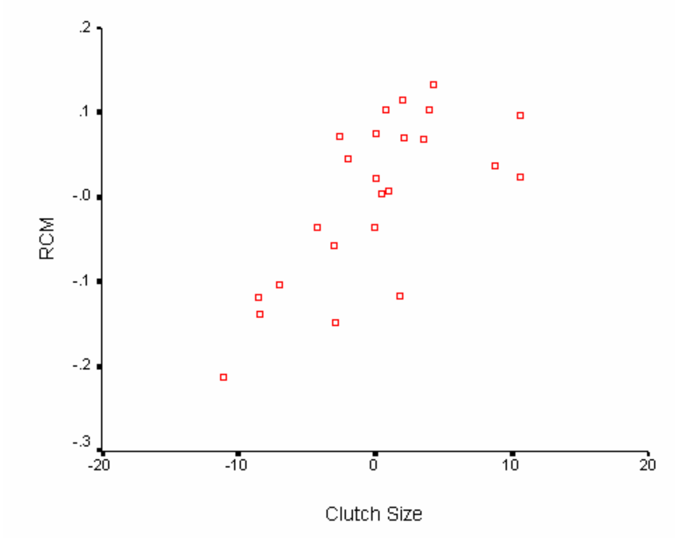


Figure 5-13. Partial correlation plot of anaconda relative clutch mass and clutch size holding SVL and condition constant (r = 0.7; p = 0.000; n = 20).

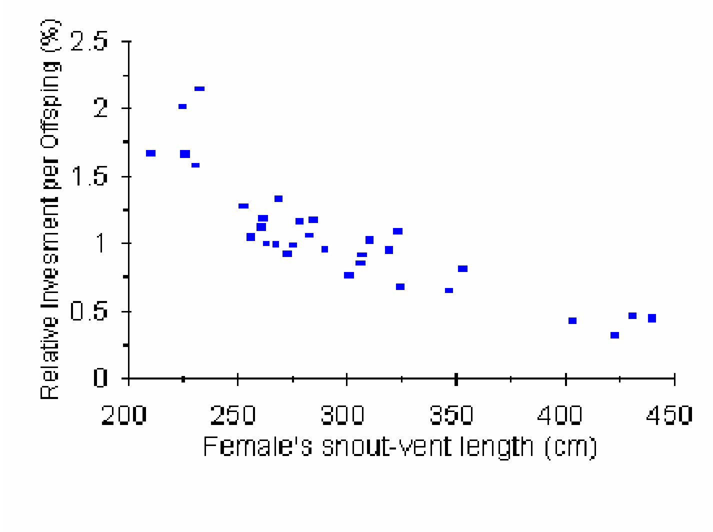


Figure 5-14. Relation between the relative invetment per oofspring and the SVL of female anacondas (r= -0.899; p< 0.000; n= 30).

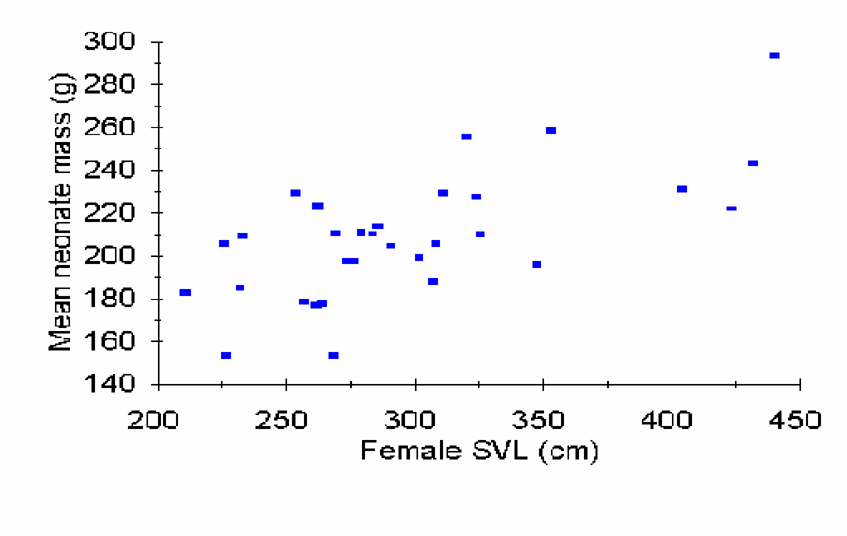


Figure 5-15. Relationship between the mass of neonate anacondas and the SVL of the female (r= 0.604; p< 0.000; n= 30).

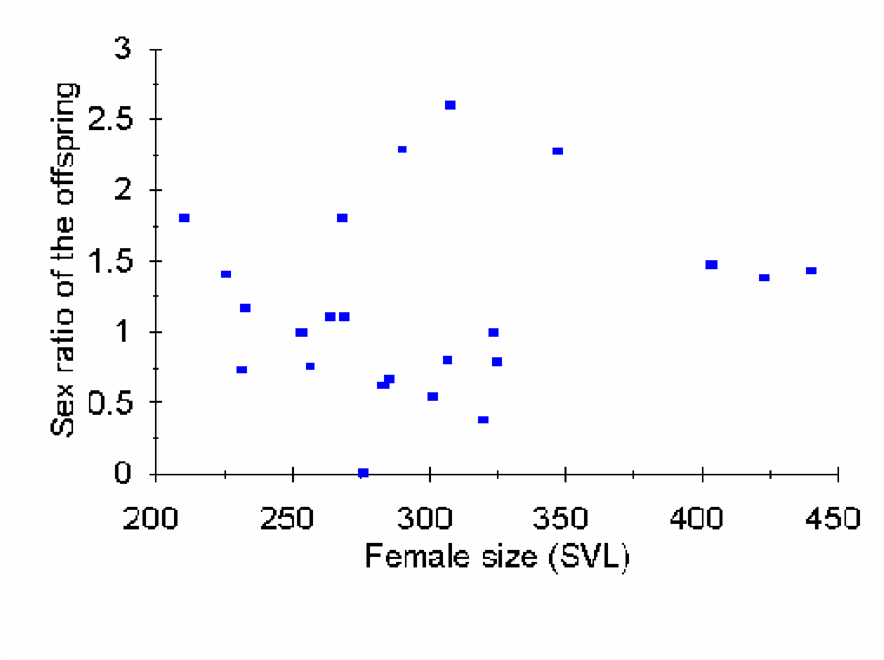


Figure 5-16. Variation in the sex ratio of the clutches of 21 anaconda clutches (r = -0.013; p< 0.964; n= 21); see Table 6-2 for statistics.

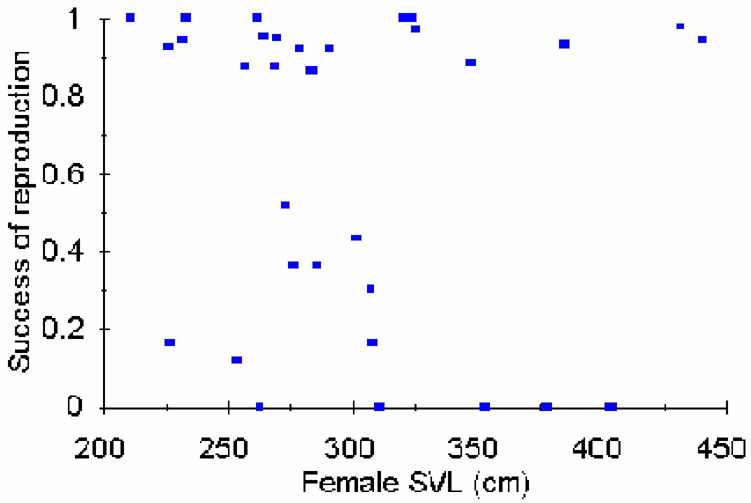


Figure 5-17. Reproductive success of anacondas that gave birth in captivity. The success of reproduction of individual females is calculated by dividing the number of live neonates by the sum of live, stillborn and infertile eggs.

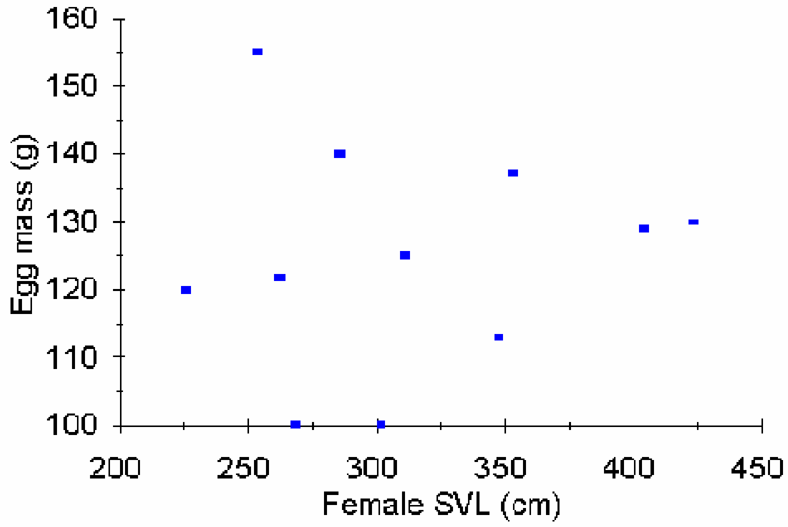


Figure 5-18. Egg mass of female anacondas in relation to female SVL (r= 0.14; p= 0.69; n = 11).

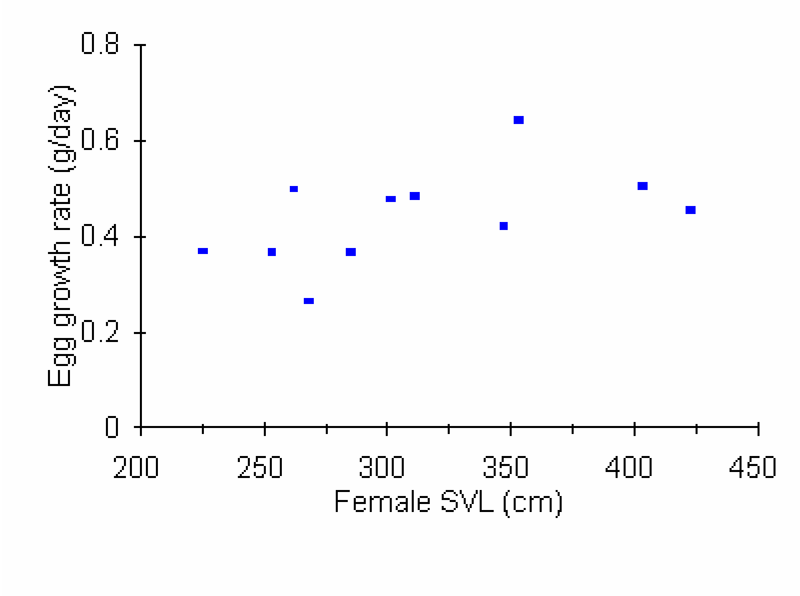


Figure 5-19. Growth rate of embryos of female anacondas in relation to female SVL (r= 0.527; p = 0.096; n = 11)

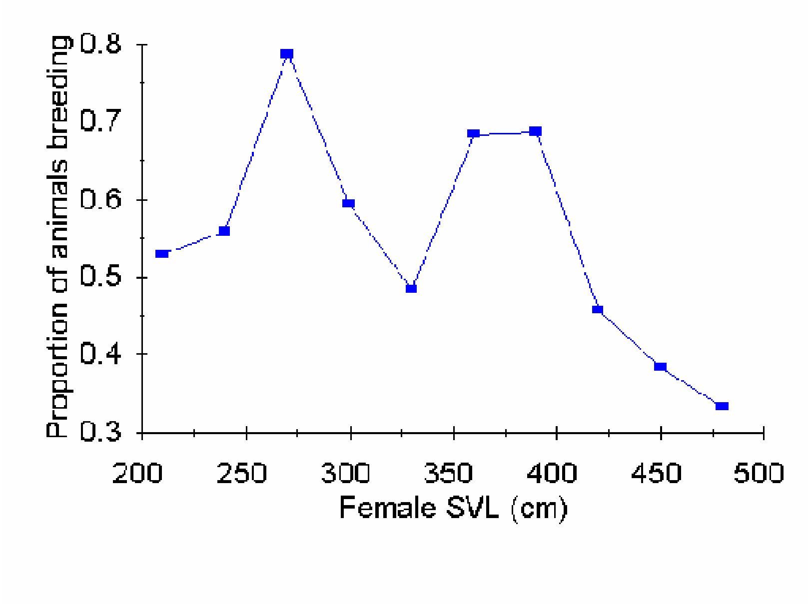


Figure 5-20. Proportion of pregnant females anaconda in different size classes. Calculated from the capture of the total sample (n =222) by using the condition index.

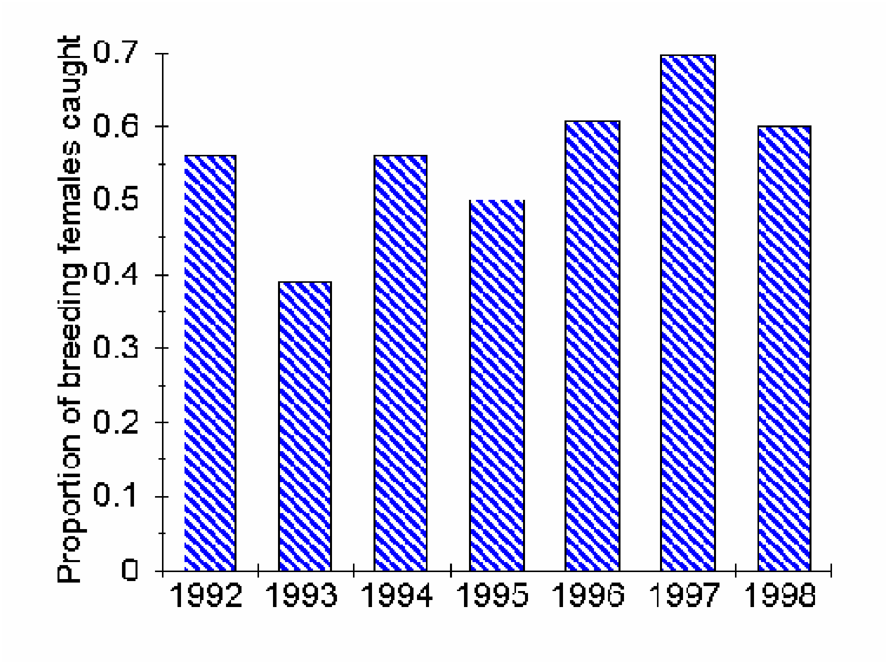


Figure 5-21. Proportion of breeding female anaconda per year of study calcualted with the condition index.

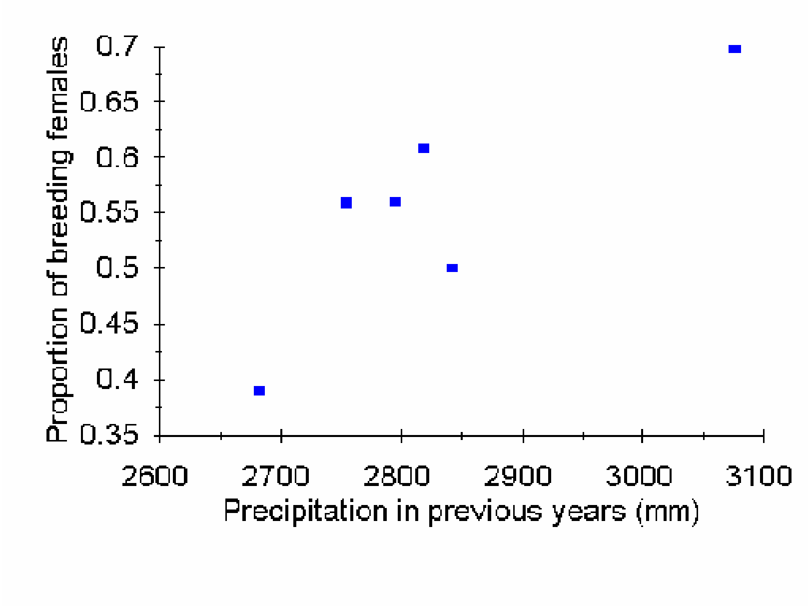


Figure 5-22. Proportion of breeding female anacondas found in relation to the total precipitation of the two former years (r = 0.66; p = 0.16; n = 6).

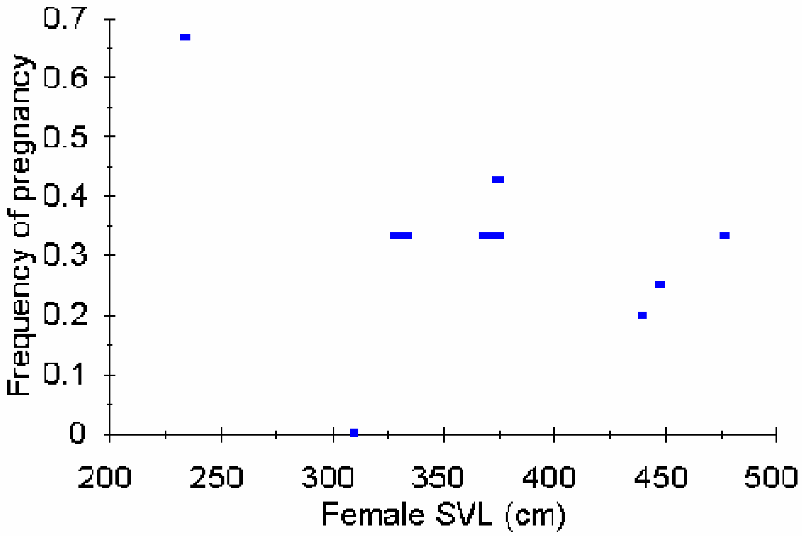


Figure 5-23. Frequency of reproduction of female anacondas that were caught in several consecutive years and were breeding in at least one (r= -0.805; p= 0.005; n= 10).

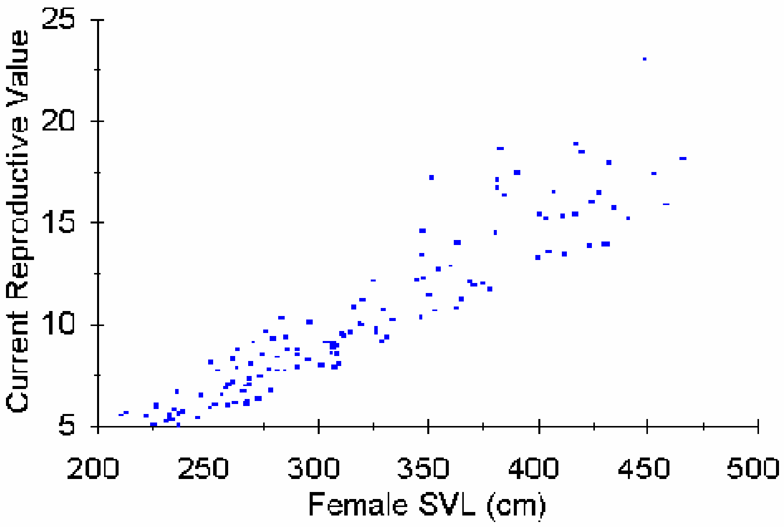


Figure 5-24. Relationship between the reproductive value (breeding frequency multiplied by the clutch size) and SVL of female anacondas (r = 0.902; p < 0.000; n = 129) .

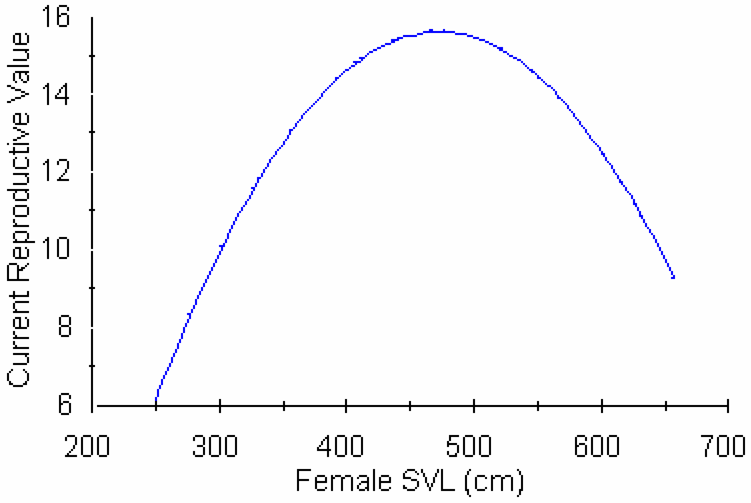


Figure 5-25. Model for anacondas of the expected ontogenetic change in the Current Reproductive Value (CRV). The CRV is calculated by multiplying the expected breeding frequency by the expected clutch size.

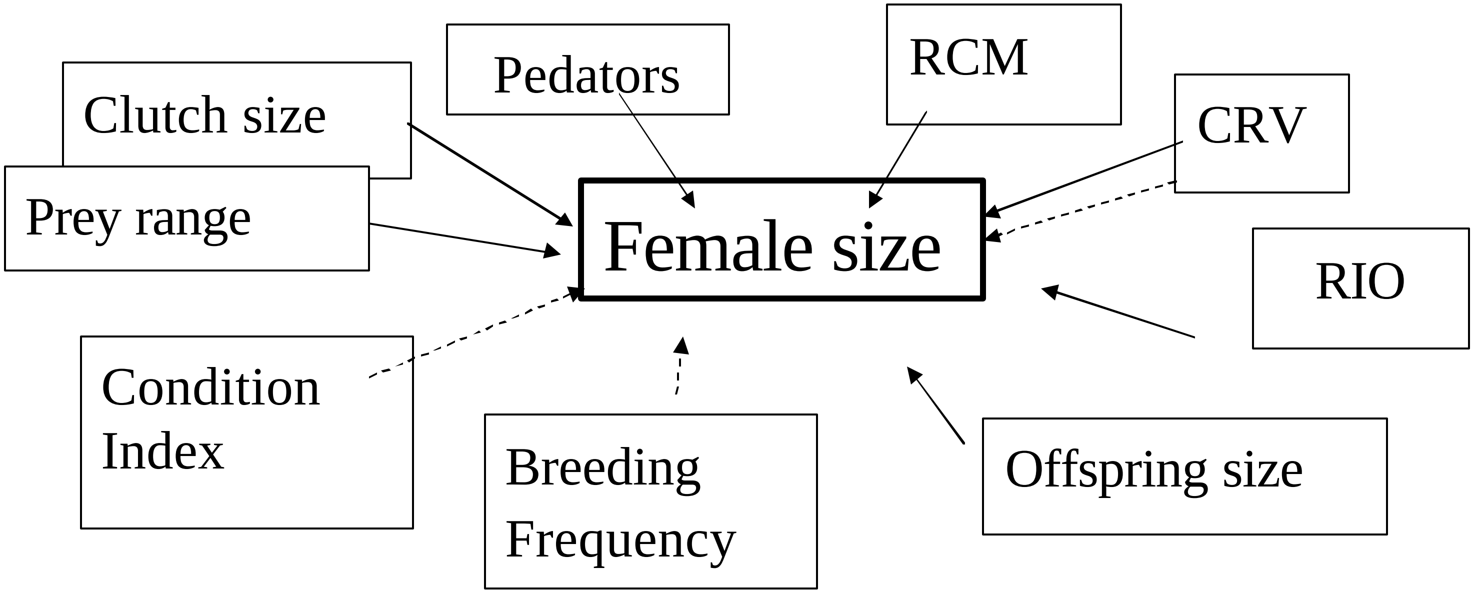


Figure 5-26 Selection presures affecting female size in green anaconda. Those selection presures that increase the female size are represented with a solid line. Those that limit or decrease female size are represented with a dashed line. RIO = relative investment per offspring, RCM = relative clutch mass, CRV = current reproductive value. CRV represents the yearly clutch size of the animal in a given size and selects for and optimum female size; so, it is represented with both arrows.

# CHAPTER 6 MATING SYSTEM AND SEXUAL SIZE DIMORPHISM OF THE GREEN ANACONDA (*Eunectes murinus*).

## 6.1 INTRODUCTION

The amount of energy that each sex invests in reproduction may not necessarily be equal. Males produce smaller gametes than females (anisogamy) and the subsequent investment and behavior of the individual is influenced by this first premise (Bateman, 1948). In general terms, males will benefit most by achieving many matings while the females will benefit most from selective matings with the "best" males. Mating with less fit individuals represents a low cost for males, and a high cost for females. Males are therefore generally polygynous while females are "choosy." However, if males have few possibilities for obtaining other mates, or if they invest a lot of resources in every mating, it may pay for them to be "choosy" as well (Arnold and Duval 1994; Reynolds and Harvey 1994; Trivers, 1972).

Mating systems can influence other traits in the life history of a species. Sexual size dimorphism has been documented in many species and has been a topic of much controversy. If males and females develop different sizes it is assumed that they are under different selection pressures. Here I summarize the most common benefit and disadvantage that each sex experiences for large and small size applied to snakes. Both sexes benefit from large size because of: 1) increased number and kinds of prey available and the range of prey sizes that it can ingest, 2) deterrence of predators and reduced vulnerability to their attacks (Curio 1976), 3) lower relative energetic costs and higher thermal inertia, which allow them to cope better with temporary shortage of food (Pough 1973). For females in particular, large size benefits in: 1) higher fecundity related to a large coelomic cavity, and 2) the production of large offspring that can potentially have a better chance of survival (Ford and Siegel 1989*a*; Shine 1994*b*; Chapter 5). Males benefit from large size because: 1) it may allow them to win mating tournaments and accomplish more matings, and 2) it increases sperm production due to allometric increase in testis size that gives them advantage in sperm competition (Andersson 1994). Large size also can be costly since it involves higher cost of maintenance and increases the risk of starvation in time of prolonged food shortage (Clutton-Brock et al. 1985; Wikelski et al 1997). While larger animals can go without food for a longer time than smaller ones due to their larger reserves, they have larger daily expenses in survival. For instance, male marine iguanas (*Amblyrhynchus cristatus*) are under strong selection pressure for large size due to mating advantages, but each time that the El Niño effect is strong, the largest suffer much higher mortality than the smaller animals due to food shortage (Wikelski et al. 1997). Also, with larger size there may be a higher absolute cost of mobility, which is especially costly in males that have to look for females for mating. In addition, there is a greater detection chance by predators (Shine 1993). Finally, larger size involves longer maturation time (Table 6-1 for a summary; Andersson 1994).

In some species larger males can win more combats, drive away more rivals, and thus monopolize more females (Darwin, 1871; Trivers, 1972). For example, large size enables males to out-compete other males and obtain more mates in mammals (Clutton-Brock 1988), lizards (Dugan, 1982; Rodda, 1992; Stamps, 1983), and snakes (Madsen et al. 1993; Madsen and Shine 1993; Schuett and Gillingham 1989; Shine and Fitzgerald 1995; Weatherhead et al. 1995).

In some male lizards, large body size allows forced copulation with smaller sized females (Dugan, 1982; Rodda 1992). However, in snakes, males are apparently unable to forcibly copulate with the females (Devine 1975; 1984; Shine, 1993).

The underlying causes of Sexual Size Dimorphism (hereafter SSD) in snakes has been a subject of much controversy. Shine (1994*a*) reviewed sexual dimorphism in snakes related to male-male combat and provided a revised theoretical model. Although males are generally larger compared to conspecific females in those species that have male-male combat, the relationship is not universal. Shine (1978) argued male biased SSD occurs when males fight physically over females and large size enhances the opportunities of the males to mate. Later (Shine 1993; 1994*a*) he added that the determinant for SSD is the Operational Sex Ratio (OSR). If the probability of encounter of two or more males with a female is low, then male-male combat is not likely to occur. Hence, there is no selection pressure for the evolution of large body size in males. Rather, sexual selection acts to refine abilities to locate the female (scramble competition; Andersson, 1994). Shine (1993) speculated that this should occur when species are in low densities, in aquatic or arboreal habitats, or utilize locomotion methods that do not leave a continuous track, such as side-winding. If there is no selection for large size in males, females biased SSD is a result of natural selection for large female size. There are other species, however, where males fight over the females or obtain more matings if they are larger, and yet females are the larger sex. This has been found in the European adder snake (*Vipera berus* Madsen et al. 1993); European grass snake (*Natrix natrix;* Madsen and Shine 1993*b*), and Northern water snake (*Nerodia sipedon*; Weatherhead et al. 1995).

The paucity of data on natural mating of snakes, and the poor diversity of taxa studied, compromise our understanding of the issue. Although the knowledge of reproductive ecology of snakes has improved greatly during the last few years (Duvall et al. 1993; Duvall and Schuett 1997; Gillingham 1987; Ford and Holland 1990; 1986; Luiselli 1996; Madsen and Shine 1993a; Seigel and Ford 1987; Shine 1994*a*; Shine and Fitzgerald 1995), most of these investigations have concerned North American and European natricines and vipers or Australian pythonids. Very little is known about neotropical species (Seigel and Ford, 1987).

Another major gap in our knowledge of snake ecology is the lack of information based on field research (Slip and Shine 1988). Most of the literature concerning snake mating ecology has been performed in captivity, at best with naturalistic enclosures. Published studies of the reproductive ecology of the group are dominated by notes on animals in captivity (Barker et al 1979; Carpenter et al. 1978; Gillingham and Chambers 1982; Hammond, 1988; Perry-Richardson, 1991; Schuett and Schuett, 1995; Tolson, 1983; 1991 among others). Two field studies on the ecology of diamond python, *Morelia spilota* (Shine and Fitzgerald 1995; Slip and Shine 1988) and some studies on the reproductive ecology of the west Indian boas (Tolson, 1992; Tolson and Henderson, 1993) constitute the few references available from field studies, but information about mainland neotropical species is lacking. Long-term field studies are required to understand the evolutionary forces acting on the snakes and their behavioral ecology (Duvall et al. 1993).

The study of life histories and field ethology has been seen as old-fashioned unless focused on answering specific, theory driven questions. However, objective, accurate and descriptive information of what the life of the animal is like is invaluable for an unbiased understanding of a species' ecology and evolutionary history; such observations do not lose validity with every new interpretation of natural phenomena (Greene 1993; Rivas 1997). This research is especially important in secretive species that occur in areas of low human density, such as the green anaconda (*Eunectes murinus*), where information from the field is only anecdotal at best. In this chapter I present field data of the mating system of anacondas and new interpretations in the mating system of other snakes and discuss some of the forces behind it.

## 6.2 METHODS

### Data collection

The field work was carried out during the dry seasons from 1992 to 1998. I did systematic searches by shuffling in the few water bodies that retained water and detecting the animals by feeling them with feet and poles or by visual contact (Chapter 2). In the height of the dry season, I often found masses of several snakes coiling around each other; these turned out to be breeding aggregations composed of a female and several males (hereafter, breeding balls; Figure 6-1). I captured all the animals that were in and within five meters of the breeding balls, processed them, and released them within 24 hours of the capture.

I was able to monitor the development of several breeding balls by force-feeding radio transmitters to 15 females (Chapter 2). Eleven of these females were recaptured after mating was over. These animals were kept in captivity until they gave birth (Chapter 5). I also studied the mating of four females in outdoor enclosures with all the males that where with her in the field. In addition, I monitored the duration of the breeding ball around three unmarked breeding females in the wild by visual observation and, if not evident, searching thoroughly in the places where they were seen. I attempted to film the mating behavior in captivity at the Wildlife Park (WCS, formerly Bronx Zoo) in order to make a thorough description of the mating, but the animals did not make a ball when I tried to film them. Some to the information gathered there is used for the analysis of the findings in the field.

I force-fed radiotransmitters to 28 adult males, to study the duration of males in the breeding aggregations, and to assess male's breeding investment (Chapter 2). I also collected data on duration of courtship from 16 males that I caught more than once in a breeding ball, as well as 3 males held in outdoors enclosures on the ranches where the study was carried out. Nine radio-implanted males were studied after they found a female. Seven of them rejoined the breeding ball after the breeding ball was perturbed. I dropped the two males that did not re-join the ball assuming that the capture might have influenced their behavior. Ten more males were studied by following the radio-implanted females they were courting; while 11 others were re-captured by chance in the breeding ball later. This also allowed me to determine the minimum time they stayed in the aggregation. The data analyses consisted of non-parametric correlations, and mean and variance comparisons performed with SAS 6.10. I did a Levene test to compare the variances (Madansky 1988). I also used the coefficient of variance; which is a statistic that measures the variance in units of the means. Its calculation and statistical inferences are in Sokal and Braumanm (1980; Chapter 3).

## 6.3 RESULTS

### Breeding balls

The first striking finding from examining the composition of the animals caught is the enormous sexual size dimorphism found in the breeding balls (Table 6-2). Each breeding ball was made up of one female and 1 to 13 males (mean 3.83; median = 3; Figure 6-2). The males coil around the female in shallow water forming a mass that usually breaks the surface through the aquatic vegetation. Occasionally, the female lays on the ground at the water's edge, or partially buried in mud. Large females often were found in very shallow water or even on completely dry land. Males remain coiled around the female for many days (see below). In the breeding balls the males coil around the female sometimes covering up her entire body, but usually just the caudal end. In order to provide a description of the mating aggregation, I here summarize serendipitous observations collected in the field before the capture of the breeding balls.

While coiling around her body, the males scratch the female with their spurs, moving them very rapidly in a "tickling fashion". Males also poke the female with their spurs, inducing her to move, and attempting to place their cloaca facing her cloaca. The movement of the spurs occurs in bouts, typically 10 to 30 seconds in duration. Often the female moves or twitches as a response, allowing the male to continue maneuvering his tail under and around the female's tail. The spur movement seems to be an important feature of courtship in anacondas.

When a new male joins a ball he coils around it and starts pushing his way towards the female's cloaca. The other males responded to the arrival of a new male by tightening their coils and attempting to push out the newcomer with their bodies. On several occasions I saw males coiling around the female's neck apparently courting the "wrong end" of the female. On several occasions I also saw some males coiling and "courting" around the tail of a large male, apparently confusing him with the female due to his large size. In one instance a very small female (275 cm TL, 11 Kg) was courted by four males, two of which were relatively large specimens (277 cm TL, 8.75 Kg and 280 cm Tl, 8 Kg) I saw these males being courted with spurs and coiled by other males in the breeding ball. In another ball a very large male (310 cm and 11.5 Kg) was courting a very large female (470 cm 68 Kg) with other 9 males of various sizes. I caught them all and put them in a cage to observe the mating. The animals resumed the breeding ball shortly after processing, and mating continued for another 12 days. On one occasion the female moved out of the water and the males hung on to her. Some males, however, were knocked off the female and were scrambling over each other to regain their positions. At that moment the large male who was following the female was clearly mistaken for the female, and several males (sizes ranging from 2.75 Kg to 5.5 Kg) coiled around him performing the spur courtship on his body (Figure 6-3).

In all the events I observed, I never saw any actual or ritualized combat, as described in the literature for other snake species (Gillingham 1987; Gillingham, et al 1983; Tolson 1992). However, the males can only mate if their vent is near the female's, so slow motion wrestling might be happening, where males push each other from the female's cloaca. The mating aggregation does not reveal much movement to the human eye, and it is difficult to appreciate what happens in it. Preliminary analysis of time lapse video taken from a wild caught breeding ball mating in a cage shows that the males are breathing very heavily; by speeding up the footage the generalized panting of the males is obvious, but it cannot be studied in real time. This panting is not apparent in time lapse footage of single male mating couples staged in captivity at the Bronx zoo. This supports the idea that the animals in the breeding balls are, indeed, struggling physically even though there is no obvious fighting.

On 13 occasions I documented actual copulation during the capture of 11 of these breeding balls (two breeding females were seen mating twice). Hence, courtship and mating do take place within the mating ball. In one instance, I observed actual copulation occurring (i.e. hemipenis inside of the female's cloaca) before I captured them. The copulation lasted for 100 minutes, until dusk, when I had to disturb the animals to collect body measurements. Even at the moment of capture, the male tightened his coils, preventing my hand from getting between his loops. When the resistance of the male was finally overcome the female coiled her tail, gripping the male and preventing him from being removed from his position. Up to this point, the animals were not aware of my presence due to their heads and eyes being under the water and mud. The behavior probably was intended to prevent an arriving male from replacing the mating one. This observation also suggests that females are active participant in mating and not just passively accepting a copulating male.

### Breeding season

Breeding balls were observed from mid-February until the end of May (Figure 6-4). Early in the dry season (January, February, and March) it is common to see males actively tongue-flicking, presumably tracking females across different water bodies. It is even possible to find breeding females by radio-tracking searching males (Chapter 2). Searching males move long distances, tongue-flicking thoroughly both the substrate and the air, often crawling on dry land and shallow water (Chapter 3). Larger females were found breeding later in the season than smaller ones as suggested by the modest negative correlation between the size of the female and the date that it was found mating ($r= -0.25$; $p= 0.095$; $n= 46$; Figure 6-5); perhaps a consequence of their larger size that needs more time to gather the heat they need. I was able to monitor the duration of 21 breeding aggregations. The breeding balls lasted for an average of 18 days (range 2- 46; Figure 6-6).

Most breeding balls were captured when first sighted, in order to record data from the individuals. On average, individual males stayed 14 days in the breeding balls; some males stayed with the female until the end of the attractive period (range = 5 - 40; Figure 6-7). I have no information about receptivity of the female to males, so by attractive period I mean the period during which the males are attracted to the females. Again, most animals were found in breeding aggregations and the reported duration probably underestimates the actual time that the each male invests in each female, yielding an OSR of 1:3.83. The sex ratio found in mark and recapture of the entire adult population was nearly even (1:1.22; Chapter 3), so not all the animals in the population are participating in breeding balls every year. Adult female anacondas are longer than males ($t= 15.67$; $p < 0.000$) and heavier in mass ($t -17.64$; $p < 0.000$). Males showed a smaller variance in sizes than females (Levene test, $F= 71.51$; $p < 0.0001$;Table 6-2; Figure 6-8).

Male tails are shorter (37.44) than female tails (49.06) in absolute size ($t= 5.48$; $df= 195$; $p<0.000$;), due to the large sexual size dimorphism. However, the relative tail length (RTL, tail length/svl) in males is larger than in females (t-test; $t= 7.35$ $p< 0.000$; $df= 195$). Males have longer and more slender tails than do females. The variance in tail length is smaller for males than for females (Levene test; $F= 11.58$ $p<0.001$). The CV of the tail length is also significantly different between males (0.155) and females (1.021; $t= 28.54$; $df = 223$; $p< 0.000$;) with males showing much smaller variance than females. The RTL of smaller males is significantly larger than the RTL of lager animals (Figure 6-9; r= -0.388; p<0.000; n = 177).

It is also possible to differentiate sex by the size of the spurs, as they are much larger in males than in females (Figure 3-6). Males have absolutely longer spurs (7.47 mm) than the females (5.13 mm; t= 8.49; p<0.000; df= 51) despite the difference in size of the females. The variance in spur length of the sexes did not differ (Levene test; F= 1.39 p< 0.243) but the coefficient of variation of males (0.784) is significantly smaller than the CV of females (0.98; t= 2.17; p< 0.025). There was no obvious difference in coloration or pattern between sexes.

## Mating System

Due to the long duration of mating aggregations and the fact that they usually take place under water or under vegetation, it was not possible to perform detailed observations of mating in the field. However, I did not observe combat interaction among the males other than pushing. Presumably, the largest male can push other animals from the area around the cloaca, preventing them from mating. Hence, a mating advantage for large animals should be expected. During some of the captures, I managed to keep track of the animals that were mating or around the cloaca in multi-male aggregations. The male coiled around the cloaca was the largest of the group in only 8 of the sixteen balls analyzed. Thus, evidence for advantage for large size is inconclusive. Eight out of sixteen does not seem different than chance for a null hypothesis of 50% probability of occupying that position, but if we consider that the breeding ball is composed by more than 2 (average 3.83) males, then 0.5 might be different than chance. Sadly the variance in the size of the breeding balls and small sample size prevents any simple solution to this problem. In some breeding balls that were in cages, it seemed that the smaller males abandoned the ball first as if they had been excluded from the female; but the fact that they did court a joined the female for several days prevent from drawing any conclusion. In any instance it is apparent at this point that a larger animal does not have certainty of mating and among the determinants of males' mating success, size is only one of the factors.

I documented some instances of several males copulating with one female. I found sperm plugs in 9 captured females that came out during processing. The sperm plugs are made of a friable white mass that produces a strong scent. The mean dimensions from two plugs that looked relatively complete were 7.5 x 1.9 x 0.8 cm; one plug weighted 7.5 gr. (Figure 6-10). Microscopic and pathologic analysis revealed the presence of acellular protein and moderate amount of spermatozoa. These 9 females were being courted at the time I caught them. Thus, the presence of a sperm plug does not prevent females from being courted. In one case studied in captivity, the actual mating was observed. Two days later the sperm plug came loose from the female that was still being courted and coiled by two males (the male that mated included). From another female that was in a cage I collected 5 sperm plugs in the water in a lapse of 12 days.

I did not document any instances of males mating with more than one female. Two males were found in two breeding balls during the same year, but due to our intervention (catching the animals), I cannot be certain that the male would have joined the second ball without being interrupted the first time. The seven radio-implanted males that were successful in finding females, and that I could follow during the entire period, each found only one female in the whole season. Males appear able to breed every year. Three males were found in breeding balls in consecutive years, while this was never found in females. Females seem to breed every other year or even less often in larger animals (Chapter 5).

I found a positive correlation between female's mass and the average size of the males courting her (r = 0.38; p = 0.010; n = 45; Figure 6-11). This suggests exclusion of smaller males from the breeding balls by larger animals. Larger females were also courted by a larger number of males (r= 0.48; p = 0.001; n = 46; Figure 6-12).

A partial correlation between the proportion of live offspring at birth and the number of males courting the females while holding the effect of the female size constant supports the prediction that females mated with larger number of males have a higher breeding success (r= 0.51; p= 0.027; n = 13; Figure 6-13); which suggests benefit of mating with multiple males. Some of the animals showed a relatively high number of infertile eggs as compared with other animals whose mating was not monitored; this suggests that the very monitoring of the mating might affect the results (Chapter 5).

One of the females studied, Marion (TL= 475 cm; weigh = 70 Kg) was found in an isolated section of river in the only patch of aquatic vegetation in several km of river. I radio-implanted her because I predicted that she was going to breed based on her condition index (Chapter 4) and it would afford a good opportunity to study a breeding ball from the beginning without the disturbance of the capture. I found the animal and made visual contact with her every other day at least, until the time when the savanna flooded. Despite the close monitoring, she was never seen mating or courted by males. However, based on the radio telemetry observations, she behaved as if she was pregnant; she made infrequent movements, moved little and basked frequently (Chapter 3 and 5) which made me decide to catch her shortly before the delivery season. Marion gave birth to 32 stillborn (18 females 14 males; see below) and 16 infertile eggs.

Smaller breeding females were often found covered by mud or aquatic vegetation while large ones where more often found in shallower water or on dry land. Larger females were calm and sedate while smaller ones were more likely to bite and more ready to flee.

## 6.4 DISCUSSION

### Breeding balls and the Operational Sex Ratio

This is the first study of the mating system of any South American boid in the wild and the first contribution to the study of anaconda reproductive biology. Although some reports of anacondas forming aggregations exist in the literature (Blomberg 1956; López 1984) no formal attempt to identify the sex of the animals involved was made; this thus, the first documentation of a mating aggregation of breeding anacondas and the first record of their extraordinary SSD.

The breeding balls show a highly male biased OSR (1:4.2), despite the fact that the adult sex ratio is fairly even. Females make a large reproductive investment, investing on average almost 40% of their post-birth body mass in reproduction; which prevents them from breeding every year (Chapter 5). This male biased OSR increases the intra-sexual selection in males, and the competition for access to the females.

The activity in the breeding ball is very hard to observe since it occurs in the water under vegetation and with several snakes intertwined, which make systematic observations difficult to do. The spur movement seems to be a way to court the female as well as locate the female's cloaca and manipulate her into position for mating. The female clearly reacts to the males poking at her by moving and allowing the males to maneuver with their tails. The difference in size of the spurs between males and females, and the smaller variance in spur size in males, suggest that they are under the effect of selection, perhaps related to mating advantages. The spur movement observed was similar to that found in courtship of other snake species (Carpenter et al. 1978; Charles et al 1985; Gillingham and Chambers 1982; Slip and Shine 1988; Tolson 1980; 1992)..

The duration of copulation is variable among the few boids which have been studied. In captive *Epicrates* spp, courtship can last for about two weeks and copulation can last from 30 minutes to nine hours (Tolson, 1992). In *Morelia spilota* mating aggregations can last 4 to 6 weeks (Slip and Shine 1988; Shine and Fitzgerald 1995). Strimple (1996) reports that the mating in captive anacondas can last up to two hours anacondas. Hence, wild anacondas fall within the range reported for other large-sized species. Risk of predation is a limit for mating time and mating aggregations in other smaller-sized snakes. This constraint perhaps does not apply to anacondas due to their large size. The large size of the animals also contributes in decreasing the frequency of eating, since due to their large size the anacondas can endure the long fasting associated with courtship and mating (Chapter 2).

The handling of the water in the llanos might have some influence in the time that the savanna stays flooded and potentially could affect the result found. However, the management does not involve the creation of new habitats but the change in size of the existing; given the large size of the different units it is likely that any effect of the management of the water on the results is only related to the location of the is breeding balls and not any substantial effect on data obtained.

### Male-male competition

What is the nature of the competition among the males? I have never noticed any spur combat, body or tail wrestling, or agonistic display in the breeding balls as described in the literature for other snake species (Gillingham, 1987; Carpenter et al 1978; Hammond 1988; Madsen and Shine, 1993*a*; Shine and Fitzgerald 1995). I was unable to observe the mating with sufficient detail to provide much evidence of male physical competition. However, several males coil around one female, and only the one around the cloaca can mate at the time. This male would be preventing the other males from mating by physically blocking the female's vent. Presumably, a pushing tournament might occur where males exclude each other from the mating position. The generalized panting of the males in the footage suggests that the males were actually physically struggling. This struggle is probably what happened when I tried to separate a copulating pair (see above). Furthermore, the fact that the largest male was in the cloacal position half of the times, even while there were several other males competing with it, suggests that males obtain mating benefit from being large. If there is physical competition for mating, and the largest males have an advantage, sexual selection would benefit the larger males, and large male size would be expected to evolve (Shine 1978*a*; 1993; 1994*a*; Shine and Fitzgerald 1995). This scenario does not seem to be supported by the amazing SSD found.

The positive correlation of female size and the average size of the males courting her (Figure 6-11) suggests that smaller males are excluded from the breeding balls with larger females. Therefore, active exclusion of small males by the larger ones is suggested. Another mechanism to explain this trend is by assortative mating, where smaller males court smaller females with whom they have a better chance of breeding successfully. Larger males could be selecting larger females to maximize their breeding effort. Whether it is due to exclusion of smaller males or an ontogenetic switch in mating strategy, the correlation between the size of males and females can be interpreted as further evidence of physical competition among the males. An alternative scenario to explain such correlation is by habitat selection. Smaller males might be limited to search in deeper water covered by aquatic vegetation to prevent predation and thus they are more likely to find smaller females that, for the same reason, use these habitats more than larger ones. This would produce the correlation found without involving physical competition among the males, but it would still mean a larger benefit for larger males, since larger females produce larger clutches; thus selection pressure for large size still exists. This also provides a mechanism to explain the presence of different strategies regarding breeding investment mentioned in Chapter 5.

Breeding balls are relatively common among large snakes. Starin and Burghardt (1992) report seasonal occurrence of groups of African rock python (*Python sebae*) and they speculated that they were mating aggregations. Slip and Shine (1988) reported similar mating aggregations in the carpet python *Morelia spilota* (Slip and Shine 1988), except that in anacondas the animals are all coiled around each other while in *M. spilota* the males may remain in the same areas without apparently much physical contact. This is the reason that some populations of *M. spilota* do not show male combat since the presence of other males involves the risk that a third male might mate while two males are fighting. They in turn mate with the female without combating or guarding (Slip and Shine 1988). However, other populations of the same species do show male combats and do not present aggregations normally (Shine and Fitzgerald 1995). Interestingly, long-term captive anacondas mate without the male coiling around the female (Holmstrom personal communication; Rivas unpublished). In the field however even single-male mating aggregations show the male coiling his tail around the female’s tail. Coiling might give the males more physical leverage to hold on their position when another males replace him from the female’s cloaca.

Males do not necessarily need to fight over the female to prevent other males from mating. The use of sperm plugs has been reported as a method to prevent other males from mating. Male garter snakes (*Thamnophis sirtalis*) are reported to leave a sperm plug in the female's cloaca which remains for 2 to 4 days, which functions as physical interference to prevent other males from mating (Devine 1975). The sperm plugs apparently also contain "turn off" pheromones that discourage other males (Ross and Crews, 1977). Nevertheless, they have proven to be “surprisingly ineffective” in preventing multiple insemination in garter snake (Schwartz et al., 1989; p: 269). There is no evidence among anacondas of any chemical deterrence for mating, since nine females that were being courted had sperm plugs. In a species with a lengthy breeding period, such as the anaconda, it is unlikely that the plug would absolutely prevent other males from mating mostly due to the short time that the plug stays in the female. Further, considering their strength and constrictor abilities, it is easy to imagine a mechanism by which the male could remove the plug by squeezing close to the cloaca (assuming that the female is neutral).

Males snakes can use complex and diverse reproductive tactics (Madsen, 1993). Male European Adders (*Vipera berus*) induce an uteral contraction (copulatory plug) in the female following mating (Nilson and Andrén, 1982). Male anacondas could be also making a "hugging plug" by wrapping themselves around the female's vent. Thus, there would be an advantage for strong and large animals that could achieve and keep that position. The male anacondas wrapping around the female’s cloaca preventing other males to mate resembles the behavior reported by O'Leile et al. (1994) for western diamondback rattlesnakes (*Crotalus atrox*) where the male coils over the much smaller female, covering her with his body and thus preventing other males from having physical access to her.

Due to the metabolic constrains of ectothermy and the presence of many other males, it is unlikely that a male can retain the optimal breeding position throughout the breeding period of the female, regardless of his size. A possible strategy in the mating of male anacondas it that they alternate physical competition and sperm competition by leaving a sperm plug when they can no longer maintain the position. After recovery, males might re-enter the struggle. This scenario would account for the permanency of the males in breeding balls. Even at the height of the dry season females seem to be too dispersed and unpredictable for the male to have a good chance in finding other animals in the same season (see below). Thus, males that mate more often, and prevent other males from mating by maintaining the breeding position for longer and/or by using sperm plugs, would have a higher probability of siring offspring. Future studies need to address in better detail the behavior of males in the breeding ball after mating and what variables determine it.

### The male's perspective

If males mated with the first female that they found, I would expect to find no correlation between the traits of the female and the number and size of the males. The positive correlation between size of the females and the number of males courting her; as well as the positive correlation between the average male size with female size, suggests that males actively chose to court larger females. It makes sense for the male to mate with the largest female, since larger females will have both larger clutches and larger offspring. Alternatively this trend could be explained by the female producing more pheromones and manipulating the male's behavior but in any instance it is on his benefit to mate with a larger female since, larger offspring will have higher survival, and, some of them, become into larger females. Hence, mating with larger females produces benefits both in quality and quantity of the offspring (Ford and Seigel 1989*a*, Madsen and Shine, 1992, 1994; 1997). Choosiness in males is explained by a large breeding investment. A sex would be "choosy" if a mating event forfeits future matings (Trivers 1972).

Are the males performing a large breeding investment per individual female? The sperm plug that was removed from the female's vent represents 0.1% the male's mass. It is fairly high if we consider that the sperm plug is not all the sperm that the male ejaculated and the short time that he has to replenish his sperm reserves within a short mating season. In the llanos the breeding period for anacondas is restricted to the driest part of the dry season (approximately 2 months), the period when it is easiest for males to locate receptive females due to the reduction of the size of water bodies. The time during which males are courting an individual female occupies a significant amount of the breeding season. Such a long time devoted to a female may prevent the males from looking for another receptive female within the same season (Figure 6-7 and Figure 6-4).

One of the males with a radio (Richie, 246 cm TL; 5.8 kg) was found next to a large female (Diega, 401 cm TL; 32.Kg). He followed her for 42 days until the time when she became receptive. During the time that I was following Richie, he passed close by other females that were in breeding condition (Chapter 4). He even passed went within 20 meters of an active breeding ball, and did not join it, or courted any of the other females. This strongly suggests that Richie chose to court Diega over the other females; Diega was the largest female that I found in the area.

Thus, the long time spent courting an individual female, the large amount of energy spent in sperm, the long time that the males do not feed during courtship (Chapter 2), the assortative mating with larger females, and the individual preference found in individual animals suggests that males are actually selecting quality of their mating over the quantity. The male choosiness advocates against multiple mating in males as and important selection force, since truly polygynous males should maximize the number of mates and not the quality and none of these trends would be present. Furthermore, high mortality of males associated with trailing females or even courting makes philandering less likely (Chapter 5; Rivas et al. 1999; Rivas and Owens In press)

The proximate mechanism for this male choice could be based on: 1) Larger females producing more pheromones and in that way manipulating the male's behavior, 2) Larger females being easier to find, which result in been encountered by more males (Luiselli 1996), 3) Looking for females of a particular size in the areas where they occur most (larger in shallower water, smaller in relatively deeper water), 4) Individual recognition and preference, or 5) Qualitative differences in the scent of larger females a triggering mechanism in the male's *innenwelt* that we are as yet far from understanding. More long term of studies of individually marked animals are needed to fully understand these issues.

### The female's perspective

Females would benefit by mating with larger males that would provide genes for large size, which would enhance survival of the offspring and reproductive success of the daughters (Chapter 5). If females select larger males that produce larger daughters, larger (more attractive) sons is a by product of this females preference and an added benefit of mating with a large male. Females would benefit also by siring offspring from males that have high ability to find females, or that have higher courting success.

Female anacondas mate more than one time in one season, and potentially with several males. This is suggested by the fact that several females that had sperm plugs, were also being courted. The long duration of the breeding ball and the strongly biased OSR creates opportunities for multiple mating (Barry et al. 1992). Multiple mating and insemination have been reported in several species of snakes (Stille et al., 1986; Slip and Shine, 1988; Schwartz et al., 1989; Barry et al., 1992; Höggren and Tegelström, 1995; McCracken et al. in press).

There has been some discussion about the benefits that a female receives from multiple matings. Slip and Shine (1988) argue that females mate multiply to ensure that they obtain sufficient sperm to fertilize all the eggs, and to reduce the cost of rejecting males. Indeed, some females I caught and interrupted during mating had larger number of infertile eggs when they gave birth than unperturbed females so several matings might be required. Multiple matings might be needed to provide enough sperm to fertilize all the eggs or to provide high diversity of sperm; but this mating need not be with different males since several single-mated females had normal clutches. Further, in captivity anacondas breed regularly with only one male (Holmstrom personal communication; Strimple personal communication). Loman et al. (1988) argue that multiple insemination would guard against the possibility of genetic defects and by increasing the genetic diversity of the brood in unpredictable environments, where the female cannot assess the genetic quality of the male. Offspring diversity would also decrease the competition among siblings. Zeh and Zeh (1996) argued that the use of diverse sperm is a hedge against genetic incompatibility and conflict at the suborganismal level acting among intragenomic units (see also Jennions 1997).

In a system where sperm competition is important then multiple mated females have offspring from spermatically competitive males produces a Fisherian phenomena selecting for males with highly competitive sperm (Keller and Reeve 1995). Madsen et al. (1992) found that multiple mating in *Vipera berus* results in higher proportion of ova being fertilized by males of higher genetic quality, by means of sperm competition. Olsson et al. (1994) showed similar results for *Lacerta agilis*. Seigel and Ford (in press) found that female *Lampropeltis triangulum campbelli* show increased fecundity when mated with several males as opposed to females mated multiply to the same male. My findings suggest that the females benefit also from multiple matings as suggested by the relationship among the number of males in the breeding ball and the higher success of females courted by multiple males.

Females are not expected to engage in multiple matings when a mating event increases the risk of injury or death during or after the mating (Arnqvist, 1989). In anacondas, however, the large size of females poses little risk while mating. This is consistent with the sedate behavior exhibited by large breeding animals and by the increased exposure by larger females when basking and laying on the dry land or very shallow mud. If females mate with many males, then sperm competition should be at work. Multiple matings have been argued to decrease the benefit to the males of being larger since the benefit that a large male might have of mating with a female will be diluted by the fact that other males might mate as well, and the competition may be at the spermatic level. However, larger males can benefit by having larger testes that produce more sperm. This has been found to be the case in pythons where larger males have relatively larger testes than smaller males (Shine et al. 1999*a*; Shine 1999*b*).

Madsen and Shine (1997) reported that, based on recapture of marked clutches, the survival of the clutch was highly determined by its quality and not its quantity. They thus concluded that having high quality offspring was more important than quantity in the female's fitness. If so, selecting for good mates maybe a critical trait in the mating for the females. Female choice has been reported as an important issue in the mating system of snakes (Barry et al, 1992). Male snakes are apparently unable to forcibly copulate with females due to the elongate shape of the body (Shine, 1993). Furthermore, a snake's hemipenis is not designed for forcible penetration by thrusting (Devine, 1975; 1984). For instance, in the genus *Epicrates* copulation cannot be accomplished if the female does not open the cloaca and allows intromission (Tolson, 1992); and a similar phenomenon seems to occur in other species such as *Agkistrodon contortix* (Schuett and Gillingham, 1988) and *Crotalus atrox* (Gillingham et al., 1983). Females are known to be highly selective in mating aggregations; Perry-Richardson et al. (1990) found that female *Thamnophis marcianus* reject some males, even after intromission has occurred. While breeding several generations of *Thamnophis melanogaster* in the laboratory, it has been also noted that sometimes females accept some males and not others (Burghardt, personal communication). Joy and Crews (1988) suggested some individual males may be consistently more successful than others. Female choice may be even more important in robust constrictor species where the females are much larger than the males. My observation of female behavior preventing the male from being removed from his position, suggests that the female does take an important part in the process.

The female can also use other ways to control the paternity of their offspring. Eberhard (1996) reviews the many ways that the female can exert control over the paternity of her clutch using post-copulatory mechanisms; from discarding the sperms of some males to abortion of clutches that are doomed to be killed by a new male in the group. Selective abortion of clutches that had an undesirable sex ratio has been reported in coypu (*Myocastor coypus*) (Gosling 1986). Selective development of some eggs is not among the possibilities presented in the literature, perhaps for lack of significant field evidence that suggest this possibility. The undeveloped fertilized eggs found in one of the females suggests the possibility that the female might be able to develop some individual eggs and stunt or prevent the development of some others. That the female selectively produces the death of some individuals in the womb is an interesting hypothesis that deserves to be studied (Chapter 5).

What are the proximate mechanisms by which the female selects her mates? Females that start signaling earlier in the season will have the benefit of having more males available since few are already committed in breeding balls. This would provide the female with many males to choose from and would encourage competition among them; therefore, by means of signaling prematurely she selects for larger males that can withstand longer duration of competition with other males; while she also gives more time for the largest males to establish themselves.

The analysis of RCM indicates that larger females incur a smaller investment than smaller females. However, RCM might not be the right currency to measure the breeding investment. Larger females are at a greater risk when feeding or hunting and incur a larger risk of death (Chapter 3). Another approach to measure the reproductive investment could be considering the time that the female needs to gather the energy surplus for reproduction since it would compensate for the different scenarios that the animal has to face. This other approach shows that smaller females invest in reproduction the surplus gathered during the last two years of foraging, while the larger females invest the surplus gathered in three or four years. This approach predicts that larger females should be choosier than smaller ones, since siring offspring from unfit males would cost so many years of mortality risk until the next breeding event; while a smaller female only requires two years to breed again. However, to make inferences about the choosiness of the animals is premature until more field data have been gathered and mating preferences are better understood.

Thus it appear that larger males would have an advantage in their ability to out-compete other males in the aggregation by being able to search for females in different habitats with less risk of predation, by having larger testes that gives him an advantage in sperm competition, and by being selected by the female to provide genes for large size for her daughter. Furthermore, homologous morphological traits in males and females are expected to show high genetic correlation (Halliday and Arnold 1987); hence any selection for large size in females should also increase the size of the males. All of these are advantage for large size in males. Males would, of course, suffer some disadvantage of being too large (summarized in Table 6-1), but these benefits seem to out weight the selection pressures for small size summarized.

## Sexual Size Dimorphism

Anacondas have the largest SSD reported in any tetrapod. The largest female I found was 97.5 kg: 40 times heavier than the smallest adult male found (Table 3-1; Table 6-2). This is a SSD without precedent among terrestrial vertebrates; it is rivaled only by the southern elephant seal, *Mirounga leonina* (Bryden 1972). The average female anaconsda is 4.7 times heavier than the average male size, which is larger than the SSD found in most other species of vertebrates.

Large SSD can be explained by a) selection for very large size in females, and/or b) selection for very small size in males. I have already discussed the selection for large size in females (Chapter 5). In the rest of this section I will discuss other selection pressures for male size.

The relationship between male-male combat and male size has been discussed broadly (Shine, 1978*a*; Madsen et al., 1993; Shine, 1993; Madsen and Shine, 1994; Shine and Fitzgerald 1995). These authors argue that large size in males would increase their likelihood of winning combats, and the winners would have a higher probability of breeding. Conversely, a lack of selection pressure for large body size would produce small size in males (Semlitsch and Whitfield-Gibbons, 1982). Unlike other mating aggregations, in anacondas the males are permanently coiling around the female and any struggle would be *over* the female, so the male that positions himself around the cloaca is the only one that has the opportunity to mate. It would benefit the male to stay there for as long a time as possible, either by actually mating, or by preventing other males from subsequent matings (contact guarding; Parker, 1984). Presumably females would benefit for mating with larger males (see above) thus female choice may also favor larger sized-males.

Smaller adult size of males can be explained by increased mobility, which may offer an advantage in terms of locating females and moving on dry land or very shallow water, less conspicuousness, and less energetic requirements (for a revision of the advantages and disadvantages of large size). Other than the advantage for small size summarized in Table 6-1, it can be argued that smaller male size may also be a consequence of early maturation (Weatherhead et al. 1995, Madsen and Shine 1993*c*). Younger males benefit from early reproduction because their fecundity is not dependent on size and breeding early allows them to secure reproduction. Even in those species where male combats occur and the selection for large size is present, some smaller males may have some mating success in some years due to fluctuation in the OSR (Madsen and Shine 1993*c*). The reproductive investment of the males may be relatively low and they do not forfeit much growth by breeding early (Bell 1980); so males would benefit from maturing early as this would give them some chance of breeding (Madsen and Shine 1993*c*; Weatherhead et al 1995). Female biased SSD is the most common scenario among snakes (Shine 1994*b*) and may be the ancestral condition among of the group. Phylogenetic inertia would explain the female biased SSD if there was not a strong selection pressure for large size in males. In the our case with anacondas, the magnitude of the SSD is such that one must look for other reasons. Furthermore, this explanation alone does not account for the difference in variance found between both sexes. The smaller variance in the male size suggests that they are under a stabilizing selection toward an optimum size (see below).

The possibility of cannibalism is another important element that might influence the SSD. Presumably larger males would be in better condition to prevent predation by the female so the males might benefit from being large. However, the size difference between males and females is such that an increase in male size might not be enough to save him. His size might be constrained for the other reasons (mobility, early maturation etc). Therefore, a male might benefit also from not being to good a meal for the female, and by maintaining an unworthy size that may not be profitable for the female (Chapter 5)

### Optimal male size: wearing the snake's shoes

The dynamics of the breeding ball suggests that there are both some disadvantages and advantages for large size in males. It is possible that the male's size represents the equilibrium between the interaction of several selection forces. There could be other forces leading to small size that would balance them out producing a local optimum.

Rivas and Burghardt (in prep.) proposed that in breeding aggregations the size of the female could be a sex recognition cue for males in the breeding ball by use of tail contact, since eyes and chemosensory organs are facing away. This sets the limit for the maximum size of males at the size of the smallest females, since being mistaken for a female might make the male lose time and effort needed for courting and mating. To seek and court large, bulkier animals makes sense for a male, since larger and thicker females have more offspring (Ford and Seigel 1989*a*; Chapter 5), are more likely to be breeding (Chapter 4), and they are also older and more experienced. Hence, it would benefit males to court the animals with largest girth, both for certainty of courting the right sex (and individual) and for increase of fitness. Thus, SSD could be the key for sex identification in situations where the chemosensory organs are not involved, or the pheromones of the females and scents of the males have impregnated all of the animals in the seething breeding ball. Success may belong to the male who can best discriminate males from females, maneuver into position for copulation, and thwart other males from doing likewise.

Confusion of large males with females in the breeding ball seems to be the case in those events where larger males were coiled and courted by smaller males (Figure 6-3). This confusion seems to have been the case also in the experiments of Madsen and Shine (1993*b*) with grass snakes (*Natrix natrix*), where they report that "Males seemed to become confused between the female's tail and those of other males, and the tails of rival males often become entwined" (p: 562). This also appears in the findings by Noble (1937) where he reports that two small male *Thamnophis sirtalis* courted, for half hour, a large male from another region where the animals were not reproductively active at the time. The hypothesis of SSD as a cue for sex recognition in the breeding ball seems to be supported by fact that the overlap of sizes of males and females is very small (Figure 6-8). Indeed it is possible to accurately assign a sex to an adult individual given only the size and length. If there is a complex of evolutionary forces leading to a "optimal size" in males where they are larger enough to win combat but not too large to be mistaken for a female, stabilizing selection is at work. The size range of males is much narrower than the size range of females (Figure 6-8; Table 6-2) which supports this idea; the significant difference found in the variance and coefficient of variations of males and females also supports this hypothesis. Larger variance in females could be a product of different ages with older snakes being larger than younger ones. The smaller variance in males, however, can be explained by directional selection resulting of selection toward large size to escape predators and perhaps mating advantage in the breeding ball, and a limit of maximum size not to be mistaken for a female. This confusion in males in the breeding balls may not be exclusive to anacondas and a detailed analyses of the relations among the variances females and male size in other species of snakes that form breeding aggregations could shed light on the generality of this phenomena.

In some species SSD occurs at birth, where typically males are born smaller than females (Weatherhead et al 1995; King 1997). This does not seem to be the case in anacondas where the size at birth is not different among the sexes in length or mass (Chapter 5). An explanation for the mechanism of the strong SSD and small variance of male size found is that males growth fast (like females), until they reach the optimum size where they stop. Fast growth rate allows males to escape predation and enter the breeding arena earlier, and stop the growth at some point where it is convenient to keep the optimal size for breeding. This is supported for the mark and recapture data where many males did not experienced any perceptible growth in as many as six years (Chapter 3), however but a better analysis of the population dynamics is needed.

Females experience a switch in diet after reaching about 3 meters in length. They switch towards more energy rich prey items (non-avian prey). This switch in diet from birds to mammals and reptiles might be related to the increase in energy that allows them to growth larger (Chapter 5). Thus a possible proximate mechanism by which males maintain the smaller size is by maintaining a lean bird-based diet and a relatively low feeding frequency. In fact a captive-born male at the Bronx zoo, fed *ad libitum* with mammalian prey developed an exceptional mass of 40 kg which is remarkably higher than the size attained by any of the wild individuals. Sadly, the origin of the animal is unclear since they come from the pet trade or donations that the zoo receive.

Differential maturation among the sexes may be involved in the evolution of this mechanism of sex identification. Females delay maturation since they make a larger breeding effort. Males start breeding earlier and at a smaller size than females; since females need to gather more energy to start breeding and the fecundity independent cost of reproduction is too high to produce a small clutch (Bell 1980; Madsen and Shine 1994). This differential maturation sets the scenario for natural selection to act and SSD can be selected as a method of sex discrimination. Once the females are larger and thicker the stage is set for natural selection to target it as a mechanism of sex discrimination. The idea that natural selection can act on pre-existing traits and use them for complex communication systems has been discussed broadly in the literature. In empid flies, behaviors with an original ecological significance have been incorporated into the ritual of mating and have taken on a different role than they use to (Kessel 1955).

Looking at the female perspective, what decision process is taking place in the female? In a breeding ball the females are courted by several males at the same time. It is very likely that the only way she can discriminate and choose among the males is, again, by relying on tactile cues. Does she have the ability to differentiate from the displays given by the head of the snake in her dorsum or neck, which tail is worthy of her favors? It may be necessary to observe a mating ball three dimensionally from the interior to fully understand the processes involved; using genetic markers to determine which males are successful is only a first step in the analysis needed.

### Mating system

It remains to be explained why breeding balls last for so long. Lengthy mating period involves larger exposure to predators, reduces foraging efficiency, and in males, it forfeits other matings. Here I identify several possible explanations: First, the female is randomly receptive throughout the period, and mates with different males without much discrimination; in which case she is simply encouraging sperm competition among the males (Schuett 1992; Madsen et al 1992; Westneat 1996). Second, she is not initially receptive to the males but puts out pheromone and attracts several males that would compete physically over her; by being receptive only at the end of the period she would be selecting the stronger males that have endured the struggle. Third, females lay in shallow mud making a breeding ball that is conspicuous to predators; she is safe due to her larger size but the smaller males are at risk of predation; thus the handicap principle is at work (Zahavi 1975). Fourth, she entices courtship that allows her to select the best males in the ball by mating selectively with the most appropriate using some criteria unknown to us (perhaps assessing some aspects of the courtship related to the spur movement). It is not clear at this point what the situation is and future studies should address these issues.

In species where the female mates with many males, sperm competition is at work (Parker 1970). Recent models (Westneat 1996) argue that males who mate last have greater benefits for several reasons. First, passive sperm transfer from one compartment to another in the females reproductive tract; so there are fewer sperm that have been lost from the last ejaculation. Second, the displacement of sperm from one ejaculation by another, the later male would flush the ejaculate of former males giving advantage to the later males. Third, stratification of sperm in the compartments of the female's system gives advantage to the last male to mate since when the sperm is going to be used the one that was deposited last is more likely to get to the ovules (Westneat 1996). Much controversy still remains in this issue (Wirtz 1997) but the last mate advantage model may explain the large time the males spend in the breeding aggregation.

Females anacondas are capable of sexual cannibalism (Chapter 3; Rivas and Owens, In press) or simple cannibalism (O'Shea 1994). This imposes a dilemma for the males. The longer he stays with the female the more likely he will sire her offspring and prevent others from doing so; but also the higher the risk that he might be eaten by the female at the end of the breeding period. This selects for refined abilities of the males to detect the mood of the female, and an abrupt dissolution of the ball as opposed to a gradual one. The latter hypothesis is not supported by some field observations.

Another factor to consider for the long duration of the breeding balls is the low probability of encountering other females. Females are not clumped together and have a rather unpredictable distribution; thus males looking for females must travel relatively long distances during which they must faces high risk of predation. It is possible that it does not pay for the males to leave the ball and try to find another female. It is a testable hypothesis that they are better off by trying to secure some offspring from one female once they find one. Duvall et al. (1992) argue that if the chances of the male of finding a female are low the male should improve his convincing abilities once he finds one female. Shine and Fitzgerald (1995) found that males were more insistent in courting a female in those areas where the density of animals (and thus the encounter rate) was lower.

Breeding occurs in the dry season, when the availability of aquatic habitats is low and presumably females are relatively easier to find. Due to the reduction in water level, the encounter rate between males and females increases, and the males are more likely to find the females (Shine 1993; Duvall et al 1992). The breeding season ends as soon as the rains flood the savanna and the anacondas start dispersing. The time that a female is attractive to males is remarkably long compared to the length of the mating season. It is, therefore, unlikely that a male would have enough time to track, court, and mate with another female in the same season. So, males in general might have time to court only one female in a season. Thus, a male biased OSR (driven by large RCM of the females), a short mating season, a long receptive period (perhaps driven by female choice), and high unpredictability of the breeding females, along with relatively high predation risk for males in searching for females, might be responsible for the first instance of a polyandrous mating system in snakes.

Duvall et al. (1993; 1992) proposed a model for the evolution of mating systems that predicts the mating system expected based on the female spatial predictability and female temporal availability. Several types of polygyny can evolve from Female Defense Polygyny (FDP), Prolonged mate search polygyny (PMSP), Explosive mating assemblage (EMA), and hotspot polygyny (HS). They also speculate about the possibility of resource defense polygyny (RSP) as it is present in other taxa. They argue that polyandry is constrained in snakes due to phylogenetic reasons. Anacondas do not fit into any of the patterns described by Duval et al. (1992). The anacondas' mating system in the llanos would be in the corner of the axes with low spatial predictability and lengthy receptive period under a label such as Lasting Breeding Balls Polyandry (LBBP; Figure 6-14)

The lack of the potential for the evolution of this mating system in Duvall's model is understandable due to their lack of any appropriate field data, and the fact that most studies have been conducted on a few taxa (Natricines and Viperids). This lack of geographic and systematic representation in previous studies of snakes mating system did not offer a sufficient gamut of possible mating systems in which to build a model. A better understanding of the dynamics of the breeding of snakes awaits more diversified information on the mating systems based on field studies.

### Fisher's Runaway process

Fisher's runaway process has been used to explain the evolution of exaggerated traits in a species that confer advantage in mate choice. Particularly the development of antlers, size, or other features beyond that dictated by natural selection. Sexual size dimorphism is one of these traits that can develop under a runaway process. Females select large-sized males thus most offspring are sired by a few very large animals and this preference for large males is transmitted to the female's daughters. If females prefer to mate with large males, this locks up the population in an ever increasing positive feed back loop where male's large size grows beyond the required for the survival of the individual (Fisher 1930).

Anacondas and other groups where extreme SSD is found, such as marine mammals share several common features. Such features include: breeding aggregations that suffer relatively low predation pressure, aquatic environment, and general large size; the latter is often correlated with large SSD. It has been proposed that large size marine mammals relaxes several ecological constraints such as predation pressure, competition with other species, and metabolic efficiency, allowing expression in full of the sexually selected characters (Andersson 1994; Lande 1980). Is it possible that an equivalent situation is happening in anacondas leading to the evolution of large size in females? In marine mammals the largest sex clearly obtains a benefit from mating with several females and siring that many more offspring (Le Boeuf and Reiter 1988). Is there in equivalent process in female anacondas?

Female anacondas have a very large variance in the their breeding success, and large females are selected more by choosy males. The preference of males for larger females increases the survival of her clutch, and potentially the fitness of it as well. Thus, male preference increases the female's reproductive output. These are the characteristics that increase the sexual selection gradient in a population (Duvall et al. 1992; 1993; Arnold and Duvall 1994; Wade and Arnold 1980). Thus, it is a testable hypothesis that sexual selection acts by increasing body size in females. The large size of the female can also be a consequence natural selection (Chapter 5) as well as sexual selection favoring large dimensions ("a sexy daughter"). This should be another variable to include in Figure 5-26and could also explain further the presence of females larger than the expected in the model represented on Figure 5-25. Hence, stabilizing selection acting on males for an optimum size, and sexual selection (runaway), along with directional natural selection acting on large size in females would explain the extreme SSD found.

## 6.5 GENERAL DISCUSSION

### Sexual Size Dimorphism in flooded habitats

In Chapter 5, I argued that the situations where I studied the animals are peculiar due to the hyper-seasonal savanna and I speculated what the differences would be in a different habitats such as rivers or deeper environments where the anaconda is likely to have evolved. The llanos is a very recent ecosystem (López-Hernández 1995) and the anacondas probably evolved in the neighboring rain forest or in the ancestral llanos that was some sort of interior sea, perhaps with similar seasonality but more flooded in general terms (Rivero-Blanco and Dixon 1979). In this section I will speculate what the mating system would be of anacondas in other habitats.

Flooded habitats would bring two major differences to the biology of the snakes. One of them is a decrease in the encounter rate among the animals. The rate of encounter between males and females, males and males, and anacondas with other species both prey and predators would be decreased. Deeper water would also involve a lower availability of small prey items (wading birds and fowl) so the diet of the anacondas might be more unpredictable (Chapter 5). The decrease in the encounter rate with prey and the presence of larger and more unpredictable prey would select for the development of larger size, since larger animals can withstand fasting for longer periods. Predation on smaller animals might be decreased due to the lack of encounter with predators so that the pressure for large size to fend off predation in the llanos might be relaxed, but the limitation for lack of small prey may produce a new pressure for large size.

The lower encounter rate between males and females might produce changes in the mating system. If the males find females less often the breeding balls that I found might be less common or might not happen at all. The physical competition among the males might not be as important. Instead high mobility and refined senses to track the females would be selected for. High mobility tends to select for small size since it lowers the energetic costs of moving; however, in water the expenses of locomotion might not be too high either, and this limitation may be relaxed. If the mating balls still occur then selection pressure for large size will still be present. I argued that the females in the river should reach larger sizes (Chapter 5) so the optimal size for a male may be pushed upwards. The SSD in rivers might be the same as we find in the savanna, since both males and females may be larger, but there are so many variables involved that it is difficult to make predictions. Recent studies in mating systems of snakes show an amazing variability of morphs within the same species where one population shows high SSD and no male combats, while another population in a different geographic regions shows violent male combats and no breeding aggregations (Shine and Fitzgerald 1995). At the Bronx Zoo (New York) anacondas mate without the males coiling around the female when they were in pairs (Holmstrom personal communication) and when there were several males as well (Rivas unpublished). However in wild caught single-male breeding balls the males do coil around the female. Thus variability in the males courting behavior of anacondas is also present and deserves to be studied.

### Breeding frequency

I showed how the breeding frequency of the female decreases with age and I argued that in rivers this decrease might be less steep since feeding rates might be higher; alternatively the prey might be more profitable or less risky. However, what would happen if females are fat enough to breed but less likely to be found by males in the lower density of the flooded riparian habitats during the mating season? When the females invest such a large amount of energy and effort in each breeding event, it is very important not to breed without sperm provisioning of the male. It is possible that ovulation does not even start until she is mated, or at least courted in order to ensure that her eggs are going to be fertilized. If there is no male suitor the female is better off by saving the energy for next year when she may be found by males. It has been found that some parts of the female's ovulation may be induced by the courtship, or some seminal substances that the male provides along with the sperm (Eberhard and Cordero 1997; Whittier and Crews 1989; Whittier et al. 1987). However, the female might benefit from breeding whenever she can due to the risk of dying during a feeding event or other causes of mortality; since the influence of CI on the clutch size is not as important as the influence of length (Figure 5-8). If the possibility exists that the males may not be available at the time when the female is ready to breed, she might resort to sperm storage for future reproductive events when she has it available. Long term sperm storage and even facultative parthenogenesis has been reported in several taxa of snakes (Schuett 1992; Schuett et al 1997). Long term sperm storage also might be what happened with Marion who gave birth in an isolated piece of a small river without forming a ball and almost certainly without mating that year. The fact that the offspring were males and females suggest that it was long term sperm storage and not facultative parthenogenesis since the latter produces only males (Schuett et al 1997). The null reproductive success indicates that this way of breeding is not the preferred method and the females is better off at being courted and having a large and perhaps diverse provisioning of sperm to chose from. The sperm that she stored was sperm that she did not use in her last reproduction and was presumably not from the "preferred" male(s).

### Polygyny in snakes

Even though multiple insemination has been documented before (Barry et al. 1992; Gibson and Falls 1975; Höggren and Tegelström 1995; Madsen and Shine 1993; McCracken et al. in press; Schwartz et al. 1989; Shine and Fitzgerald 1995; Stille et al. 1986), this is the first report of polyandry in any snake species. The closest that some authors have come to acknowledging polyandry is by using the word "promiscuity" (Shine and Fitzgerald 1995), but no further discussion is provided to it and all of their findings were analyzed in the light of "female defense polygyny" or "mate-searching polygyny" (p.: 496).

Up to the present all the reports of mating systems of snakes regard them as polygynous (Duvall et al 1992; 1993; Arnold and Duvall 1994; Duvall and Schuett 1997; Shine and Fitzgerald 1995). However, multiple matings by males per breeding season has been largely assumed and seldom documented (Gibson and Falls 1975, Schuett 1982). Often a male courting multiple females is considered as evidence of multiple mating in males without confirming whether those courtships were successful or artifacts of captivity (Weatherhead et al 1995; Shine and Fitzgerald 1995). Furthermore, multiple copulation by one male is not really enough to warrant polygyny, since some matings might not produce any offspring.

Evidence for multiple mating in males is limited to few studies. Blanchard and Blanchard (1942) documented multiple mating of one male *Thamnophis sirtalis sirtalis* but all their observations were on captive animals. Madsen et al (1993) provides perhaps the clearest example of a species where males European adder were found mate multiple times in a season on a regular basis. About half of the males mated with more than one female and about 2/3 of the males accomplish some mating; plus all the females mated with multiple males as well. This does not really resemble the situation of typical polygyny where few males do most of the matings and most males are delegated to bachelorhood (Clutton-Brock et al. 1988; Le Boeuf and Reiter 1988). The high variance in males mating success is the key for sexual selection to exist (Bateman 1948) and a runaway process to occur, and this is not present in the European adders.

The anaconda polyandry might not be just a rare exception to the Duvall et al. (1993) models. True polygyny might not actually be nearly as common in snakes as formerly believed. Several features of the mating system of snakes suggest this. First, the large investment that some males make in single reproductive events (Weatherhead et al. 1995; Madsen and Shine 1993*b;* O'Leile et al 1994) which lower the likelihood that the males mate with mane females. Second, the OSR of many species is male biased (Weatherhead et al. 1995, Slip and Shine 1988; Madsen et al. 1993, Madsen and Shine 1993a, Luiselli 1996) because the females make a very large reproductive investment and they cannot afford to reproduce every year (Madsen and Shine 1993*a*) creating great potential for the female to mate multiply (Barry et al 1992). Third, females have large variance in reproductive success associated with her size (Weatherhead et al. 1995, Shine 1994*b*; Ford and Seigel 1989*a*) which may lead to (fourth) male choossiness in selecting the best female in several species (Luiselli 1996; Garstka et al. 1982) and to an increase in the intensity of sexual selection in females (Wade and Arnold 1980). Finally, the most convincing argument that the dominant mating system in snakes is not polygyny is the very fact that multiple paternity has been found in nearly all the species where is has been studied in detail (Barry et al. 1992; Schwartz et al. 1989; Gibson and Falls 1975; Höggren and Tegelström 1995 Madsen et al. 1992; McCracken et al In press)

There has been great reluctance among researchers to consider that mating in snakes is not polygynous. Duvall and Schuett (1997) found that only 12 of the 28 radio implanted males *Crotalus viridis viridis* were successful in finding females, while 17 of the 21 females studied were courted and presumably mated. Only four of the males courted (and presumably mated) more than one female (9 matings in total), while 12 of the females mated with multiple males (32 mating in total). Notice that the proportion of males that mated with several females (33%) is much lower than the proportion of females that mated with several males (71%). Notice also that the average male that mated did so with 1.4 females while the average female that mated did so with 2.7 males. Surprisingly, the authors insisted in labeling this mating system as a polygynous one (p. 333) despite of the fact that it is clear that multiple mating in males is not the norm and its importance as a trend in the evolutionary scenario of the species is not certain.

Failure to identify polyandry (or at least lack of polygyny) has led to a very long lasting controversy about female biased SSD in species where males fight physically over the females. Madsen and Shine (1993*b*) argue that if females obtain more benefit by being large, then they could be larger than males despite the mating advantages of larger males. In a polygynous mating system however, the benefit of the female of being larger (natural selection) could not be higher than the benefits of males of being large and hence mating with more and larger females (sexual selection). Indeed the sexual selection gradient for the males increases with the female fecundity (Duvall et al 1993; Arnold and Duvall 1994). In other words any increase in fecundity of the female for being large will be followed by a equivalently geometric increase in the male's reproductive output by mating with several of those females with enhanced fecundity. Thus, the explanation of Madsen and Shine (1993*b*) cannot really account for the permanence of female biased SSD in species where larger males have mating advantages unless one considers that the mating system is not really polygynous.

### Sexual selection acting on females

Even in the cases where females are documented to mate multiply and get benefits from multiple mating, the authors have not considered the influence of this particular mating system on the females life history and how it affects the sexual selection gradient and intensity of sexual selection on them. Multiple mating has been considered in regards to how it affects mating success and life history traits of the males, and SSD considering only the male side (Shine and Fitzgerald 1995; Slip and Shine 1988; Madsen et al. 1992; Olsson et al 1996; Madsen and Shine 1993*c;* Madsen and Shine 1992) but no consideration has been given to the effect of it on the female's reproductive biology.

A high sexual selection gradient (SSG) can produce several trends in the mating system of the females that one can identify. To gather this information from the published literature is fairly challenging, since it has never been the aim of the papers and the information is scattered among several taxa. However, it can prompt different analyses that change our understanding of snake ecology and evolution. First, female's reproductive success can increase by accomplishing multiple mating (Madsen et al 1992 Seigel and Ford in press; Olsson et al 1994; this contribution). Second, the large size of the female increases mating success via male choice (Luiselli 1996, Garstka et al 1982; this contribution). Third, larger females have more and/or larger offspring (Ford and Seigel 1989*a*, Shine 1994*b;* Chapter 5). This means that there is some variance in the reproductive success of the females depending on their size; this sets the scenario for sexual selection on female size. It actually might be the case that anacondas meet all of the above characteristics in a more dramatic way than any of the other species or that its larger size allows the full expression of SS.

The difficulty that snake researchers have had in actually having valid data on snakes mating systems has led to much controversy. Perhaps misled by the voluminous sexual selection literature on organisms that do not grow much after adulthood (mammals, birds, and insects) and their theoretical "dogmas", they have overlooked many aspects of snake biology despite the suggestive data they had in hand. This is, perhaps, an undesirable consequence of the male bias among snake biologists (Wilson 1998) that might have prevented the snake biologist from considering the female perspective. Such bias among scientists influencing the interpretation of the biological data has been documented before (Cunningham and Birkhead 1997; Gowaty 1994). To record naively the natural system without any bias or the intention of predicting it has great potential to understand better the natural world by allowing a higher diversity of hypothesis testing in the conceptual framework (Rivas 1997). As argued elsewhere (Rivas and Burghardt in prep), through critical anthropomorphism and consideration of a species' or sexes' *Umwelt*, such research bias can be reduced.

**Snake's evolution and low encounter rate**

To assume polygyny as the general mating system of snakes may appear sensible due to the fact it is the most common mating system in the group that the snakes apparently derived from Thecoglossian lizards (Forstner et al. 1995; Lee 1997;). However, there are several traits of snakes as a group that are different from other squamate reptiles and that can be related to the lack of polygyny. Snake lack the territoriality and the male biased SSD that is the general trend on their ancestors (Phillips 1995, Wikramanayake and Dryden 1988**;** Stamp 1983; Shine 1994*a*). There is yet another important difference between snakes and varanids and it is related to the reproductive investment. Snakes tend to have much larger reproductive investment than lizards (Siegel and Fitch 1984). I believe that an evolutionary environment with a low encounter rate is a likely scenario of the evolution of snakes as a group and could explain the evolution of all these synapomorphies.

There is some controversy regarding the origin of snakes. The latest evidence suggests that the ancestor of snakes was from some maritime origin (Caldwell and Lee 1997) and the more derived groups evolved in some fossorial habitat (Forstner et al 1995**;** Gans 1975**;** Lee 1997; Rieppel 1988). In any case the encounter rate might have been low. In a fossorial environment mobility is constrained and the rate of encounter should be decreased because of this. In a aquatic habitat it would be harder for the animals to follow the scent trails and the encounter rate is also supposed to be low (Shine 1993). Thus a low encounter rate seems to have been the scenario in the evolutionary history of snakes.

I hypothesize that the polygynous mating system y from the ancestral lizard was not functionally possible due to the difficulty of finding females. A male simply could not easily find more than one female in a season due to the low mobility of the males and the high dispersion of the females. This also offers an explanation for the switch in SSD from male biased to female biased. The ancestor did not have male-male combats or territoriality due to the low encounter rates. While the benefits of large size in females continued (larger clutches, survival, wide range of prey), there was no longer a benefit for males to be large. Furthermore, being small was convenient to move around and find females, and the odds of finding other males was too small; so male combats were no longer a selection force for large size. Due to the low encounter rate between females and males (and perhaps with prey too), females might have not bred very often; thus there was no reason to save energy for the next breeding event. The odds of mortality between one breeding event and the next one were too high, so the females went into larger breeding investments in every reproduction. This would explain the higher RCM found snakes compared with lizards.

## 6.6 CONCLUSIONS

Studies of snake mating systems are not abundant, but the few that exist have been the product of long term naturalistic field investigations of high quality. Apparently, though, when these articles were written, the genuine interest of the authors in learning about the animals seemed to have surrendered to a more conventional approach to report the findings to fit the accepted style of writing (Greene 1993).

Female anacondas seem to be able to mate multiply in one season while there is no evidence for this in males. Males seem to select mates of high quality making a high investment per mating. A short mating season, high dispersion of the females, and high cost of mobility for the males might account for a "loosely" polyandrous mating system. There is evidence for spermatic competition from the presence of sperm plugs and multiple mating in females. Physical competition in the breeding balls could also be at work. The complicated dynamic of the breeding balls seem to be involved in the remarkable SSD found in this species.

I have shed some light on the anaconda's mating system but it is still far from being well understood. So far I am unable to determine exactly how males compete for the female, or whether larger males have an advantage in siring more neonates. More field studies involving radio-tagged animals, as well as laboratory experiments, are required to understand such issues as mating success, mate choice, sexual selection forces, natural selection forces, sexual selection gradients, and multiple paternity. DNA analyses are underway to elucidate these issues. A comparative study examining the relative size of the testes among several species of snakes and lizards alike, would help to understand whether sperm competition is an important aspect in the reproductive ecology of the snakes and its evolutionary ancestor.

The previous bias in the pioneer literature regarding mating systems and reproductive investment has led to a lack of understanding of the effect of variance in the female reproductive success in ectothermic vertebrates where females can grow throughout life; and hence their reproductive potential can be a function of their size. Variance in the female's reproductive success has not been yet considered in the literature perhaps due to the lack of documentation. Thus the potential for a runaway process and effect of sexual selection in females has not been properly considered and indeed it might be the key to explaining some unanswered questions in the ecology and mating systems of snakes.

Current models to explain the evolution of mating systems failed to predict polyandry as a possible scenario. The limited number of species from which the basic natural history is known limits our understanding of mating systems in snakes and seems to be responsible for the misinterpretations in the models developed. I endorse the call of several authors (Madsen and Shine 1993a, Siegel and Ford 1987; Shine 1993, Weatherhead et al. 1995) that long term field studies of individually marked animals in different taxa and different geographic regions are needed to test and develop theories regarding the mating system and sexual selection in snakes. The need to widen our horizons and acquire knowledge of natural history of more species must be retaken in order to increase the predictive power of the models and accomplish a better, more objective understanding of nature.

Table 6-1 Advantages and disadvantages of large size for males and females (Rivas and Burghardt in prep)

| | **Benefits of large size** | **Disadvantage of large size** |
|---|---|---|
| **Both sexes** | 1.- Increased number of prey and the ability to subdue them.<br>2.- Deterrence of predators and reduced vulnerability to them.<br>3.- Lower relative energetic cost and higher thermal inertia. | 1.-More easily detected by predators<br>2.- Higher basic maintenance.<br>3.- Lower survival in times of shortage.<br>4.- Higher cost of mobility.<br>5.- Longer maturation time. |
| **Females only** | 4.- Increased fecundity due to increased coelomic capacity that allows larger clutches and larger breeding investment.<br>5.- Females will have larger offspring with larger chances of survival and faster growth. | |
| **Males only** | 6.- Increased number of matings and fitness if there is physical competition for the females.<br>7.- Large testis size that by allometric correlation would produce larger amounts of sperm for sperm competition. | 6.- Increased cost for moving and dispersing in males that are tracking females for mating. |

Table 6-2 Measures of adult anacondas found involved in breeding aggregations. 177 males and 48 females.

| | Total Length (cm) | | | | Snout-Vent Length (cm) | | | | Mass (kg) | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Mean | SD | Min. | Max. | Mean | SD | Min. | Max. | Mean | SD | Min. | Max. |
| Females | 370.4 | 70.6 | 242.7. | 517.3 | 326.2 | 65.9 | 210.7 | 477 | 32.60 | 18.59 | 9.25 | 82.500 |
| Males | 263.2 | 28.3 | 188.3 | 333.7 | 225.9 | 24.7 | 159.3 | 293.7 | 6.96 | 2.07 | 2.45 | 14.300 |

Figure 6-1. Breeding female (Benita, 410 cm TL; 44 kg) at the shore of a canal being courted by 12 males. Photo Tony Rattin.

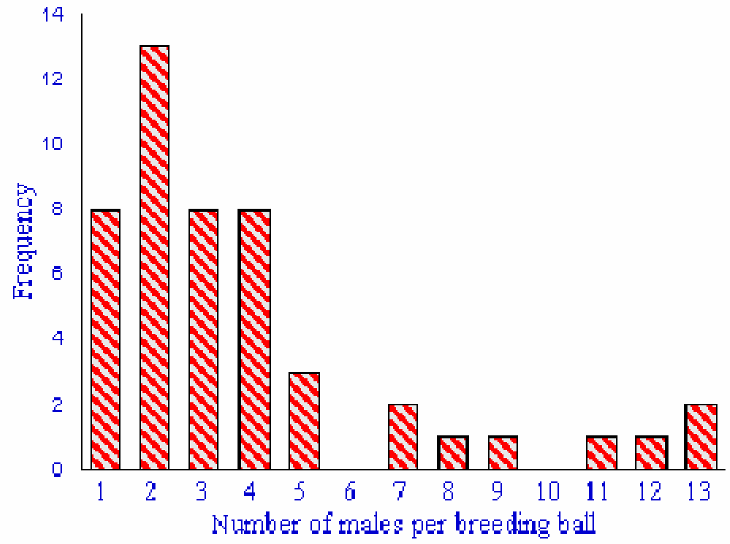


Figure 6-2. Composition (number of males) of the breeding aggregations of anacondas found

Figure 6-3. Mating aggregation of anacondas involving a very large female and some large males. The female moved out of the water and dragged with her some of the males that where coiled around her (A). Other males were removed from their positions and tried to find the female again to continue courtship. However, some smaller males have mistakenly coiled around a very large male and are courting him (B).

Figure 6-4. Number of breeding aggregations of anacondas found during the breeding season in a locality of the Venezuelan llanos. Each bar represents a two-week period.

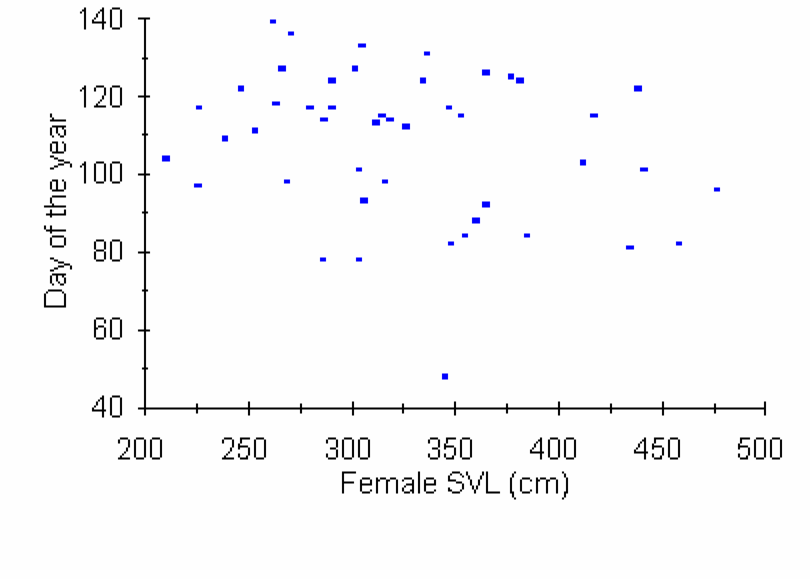


Figure 6-5. Relation between the date in which female anacondas mated and their size. (r = -0.25; p = 0.095; n= 46)

Figure 6-6. Minimum number of days that each breeding ball of anacondas was seen together.

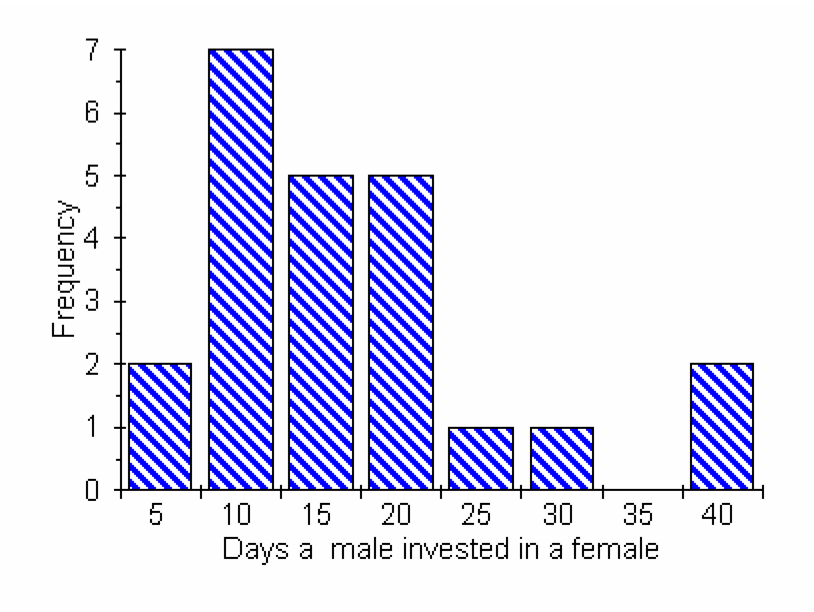


Figure 6-7. Time spent by individual males with a particular female. The time spent was determined by following radio implanted animals or by re-catching them at different times.

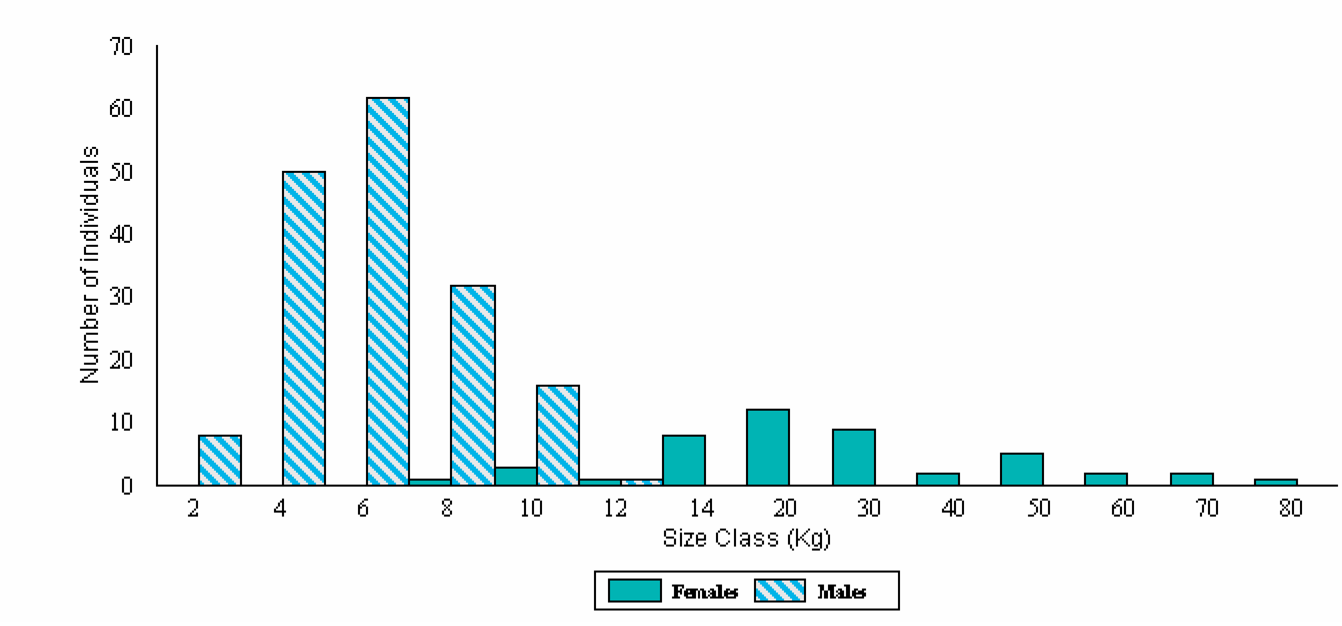


Figure 6-8. Size distribution of the adult population of anacondas. The criteria to determine adulthood was finding them involved in a breeding aggregation. Notice the change in the scale of the “x” axis after 14 Kg.

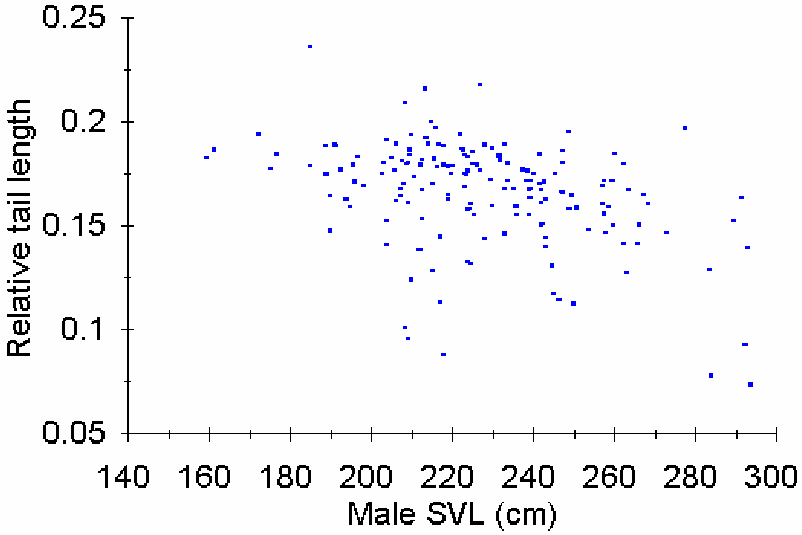


Figure 6-9. Relation between relative tail length (tail length/SVL) of adult male anacondas and the size of the animals. Coefficient of correlation r = -0.388, p<0.000; n = 177.

Figure 6-10 Sperm plug obtained from a breeding female anaconda (see text for dimensions).

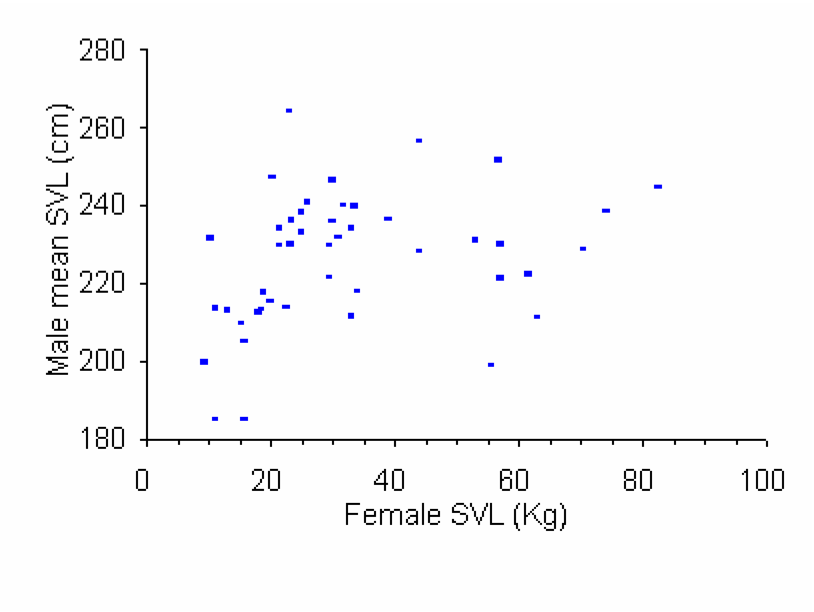


Figure 6-11. Relation of length of the female anaconda and the average length of the males in the breeding ball (r= 0.38; p = 0.009; n = 45).

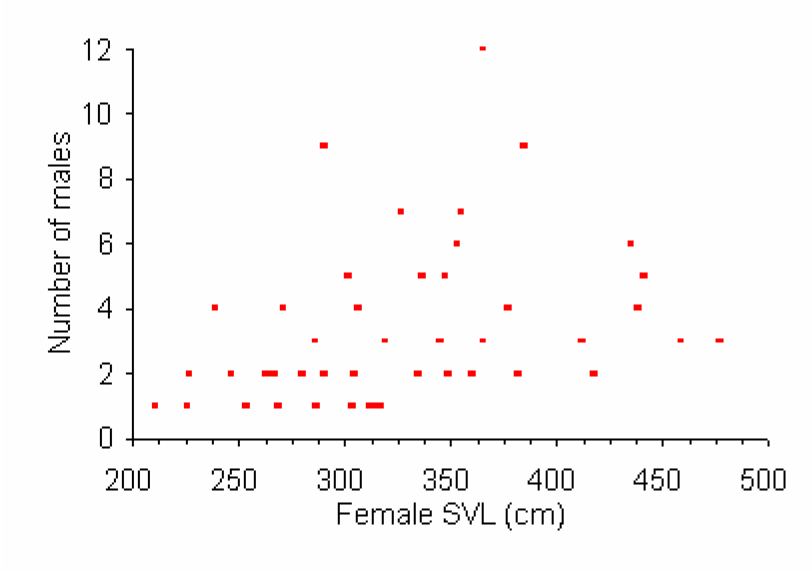


Figure 6-12 Relationship between number of male anacondas in a breeding ball and the length of the female in it (r= 0.48; p= 0.001; n= 46).

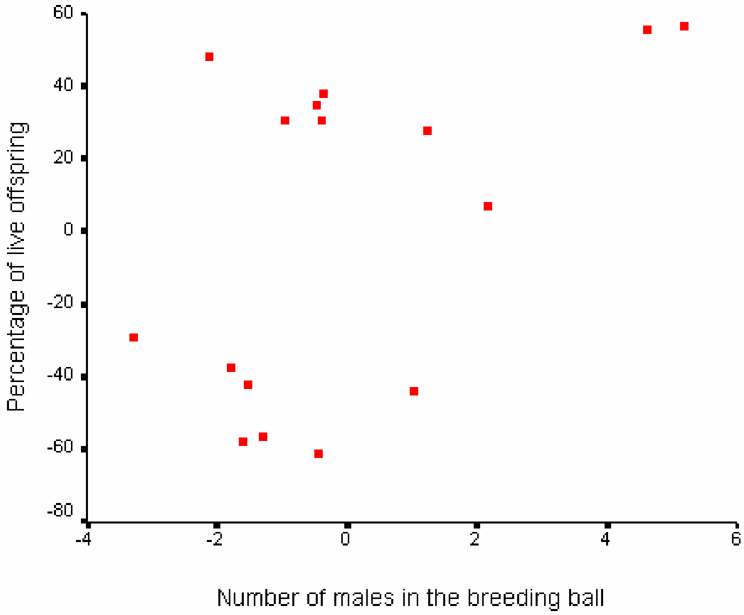
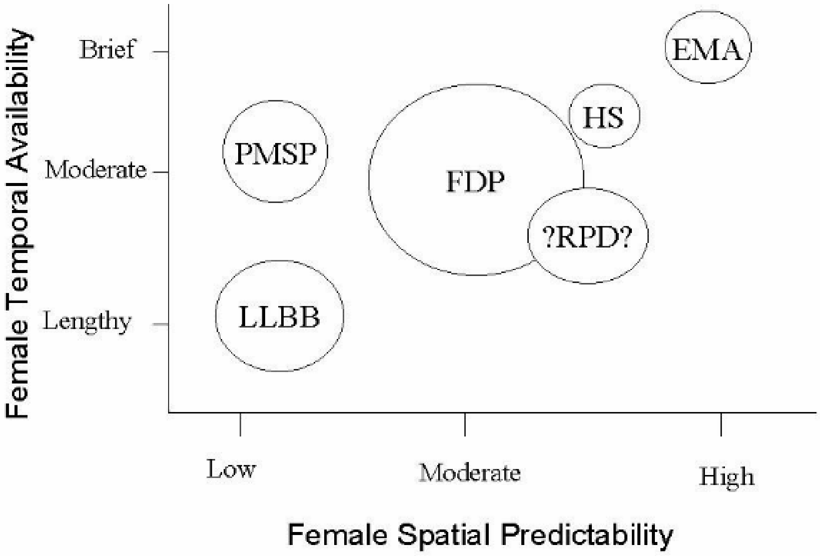


Figure 6-13. Partial regression plot between the proportion of live offspring in female anacondas and the number of males that mated with her holding the effect of female size constant (r = 0.51; 0 = 0.027; n = 13, one-tailed test).

Figure 6-14. Mating system predicted by the female temporal availability and the female spatial predictability



by Duval et al. (1993). Female Defense Polygyny (FDP), Prolonged mate search polygyny (PMSP), Explosive mating assemblage (EMA), and hotspot polygyny (HS). They also speculate about the possibility of resource defense polygyny (RDP) as it is present in other taxa. Long-Lasting Breeding Balls (LLBB) appears as a new mating system reported in this contribution.

# CHAPTER 7 .CONSERVATION AND MANAGEMENT

In this chapter I summarize the basic problems of conservation regarding anacondas, and I discuss the findings of my research that apply directly to conservation of anacondas and their habitats. I present some possibilities for the rational use of the species with a discussion of how to implement these possibilities. Much of the information presented comes from my research, and some comes from my own experience working for the Venezuelan Fish and Wildlife Service (Profauna).

## 7.1 INTRODUCTION

The economic crisis of developing Latin American countries, compounded by constant population growth, has produced increasing pressures on natural resources and rural areas. The lack of official awareness about environmental issues, little public education in rural communities, and the virtual economic shutdown of many local economies is resulting in increasing damage to pristine habitats. This problem is even greater if we consider that most developing countries are located in the tropics where the most fragile and diverse ecosystems occur.

The sustainable use of natural resources has been offered as one potential solution to economic problems. The rational use of wildlife has also been proposed as an alternative to destruction and replacement of natural habitats by other uses of the land, such as timbering or agriculture (Balick and Mendelsohn 1992; Bodmer et al 1997; Robinson and Redford 1991; Shaw, 1991). The sustained harvest of wild populations has been implemented in several countries for subsistence (Silva and Strahl, 1991; Vickers, 1991) and for commercial uses such as harvesting wildlife for hides, flesh, or live pets (Beissinger and Bucher, 1992; Fitzgerald et al. 1991; Groom et al., 1991; Iñigo-Elias and Ramos, 1991; Joanen et al 1997).

Venezuela has been withstanding the economic crisis better than other Latin-American countries due to the fact that all the countries oil reserves belong to the government. However, from 1982 to the present there has been a slow but consistent decline in the economy (related to dropping oil prices) that is affecting the lifestyle of the people and, ultimately, the environment and wildlife. As the economy of the country worsens and the wages of the local people fall well below the minimum necessary to survive, people start using resources they would have disregarded otherwise. For instance, in the past the use of capybara meat was only restricted to the week before Easter when it was tradition to eat capybara in some cities of the country. Lately, illegal hunting of capybaras has expanded throughout the year, as people have resorted to capybara as a staple food source. Traditionally the ranch that produced most of the country's capybara meat was El Frío. For more than 30 years, El Frío sustained an estimated population of roughly 30,000 capybaras; of which 10,000 were harvested every year (see Ojasti 1991 for a full description of the harvest program). However, in 1986 I participated in a survey of El Frío capybaras where we counted slightly more than 4,000. Later surveys of the area indicate an even further decrease in the population, and poaching has been acknowledged as the leading cause of the population crash. Similar cases of significant poaching have occurred with other species including white-tailed deer, caiman, iguanas, side-necked turtles, and peccaries, among others. This trend is, not surprisingly, expected to continue and extended to other species as well.

Although any use of the green anaconda is forbidden by Profauna, they are currently being harvested illegally. There have been several seizures of anaconda skins in Venezuela. In two different years (1988 and 1990) Profauna confiscated a total of 2,138 anaconda skins (Profauna files). In 1992, I learned from some local people that the tanneries were paying Bs.1,000 ($16.67) per meter of skin. This is a significant amount for a worker who makes approximately $3.50 a day. Aside from the skins, anaconda meat can be used as a source of protein, and the live individuals are in demand for the pet trade.

I learned from conversations with some of the tanners that the scales of the anacondas were too large and inconvenient to use for luxury articles. They insisted that smaller-scaled skins such as boa constrictor, reticulated pythons, or tegus were of higher value in the skin trade. Due to the large sizes of the scales, the skins of anacondas can only be used in rustic articles such as cowboy boots, belts, or maybe in purses, but could not for higher quality (and pricier) items. I tried to learn the prices paid for anaconda skins in the international trade market, but tanners are very reluctant to talk about prices of animals that are not under legal management (perhaps for fear of being investigated). They often claimed not to know the prices or that the prices were very low and the skins were of little value. However, the confiscation of several anacondas skins in other countries suggest that they have some value. In light of these facts, what viable options are available regarding sustainable management of the species? It is clear that an illegal, uncontrolled market threatens the populations due to the likelihood of over-harvesting (Thorbjarnarson et al. 1992). The best way to combat the illegal, uncontrolled use of a resource is by developing a legal and rational market that outcompetes the black market. The rational use of wildlife has been used as an alternative to its destruction. For example, several populations of crocodilians that have been seriously threatened are now recovering due to effective harvesting practices (Thorbjarnarson et al. 1992 for a review). In the following section I will summarize the different forms of management and how they can be applied to anacondas.

### 7.2 WILDLIFE MANAGEMENT AS A TOOL FOR CONSERVATION: HARVESTING VS FARMING

The most common methods of extractive wildlife management are farming, harvesting, or a combination of both. In a farming model, animals are kept in captivity, and all their needs are provided for y the keepers. This is a relatively expensive activity, preferable for those animals that have large growth rates, low maintenance expenses, and can be housed in large densities. Wildlife farming has been practiced successfully with the green iguana (*Iguana iguana*) in Panama (Werner 1991). Farming does not represent a threat to the wild population since only a few animals are originally collected from the wild, and if the project fails, only the animals that were in the farm are in jeopardy. Also, due to the localized nature of the activity, it is potentially easy to monitor and enforce the existing regulations. Farming, however, is an activity that benefits the few people working on the farm, and does not constitute a real incentive for conservation of habitats (Thorbjarnarson 1999).

Another possible management method is ranching or open farming. It involves collection or eggs or juveniles from the wild, growing them in captivity for a relatively short time, and commercializing them after they reach a certain size. In some cases, a specific percentage of the animals must be released into the wild to compensate for the extraction. This method is used often in species that have a high mortality in early ages, and the extraction of neonates can be compensated for by the later released of a number of larger individuals into the wild (Thorbjarnarson et al 1992). The fact that the adults are not being kept in captivity decreases food and facility expenses significantly. Also, because this method relies on natural populations, it has a great potential to promote conservation among local communities (Thorbjarnarson 1999).

On the other end of the spectrum is harvesting or cropping. In a cropping system, animals are harvested from the wild; thus a direct link exists between the economic activity and the conservation of the species and its habitats. This activity is better for animals that occur in high densities and are easy to find and catch. It requires a much lower overhead since the only investment involves finding and catching the animals that are going to be harvested. However, due to the more extensive nature of the harvest, it has a much greater potential to have a detrimental effect on the natural population. Monitoring and control of the harvesting activities are a great priority, but it can be very expensive and troublesome. A representative example of this model in a reptile is the harvest of spectacled caiman (*Caiman crocodilus*) in Venezuela (Thorbjarnarson 1991**;** Thorbjarnarson and Velasco 1999). This was an important source of revenue for the country and for the local economy for several years, and some long term investment in conservation was encouraged. Sadly, this program's success eventually deteriorated due to international drops in the prices of the skins (Thorbjarnarson and Velasco 1999) and to difficulties in the management that resulted in local population crashes in the areas where cropping was occurring (personal observations).

### 7.3 CROPPING ANACONDAS: pros and cons

By far the main economic activity in the llanos is cattle ranching. Most of the land is devoted to low density cattle ranching. This is perhaps due to the fact that the poor soils and extreme seasons prevent much agriculture and most other such activities. The management of the land for cattle ranching in the llanos utilizes dikes to hold the water during the dry season. This has extended the time that the savanna is flooded, increasing the carrying capacity for many species dependent upon relatively large bodies of shallow water, such as fish, waterfowl, herons and other wading birds, capybaras, and caimans. It may have also enhanced the carrying capacity for anacondas, both by increasing the available habitat and enhancing the number of prey. Here I consider the different stages of harvesting and how they can be applied to anacondas.

#### Population estimations

Before attempting the management of any species, it is important to understand its basic life history. Even modest success at wildlife management depends upon a knowledge of the population parameters, demography, and the maximum sustainable yield a population can support (Caughley 1977). The main population parameters are: abundance, rate of increase, fecundity, mortality, recruitment, and dispersal. First, population size followed by the intrinsic rate of increase of the population should be determined. These statistics should enable us to calculate the maximum sustainable yield (MSY) which is the maximum amount of individuals that can be removed from the population while keeping the population essentially constant (Caughley 1977; Caughley and Sinclair, 1994).

The first problem encountered when attempting to harvest anacondas is their secretive nature. To harvest a population rationally, we must be able to count how many animals there are in order to propose a sustainable harvest rate. Not having a total number of animals available, the alternative is to have some estimate of the population size in the form of an index of relative abundance (e. g. number of snake seen per km of road, or per hour traveled). This way we can make an educated guess about the MSY, and refine it by monitoring its impact on the population by changes in the index of abundance. In this way we detect any problem and fix it in a timely fashion (Caughley 1977).

To date, we do not have any of these surveying tools with respect to anacondas. To estimate the abundance of the population necessitates long term mark and recapture studies that are too time consuming to apply to the large scale management of the species. We do not have any index of relative abundance either. Due to their secretive nature none of the traditional methods of counting anacondas by transects can be applied in a simple manner. A possible method of developing an index of relative abundance for the population of anacondas may be by using the sighting of pregnant females at the river banks or edges of roads. Because pregnant females bask frequently along river banks and near the roads, it might be possible to use the frequency of sightings related to distance and duration of surveying to develop an index of relative abundance. Since we cannot monitor the impact of the program, harvesting of anacondas should not be implemented due to the risk of over harvesting.

### Harvesting

Capturing the animals for harvest offers another challenge for several reasons, aside from the problems of finding the animals. One of them is that local people feel very strong fear and dislike for the snakes; this would make it very difficult to find a crew to do the harvest. In some instances when I needed extra help catching some of the anacondas, it was very difficult to find a volunteer willing to help me. The other problem is the number of hours needed to find only a few animals. Paying a crew to look for anacondas might not be cost effective considering the low frequency of capture that I encountered. One alternative strategy to overcome the low encounter rate with anacondas is to put together a crew that harvests other species as well; such as caimans, turtles, iguanas, and tegus (Thorbjarnarson and Velasco 1999). All of these reptiles occur in relatively high density and are potentially manageable. Indeed, the word “tropics” normally brings up the word “diversity” to many biologists’ minds, yet surprisingly those involved in wildlife management and decision making have failed to take advantage of the high diversity of these areas. However, in order to implement sustainable management there is much that has to be learned about the species, as well as improvement in the organizational skills of Profauna in their attempts to manage all of these species correctly (see below).

Other problems that would be encountered with anaconda harvesting are related to SSD and the enforcement of the harvest. Hunters typically tend to target the largest individuals first, which are usually males in many game species. In polygynous species this is potentially sustainable since most of the matings are performed by a few males, and there is a theoretic surplus of males that are not breeding at a given time. In anacondas, however, it is certain that harvesting larger animals will involve harvesting the females that make the largest contribution to the population. Females larger than 340 cm are responsible for 59.5% of the new offspring every year (Chapter 5), and females larger than 300 cm contribute to 74.8% of the total number of newborns in every generation. In other words, any harvesting of large females would impact dramatically the population numbers, making cropping extremely risky to implement.

It could be argued that harvesting males is a more feasible alternative as they are easier to find (Chapter 3) and can be gathered in greater numbers in the breeding aggregations (Chapter 6). Having smaller size and feeding on less dangerous prey, males tend to have better hides with fewer scars (Chapter 3) thus increasing the quality of the product. If the program is created in a manner to encourage the collection of smaller animals, the odds of success are better, since they are more likely to be males and thus will have skins with less wounds (Chapter 3) and smaller scales. Even this alternative might be unfeasible given the practical problems mentioned earlier. Furthermore, if females that are courted by several males have higher reproductive success (Chapter 6), the quota of males for the harvest would have to be assessed very carefully.

Commercial use of large snakes is practiced in Sumatra where reticulated pythons (*Python reticulatus*), blood pythons (*Python brongersmai*), and short-tailed pythons (*Python curtus*) are harvested serendipitously near plantations and villages. The snakes are kept alive in bags and taken to slaughter houses where the animals are processed (Shine et al 1999*a*). This method targets mostly males due to their higher mobility, and produces a variable rate of harvest that changes with snake abundance. Given the nature of this kind of harvesting, in which the hunters are not going out just to catch snakes, this method of hunting has the potential to be self-regulating. A drop in the population will produce a lower encounter rate with people that will result in a lower harvest. Given the cryptic nature of these species, it is unlikely that they can be hunted out or driven to extinction by harvesting. In the cases of *P. curtus* and *P. bongersmai,* the animals feed heavily on rats in the plantations, and are thus also perceived as performing a pest control role, which helps the survival of local populations.

A similar method is used in British Guyana with green anacondas. Fishermen gather snakes opportunistically and keep them in bags to take to the tanners where the snakes are killed for skins. If the tanner considers an individual snake to be inappropriate for the market (too small, too many scars, too large), the animal may be turned loose (Quero personal communication). Although this has the potential to disrupt local genetic structures, this risk might not be very high since the tanneries are generally near the places where the animals are caught. Similar to the python harvest, this method seems to be sustainable since this low rate of cropping is not expected to threaten the population. However, any harvest based on encounter rate with people must still be regulated by a quota since increases in human density or in the prices of the skin could dramatically increase the harvest rate and eventually reach a level which might not be sustainable.

### 7.4 FARMING ANACONDAS

Farming anacondas in a closed system is unlikely to be successful. The cost of facilities and maintenance is probably prohibitively high. It is unlikely to be cost effective to maintain a species that takes several years to reach adulthood, and where females will not breed every year but every other year at best (Chapter 5). However, the possibility of an open farm system exists. Large pregnant females can be found along the riverbanks (Chapter 3 and 5), caught and kept in captivity, and released after they deliver. Due to their high fertility (Chapter 5), a large number of individuals can be produced in short-term farming or in the pet trade. Neonates have a high natural mortality in the field (Chapter 3), and protecting them in captivity and releasing some later would result in the same proportion that would have survived to that age and should not affect the natural population. Neonates can have a relatively fast growth rate (Holmstrom 1982), and, after a short time, can provide excellent, scar-free, small-scaled skins that would have a high value on the legal market. In addition, young individuals have a sharper pattern and more attractive skin.

Throughout my field research I tried to promote experimental farming of neonate anacondas to study its feasibility. For two years Profauna experimented with neonate farming, but both times it was implemented poorly and gave inconclusive results. Future attempts should be made to more adequately assess whether it is feasible and what is necessary to ensure cost effectiveness without over-exploiting the resource.

With respect to the use of anacondas in the pet trade, anacondas do not make good pets. They quickly outgrow their cages, and become a risk to other pets and even people. The have an aggressive temperament and never become an easy (or safe) animal to handle. They also release an aversive musk when handled and disturbed. However, due to the popularity of the animal, anacondas are in large demand in the pet trade (approximately $250/neonate, retail). The illegal import of live reptiles for the pet trade is a growing market in the US (Hoover 1998). The number of pet keepers and the demand for reptiles for pets grows with increases in the human population and also with the increasing trend in smaller housing for people in large cities that makes conventional pets more troublesome. Because most reptiles can survive for many hours without water or food the animals can be smuggled into the country in many ways. This market is very hard to control and the number of animals being extracted is difficult to quantify (Hoover 1998). Thus a legal source of neonates that come from a sustainable system would be a way to promote protection of the wild population.

## 7.5 CONSERVATION OF THE ANACONDA: PRESENT AND FUTURE.

Anacondas and other boids are in appendix II of CITES. This means that they cannot be the subject of commercial trade unless local permits are obtained. In Venezuela, anacondas are still relatively abundant due to the large expanses of wetland habitat that lack human development, are relatively undisturbed, and have low human density. There is no legal commercial trade of anacondas in the country, however, there is an illegal local market for the skins. Due to the low profile of this activity, the pressure on the population is not too high and, at the moment, does not constitute a threat to the population.

The flesh of the anaconda, although edible, is not preferred by the local people and the anacondas are not killed for it. Other than the skin, the only product of the anaconda that people seek (and more so than the skin) is the fat. Anaconda fat, melted under the sun in a closed container or in a fire, is considered as a medicine for throat problems, asthma and other respiratory problems, but at present the demand is not very high.

Selling anaconda skins is illegal and troublesome for the campesinos, so most people do not engage in this activity. The main reason that local people kill anacondas is because they fear and dislike them so much that they will kill them on sight. Arguments that anacondas eat poultry, livestock, pets, or even people are often used to justify killing the snake. The truth is that people traditionally dislike and kill snakes even when they are nowhere near any of their livestock or houses. On some live animals that I studied, I observed straight, long scars or wounds that could only have been made by a machete. This was especially true in the ranches that offer less protection to wildlife.

Habitat degradation in the llanos has not yet been a serious problem, since much of the land management for the cattle involves increasing the surface of land that contains water for a longer time. The impact of this extensive cattle ranching on wildlife is much lower than the impact found in the US or other countries where cattle are kept in higher densities. However, old-fashioned ranching practices involve cutting the gallery forests to ease the handling of the cows (that often hide in the forest and become feral) and to allow easy access for the animals to water in dry season. Federal laws prohibit gallery forests from being cut up to 50 meters from the river, on both sides, but this regulation is seldom enforced. Deforestation in the llanos was not an important trend in the past, but it has been increasing dramatically in the last few years, and it is encountering an unsettling leniency with government authorities. The river banks often develop caves that are supported by the roots of the trees in the forest; frequently these caves are used by anacondas to hide and spend the dry season (Chapter 3). In the treeless savanna, anacondas have fewer places to hide and protect themselves from extreme drought. This might be very significant in atypical years where the anacondas may be exposed to extreme heat or droughts (Chapter 3). The caves found in the segments of the rivers without forest are considerably less abundant and smaller than the caves found in other areas because without the roots the river erodes and destroys the caves. Cutting of the gallery forest does represent a direct threat to the anaconda's welfare. Or course, this is additive to the obvious effects that deforestation has on the populations of prey species and other components of the ecosystems including all the forest-dwelling species.

Information on the international illegal trade in anacondas is difficult to obtain, but the trade may not be too high since the animals are hard to find and the demand for skins with larger scales is limited. Perhaps the dynamics of the market is that the tanners buy skins that hunters occasional bring them, and when they accumulate a sufficient number, they smuggle them out of the country or use them in national products that are exported later. At the present, anaconda population numbers are high and there is no immediate threat to their survival in the llanos. However, the safety of the anaconda relies heavily on the low likelihood of encounters with humans and the low degree of degradation of the habitat. The increase in the human population will produce increased encounters with anacondas that will invariably lead to more snakes being killed. The struggling economy will lead to an increase in the degree and intensity of land use and development, and this will undoubtedly have a negative effect on the life of the anacondas by decreasing suitable habitat for them and their prey.

### 7.6 WILDLIFE MANAGEMENT AND CONSERVATION: A TROPICAL PERSPECTIVE

The possibility of management as a method to incorporate anacondas into economic development is not easy, and much more research is needed. Harvesting males, as well as farming of neonates, are possible alternatives that can be explored. However, both of these possibilities involve many practical problems as well as ethical issues that cannot be ignored. Killing animals for human comfort and leisure is a theme of heated debate on several levels between those concerned with conservation and those who manage wildlife for profit (Joanen et al 1997; McLarney 1999; Medellín 1999; Robinson, 1993; Struhsaker 1998). Changes in fashion or drops in economies around the world can dramatically affect the demand for, and prices paid for the animal products along with the faith in conservation measures based on it (Thorbjarnarson 1999). New regulations adopted by the international community regarding import of exotic wildlife, either in the name of conservation or in the name of animal welfare, can further limit the market and put in jeopardy all the investment made by the producers. Importing live animals leads to even harder ethical issues regarding the welfare of the animals as pets that might end up in the hands of novice pet owners who will not keep the animals in optimal conditions. In the case of larger reptiles, the problem will always be raised of what to do with the animal after it reaches a size where it cannot be kept in the facilities where it used to live. Frequently the animal is turned loose in an exotic environment where it will, at best, die in a short time from exposure or starvation; although sometimes it survives and reproduces causing further problems as an exotic invader in a foreign ecosystem (Atkinson 1989).

The rationale for harvesting programs as an appropriate way to achieve the goals of conservation is that the use of wildlife for profit can invigorate local economies. Inhabitants of rural areas would then realize that the species being used can produce some profit for them, and they should then protect the resource and use it in a rational manner. This approach often fails to consider the philosophy and customs of the people that are supposedly targeted. To develop this point I will use the example of caiman harvesting in Venezuela, which has been thoroughly described in the literature (Thorbjarnarson 1991; Thorbjarnarson and Velasco 1999), and of which I am personally familiar.

This program operates on private lands, where the owners hire a technician to survey the population size, and, based on the population size estimate (or other surveys of the area), Profauna gives a license for a given quota. The owner then hires people to harvest and process the animals. This program provides some benefit to the land owner, to the local worker that performs the harvest and works in the processing, to the biologist that does the survey, and to the tanners that commercialize and export the hides. It is based on a very prolific species that had a very high commercial value, is very easy to count and harvest, and belongs to a group that has proven to be fairly resilient (Thorbjarnarson 1999). In short, a “perfect” species for sustained management.

However, in this program no consideration was given to the philosophy and customs of the local people. I will use a blooming mango tree to illustrate a piece of philosophy that is very common in Venezuela and perhaps throughout the tropics. For those that did not have the privilege of growing up in a tropical country I will explain what it is all about. When the mangos mature in the middle of the dry season, there are 40-50 foot tall mango trees with their extended canopies loaded with juicy mangos. At this point everybody, kids and adults alike, climb up the trees or reach with poles to knock over mangos by the dozens. Everybody gets to enjoy the delicious fruit that is incredibly abundant at this time of the year. Such is their abundance that people are unable to eat all that are available, and one month later the soil is covered by a carpet of mangos rotting in the baking tropical sun. A month later all the mangos are gone, and whoever did not feast on them will have to wait until the following year in order to enjoy this wonderful fruit. No one saves mangos or stores them for later. The people simply eat what they can, and when the mango season is over, the guajaba fruit comes into season! This is, essentially, the philosophy that the local people on the llanos had regarding the sustainable use of caimans in the llanos.

Regardless of the well intended efforts of Profauna in running a biologically sound program, from the beginning Profauna was involved in an battle of wits with the poachers and other sectors that took advantage of the loopholes in the regulations. After the word got out that every square foot of caiman skin was worth $40, there was no safe haven for the animals. Every improvement in the legislation was matched immediately by new ways to circumvent the law. One of the problems that the program had was that landowners would kill and market the caimans on other lands to keep their own populations high for future surveys, or simply because they did not have enough animals to meet their quota (typically they would have filed manipulated survey results to get a higher quota). Profauna then decided to count the skulls and carcasses of the caimans that were harvested and match it with the number of skins as a way to ensure that the caimans were actually killed on the lands of the producer (and thus within the permitted quota). This regulation immediately spawned a new breed of small businessmen in the llanos. Their business consisted of carrying a truck loaded with rotting caiman carcasses that were then rented out to crooked landowners who had hunted caimans illegally and needed the carcasses to match the skins they had poached (carcasses are too heavy to carry on a burro's back, which is the reason that poachers only retrieve the skins from the site of the kill). Eventually Profauna decided to burn the carcasses that they counted to prevent recounting them in other ranches. This is only one example of the many tricks that Profauna had to uncover in their effort to implement the program. Most of the people that were supposed to get involved in management and start protecting the resource for sustainability never perceived it as something different than an ephemeral source of wealth that, not unlike the blooming mango, was there to take advantage of while it lasted. Of course, this uncontrolled rate of harvest resulted in a population decline that (along with a drop in international prices) decreased the profit of the harvest, bringing the program to "the brink of extinction" and reinforcing the idea that the caiman harvesting was indeed ephemeral!

This is one example of a program that had, on paper, a perfect profile for sustainable harvest, but which failed to consider other aspects just as important as the species biology: the culture and education of the people being targeted. Although I believe that there are many species that can be harvested in an integrated conservation plan (see above), I have serious doubts that, after failing to manage one species with such fine management prospects, we can realistically expect to succeed managing several species at once. Perhaps the "blooming mango philosophy" can be overcome with education, but we must be aware that a short campaign stating the benefits of a rational harvest will not change a lifestyle that may be engrained in the culture for many generations past. Finally, we should study how common this "blooming mango philosophy" is in other tropical countries, and how their government agencies can overcome them if they do exist. For the long term, it is likely that people involved in management will learn that they must use the resource rationally, but the resource must last beyond the first stage of learning! Furthermore, to learn to use one or a few species does not really constitute a tool for conservation if this is not also extended towards other species and involves some respect or feeling for the integrity of the ecosystem (Rivas and Owens 1999).

In my opinion, the most clear and least controversial benefit that local communities can gain from anacondas is from the lure that anacondas, as "charismatic mega-fauna," present for ecotourism. The llanos has a tremendous and unrealized potential for ecotourism due to the large abundance and diversity of wildlife comparable to the diversity of the rain forest (Rodriguez and Rojas 1996). Unlike the rain forest, in vast savannas of the llanos the animals can be readily spotted and appreciated due to the lack of trees and the forest's patchy distribution. However, for tourism to become a leading economic force, a very strong environmental awareness program must be implemented in all levels of the population with emphasis in the rural areas especially, at grade school levels (Rivas and Owens 1999). Sadly, this does not seem to be the path that governmental institutions or other conservation institutions are taking.

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# Vitae

Jesús A. Rivas was born in Caracas, Venezuela on February the 13th, 1964. He attended to the Universidad Central de Venezuela where he obtained his undergraduate degree in Biology. Since the beginning of his undergraduate career in 1980, Mr. Rivas worked actively in the University's Fire department as a firefighter while working in his undergraduate degree. In 1986 and 1987 he was an intern at the Venezuela Fish and Wildlife Service (Profauna). For his undergraduate thesis he studied the foraging ecology of the green iguana (*Iguana iguana*) in an extensive study which included the of stomach contents analysis of more than 300 animals. Upon graduation on 1990, he was involved as a field assistant in several research projects of the biology of the Venezuelan fauna, including the green sea turtle (*Chelonia mydas*), hoatzin (*Opisthocomus hoazin*), Orinoco crocodile (*Crocodilus intermedius*), and spectacled caiman (*Caiman crocodilus*). With funding from Wildlife Conservation Society (WCS), he also continued his research on the biology of the green iguana involving population dynamics, reproductive biology, and social antipredator behavior of neonates.

In 1992 he started an ambitious field project on the life history of the green anaconda sponsored by the Convention for the International Trade of Endangered Species, WCS and Profauna, that later developed into his Ph.D. research, when he joined the University of Tennessee at Knoxville in 1993. He has recently been hired by Boston University to teach a field-based course of Tropical Ecology in Ecuador while a publishing company considers the publication of this dissertation as a book,