NATURAL HISTORY OF THE GREEN ANACONDA (EUNECTES MURINUS) IN THE VENEZUELAN LLANOS

JESÚS A. RIVAS¹, MARÍA C. MUÑOZ², JOHN B. THORBJARNARSON³, GORDON M. BURGHARDT⁴, WILLIAM HOLMSTROM⁵, AND PAUL P. CALLE⁵

ABSTRACT.—During a six-year study in the Venezuelan llanos, 575 (345 \circ , 230 \circ) Green Anacondas (Eunectes murinus) were processed. Snakes were found by wading in the shallow water of módulos, borrow pits, lagoons, and rivers, and they were most often encountered in bodies of water covered with aquatic vegetation (especially Eichornia spp.). Most individuals were encountered during the dry season when water levels were low. Green Anacondas were active at all hours of the day and night, but, in general, activity was depressed during the hottest hours of the day (with the potential to overheat during the dry season). They consumed a wide range of prey via ambush predation, and often suffered wounds (and associated infections) inflicted by prey (e.g., Capybaras). Females (35 of 38) exhibited more wounds than males (25/56), and this may be a reflection of larger female size and the larger prey on which they feed.

INTRODUCTION

Early studies of the natural world were primarily based on careful observations. However, for some time, the study of natural history has been considered oldfashioned and scientifically suspect (Greene, 1986). The current focus on hypothesis-driven questions and theoretical work can result in dismissal of natural history observations as solid science, although some scientists stubbornly resist this trend (Greene, 1986, 1993; Noss, 1996; Rivas, 1997). We contend that natural history studies remain an invaluable source of information concerning species and natural systems; indeed, descriptive fieldwork often provides scientific knowledge that will provide baseline data in a changing world, outlive current models and interpretations, and be available for testing future hypotheses (Rivas, 1997).

Although interest in the natural history of anacondas has existed for a long time, studies were not initiated until practical needs justified funding. Herein, we report results from investigations triggered by the need for baseline data on Green Anacondas (Eunectes murinus) for making management decisions. Some of our fieldwork has been published previously: health

'Department of Ecology and Evolutionary Biology, University of Tennessee, Knoxville, Tennessee 37996, USA (current address: Department of Mathematics and Natural Sciences, Somerset Community College, 808 Monticello Road, Somerset, Kentucky 42501, USA). E-mail: jesus@anacondas.org

²Graduate Program in Ecology, Departamento de Biología de Organismos, Universidad Simón Bolívar, Caracas Venezuela.

³Wildlife Conservation Society, P. O. Box 357625, Gainesville, Florida, 32635-7625, USA.

⁴Department of Ecology and Evolutionary Biology and Department of Psychology, University of Tennessee, Knoxville, Tennessee 37996, USA.

⁵Wildlife Conservation Society, 2300 Southern Blvd., Bronx, New York 10460-1099, USA.

status of wild populations (Calle et al., 1994; Calle et al., 2001), safely handling large anacondas (Rivas et al., 1995), predation (Rivas et al., 1999, 2001; Rivas and Owens, 2000), mating (Rivas and Owens, 2000; Rivas and Burghardt, 2001), methods for implanting transmitters (Raphael et al., 1996; Rivas, 2001), and general natural history (Rivas, 1998, 2000, 2004).

METHODS

Study Site: The Llanos

The "llanos" is a large geosyncline (approximately 450,000 km²) tilted to the east and located at the intersection of the Andean and Caribbean ridges in northern South America (Rivas et al., 2002). Flooded areas in the west drain into the Orinoco River. This study was carried out in the alluvial overflow plains of Apure State. The dominant vegetation associated with this region is a savanna with few trees. Gallery forests bordering the rivers and patches of dry forest adjacent to them interrupt the otherwise continuous plain. In the wet season, rivers overflow and flood most of the savanna.

The climate is intertropical and hyperseasonal. The area receives an annual average of 1,575 mm of rain, with over 90% falling between April and November. The period from January to April is considered the dry season, during which all bodies of water shrink dramatically. During the wet season, from July to October, the savanna floods and standing water is abundant due to rainfall and overflowing rivers. The months between seasons are transitional (Rivas, 2000; Rivas et al., 2002).

From 1992 to 1997, we conducted most of a study on Green Anacondas (Eunectes murinus) at Hato El Cedral, a 54,000-ha cattle ranch in the Muñoz District, Apure State (7° 30' N, 69° 18' W). This location was

chosen for its dense E . *murinus* populations, the vigilance of the owners in discouraging poaching, and the presence of good roads for travel during the wet season. A series of dikes have created more permanently flooded habitats ("módulos"), which diminish the impact of the dry season. Gates of dikes are closed at the end of the wet season to hold water for pastures and cattle (0.15-0.40 cows/ha). Each módulo covers approximately 7,000 ha.

Dikes provide adequate and reliable roads to move around the ranch even during the peak of the wet season. The construction of dikes (and roads) also produced borrow pits, which are used by E . murinus. Borrow pits are small quarries from which fill was taken to build the raised road. Borrow pits are found along roads and their variable size and depth determines how long into the dry season they can hold water. Different communities of aquatic vegetation grow in them as the seasons change.

Finding Green Anacondas

Despite its size, E . *murinus* can be very inconspicuous. Its secretive nature, preference for aquatic habitats (frequently with murky water and dense vegetation), and its cryptic coloration combine to make finding these animals difficult. Green Anacondas are most easily found during the dry season, when snakes are concentrated in remaining bodies of water. Early attempts to seine water bodies were unsuccessful as most water bodies were filled with rooted or floating aquatic vegetation.

We found that the most effective way to find E . murinus was by systematically searching shallow $(< 50$ cm deep) water in módulos, borrow pits, lagoons, and rivers. Searching in deeper water proved to be unsuccessful due to the restricted mobility of researchers and the increased ease of escape by snakes. Searches were conducted by slowly wading while probing areas of drying mud or accumulations of aquatic vegetation with poles. Green Anacondas also were found by searching natural cavities along the banks of ponds, drying rivers, and nearby shaded locations, such as under bushes adjacent to water. Snakes were found occasionally in crevices in man-made structures such as bridges.

We discovered that E. murinus is rarely encountered during the early morning, and that its activity levels also are low during the temperature peaks of the day. Consequently, searching for animals began in the morning (around 0800 h) and continued until afternoon, depending on success rates. By 1000 h, we sometimes captured more animals than we could process during the rest of the day. However, on other days, the search went on for several hours without success. On those days, we would stop around 1300 h and resume around 1530 h and continue searching for snakes until it became too dark to see them.

Another search technique was to systematically patrol the study area looking for moving or basking animals. This was done either by riding on top of a truck, on horseback, or by motorboat, depending on water levels. Intensive searches were more effective in very dry areas, whereas patrols proved useful in areas that had more water and where wading was not feasible.

Capturing and Restraining Snakes

Submerged snakes were located by detection with one's feet or poles. Once the presence of a snake was confirmed, the animal was captured by grabbing it behind the head and allowing it to exhaust itself. When the water level was too high to control a snake, we dragged it to shallower water or to the shore, where it was more easily subdued. Although strong, Green Anacondas are bulky, heavy, and move slowly on land. When animals became defensive and attempted to bite, we anticipated such behavior, and due to their slow movements, moved out of the animals' reach to avoid injury. When snakes were in caves, they were gently poked with a pole. After a short time, animals would move to the water where they were subdued as above. Individuals often tired within 15 minutes, with larger animals tiring more quickly. Once a snake was controlled, it was placed in a large sack or a 200-l metallic drum, depending on the size of the animal.

Initially, several people were needed to subdue and process each snake, but, as the project advanced, fewer people were required to restrain snakes. An important discovery was that, once the head had been seized, snakes formed powerful loops with the anterior parts of their bodies. This loop forces the hand of the holder forward (from neck to nose), causing the person to lose his/her grip. The snake then would wrap around the hand of the holder, leading to complicated situations because the snake's head was now free and the "holder" was held. Formation of loops appears to be an innate behavior (e.g., Fixed Action Pattern; FAP) during which snakes protect their heads with their muscular bodies when threatened. By keeping the first fifth of an animal's body stretched, we could prevent the animal from developing the loop. The drive to perform this FAP is so strong that, if we focused on preventing large animals from performing it, they would expend all their energy and endurance trying to protect their heads, resulting in them tiring out quickly while presenting little risk to handlers. After this discovery, one individual (JAR, 178 cm, 86 kg) could control animals to 5 m in length.

Processing Snakes

At the time of capture, we recorded information on the capture site (e.g., substrate, vegetation) and animal activity. After capture, snakes were usually transported back to the central processing station, where they were kept for periods from a few hours to one day, unless they had recently eaten, in which case we kept them in a metal drum until they defecated (normally within a week). To process an animal, we used a sock as a muzzle, which lowers their stress level and renders working with them much easier (Rivas et al., 1995). We recorded total length, tail length (to the nearest 0.5 mm in large animals and to the nearest 0.1 mm in snakes < 1 m in length), body mass (to the nearest 100 g in large animals, to the nearest 5 g in small individuals), and sex. To determine sex, we used standard probes to determine the length of the cloacal pouch (Rivas and Ávila, 1996). However, because Green Anacondas are so strong, they may oppose the introduction of the probe muscularly and cause a male to be mistakenly sexed as a female by an inexperienced person. We found that the easiest and most reliable way to identify the sex of adults is by examining the pelvic spurs, which are much longer in males than in females (see Rivas et al., this volume).

Snakes were marked by scale-clipping on both sides of the body, using the pelvic spurs as a point of reference. Each animal was identified by a unique combination of clipped scales that allowed for future recognition. Even though clipped scales re-grow, regenerated scales have a darker color than the originals, making reliable identification of an animal possible for several years. A backup method for identification of individuals was to record the pattern of dark spots on the first 15 subcaudal scales.

For 56 males and 38 females, we also recorded injuries and scars. Scars \leq 2 cm in length were classified as small, scars from 2 to 5 cm as medium, and scars \geq 5 cm as large. We also recorded anecdotal evidence of instances during which snakes were severely injured or killed by their prey.

RESULTS AND DISCUSSION

Capturing and Handling Green Anacondas

Recaptures of 121 healthy Eunectes murinus (of 780 initial captures) suggest that capture and handling of the snakes did not adversely affect individuals. Only two captured animals showed an adverse effect. Two large females had recently eaten large meals (Whitetailed Deer, Odocoileus virginianus), which subsequently were regurgitated (Fig. 1). Both snakes died shortly thereafter. Necropsies revealed no injuries to the digestive system that would account for their deaths, and at least one of the animals was alive after regurgitating, so death by asphyxia is unlikely. After these two unfortunate incidents, we stopped manipulating large animals that recently had ingested large meals. Instead, we tracked those animals for two or three weeks (they generally do not move more than 20-30 m from the site of a kill) before capturing and keeping them in a drum to identify the meal by fecal analysis. On occasion, we did not realize that a snake

William Holmstrom

Fig. 1. Shortly after capture, this female Eunectes murinus (SVL 363 cm, 40 kg) regurgitated the 10-kg White-tailed Deer (Odocoileus virginianus). The deer had two broken ribs, presumably from constriction by the snake. Unfortunately, the snake died for unknown reasons several hours after regurgitating the deer.

132 J. A. Rivas, M. C. Muñoz, J. B. Thorbjarnarson, G. M. Burghardt, W. Holmstrom, and P. P. Calle

Fig. 2. Size distribution of a *Eunectes murinus* population in the Venezuelan llanos.

had eaten recently until after its capture. In such cases, if the animal regurgitated relatively large prey, we kept it in an outdoor enclosure. These animals showed no ill effects.

Occasionally, handlers were bitten by snakes, resulting in fairly severe wounds, especially if the person reflexively withdrew the bitten member. The curved shape of the teeth prevents an easy release, and teeth tore flesh and muscle tissue or came loose and were left in the person's flesh. However, if the bitten person avoided the natural reaction of withdrawing and instead seized the snake's neck with the other hand, pushing the hand farther into the mouth, injuries were reduced and the release of the hand was facilitated. An animal's normal reaction is to open the mouth and try to bite the gripping hand, thus releasing the bitten member and leaving only the painful imprint of the teeth, but no serious wound.

Smaller animals were much more disposed to bite than larger individuals. This may be due to the lack of predators on larger snakes and the fact that active responses are metabolically costly. A similar trend of reduced antipredator behavior in larger (older) individuals was found in other snakes (Herzog et al., 1989). We captured 125 individuals > 3.5 m in length, and none tried to bite when first handled. Most snakes tried to escape until they were seized by the neck or, after many unsuccessful attempts to escape, being pulled repeatedly by the tail or midbody. However, animals that had been captured previously behaved differently. As soon as they were seized, they turned and fought ferociously, thereby posing a greater danger to the researchers. In many instances, we could tell whether an animal had been captured before based solely on its behavior.

Population Sampling

We collected 575 animals (345 males and 230 females) in six years (Fig. 2). Intensive searches yielded more captures in all years (Fig. 3). Males were found more often in most years (Fig. 4), perhaps as a consequence of their higher activity and the fact that many were found in breeding aggregations. The capture efficiency by day was not high in any season. The number of animals captured from year to year varied considerably, even after the first couple of years, during which we became increasingly experienced. This may be due to differences in the amount of rainfall during the previous year, the handling of water in the "módulos" by ranchers, and the time spent in the field in a

120 animals per year, but the actual effort was largely restricted to the peak of the dry season (estimated to average 55 days of sampling per year), so the average number of animals captured per day was 2.27. In dry years (i.e., in dry seasons preceded by relatively dry wet seasons), animals were easier to find and catch.

None of our methods were effective in detecting small snakes (Fig. 2). The cryptic habits of small individuals made them hard to see when road-cruising, and their small size precluded detection during intensive searches. Small snakes were hard to distinguish from the roots of water hyacinths and other aquatic vegetation when using our feet or poles, and this contributed to their poor representation in the sample. Attempts to catch juveniles using minnow traps were also fruitless, perhaps due to their low mobility.

Intensive searches were much more effective during the dry season, whereas road cruising is a better method during the wet season and transitional periods (Fig. 6). The relatively high number of animals found during the height of the wet season largely represents pregnant females that are easy to find basking at that time of the year.

Activity Patterns

Hunting "activity" may simply mean being alert to passing prey, with no evident physical movements. Consuming a meal $(6 h)$, digestion $(4 m)$, and even mating (Rivas et al., this volume) seem to take much longer in large than in smaller animals. Pregnant females are frequently seen basking. During the hottest times of day, however, they seek refuge and are not easy to locate, but they tend to reappear toward evening. Thus, times of capture by road cruising showed a bimodal daily pattern (Fig. 7). Our survey was useful in assessing demographic and population trends and to target sampling efforts, but it should not be considered an effective means of assessing activity patterns of individual animals. Snakes often spend a week or more without moving. A bimodal curve would probably not accurately describe the behavior of any individual.

Eunectes murinus is reportedly nocturnal (Lancini, 1986). However, our data do not completely support this notion. Although anacondas are more active in the evening and at night, we found snakes moving, foraging, constricting prey, and mating at all times of the day and night. Being an ambush hunter, they attack prey adventitiously. Once warmed in the morning, snakes frequently move. Opportunistic observations of animals that had recently fed revealed that an animal can

Fig. 5. Annual precipitation during the years of our study from the Estación Meteorológica de Mantecal (Ministerio del Ambiente y de los Recursos Naturales Renovables), located aproximatedly 30 km from the study area.

Fig. 6. Average number of *Eunectes murinus* captured each month using different searching methods.

Fig. 7. Daily activity of Eunectes murinus in the Venezuelan llanos assessed from road-cruising during the dry season.

Biology of the Boas and Pythons 133

go for several weeks after a meal without moving at all. Mating, which can occur at any time, can go on for several weeks without showing any clear pattern of activity.

If we were to attempt to describe a daily pattern, animals appeared to move (including males searching for females) primarily after the hottest hours of the day. This trend of moving when temperatures drop was also apparent on cloudy days, when snakes were more active at all hours, suggesting that temperature, not necessarily time of day, controls this behavior.

The activity of animals at the time of capture is informative, but is bound to be biased toward animals that were easier to locate. This information is crucial. however, in future studies aiming to locate snakes or evaluate potential management plans that involve surveying or harvesting. Animals that are moving (26.5%), basking (7.4%) , and mating $(28.2\%; Fig. 8)$ are more likely to be detected than animals that are under cover. Despite this bias, we found a lot of snakes hiding, whether under bushes (2.9%) , in caves (5.3%) , underwater (14.4%) , or buried in mud $(12.5\%; Fig. 8)$. A breakdown by sex shows a much larger number of males moving and mating than females, which is undoubtedly responsible for the higher representation of males in the our samples (Rivas et al., 1999; Fig. 9).

Habitat Preferences

At the height of the dry season most rivers stop flowing, and many bodies of water in the area tend to become covered with aquatic vegetation, some of which is rooted. This vegetation is composed mainly of spiny scrubs (Barinas, Cassia aculeata; Guaica, Randia armatta; Mimosa spp.), grasses (Trachypogon spp., Paspalum spp.), and floating plants (Eichhornia crassipes, E. azurea, Salvinia sp.). At this time of year, snakes were concentrated in these heavily vegetated bodies of water (84.9%), particularly in areas covered with *Eichhornia* spp. (Fig. 10). The presence of vegetation appeared to be more important than the nature of the body of water, as we found snakes in módulos, flooded savanna, and vegetated creeks and borrow pits. Animals found in creeks without extensive vegetation often were in caves in the riverbank. Eunectes murinus may be found in flowing rivers or pools without aquatic vegetation, where it often is quite visible, but the presence of snakes in those situations are apparently transitory.

Predation on Green Anacondas

Eunectes murinus appears to suffer high mortality during the first year of life (Rivas et al., 2001). Predators

Fig. 8. Activity of *Eunectes murinus* when captured ($N = 514$). Except for animals that were moving, mating, or basking, all other snakes were hidden under the specified type of cover.

Fig. 9. Activity of male and female *Eunectes murinus* when captured during the mating season. Except for animals that were moving, mating, or basking, all other snakes were hidden under the specified type of cover.

include mammals (Rivas et al., 2001), other reptiles (Rivas et al., 1999), and larger conspecifics (Rivas and Owens, 2000). Larger animals seem to suffer lower rates of predation, as few predators will attack full grown individuals.

Parasites and Diseases

In March 1992, we captured a female (356 cm TL, 20.5 kg) in which a radiotransmitter had previously been implanted. This snake 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

Fig. 10. Habitats where Green Anacondas *(Eunectes murinus)* were captured: Brrw = borrow pits without vegetation, Brrw. vg. = borrow pits with vegetation, Crk. vg. = creek with vegetation, Crk. = creek without vegetation, M6dulo (always with vegetation), Fld. Sv. = flooded savanna, Dry sv. = dry savanna.

rendered one eye useless. We drained the abscess and cleaned *it* with *peroxide* and iodine. We *also adminis*tered preventive antibiotic treatment (enrofloxacine) as part of the surgical protocol for the implantation of the transmitter (Raphael et al., 1996). In the next two weeks, we saw the swelling return, indicating that the abscess was probably still present. We followed this female for an entire year, during which she reproduced. One year later, the swelling was still evident. Just before the transmitter expired, the snake was seen with a recent meal. We noted other incidents of animals surviving long-term infections with little apparent harm (Rivas et al., 1999).

Snakes were frequently discovered with wounds and associated infections. Sometimes we found completely toothless animals as a result of stomatitis, presumably from tooth loss during encounters with prey or predators (Ross and Marzec, 1990). However, wild anacondas appear to recover from such infections, as some infected animals were subsequently recaptured with fully healed mouths (Calle et al., 1994; Rivas, 1998).

In some cases, we found dead animals for which a clear cause of death could not be assigned. During necropsies, we noticed dark spots $({\sim}1 \text{ mm}^2)$ in fatty tissue and other parts of the body. In April 1997, a female (420 cm TL, 44.5 kg) was found alive but not moving. We found her dead later that day. Superficially, she looked healthy other than having several old, small wounds on her tail that had been inflicted by a small Capybara *(Hydrochaeris hydrochaeris).* Histopathological analysis of her fatty tissues revealed that the animal had a lymphatic cancer (lymphosarcoma) that probably caused her death. We had captured this snake each year since 1992, when we determined that she had a *Hemoproteus* (reptilian malaria) infection (Calle et al., 1994). She had reproduced twice in the intervening years, and large amounts of body fat and eggs in early stages of development suggested that she would have reproduced the following year.

Risk of Injury during Predation

We observed individuals wounded or even killed by their prey. In April 1992, we were tracking a female (455 cm TL, 46 kg) and found her floating dead in the middle of a pond. Her head was missing, but no other injuries were evident. The next day a young Capybara (ca. 2.5 kg) was found dead and floating in the pond. The Capybara had been dead for approximately 24 h, showed clear scratches and anaconda tooth marks, and its spine was dislocated at the cervical level (Rivas, 2004). We surmise that the snake attacked it and in turn *was* attacked by *adult* Capybaras. Piranhas or other scavengers might have eaten the snake's head.

Another Capybara-inflicted injury occurred in March 1997, when a female (401.3 cm TL, 32 kg) killed and ate a solitary juvenile Capybara. The Capybara managed to bite the snake during the final struggle (Fig. 11). Capybaras are heavy-bodied rodents with long, sharp incisors capable of inflicting serious wounds. Defensive bites by Capybaras on Green Anacondas appear to be relatively common; Capybara teeth clearly caused the scars and wounds we recorded on several individuals.

Other prey species can also pose a danger to E. *murinus.* In February 1993, we were notified that a large anaconda was eating a large turtle *(Podocnemis* sp.) near a road. Shortly thereafter, we saw a large snake (485 cm TL, 61.3 kg) at that site. After capture, we saw a 20-cm tear through the snake's throat and neck. She died two days later. We found epidermal scutes of *P vogli* that matched the scutes of a turtle shell 20.3 cm in length. The turtle probably was too large for the snake to swallow, or perhaps it was in the wrong position, tearing the esophagus and skin of the snake as she ingested it.

A third event was recorded in February 1997. A male anaconda (268 cm TL, 10.7 kg) was swallowing a catfish *(pseudopimelodus apurensis;* 29 cm TL, 425 g) on the bank of the Cano Guaritico River. These fish

(Gomez-Dellmeier and Crigan... 1989). However, birds tend to be relatively lean and lightweight, and consuming them may not compensate for the metabolic costs of capture and digestion, especially by large snakes (Secor and Diamond, 1997; Rivas, 2000). Furthermore, strategies for capturing birds may differ substantially with those used to catch other, potentially more profitable and nutritious prey. In fact, excluding smaller prey from the diet as a snake grows larger is a common trend among snakes (Arnold, 1993; Rivas, 2000). In E. murinus, however, a switch

Fig. 11. A Green Anaconda (Eunectes murinus) ingesting a Capybara (Hydrochaeris hydrochaeris) that inflicted the bite responsible for the large wound.

have wide heads and long, sharp spines. These spines had punctured the snake's esophageal wall, muscle, and outer skin. The fish, still alive, was biting the snake's esophagus and was held in place by its spikes. We captured the animal, extracted the catfish, and held the snake without treatment until it healed completely, two months later. While in captivity, the snake ate a Green Iguana (Iguana iguana).

Scars and Wounds

Many anacondas sported scars, probably attributable to attacks by potential predators or defensive efforts of captured prey. Females were more frequently scarred (35 of 38 animals) than males (25 of 56; $\chi^2 = 20.1$, df $= 1, P < 0.001$; Fig. 12). This apparently reflects larger female size (Rivas, 2000; Rivas and Burghardt, 2001), as larger (= older) animals have more scars (Fig. 13). Logically, animals would accumulate more scars as they age, and because larger snakes presumably attack larger, more dangerous prey. An alternative explanation is that males experience higher mortality than females, possibly while tracking females. However, if this second scenario was true, one would expect a female-biased sex ratio, which was not supported by our data (Rivas, 2000; Fig. 2).

Predators should avoid prey that can injure them, because recovering from wounds can be more costly than the benefits of a meal. Why then do Green Anacondas attack prey that can and does inflict serious injuries? Perhaps no other prey is available. The abundance of waterfowl and other relatively "safe" birds in the llanos does not appear to support this hypothesis from birds to larger prey means capturing more dangerous mammals or non-avian reptiles. A similar switch in the diet of Reticulated Pythons (Python reticulatus) over 3 m TL has been documented (Shine et al., 1998), but does not seem to involve the same increased risk of injury we observed in anacondas.

The evolution of streptostylic jaws in early macrostomatan snakes facilitated the swallowing of large prey and enabled exploitation of new habitats. However, more mobile jaws with fewer rigid bones (Rieppel, 1988) undoubtedly involved the loss of some crushing power. Lacking the ability to kill or neutralize large prey with bites or crushing them with their jaws, snakes might be subject to different risks during predation than carnivorous lizards, mammals, and crocodilians.

Fig. 12. Scars on *Eunectes murinus* classified by relative size (see text).

Fig. 13. The number of scars increases with length in both sexes of Eunectes murinus.

Having neither a crushing jaw nor limbs to pin or strike prey increases the risk of being wounded by relatively large prey, and probably contributed to the evolution of sophisticated killing methods, such as venom and constriction.

Other Causes of Mortality

Another cause of mortality is accidental overheating, which may be prevalent during the hot dry season, when snakes are stranded in small, isolated pools or ponds. Although anacondas might remain in mud until the onset of the wet season, if they are disturbed or attempt to move to deeper water, they risk becoming

stranded and overheating (Fig. 14). On one occasion, we found 34 individuals in a mud hole that measured approximately 20×10 m. These animals had congregated in one of the last suitable places in the area (Rivas, 2000).

CONCLUSIONS

Green Anacondas are models useful for studying the evolution of large body size and extreme sexual size dimorphism. neonatal biology, and predatorprey relationships. However, the difficulties in collecting natural history data are evident, considering that seven years of fieldwork were necessary to collect data on fifty mating aggregations (Rivas et al., this volume). That long-term field research has decreased greatly in recent years is not surprising. This trend is compounded by pressures on scientists to study questions easily formulated and quickly testable. In a time of scarce research funding, extended field-based studies often are too risky and require a considerable investment of time, energy, and funds with no guarantee of results. Nevertheless, no alterative exists for dealing with species whose natural histories are poorly known.

This study began as a two-year program to study the possibility of sustainable use of Green Anacondas. However, because these snakes command attention, some media organizations sponsored a longer-term study. The need for similar studies of many other species that receive little or no public attention is equally critical. Consider, for example, that a great majority of amphibian species, many of which are declining rapidly, are known only as taxonomic entities.

Most of the results obtained in this study had little to do with the original goals. Too often, biologists are required to limit themselves to the specific data needed to address narrowly focused research goals, and are unable to expand the scope of their work as we did, to the detriment of good science.

Acknowledgments.—We thank the Wildlife Conservation Society, the National Geographic Society, the Convention for the International Trade of Endangered Species (CITES), the Venezuelan Fish and Wildlife

Tony Croccetta

Fig. 14. Carcass of a Green Anaconda (Eunectes murinus) found on the parched savanna. Snakes move in the dry season looking for water and occasionally fail to find a safe, cool refuge before the peak heat of the day.

Service (Profauna), The Miami Museum of Science, CONICIT, COVEGAN, The University of Tennessee, and Estacion Biologica Hato El Frio for providing financing and logistic support and allowing us work in their facilities. We also thank P. Azuaje, Mirna Quero, M. Urcera, A. Atensio, T. Aguliera, and E. Arrieta for their help and cooperation in the project and F. Provenzano for identifying icthyological samples. S. Corey provided important editorial comments and revisions. Dorcas Schaeffer and Phil Bochsler helped with key veterinary and pathological advice. Last but not least, we thank a long list of volunteers that helped us catch and process animals.

LITERATURE CITED

- ARNOLD, S. 1993. Foraging theory and prey-predator-size in snakes. Pp. 87–115 $In R. A. Seigel and J. T. Collin (Eds.),$ Snake Ecology and Behavior. McGraw-Hill, New York.
- CALLE, P. P., J. A. RIVAS, M. C. MUÑOZ, J. B. THORBJARNARSON, E. DIERENFELD, W. HOLMSTROM, E. BRASELTON, AND W. KARESH. 1994. Health assessment of free-ranging anacondas (Eunectes murinus) in Venezuela. J. Zoo Wildl. Med. $25:53 - 62.$
	- , W. HOLMSTROM, AND W. B. KARESH. 2001. Infectious disease serologic survey in free-ranging Venezuelan anacondas (Eunectes murinus). J. Zoo Wildl. Med. 32:320-323.
- GOMEZ-DELLMEIER, F., AND A. T. CRIGAN. 1989. Biology Conservation and Management of Waterfowl in Venezuela. Editorial Ex Libris, Caracas, Venezuela.
- GREENE, H. W. 1986. Natural history and evolutionary biology. Pp. 99-108 In M. E. Feeder and G. V. Lauder (Eds.), Predator-prey Relationships: Perspectives and Approaches from the Study of Lower Vertebrates. The University of Chicago Press, Chicago, Illinois.
- -. 1993. What's good about good natural history. Herpetol. Nat. Hist. 1:3.
- HERZOG, H. A. J., B. B. BOWERS, AND G. M. BURGHARDT. 1989. Development of antipredator responses in snakes: IV. Interspecific and intraspecific differences in habituation of defensive behavior. Develop. Psychobiol. 22:489-508.
- LANCINI, A. R. 1986. Serpientes de Venezuela. Talleres de Gráficas Armitano, Caracas, Venezuela.

Noss, R. F. 1996. The naturalist are dying off. Conserv. Biol. $10:1-3.$

- RAPHAEL, B. L., P. P. CALLE, W. KARESH, J. A. RIVAS, AND D. LAWSON. 1996. Technique for surgical implantation of transmitters in snakes. Proc. Wildl. Dis. Assoc. 1996:82.
- RIEPPEL, O. 1988. A review of the origin of the snakes. Evol. Biol. 22:37-130.
- RIVAS, J. A. 1997. Natural history: hobby or science? Conserv. Biol. 11:811-812.
- -. 1998. Predatory attack of a Green Anaconda (Eunectes murinus) on an adult human. Herpetol. Nat. Hist. 6:158-160.

2000. Life History of the Green Anaconda with Emphasis on its Reproduction Biology. Unpublished Ph.D. dissertation. University of Tennessee, Knoxville.

- . 2001. Feasibility and efficiency of transmitter force-feeding in studying the reproductive biology of large snakes. Herpetol. Nat. Hist. 8:93-95.
- . 2004. Eunectes murinus (Green Anaconda): subduing behavior. Herpetol. Rev. 35:66-67.
- , AND T. M. ÁVILA. 1996. Sex differences in hatchling Iguana iguana. Copeia 1996:219-221.

, AND G. M. BURGHARDT. 2001. Sexual size dimorphism in snakes: wearing the snake's shoes. Anim. Behav. 62:F1-F6.

- -, M. C. MUÑOZ, J. B. THORBJARNARSON, W. HOLMSTROM, AND P. P. CALLE. 1995. A safe method for handling large
- snakes in the field. Herpetol. Rev. 26:138-139. -, AND R. Y. OWENS. 2000. Eunectes murinus (Green
- Anaconda): cannibalism. Herpetol. Rev. 31:44-45.
- -, AND P. P. CALLE. 2001. Eunectes murinus (Green Anaconda): juvenile predation. Herpetol. Rev. 32:107-108.
- -, J. V. RODRIGUEZ, AND C. G. MITTERMEIER. 2002. The llanos. Pp. 265-273 In R. Mittermeier (Ed.), Wilderness. Cemex, México.
- -, J. B. THORBJARNARSON, R. Y. OWENS, AND M. C. MUÑOZ. 1999. Eunectes murinus: caiman predation. Herpetol. Rev. 30:101.
- Ross, R. A., AND G. M. MARZEC. 1990. The Reproductive Husbandry of Pythons and Boas. Institute of Herpetological Research, Stanford, California.
- SECOR, S. M., AND J. DIAMOND. 1997. Determinants of the postfeeding metabolic response of Burmese Pythons, Python molurus. Physiol. Zool. 70:202-212.
- SHINE, R. G., P. S. HARLOW, J. S. KEOGH, AND BOEADI. 1998. The influence of sex and body size on food habits of a giant tropical snake, Python reticulatus. Funct. Ecol. 12:248-258.