

on the screen may have differentially affected their ability to visually respond to the moving stimulus. Toads, on the other hand, have a larger anterior binocular field along the horizontal meridian that allows them to stalk terrestrial prey efficiently (Fite, 1973). Because the cricket was restricted to the lower portion of the video screen, the stimulus may have been out of the Green Frog's sight lines.

The present study corroborates previous experiments by Ewert (1980), Ingle (1968), and Freed (1988), showing that small moving objects may trigger prey-catching behavior in anurans. By using a natural prey item as a model, the stimulus conforms to the guidelines established by Ewert (1980), Ingle (1968), and Freed (1988) as a good visual releaser of prey-catching behavior in anurans. The current study differs from previous tests in that a televised, two-dimensional stimulus has been shown to elicit an attack response. Further, this study, unlike Ewert's (1980) previous experiments, allowed the test subjects to approach and attack the video image as an indicator of positive prey recognition. During the experiments performed by Beck and Ewert (1979) and Ewert (1980), toads were kept in glass vessels and could not approach the stimulus.

This technique has tremendous potential because identical stimuli may be presented to all test subjects. Further, the background, contrast, intensity, behavior, and morphology of the stimuli can all be varied independently with computer animation. Each stimulus also may be used repeatedly with no variation in presentation. Using video imaging, an array of prey species can be tested, or various aspects of specific prey items may be manipulated and modified to determine their importance in triggering a feeding response.

LITERATURE CITED

- BECK, A., and J.-P. EWERT. 1979. Prey selection by toads (*Bufo bufo* L.) in response to configurational stimuli moved in the visual field z,y-coordinates. *J. Comp. Physiol.* 129:207-209.
- CLARK, D. L., and G. W. UETZ. 1990. Video image recognition by the jumping spider, *Maevia inclemens* (Araneae: Salticidae). *Anim. Behav.* 40:884-890.
- _____, and _____. 1992. Morph-independent mate selection in a dimorphic jumping spider: demonstration of movement bias in female choice using video controlled courtship behavior. *Ibid.* 43:247-254.
- EVANS, C. S., and P. MARLER. 1991. On the use of video images as social stimulus in birds: audience effects on alarm calling. *Ibid.* 41:17-26.
- EWERT, J.-P. 1980. Neuroethology: an introduction

to the neurophysiological fundamentals of behavior. Springer-Verlag, Berlin, Germany.

- FITE, K. V. 1973. The visual fields of the frog and toad: a comparative study. *Behav. Biol.* 9:707-718.
- FREED, A. N. 1988. The use of visual cues for prey selection by foraging treefrogs (*Hyla cinerea*). *Herpetologica* 44:18-24.
- INGLE, D. 1968. Visual releasers of prey-catching behavior in frogs and toads. *Brain Behav. Evol.* 1:500-518.
- _____. 1973. Size preferences for prey-catching in frogs: relationship to motivational state. *Behav. Ecol.* 9:485-491.
- _____, and J. COOK. 1977. The effect of viewing distance upon size preferences of frogs for prey. *Vision Res.* 17:1009-1013.

NICHOLAS O. ROSTER, *Department of Biology, Central Michigan University, Mount Pleasant, Michigan 48858*; DAVID L. CLARK, *Department of Biology, Alma College, Alma, Michigan 48801*; and JAMES C. GILLINGHAM, *Department of Biology, Central Michigan University, Mount Pleasant, Michigan 48858*. Send reprint requests to NOR. Submitted: 23 April 1993. Accepted: 21 July 1994. Section editors: D. Cundall and F. Irish.

Copeia, 1995(2), pp. 498-501
© 1995 by the American Society of
Ichthyologists and Herpetologists

GROWTH OF CAIMAN CROCODYLUS CROCODYLUS IN CENTRAL AMAZONIA, BRAZIL.—*Caiman crocodylus crocodylus* is considered to reach sexual maturity at 3-4 years of age (Stanton and Dixon, 1977; Ouboter and Nanho, 1989) whereas most other crocodylians require more than nine years for females to reach sexual maturity (Webb et al., 1983; Magnusson and Lima, 1991). However, growth rates of *C. c. crocodylus* vary among habitats, and individuals in some populations in the Venezuelan Llanos (Ayarzagüena, 1980) and the Guianan shield in Venezuela (Gorzula, 1978) appear to have much lower growth rates (Gorzula and Seijas, 1989).

Not all methods of age estimation are equally reliable for crocodylians. Size frequency analyses are difficult to interpret because of large individual variation and the possibility that reproductive failure may mean that some year classes are missing. Well-calibrated studies using bone histology may be precise, but knowledgeable animals are necessary to determine the rate of annulus formation, and it is often necessary to kill the animal to obtain the appropriate bone sample. Integration of growth-rate-on-size re-

lationships obtained from capture-recapture studies is frequently used to estimate size-age relationships (Andrews, 1982). However, many models are available, and there may be no a priori reason to accept any particular model (Brisbin et al., 1987). Age can be determined directly by marking juveniles at birth and measuring them at known intervals. Despite its accuracy, the difficulty of recapturing crocodylians and the similarity of their longevity to that of humans reduces the utility of this method. In this study, we used a combination of the latter two methods to estimate the relationship between size and age for a population of *C. c. crocodylus* inhabiting two small lakes near the mouth of the Tapajós River, Pará, Brazil.

The study was done in Lago Mangueira and Lago Piranha, located on a peninsula which juts into the Tapajós River, about 2 km north of the township of Alter do Chão (2°31'S, 55°00'W). The Tapajós is a clear-water tributary of the Amazon River (Sioli, 1975). The lakes are formed by overflow from the Tapajós River and have no permanent affluents. Lago Piranha is about 1.9 km long and 0.5 km wide. Lago Mangueira is circular, about 200 m in diameter and separated from Lago Piranha by a strip of land about 150 m wide covered by fringing forest and savanna. The lakes are connected at high water. The depth of each lake varies from ~7 m to < 1 m seasonally. Mean daily rainfall for the area was provided by the Ministério da Aeronautica, Santarem Airport. The recording station is 20 km from the study area and has similar rainfall.

Caimans were captured at night by hand, with Pilsstrom tongs or in gill nets. The nets were set in the water and formed an arc along the bank. They were anchored to the bottom and the bank with sticks, and rotting fish were suspended from bushes as bait. Caimans that swam over the net were scared into diving by the fast approach of the researchers. The method is a modification of the drop-net technique of Webb and Messel (1977). Captures were made at irregular intervals between Dec. 1985 and Nov. 1990. We marked 81 individuals and recaptured 28 of them between one and three times for a total of 42 recaptures.

Snout-vent lengths (SVL; measured to the anterior edge of the cloaca) were calibrated with tapes accurate to 0.05 cm. The caimans were marked by excising unique combinations of tail scutes, and their sex was determined by visual examination of the penis/clitoris.

The relationship between growth rate (GR) and snout-vent length was complex (Fig. 1B), and attempts to fit the Richard's model of sig-

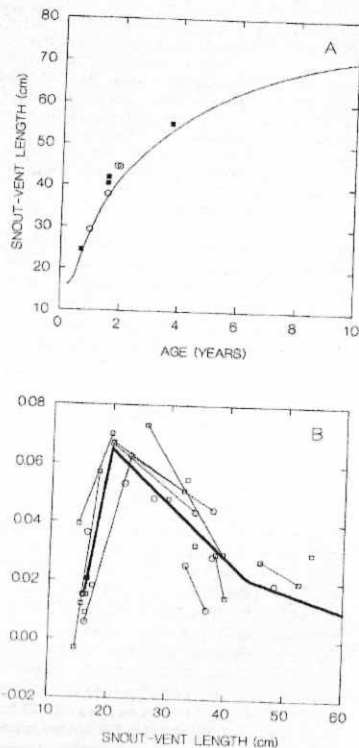


Fig. 1. (A) The relationship between length and age of *Caiman crocodylus* (line) was estimated by integration of the data in part B. Open circles represent sizes of known-age females, and closed squares represent sizes of known-age males that were used to verify the accuracy of the relationship. (B) Relationship between growth rate (GR) and length (SVL) for *C. crocodylus*. Circles represent females and squares represent males. Fine lines join data for the same animal. The thick lines represent the relationships between growth rate and age used to construct part A by integration of the straight line segments (Andrews, 1982). In sequence from left to right the linear segments are defined by the following equations: $GR = -0.175 + 0.011988 SVL$, $GR = 0.102 - 0.001861 SVL$, $GR = 0.050 - 0.00067 SVL$.

moidal growth (Brisbin, 1988) produced results that were not biologically feasible. This occurred even when we stipulated asymptotic sizes between 70 cm and 85 cm, suggesting that the

underlying relationship is not a special case of the Richard's family of curves. We, therefore, used linear models to represent different segments of the growth-rate-on-size relationship (Webb et al., 1983). The break points were determined by piecewise linear regression in the NONLIN module of the SYSTAT statistical program (Wilkinson, 1990). The general model was $GR = a + b_1 * SVL + b_2 * (SVL - intercept) * (SVL < intercept)$ where a , b_1 , and b_2 are constants and the intercept of the two lines is to be estimated. The program identified an intercept at 20 cm SVL (Fig. 1B). We then applied the model to the data for animals larger than 20 cm, and the program identified another intercept at 43.6 cm. Each animal was used only once for estimation of the relationship. For animals with multiple recaptures, we used the following criteria. For animals with $SVL < 20$ cm at first capture, we used the first recapture interval. For animals with $SVL \geq 20$ cm at first capture, we used the second recapture interval. This model is purely empirical. We justify its use below.

The second break point (43.6 cm SVL) appears realistic. However, the program estimated a positive slope for the last segment of the curve. The relationship between growth rate and size may approximate zero inclination (e.g., Webb et al., 1983). However, a positive slope is biologically unlikely and could not be maintained for long. We, therefore, assumed a constant rate of decrease in growth rate from 43.6 cm SVL to an asymptote of 75 cm SVL. There was no apparent difference in growth rates between males and females for any segment of the curve (Fig. 1B). However, males attain larger sizes than females (Gorzula and Seijas, 1989), and they must have higher growth rates at larger sizes than we measured. An average maximum size of 75 cm SVL for females is realistic based on what we know of other populations in Amazonia and Venezuela (Gorzula and Seijas, 1989). However, setting the asymptote at 70 cm or 85 cm would have little effect on any of the conclusions we make.

The model we have chosen is deliberately conservative. If it is biased, it will underestimate size at any age. We tried other composite models such as logistic growth until 43.6 cm and exponential from there on. However, these gave results similar to those for the segmented linear model so we used the simpler model.

We had most data for the central segment of the growth curve. In this segment, there was no significant effect of sex or the mean daily rainfall during the recapture interval on size-spe-

cific growth rates ($F_{1,14} = 0.46, P = 0.51; F_{1,14} = 0.03, P = 0.87$, respectively).

As with *C. johnstoni* (Webb et al., 1983), multiple recaptures indicate that the variance around the growth-rate-on-size relationship is caused by individual animals following different, but generally parallel, growth trajectories rather than by random fluctuations in the growth rates of individual animals. Therefore, differences among individuals in the relationship between SVL and age will increase with time, and this will increase the variance in age at a given length.

Multiple recaptures also confirm that growth rates increase during the first year and then show a declining concave relationship with size. Growth rates of large reptiles usually decline monotonically with age (Andrews, 1982). Without multiple recaptures, the most parsimonious procedure would be to fit a single exponential model to the data. This would grossly underestimate average growth rates at some sizes.

As outlined above, our empirical model was deliberately conservative and probably underestimates growth rates. However, comparison of the integrated form of this model (Fig. 1A) with eight animals captured as hatchlings (possible error of estimation of hatching date approximately ± 30 days) indicates that it only slightly underestimates SVL up to about 55 cm SVL and four years of age. We have no empirical verification of the model above this age, but we are confident that it is fairly accurate and still biased toward overestimating age.

The occurrence of nests indicates that only one or two females regularly breed in the lakes. We have seen adult caimans (~70 cm SVL) accompanying pods of hatchlings but have been unable to catch them. Based on an average size of 120 cm TL (~60 cm SVL) for females at sexual maturity (Gorzula and Seijas, 1989), females at Alter do Chão would reach maturity at between five and six years of age. This is much less than the age at maturity of females estimated for other crocodylians [Webb et al., 1983; Magnusson and Lima, 1991; but the model of Brislin (1988) indicates that *Alligator mississippiensis* could reach reproductive size at a similar age].

The reason for the abrupt changes in growth rates is not obvious. The first break point occurs at about the time that hatchlings disperse from pods, but there may also be seasonal changes in food abundance. As with *C. johnstoni* (Webb et al., 1983), the second break point occurs before sexual maturity, and there is no evidence for an abrupt change in diet at this size in either

species (Magnusson et al., 1987). The very abrupt decreases in growth rates of the two animals with multiple recaptures between 30 and 40 cm SVL (Fig. 1B), indicate that individuals may face some biological barrier at that size.

Acknowledgments.—R. Cintra, V. da Costa, M. Hero, A. Lima, and M. Yamakoshi helped with recaptures. P. Bayliss helped with recaptures and discussion of methods of analysis. This study owes much to the help and hospitality of S. Sardinha, N. Sardinha, S. Sardinha, B. Sardinha, and their families at the Village of Alter do Chão. Financial support was provided by grants (40081/09-7, 301299-86, 408064/84) from the Brazilian Conselho Nacional de Desenvolvimento Científico e Tecnológico to WEM. The manuscript was much improved by comments from I. L. Brislin and S. Gorzula.

LITERATURE CITED

- ANDREWS, R. M. 1982. Patterns of growth in reptiles, p. 273-320. In: *Biology of the Reptilia*. Vol. 13. Physiology D. C. Gans and F. H. Pough (eds.). Academic Press, New York, New York.
- AVARZAGÜENA, J. 1984. *Biología y ecología de la baba (Caiman crocodilus) en los Llanos de Venezuela*. Doñana Acta Vertebrata, Série Monografías, Sevilla, Spain.
- BRISLIN, I. L. 1988. Growth curve analyses and their application to the conservation and captive management of crocodylians, p. 116-145. In: *Proceedings of the Ninth Working Meeting of the IUCN/SSC Crocodile Specialist Group*. F. W. King (ed.). IUCN, Gland, Switzerland.
- , C. T. COLLINS, G. C. WHITE, AND D. A. MCCALLUM. 1987. A new paradigm for the analysis and interpretation of growth data: the shape of things to come. *Auk* 104:552-554.
- GORZULA, S. J. 1978. An ecological study of *Caiman crocodilus crocodilus* inhabiting savanna lagoons in the Venezuelan Guyana. *Oecologia* 35:21-34.
- , AND A. E. SEIJAS. 1989. The common caiman, p. 44-61. In: *Crocodyles: their ecology, management and conservation*. P. Hall and R. Bryant (eds.). IUCN, Gland, Switzerland.
- MAGNUSON, W. E., AND A. P. LIMA. 1991. The ecology of a cryptic predator, *Paleosuchus trigonatus*, in a tropical rainforest. *J. Herpetol.* 25:41-48.
- , E. V. DA SILVA, AND A. P. LIMA. 1987. Diets of Amazonian crocodylians. *Ibid.* 21:85-95.
- OUBOTER, P. E., AND L. M. R. NANHOE. 1989. Notes on the dynamics of a population of *Caiman crocodilus* in northern Surinam and its implications for management. *Biol. Conserv.* 48:243-264.
- SIOLI, H. 1975. Amazon tributaries and drainage basins, p. 199-213. In: *Coupling of land and water systems*. A. D. Hasler (ed.). Springer Verlag, Berlin, Germany.
- STATON, M. A., AND J. R. DIXON. 1977. Breeding biology of the spectacled caiman, *Caiman crocodilus crocodilus*, in the Venezuelan Llanos. *U.S. Fish Wildl. Serv. Wildl. Res. Report* 5:1-21.
- WEBB, G. J. W., AND H. MESSEL. 1977. Crocodile capture techniques. *J. Wildl. Manage.* 41:572-575.
- , R. BUCKWORTH, AND S. C. MANOLIS. 1983. *Crocodylus johnstoni* in the Mckinlay River area, N. T. III. Growth, movement and population age structure. *Aust. Wildl. Res.* 10:383-401.
- WILKINSON, L. 1990. SYSTAT. The system for statistics. SYSTAT Inc., Evanston, Illinois.
- WILLIAM E. MAGNUSON AND TÂNIA M. SANATIOTTI, *Departamento de Ecologia, Instituto Nacional de Pesquisas da Amazônia, Caixa Postal 478, 69011-970 Manaus AM, Brasil*. Submitted: 30 July 1993. Accepted: 13 Jan. 1994. Section editors: D. Cundall and F. Irish.

Copeia, 1995(2), pp. 501-505
© 1995 by the American Society of
Ichthyologists and Herpetologists

HISTORY OF THE GENERA *LEBIA* OKEN 1817 AND *LEBIAS* GOLDFUSS 1820 (TELEOSTEI: CYPRINODONTIFORMES: CYPRINODONTIDAE) WITH DESIGNATION OF A TYPE SPECIES FOR *LEBIAS*.—The history of *Lebia* Oken 1817 and *Lebias* Goldfuss 1820 has been marked by unnecessary confusion owing, in part, to the unwarranted assumption that the latter name is a spelling variant of the former. In recent literature, such as in Eschmeyer and Bailey (1990), *Lebias* has been dismissed without any investigation of its history. The literature appropriate to the understanding of the nomenclatural status of these genera was reviewed by Garman (1895) in his monumental revision of the cyprinodonts. Unfortunately, Garman's work, at least as it pertains to *Lebia* and *Lebias*, has gone unnoticed in subsequent treatments of cyprinodont genera and species. With the law of priority in mind, a careful reading of Garman could have been used to ascertain the status of both genera.

Cuvier (1816) introduced a new genus using the vernacular "Les Lebias." Cuvier's vernacular name is not available [International Code of Zoological Nomenclature (ICZN), 1985: Article 11]. Because of the inherent ambiguity of "Les Lebias," it is not possible to determine whether Cuvier had *Lebia* or *Lebias* in mind as the latinized version of his new genus. Oken (1817), in a work that contrasted his systematic