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Human Influence on the Wariness of *Melanosuchus niger* and *Caiman crocodilus* in Cuyabeno, Ecuador

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ABSTRACT.—The effect of mark-recapture experiments on the wariness of *Caiman crocodilus* and *Melanosuchus niger* in two lakes in Amazonian Ecuador was examined. Three experiments were conducted with five, seven, and 10 sampling replicates, respectively. Each sampling replicate consisted of one nocturnal spotlight count around the lake, during which caimans were captured, marked, and released. There were negative correlations between the number of individuals seen in each sampling replicate and sampling replicate sequence in both lakes and both species. In one lake, there was a positive correlation between the percentage of wary caimans and the sequence of sampling replicates. Our findings indicate that observation and capture, even if harmless, affect the spatial distribution and wariness of crocodilian populations.

RESUMEN.—Examinamos el efecto de la conducción de experimentos de captura-recaptura en la cautela de *Caiman crocodilus* y *Melanosuchus niger* en dos lagunas de la Amazonía Ecuatoriana. Se llevó a cabo tres experimentos con cinco, siete y 10 muestreos respectivamente. Cada muestreo consistió en un conteo nocturno al rededor de la laguna a lo largo del cual se capturó, marcó y liberó caimanes. En ambas especies se observó correlaciones negativas entre el número de individuos vistos en cada muestreo y la secuencia de los muestreos. En una de las dos lagunas hubo una correlación positiva entre el porcentaje de caimanes ariscos y la secuencia de los muestreos. Los resultados de este estudio indican que influencias humanas, incluso si son inofensivas, afectan la distribución y cautela de las poblaciones de cocodrilianos.

Predation is an environmental pressure that greatly influences animal survival. Therefore, behavioral traits, such as wariness, that allow successful escape from predators may have a strong impact on individual fitness. "Wariness" is defined here as the disposition of exhibiting avoidance behaviors toward potential predators. The degree of wariness might reflect a cost-benefit relationship that is in equilibrium when the disadvantageous costs of being wary (e.g., increased energy expenditure owing to escape responses, decreased time devoted to foraging or reproductive activities) are balanced by the benefit of successful avoidance of predators.

Human activities, such as hunting, nocturnal observation, and capture of crocodilians, might affect wariness (e.g., Bustard, 1968; Webb and Messel, 1979; Montague, 1983; Woodward et al., 1987; Pacheco, 1996) by influencing the genetic and learned components of evasive behaviors. Although the relationship between human-generated disturbance and wariness has been assumed widely by crocodilian biologists, its quantitative nature has not been determined. Bustard (1968) reported that juveniles of *Crocodylus porosus* were more difficult to approach after capture attempts. Montague (1983) reported that hunted populations of *C. porosus* and *C. novaeguineae* have longer flight distances than do those of non-hunted populations; however, no tests were performed to confirm the statistical significance of these observations.

Influences on wariness are also important because they can bias abundance estimates derived from nocturnal spotlight counts (Bayliss, 1987; Pacheco, 1996). Surveys of less wary populations may yield higher counts than those of more wary populations. Nocturnal spotlight counts are the most widely used method of sampling crocodilians (Magnusson, 1982). Mark-recapture experiments also are an important tool to assess absolute abundance and density of wild populations. However, there is no statistical analyses to predict and correct for the possible effect of monitoring techniques on wariness and, therefore, the effect of these techniques on estimates of relative or absolute abundance derived from such surveys.

Attempts have been made to relate wariness of crocodilians to animal size, hunting pressure (Webb and Messel, 1979; Montague, 1983; Pacheco, 1996), and several abiotic factors (Ron, 1995; Vallejo, 1995; Pacheco, 1996). The only variable that has been proven repeatedly to be related with wariness is animal size—i.e., larger crocodilians tend to be more wary (Webb and Messel, 1979; Montague, 1983; Pacheco, 1996).

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During the course of three mark-recapture experiments, to determine the size of populations of *Caiman crocodilus* and *Melanosuchus niger* in three lakes in the Ecuadorian Amazon, we observed a progressive increase in wariness. This is the first published study to correlate statistically human disturbance with the wariness and distribution of wild crocodilian populations.

MATERIALS AND METHODS

The studies were conducted in 1993–1994 in two black-water lakes located in the Provincia de Sucumbíos in Amazonian Ecuador. The lakes are in a protected area, the Reserva de Producción Faunística Cuyabeno, which is part of the Tropical Humid Forest Life Zone (Cañadas-Cruz, 1983). The elevation is 260 m, the mean annual precipitation is approximately 3000 mm, and the daily mean temperature typically is 20.9–28.2°C.

Laguna Mateococha (MT) is a 0.32 km^2 lake located at 0°1′S and 75°14′W in the Río Cuyabeno lacustrine system. Laguna Zancudococha (ZC) is a 4.37 km^2 lake located at 0°35′S and 75°30′W on the southern border of the Río Aguarico. Both lakes are surrounded by black-water flooded forest or igapo.

The common caiman, *Caiman crocodilus crocodilus*, and the black caiman, *Melanosuchus niger*, occur in both lakes, but in different relative abundances. In MT, the ratio of individuals *C. crocodilus: M. niger* observed during nocturnal spotlight counts is 28.4:1 whereas in ZC the ratio is 1:9.2 (Ron, 1995; Vallejo, 1995).

A mark-recapture experiment was conducted in ZC in January 1993. High water levels reduced the caiman population accessible for capture and resulted in small sample sizes that impeded estimation of population size. However, there were sufficient observations of caiman to allow us to perform an analysis of wariness; five sampling replicates were conducted during five consecutive nights. During the dry season of January and February 1994, low water levels facilitated seven and 10 sampling replicates to be conducted in MT and ZC, respectively. None of the experiments lasted more than 10 consecutive nights (one or two nights per sample). Each sampling replicate consisted of a nocturnal spotlight count around the lake during which we captured as many caimans (<170 cm in total length) as possible. The nocturnal spotlight count methodology used was described by Magnusson (1982). Caiman total length was estimated by direct observation. Individuals less than 1 m in total length were captured by hand, whereas those ranging from 1.0 to 1.7 m were captured with a noose (as described by Jones, 1966). Caimans, detected by their eye-reflection, often avoided capture with evasive movements. If the caiman was caught, it was brought into the canoe and its identity, sex (by cloacal examination), and general measurements were recorded. Each individual was marked with numbered #1 or #2 Monel (Natl. Band and Tag Co., Newport, KY) metallic tags inserted in the web between the third and fourth digit of the right rear foot. All caimans were released immediately after we recorded the data.

The species and estimated length of all caimans observed were recorded. At ZC, we used a 12-V spotlight during the first four surveys, but later realized the capture attempts were more successful with a less intense light (6-V head lamp). At Mateococha, we used only the 6-V head lamp. All surveys were conducted by the same two people to avoid any bias that might result from differential experience and capture ability between working teams.

Water level is the most influential abiotic factor affecting the numbers of caimans seen in nocturnal spotlight counts performed at time intervals of approximately one month (Ron, 1995; Vallejo, 1995). During the experiment, the variation of water level was recorded to determine possible influences on wariness.

The effect of the mark-recapture experiment on population wariness was judged by two criteria. First, we recorded the total number of caimans seen in the samples. We assumed that a progressive reduction in the number of individuals seen during the course of the surveys might reflect an associated increase in wariness. Second, we determined the proportion of caimans that could not be approached closely enough to make either species identification or size estimation ("eyes only" = EO; Webb and Messel, 1979; Montague, 1983; Seijas, 1988; Pacheco, 1996). We assumed that an increase in this latter proportion reflects increased wariness.

We also tested the relationship between wariness and caiman size. Wariness was measured as the proportion of the number of caimans observed that were captured in each sample. We assumed that higher capture proportions indicated lower wariness levels.

Linear regressions were performed to determine the significance of the relationship between the total number of caimans observed (dependent variable) and the number that the sample occupied in the replicate sequence (first, second, third, etc.; independent variable). Linear regressions also were performed on the relationship between the number that the sample occupied in the sequence (independent variable) and the EO caimans seen (dependent variable). In all cases ANOVAs were computed to test the significance of the association between the dependent and independent variables ($\alpha = 0.05$).

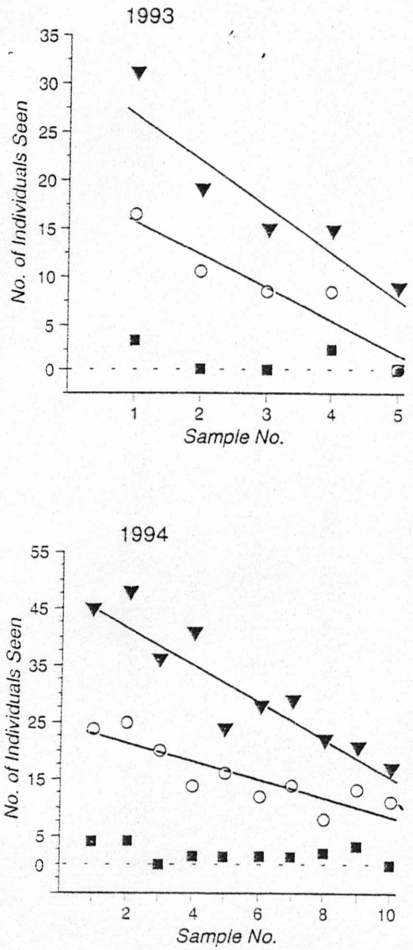

FIG. 1. Number of caimans observed during the mark-recapture experiments performed in Laguna Zancudococha in January 1993 and January 1994. The experiments in 1993 and 1994 were performed over a period of five and 10 consecutive nights, respectively. Regression lines plotted only for significant relationships. Total number (*Melanosuchus niger* + *Caiman crocodilus* + EO) observed in 1993 = 31.2 − 4.8x; R^2 = 0.856. Total number observed in 1994 = 48.2 − 3.3x; R^2 = 0.852. Number of *M. niger* observed in 1993 = 18.6 − 3.4x; R^2 = 0.881. Number of *M. niger* observed in 1994 = 24.5 − 1.6x; R^2 = 0.754. ▼ = total; ○ = *M. niger*; ■ = *C. crocodilus*.

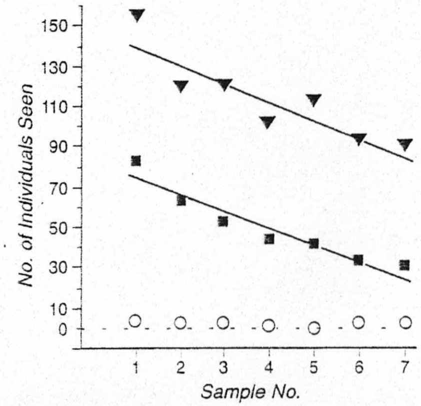

FIG. 2. Number of caimans observed during the mark-recapture experiment performed in Laguna Mateococha in January 1994. The experiment was performed over a period of 10 consecutive nights. Regression lines only plotted for significant relationships. Total number (*Melanosuchus niger* + *Caiman crocodilus* + EO) observed = 146.4 − 9x; R^2 = 0.796. Number of *C. crocodilus* observed = 82.1 − 8.2x; R^2 = 0.909. ▼ = total; ○ = *M. niger*; ■ = *C. crocodilus*.

Hatchlings (individuals <40 cm in total length) were not considered in the analyses. They tend to be congregated in pods and, therefore, do not represent independent observations. We did not perform analyses on samples of *Melanosuchus niger* from MT or *Caiman crocodilus* from ZC owing to small sample sizes.

RESULTS

Significant relationships exist between sample sequence and the total number of caimans observed (*Melanosuchus niger* + *Caiman crocodilus* + EO). The relationship was also significant for *M. niger* in ZC and *C. crocodilus* in MT (Figs. 1, 2; Table 1).

There was a significant relationship between EO percentage and sample sequence in the data from MT (F = 48.02, df = 6, P = 0.001; EO percentage = 40.208 + 3.704x, R^2 = 0.906). The relationship was not significant in the experiments performed at ZC (1993 experiment: F = 1.85, df = 4, P = 0.267, R^2 = 0.382; 1994 experiment: F = 0.36, df = 9, P = 0.561, R^2 = 0.044).

Water level had no significant influence on the total number of individuals of *Melanosuchus niger* in ZC and *Caiman crocodilus* in MT, or on the number of EO observed in the samples (P > 0.11 in all cases). The range of variation in water level during the experiments was of 43 cm in MC and 33 cm in ZC.

Wariness was dependent on size in *Caiman*

TABLE 1. ANOVAs for the linear relationships between the survey sequence and the number of caimans seen during the mark-recapture experiments at Laguna Mateococha and Laguna Zancudococha. Total number corresponds to the sum of *Melanosuchus niger, Caiman crocodilus*, and EO caimans observed on surveys. See text for details.

	df	F	P
Total number Zancudococha (1993 experiment)	4	18.000	0.024
Melanosuchus niger Zancudococha (1993 experiment)	4	22.231	0.018
Total number Zancudococha (1994 experiment)	9	45.991	0.0001
Melanosuchus niger Zancudococha (1994 experiment)	9	24.567	0.001
Total number Mateococha	6	19.542	0.007
Caiman crocodilus Mateococha	6	50.209	0.0009

crocodilus in MC (G = 10.20, df = 4, P = 0.037) and *Melanosuchus niger* in ZC (G = 11.58, df = 4, P = 0.02). Both species showed similar wariness responses: there was an increase in wariness in the first four classes, whereas a greater proportion of individuals seen were captured in the 151–170 cm class (Fig. 3).

DISCUSSION

This study indicates that surveys with capture attempts influence the wariness and spatial distribution of wild crocodilian populations. A progressive decrease in the number of observations of both *Caiman crocodilus* and *Melanosuchus niger* was evident in both lakes. Because the experiments were carried out during periods of fewer than 10 d, it is unlikely that the decreases resulted from changes in the absolute abundance of caimans. Nor did differences in water

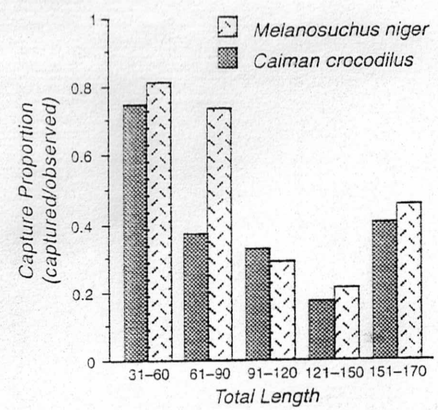

FIG. 3. Proportion of capture (number of individuals captured/number of individuals observed) by size classes of *Caiman crocodilus* in Laguna Mateococha and *Melanosuchus niger* in Laguna Zancudococha during the experiments of capture-recapture performed in 1994. Wariness indices were dependent of size class in both species. See text for details.

level correlate with the decrease in the number of caimans observed. The decrease in the number of caimans observed can be attributed primarily to movements by the caimans to positions unreachable by our lights. These positions might be located in the flooded forest that surrounds the lake. Similar findings have been reported for the green iguana, *Iguana iguana*, for which capture and handling led to a lower probability of sighting the individual again and to changes in home ranges of individuals (Rhoda et al., 1988).

Seasonal variation in water level is the most important factor affecting the spatial distribution of crocodilians in the upper Amazon Basin. During the rainy season, most *Caiman crocodilus* and *Melanosuchus niger* remain in the flooded forest. During the dry season (when this study was carried out), the flooded forest dries and the caimans gradually retreat to the deepest areas of the lakes. Caimans remain there until the end of the dry season (Asanza, 1992; Ron, 1995; Vallejo, 1995). Apparently, direct disturbance by humans can revert that tendency, forcing caimans to move to possibly suboptimal locations.

The increase in the proportion of wary caimans (as indicated by EO%) in MT might reflect an increase in wariness as result of learning. When repeatedly disturbed, caimans may tend to escape at increasing distances from the source of the disturbance. However, this behavior was not evident in ZC. The reasons for these differences remain unclear, but the change in light intensity during the experiment in ZC might have contributed to lack of significance of the relationship between EO percentage and sample sequence. Different disturbance intensities between lakes and/or different responses between species might be other sources of variation.

The intensity of the disturbance during the experiments might have played an important roll in revealing the effects of the samples in the wariness and spatial distribution. Most mark-recapture experiments involving crocodilian populations (e.g., Bayliss et al., 1986; Hutton and Woolhouse, 1989) differ from our studies in that they lasted longer and the areas sampled were larger. Additionally, tags visible from long distances were attached to crocodilians so "recaptures" required only sighting of the tags instead of an additional capture (=additional disturbance). These differences in experimental approach may have impeded the identification of effects on wariness.

Previous studies on the association between wariness and crocodilian size reported positive relationships (Webb and Messel, 1979; Montague, 1983; Pacheco, 1996). This also was true for this investigation for the size classes below 150 cm in total length. However, the decrease in wariness observed in the 151–170 cm class with respect to the previous class, does not fit that pattern. This may be the result of differences in the genetic and/or learned components of wariness among the studied species and populations and/or differences in movement patterns between size classes.

In conclusion, the effects on wariness of the monitoring of crocodilian populations can generate changes in sampling proportions that can bias demographic estimates. Therefore, monitoring methodologies should be designed to minimize direct interactions with crocodilians. Induced changes in wariness should be determined to correctly estimate abundance trends through time. This study also has shown that human interactions with crocodilians, even if causing no direct injury, can influence their distribution and wariness and, therefore, might affect their survivorship and/or reproductive output in the long term.

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