

Gravid females, eggs and juveniles of *P. astriata* have been observed in all months of the year with no discernible peak in reproductive effort (Gardner, 1984). The high number of co-occurrences between males and females recorded in this study probably reflects year round mating.

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## Wariness of Caiman Populations and its Effect on Abundance Estimates

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Management of wild crocodylian populations has relied heavily on abundance estimates derived from night spotlight counts, under the assumption that sighting proportions (the relationship between the counts and the total population) remain constant through time (Woodward and Moore, 1993). When conducting spotlight surveys, differences in wariness or activity level of the animals may affect count results. Surveys of less wary populations may give higher sighting proportions than more wary populations, even when activity levels are equal. Hunting, capture and release programs, and individual age (size) are the main factors that affect the wariness of crocodylian populations (Webb and Messel, 1979; Montague, 1983; Woodward et al., 1987). Therefore, the effects of wariness on spotlight counts should be considered both when comparing abundances between crocodylian populations and when monitoring population trends. Localities having similar indices of wariness should give comparable abundance estimates, if surveyed under similar environmental conditions.

This study was designed to help evaluate abundance estimates within a monitoring program of crocodylians in the Beni Biosphere Reserve Estación Biológica Beni (BBR), Bolivia (14°30'-14°50'S and 66°00'-66°40'W). The BBR has an average altitude of 225 m and covers 135,000 ha. Vegetation is mainly forest, interspersed with patches of open swamps and savannas. Mean annual temperature is 26.1°C (6°C-38°C), and mean annual rainfall is 1830 mm (Miranda et al., 1991).

Four lagoons were studied; three of them, Cedral = CE (ca. 6.5 km shoreline), Normandia = NO (ca. 7.3 km) and Ojo de Buey = OB (ca. 2.9 km) are within the BBR, and Los Puros = LP (ca. 6.5 km) is outside the BBR limits. All surveys were done during the low water period (late May through October) to control for its effects on counts.

Three of the five species of crocodylians occurring in Bolivia (Ergueta and Pacheco, 1990) are present in the BBR: *Caiman yacare*, *Melanosuchus niger*, and *Paleosuchus palpebrosus*. Few data on *P. palpebrosus* were collected, so analysis was restricted to the other two species. Caimans were classified into the following life stages (size classes): I = all hatchlings and probably some yearlings in both species. II = juveniles and subadults of *C. yacare* and juveniles for *M. niger*. III = adults of *C. yacare* and subadults for *M. niger*. IV = mainly mature males of *C. yacare* (Medem 1981, Thorbjarnarson 1991) and the largest subadults and

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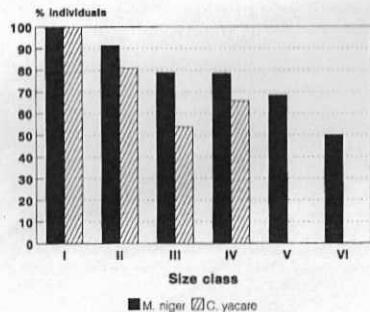


FIG. 1. Proportion of crocodilians, by species and size class, with escape distance <1.5 m. The frequency of individuals with escape distance <1.5 m is not independent of size for either *M. niger* ( $G = 110.4$ ,  $df = 5$ ,  $P < 0.0001$ ) or *C. yacare* ( $G = 17.1$ ,  $df = 3$ ,  $P < 0.001$ ).

smallest adults of *M. niger*. V = adult *M. niger* of both sexes. VI = mainly mature males of *M. niger* (Medem 1981).

Twenty spotlight counts were conducted in Cedral lagoon, and 1–3 surveys in the rest of the lagoons. Two wariness indices were obtained for each locality: the proportion of caimans that could be approached to <1.5 m (caimans closely approached—CCA) and the proportion of caimans that could not be approached closely enough to make species identification ("eyes only"—EO; Webb and Messel 1979, Montague 1983, Seijas 1988).

Using the 20 surveys from CE, multiple regression analysis was performed using the two wariness indices as dependent variables (separately) against seven environmental variables. Water temperature, wave height (in cm), wind speed (in k.p.h.), cloud cover (measured in octaves), and air temperature were measured before and after each survey. The other two variables were moon phase (1 = new moon to 14 = full moon) and maximum diurnal air temperature. Water temperature and wave height were dropped from analysis because of their high correlations with air temperature ( $r = 0.92$ ,  $P = 0.0001$ ) and wind speed ( $r = 0.98$ ,  $P = 0.0001$ ), respectively. Both dependent variables were transformed to natural logarithms (arcsine transformation was first tested) to linearize data (Ott, 1988), only for the multiple regression analyses.

The independence of wariness and size was tested by comparing size-class distributions of caiman that could be approached closely (<1.5 m, = CCA), for both species separately vs. those that could not, using a G test (Zar, 1984). Data from all the surveys and all localities were used for this analysis. Frequency distributions of CCA by size class were compared among populations using either a G test or a Fisher's exact test as necessary (Zar, 1984). Size classes >II were lumped together to fulfill test requirements. Size class I was excluded from analysis because >99.5% of these animals (both species) were closely approachable.

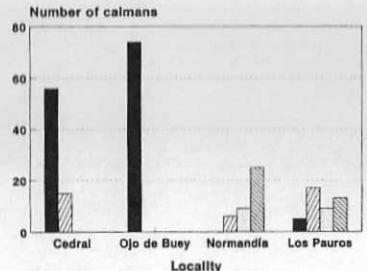


FIG. 2. Frequency distributions of *M. niger* and *C. yacare* with escape distance <1.5 m, by size and locality.

The mean proportion of EO individuals in CE was compared to the proportions from the other lagoons (Bayliss et al., 1986) using a two sample t-test with arcsine transformation (Zar, 1984). A single survey was carried out in CE on 18 May, 1993. Data from this survey were compared to those from the 1992 surveys to detect possible changes in wariness for CE, after caimans were captured and marked in 1992. Finally, pairwise comparisons of the proportion of EO among localities were done using a Z test (Zar, 1984). Within locality comparisons were first done for OB and NO, where more than one survey were conducted, to test for consistency within a locality.

None of the five variables considered affected significantly either the proportion of CCA ( $R^2 = 0.35$ ,  $F = 1.485$ ,  $df = 5, 14$ ,  $P > 0.2$ , full model) nor the proportion of EO ( $R^2 = 0.30$ ,  $F = 1.156$ ,  $df = 5, 14$ ,  $P > 0.3$ , full model). Consequently, data from all the surveys were combined for the following analysis. Escape distance (number of CCA) is not independent of the size of the caimans for *M. niger* ( $G = 110.4$ ,  $df = 5$ ,  $P < 0.0001$ ) or *C. yacare* ( $G = 17.1$ ,  $df = 3$ ,  $P < 0.001$ ). Larger caimans were more wary than smaller ones (Fig. 1).

Differences in the frequencies of CCA were found among all localities surveyed for *M. niger* (CE, OB, and LP,  $G = 66.38$ ,  $df = 2$ ,  $P < 0.0001$ , Fig. 2). No difference in proportion of CCA was found between *C. yacare* in NO and in LP (Fisher's exact test  $P > 0.52$ , Fig. 2). Data on *M. niger* from NO were excluded from analysis to fulfill G-test requirements. Pairwise comparisons for CE, OB, and LP indicated that wariness of *M. niger*, as measured by CCA, was different for all three localities (Fisher's exact tests  $P < 0.0001$  for all three comparisons).

No difference in wariness was found between species for LP (Fisher's exact test  $P > 0.33$ ). Data were insufficient for statistical comparison between species for NO and CE. Following this result, data for both species were lumped together to compare wariness between NO and LP caiman populations, which showed no significant differences (Fisher's exact test  $P > 0.56$ ).

The proportion of EO individuals counted in CE in 1992 was lower than for any other lagoon, except OB. Furthermore, in CE itself EO proportions did not differ between 1992 and 1993 (Table 1). No differences in the proportion of EO were found among surveys within the same locality for either OB (two surveys,  $Z = 0.519$ ,  $P > 0.3$ ) or NO (three surveys,  $P > 0.15$  for all three comparisons). Thus data from all the surveys within the same locality were lumped together for among-locality comparisons. Pairwise comparisons among all the lagoons indicated differences in wariness (as measured by the proportion of EO) among all lagoons ( $P < 0.001$  for all tests), except between NO and LP ( $Z = 0.96$ ,  $P > 0.16$ ).

Summarizing, both indices detected differences in wariness among all the localities surveyed, except between NO and LP. The only inconsistency between the two indices was for CE and OB, for which no difference was found for the EO category, while the comparison of CCA did show differences in wariness.

Wariness, as defined here, was not demonstrably affected by any of the environmental variables considered, even when some of these variables (wind speed, cloud cover, and maximum diurnal air temperature) affect the sighting proportions in a single survey (Pacheco, 1993). The popular belief that crocodilians are more wary when moon is full was not supported in this case. Rand (1964) reported that *Anolis lizard*s are more wary when their body temperature is high than when it is cooler. This appears not to be the case in crocodilians. Webb and Messel (1979) postulated that if any relationship between wariness of *C. porosus* and air temperature exists, this will be of minor importance, which agrees with the findings of this study.

The relationship between size and wariness found for *M. niger* and *C. yacare* in this study was also observed in *Crocodylus porosus* (Webb and Messel, 1979) and *C. porosus* and *C. novaeguineae* (Montague, 1983). Hatching *Alligator mississippiensis* were found to show little or no avoidance behavior (Woodward et al., 1987), similar to what was found here for hatching *M. niger*. According to Webb et al. (1989), increased size appears to be inherently associated with increased wariness (in *C. porosus*), and they postulated that wariness is not totally explicable on the basis of learned behavior. However, larger crocodilians become wary on the basis of experience, which increases with age. Differences in the types of experience (i.e., hunting, capturing) to which a population is subjected will determine differences in wariness.

A mark-recapture study was undertaken on the population of *C. yacare* in Normandia lagoon during 1985–1988 (Ruiz, 1988). Furthermore, the population of *M. niger* inhabiting this lagoon was introduced in 1990 (Pacheco et al., 1991). The similarity of wariness between NO and LP may be an indication of similar disturbances occurring in both lagoons. LP is outside the BBR, which may help explain this result.

Lack of differences in wariness between *M. niger* and *C. yacare* in LP suggests that factors influencing wariness may affect both species in the same way. For instance, since hunting is not species-selective, it might have similar effects on both species.

The inconsistency of the wariness indices when comparing CE and OB may be attributed to the small number of large caimans seen in OB. Since wariness

TABLE 1. Comparison of the proportion of EO individuals of Cedral lagoon (1992 counts) with those of the other lagoons.  $p$  = proportion of EO individuals out of the total counted. The values presented here are not transformed to arcsine. Values were transformed only for statistical analysis. CE = Cedral, OB = Ojo de Buoy, NO = Normandia, LP = Los Pauros, N = number of surveys.

| Lagoon    | Mean $p$ (N) | St dev. | df | t     | P      |
|-----------|--------------|---------|----|-------|--------|
| CE (1992) | 0.037 (20)   | 0.0261  | —  | —     | —      |
| CE (1993) | 0.037 (1)    | —       | 19 | 0.19  | 0.77   |
| OB        | 0.064 (2)    | 0.0178  | 20 | -1.18 | 0.2484 |
| NO        | 0.341 (3)    | 0.0603  | 21 | -4.38 | 0.0003 |
| LP        | 0.0921 (1)   | —       | 19 | -4.91 | 0.0001 |

is dependent on size, and the EO category tend to include mostly large caimans (pers. obs.), the EO index may be more appropriate in this case. Should we use the proportion of CCA index, size structure differences would make wariness comparisons less reliable. The results indicate that abundance estimates between OB and CE may be comparable for *M. niger*, as well as between NO and LP for both species. All other abundance comparisons may not be appropriate.

In conclusion, wariness is affected by size of the individuals, either as learned behavior or as an inherent property of age. Wariness is greater in disturbed lagoons than in less disturbed localities. Factors affecting wariness appear to be acting in a similar way upon both *M. niger* and *C. yacare*. Abundance comparisons among crocodilian populations should not be done without comparing wariness first. Both types of data used here are easily obtained while surveying. Wariness comparisons may be most effective if both indices are employed.

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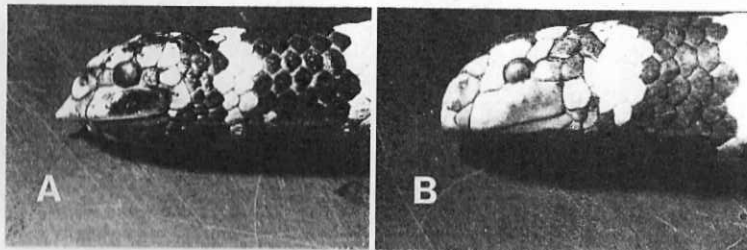


FIG. 1. Sexual dimorphism in the head of the sea snake *Emydocephalus annulatus*. (A) Male (NTM R21254; SVL = 54.5 cm) with the spine on the rostral scale and the enlarged second supralabial scale. (B) Female (NTM R21255; SVL = 74.0 cm) lacking the spine on the rostral scale but possessing the enlarged second supralabial scale.

coition in *Laticauda colubrina* (Guinea, 1986). Twenty-five minutes elapsed from the start of coition to when the pair parted and surfaced together with the male still prodding the body of the female. Each took a single breath and returned to an area close to the crevice in which they had been positioned. Although the male continued to prod the head and neck of the female, she moved away with each touch and shifted to another location. Two hours after observations began the pair were collected, measured, weighed and released at the same coral patch. The female was larger in snout-vent length (SVL = 66.0 cm) and weight (300 g) than the male (SVL = 54.0 cm and 200 g).

The importance of tactile contact during courtship was demonstrated by an unsuccessful mating by *E. annulatus*. The pair were observed in 3 m of water where the male kept close and incessant contact with his rostral spine on the back and head of the female. After 15 min, the female initiated the ascent to the surface. The male followed closely but lost contact with her. The female took a single breath and had commenced her descent as the male reached the surface. Although she returned to the same coral head, the male was unable to locate her. From the surface, I could see both snakes within a meter of each other. The female was motionless and remained so for some minutes. The male moved slowly, making forward-darting movements of his head as if to regain contact with the female. For twenty minutes more he erratically covered the coral patch of about 2 m<sup>2</sup> in area. The female moved about 50 cm from where she had initially rested on descent and came to within 30 cm of the male. He eventually moved off the coral patch into deeper water still making the same forward-darting movements of his head.

Snakes were observed as they fed. They moved over the coral and investigated crevices with their heads. This I interpreted as foraging behavior. I watched a male *E. annulatus* investigate a coral head (*Acropora* sp.). The snake was in 2 m of clear water and apparently oblivious to my presence. As the coral head was only 30 cm in diameter, the entire body of the snake was clearly visible. Its body was braced between branches of the coral, and its head placed beside another branch. The snake kept the supralabial scale in contact with the coral branch and rapidly nodded his

head dorso-ventrally along the coral branch. I snorkelled to within 30 cm and noticed that the mouth was closed but there was a gap of about 3 mm between the second supralabial and corresponding third infra-labial scale on the side touching the coral. The snake performed several episodes of rapid head movement along the same coral branch without changing the position of his body. Between bouts of rubbing the coral with his labial scales, the snake darted his head forward with his mouth open, and snapped up something in the water. I was unable to identify the objects that the snake ate because of their small size and the speed at which they were ingested. Two Neon Damsel Fish (*Pomacentrus coelestis*) (Allen and Swainston, 1988) were very agitated by the snake's presence and made repeated attacks at its head. The snake ceased its activity momentarily but continued with the rapid head movements. No sign of aggression was shown toward the fish.

I interpreted the snake's behavior as one of feeding by using the enlarged supralabial scale to scrape the eggs of the Neon Damsel Fish from the coral branch. Eggs which had been dislodged and were drifting away were plucked from the water with the open-mouth head movements. Suction was not involved as there was neither depression of the gular region nor an enlargement of the throat or any other part of the body. As the rostral spine of this male did not touch the coral, I conclude that this scale is not used in this type of feeding.

Damsel fish belong to the family Pomacentridae and attach their eggs to the substrate by adhesive strands. Males zealously defend their territory and guard the eggs (Allen and Swainston, 1988). After the above observations, Neon Damsel Fish were not seen at the small coral head and presumably the pair had abandoned the site.

Each day, I watched at least two *E. annulatus* scrape coral branches with the enlarged supralabial scale. Their feeding behavior did not differ from that reported above. The presence of damsel fish in the vicinity of foraging snakes indicated the possibility of a successful feeding event being imminent. However, twice pairs of the Jewel Damsel Fish (*Plectroglyphidodon lucrymatus*) successfully defended their territory and possibly their eggs by repeated attacks at the