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MARK–RECAPTURE TO ASSESS FACTORS AFFECTING THE PROPORTION OF A NILE CROCODILE POPULATION SEEN DURING SPOTLIGHT COUNTS AT NGEZI, ZIMBABWE, AND THE USE OF SPOTLIGHT COUNTS TO MONITOR CROCODILE ABUNDANCE

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SUMMARY

(1) Changes in the absolute abundance of Nile crocodiles (*Crocodylus niloticus* Laurenti) at Lake Ngezi, Zimbabwe, were followed in 1979–82 by mark–recapture in three size-classes (< 1·2 m, 1·2–2·5 m, > 2·5 m total length).

(2) Throughout the study period, there were twenty-eight crocodiles > 2·5 m long and forty crocodiles of 1·2–2·5 m in the population, but the number of animals < 1·2 m long declined from fifty-four in 1979 to eleven in 1982.

(3) Over the same period, forty-six spotlight counts, standardized with respect to observer, route, speed and time of night, were conducted. Twelve environmental variables of probable importance to crocodile activity or visibility were measured during each count. These were included in a multiple regression analysis to quantify the effect of the environment on the proportion of the population seen during counts.

(4) The proportion of the population counted by spotlight ranged from 0·10 to 0·63 with a mean of 0·36 ± 0·13 (S.D.) over the study period.

(5) Two environmental variables, water-level and the difference between water and air temperatures, accounted for 64% of the variation in the proportion of the total population seen during counts.

(6) Correction factors to convert spotlight counts to absolute numbers were calculated for the whole population and separately for each size-class.

(7) Analysis shows that uncorrected counts undertaken in October/November at the time of lowest water and highest temperatures would have been useful indices of abundance at Ngezi. The use of simple standardized spotlight counts to monitor crocodile abundance is discussed.

INTRODUCTION

In river and lacustrine habitats, crocodiles occur in shallow water at the land–water interface. A standard method of estimating the abundance of crocodiles is to count animals in this narrow zone in the beam of a spotlight at night, usually from a boat cruising offshore. Spotlight counts indicate the minimum number of animals in the population, but the relationship between this and the total number is not often known. Because of the simplicity of the technique, numerous attempts have been made to use spotlight counts as indices of relative abundance for long-term monitoring in management programmes (Woodward & Marion 1978; Messel, Wells & Green 1981; Bayliss *et al.* 1986; Taylor 1988). However, a number of factors affect the proportion of a crocodile population seen during counts and, although this is widely appreciated, the variability of these indices has never been properly measured.

Chabreck (1966) rigorously standardized spotlight counts of the American alligator (*Alligator mississippiensis* Daudin) in an attempt to stabilize them as indices. Woodward & Marion (1978) tackled the same problem by measuring eleven environmental variables and relating these, in a multiple regression analysis, to the number of animals seen in sixty-seven spotlight counts. In this way, they accounted for 90% of the variation in the number of alligators seen. However, the actual number of animals in the population was unknown and the technique relied on the assumption that the population was stable. Messel, Wells & Green (1981) used similar methods to estimate absolute numbers in a population of the estuarine crocodile (*Crocodylus porosus* Schneider) but the method was not tested against other estimation techniques nor in a population of known size. Bayliss *et al.* (1986) conducted a mark–recapture experiment to estimate numbers of estuarine crocodiles and were therefore able to calculate a correction factor for simultaneous spotlight counts. However, the study was over a short period during which abundance was assumed to remain constant.

Working with alligators, Murphy (1976) similarly correlated spotlight counts with estimates of abundance from mark–recapture over a short period. Data from counts were used in a Hanson plot removal estimate (Hanson 1968) and absolute abundance estimated in this way was comparable to that from mark–recapture. Unfortunately, the theoretical basis of the Hanson estimate is dubious (Enright & Wormuth 1969) and it has not been used elsewhere.

This paper reports part of a study of the population ecology of the Nile crocodile, *Crocodylus niloticus* Laurenti, undertaken at Lake Ngezi, Zimbabwe, in 1979–82 (Hutton 1984). The principal objective of the work reported here was a detailed examination of the factors affecting crocodile numbers seen during spotlight counts. In order to achieve this: (i) the absolute abundance of crocodiles in three size-classes was estimated and monitored in a 3-year mark–recapture experiment; (ii) repeated, standardized spotlight-counts of the population subject to mark–recapture were made over the same period; and (iii) the effect was measured of twelve environmental variables on the variation in spotlight counts and their deviation from the estimated absolute number of animals present.

From this information, correction factors were derived to convert spotlight counts to absolute numbers, and in this way the study is akin to that of Bayliss *et al.* (1986). However, the duration of the mark–recapture experiment is unique in crocodilian studies and allowed account to be taken of fluctuations in abundance during the study period. The results allow some general observations to be made about the monitoring of crocodile abundance through spotlight counts.

STUDY AREA

Lake Ngezi, an artificial impoundment completed in 1945, lies at 1220 m above sea level between 30°20′/30°29′S and 18°39′/18°44′E. The area has a hot-rainy season between November and March, followed by a cool-dry season until September and a hot-dry season until the start of the rains.

The lake is narrow and irregularly shaped, closely following the course of the old river, and covers 580 ha. The main body of water has gently shelving banks with wide beds of perennial hydrophytes such as *Echinochloa stagnina* (Retz.) Beav. and *Cyperus digitatus* Roxb. Over 30% of this area is <2 m deep and supports a dense growth of aquatic macrophytes, notably *Ceratophyllum demersum* L. The shoreline, including both banks of the river, is *c.* 36 km. The prevailing wind is south-easterly and the long exposed north-west shore is characterized by rough water, particularly during the cool-dry season. The water-level is variable, responding to downstream requirements, but is generally close to its maximum for 7–9 months.

Crocodiles occur naturally in the lake and have been protected since 1967.

MATERIALS AND METHODS

Capture and marking

Crocodiles were captured by the methods of Hutton, Loveridge & Blake (1987), marked and released at the site of capture. All animals were given permanent individual marks by coded toe-clipping or tail scute notching. In order to make each animal identifiable at a distance, colour-coded tags were attached to the tail scutes. Individuals >2·5 m total length (TL) were also fitted with head caps using a modification of the technique described by Yerbury (1977). Some head caps served as the attachment for radio transmitters; all carried individually colour-coded light reflectors (Hutton 1984). Capture and marking were conducted up to ten times during each year of the study.

Spotlight counts

Spotlight counts rely on the fact that crocodiles can be located from over 200 m at night by the reflection of red/orange light from the tapetum of the eye. Counts were made from a 3·7-m boat powered by a 10-hp outboard motor. A standard 12-V spotlight was adapted with a screen to produce a narrow, intensive beam of *c.* 100 000 candle power. The boat was painted with matt black paint to reduce reflections. Surveys always started at the dam and proceeded in an anticlockwise direction, parallel to, and *c.* 50 m from the shore. The driver found his course from hand signals given by the observer in the bow. A constant speed of *c.* 8 km h^{-1} was maintained around the main waters of the lake, but this was reduced to *c.* 4 km h^{-1} in the river when both banks were being counted.

When cruising >50 m from the shore, binoculars were used to spot juveniles and to make identification without having to approach the animals closely. Large animals that had been tagged with head caps could often be identified from 30–40 m, but smaller crocodiles, marked only with tail tags, required closer approach. When animals could not be identified from a distance, they were approached slowly. Crocodiles of all sizes were more approachable when the engine was running. However, in shallow water it was often necessary to paddle or wade.

Each sighting of an animal was recorded to within 10 m on a 1:20 000 map. This was aided by division of the shoreline into 0·5-km intervals with reflective markers. Also recorded were time, water depth and identity of tags, together with the estimated size and general demeanour of the animal and any obvious association with other individuals. When possible, TL was estimated but it was also common to estimate head length (HL) from which TL was later calculated (Hutton 1987). Total length was estimated in feet and size-classes with intervals of 1 foot were therefore adopted in the field though these were subsequently combined into three broad size-classes. A total of forty-six spotlight counts of the whole lake, conducted between 1979 and 1982, provides the basis for this report.

Environmental variables

In order to examine the effect of the environment on the number of crocodiles seen, the following twelve variables were recorded for each spotlight count.

(1) Number of juvenile, intermediate and adult crocodiles seen, x, y and z, respectively. Also the number of crocodiles not allocated to a size-class (u) and the total number of crocodiles seen, $n_i = x_i + y_i + z_i + u_i$.
(2) Water-level above (+) or below (−) the crown of the dam, recorded at the beginning of each count to the nearest 0·05 m (WL).
(3) Moon phase given a value from 1 (new moon) to 14 (full moon) (MP).
(4) More or less than 50% cloud cover during the count (CL).
(5) Presence or absence of moonlight during the count (ML).
(6) Presence or absence of wind during the count (WI).
(7) Presence or absence of waves during the count (WA).
(8) Mean air temperature (°C) during the count recorded at seven fixed stations (MA).
(9) Mean water temperature (°C) during the count at the same seven stations (MW).
(10) Maximum air temperature (°C) 24 h before the count (MX).
(11) Minimum air temperature (°C) 24 h before the count (MN).
(12) The difference between mean water and mean air temperatures during the count (TD).

The chosen environmental variables were, by and large, those reported in the literature as being important to the behaviour and hence visibility of crocodilians, e.g. wave action as noted by Graham (1968). However, maximum and minimum temperatures were included as it was believed that temperatures in the 24 h before a count might affect behaviour and therefore visibility. The month of the survey was considered in subsequent analysis to determine whether there was any gross seasonal variation in visibility not accounted for by water-level and temperatures.

Mark–recapture

Spotlight counts provided data on the number of crocodiles seen at time i, n_i and on the number of marked individuals seen. Initial analysis was carried out using Petersen Estimates modified after Bailey (1951). This method requires information on the number of marked animals available for 'recapture' at time i, M_i. M_i varied as more individuals were marked and was potentially subject to attrition through mortality and loss of marks. M_i was obtained retrospectively as the number of marked animals seen at any time t where $t > i$. These animals must therefore have been available for recapture at time i. The number of marked animals seen at time i, M_i, thus included only those individuals that were seen on at least one subsequent visit. This procedure has the advantage that each Petersen Estimate can be considered instantaneous and recruitment, mortality and loss of marks can be ignored.

The crocodile population was stratified into three size-classes: < 1·2 m TL (juveniles), 1·2–2·5 m TL (intermediates) and > 2·5 m TL (adults). The size-classes differed in behaviour, life-history and method by which they were marked (Hutton 1984). Mark–recapture data were analysed separately for each size class. Crocodiles seen but not approached closely enough to ascribe to a size-class were not included in the mark–recapture data (but were included in the total spotlight counts). Juvenile crocodiles were almost all found in a 6-km stretch of the Ngezi River and additional counts were made to census juveniles in this area.

For periods when mortality and emigration within a size-class were negligible (see Results), a weighted-mean Petersen Estimate was calculated (Begon 1979):

$$\hat{N} = \frac{\Sigma_i M_i n_i}{(\Sigma_i m_i) + 1}$$

with standard error:

$$\text{S.E. } (\hat{N}) = \hat{N}\left(\frac{1}{(\Sigma_i m_i) + 1} + \frac{2}{((\Sigma_i m_i) + 1)^2} + \frac{6}{((\Sigma_i m_i) + 1)^3}\right)^{\frac{1}{2}}$$

Leslie's (1958) test for random sampling of marked individuals was applied to the juvenile size-class for the period up to November 1979 (this was the most abundant size-class and so provided the best data for this test).

Recruitment into the population was ignored; hatchlings appeared seasonally and were readily distinguished from juveniles. The level of migration was assessed by the examination of spoor in a sand-pit constructed between the lake and the lower Ngezi River.

Most mortality occurred when the water-level was lowest, usually in mid-November (Hutton 1984). This pattern was approximated by assuming all mortality to occur on 15 November and dividing the results into November–November periods (November 1979 to November 1980, for example, is subsequently referred to as the year 1980) (see Fig. 1). For all size-classes, weighted Petersen Estimates were calculated for each November–November period.

Acuminated population estimates

In order to obtain an overall 'best' estimate of crocodile abundance, three sources of information were employed in addition to mark–recapture. These were: (i) counts of the total number of individuals marked (allowing for mortality); (ii) the maximum number of individuals seen during any one spotlight count (providing a lower bound to the abundance estimates); and (iii) plotted map distributions related to home-range behaviour (see Hutton 1984). Comparison of abundance estimates made by this range of methods provided an indication of the reliability of the estimates employed in subsequent analyses and were combined to give an acuminated population estimate for each November–November year as described in the Results (Fig. 1).

Regression analysis

The object of this analysis was to measure the effect of twelve environmental variables on the proportion of animals seen and obtain the best possible set of predictors for this proportion. The dependent variables were the proportion of juvenile, intermediate, adult and all crocodiles seen: P(x), P(y), P(z) and P(n), respectively. These were obtained by dividing x_i, y_i, z_i and n_i values by the acuminated population estimates. Note that n_i includes crocodiles seen but not allocated to a size-class. The proportions seen were related to the measured environmental variables using stepwise regression. Two stepwise methods were used to obtain the best regression equations, forward and backward selection (Sokal & Rohlf 1981) with a P-to-enter/drop value of 0·10. At each step, the regression models were examined to ensure that previously included/excluded variables should not be dropped/readmitted. However, this basic procedure was modified to allow for correlations between environmental variables, calculated as product–moment correlation coefficients. No two variables were accepted in a final model if they were significantly correlated at the 5% level. In forward selection analysis, when two such variables entered the model the selection procedure was bifurcated; each of the correlated variables was continued separately. The final models arrived at were then compared for

TABLE 1. Estimates of abundance of crocodiles from mark–recapture

Period	Juveniles	Intermediates	Adults
Up to November 1979	$49{\cdot}4 \pm 4{\cdot}1$	No estimate	No estimate
November 1979 to November 1980	$22{\cdot}9 \pm 4{\cdot}1$	No estimate	$29{\cdot}6 \pm 4{\cdot}4$
November 1980 to November 1981	$8{\cdot}3 \pm 3{\cdot}6$	$37{\cdot}5 \pm 12{\cdot}6$	$25{\cdot}6 \pm 3{\cdot}7$
After November 1981	$6{\cdot}9 \pm 3{\cdot}1$	$38{\cdot}3 \pm 21{\cdot}8$	$26{\cdot}0 \pm 10{\cdot}3$

best fit. An analogous procedure was used for backward selection. The forward and backward selection models were then compared for best fit.

The residuals of all final models were examined for correlations with time (scored from 1 to 46) and were also plotted against month in order to check for evidence of seasonal effects.

Stepwise regression analysis was also carried out for the proportion of crocodiles not allocated to a size-class, $u_i = 1 - (x_i + y_i + z_i)/n_i$. The best-fit model was examined for correlations with residuals as above.

Applying the model: estimating the population in 1987

The above procedure gave regression equations that could be used to correct a spotlight count and provide estimates of absolute abundance. Note that there are two possible methods of estimating total crocodile abundance: directly through estimating P(n), and indirectly by combining abundance estimates for each size-class (see Results).

An additional spotlight count was conducted in July 1987, 5 years after the main study period and 3 years after a major drought during which Lake Ngezi almost dried up. Data from this count are used to illustrate the application of the regression models.

RESULTS

Absolute abundance

The three size-classes differed in their catchability (Hutton 1984) and small samples precluded Petersen Estimates of abundance for adults until 1980 and intermediates until 1981. Thereafter, no changes in numbers were detected and these sections of the population appeared to be stable (Tables 1 and 2). However, successive estimates did show a reduction in juvenile numbers during the course of the study (Tables 1 and 2; Fig. 1).

The maximum number of animals seen during any spotlight count provided lower limits for acuminated estimates. For juveniles these were 37, 23, 10 and 11 for the years

TABLE 2. Acuminated estimates of crocodile abundance (see text)

Period	Juveniles	Intermediates	Adults	Total
Up to November 1979	54	40	28	122
November 1979 to November 1980	23	40	28	91
November 1980 to November 1981	10	40	28	78
After November 1981	11	40	28	79

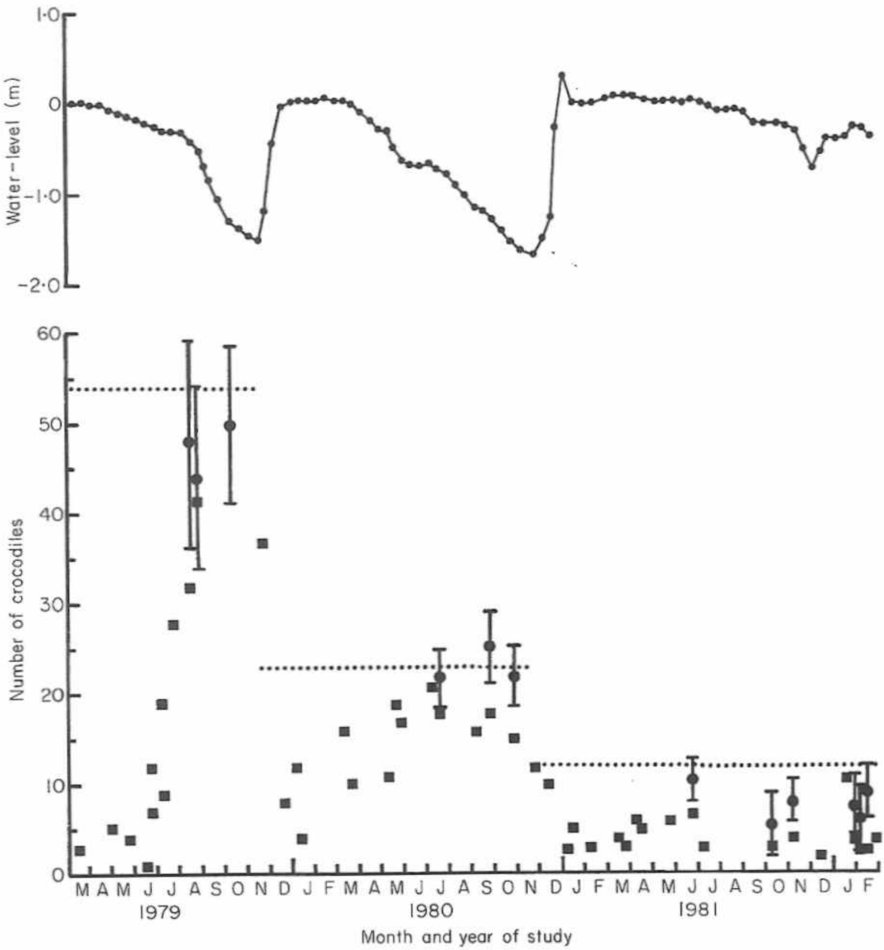

FIG. 1. Number of juvenile crocodiles seen during spotlight counts (■), number of juveniles in the population as estimated from mark–recapture (●) (±S.E.), acuminated estimate of the number of juveniles when all mortality is assumed to occur in mid-November (······) (see text) and water-level at Ngezi from March 1979 until February 1982. Note that the first and second 1979 mark–recapture estimates are, respectively, means of five estimates in mid-August and three in late August. The first 1982 estimate is the mean of two estimates from early February. The 1979 acuminated estimate includes five animals not subject to mark–recapture.

1979, 1980, 1981 and 1982, respectively. The last two values exceeded the mark–recapture estimates but are not outside their confidence limits. In 1979, five juveniles were observed outside the river where they had been intensively sampled. These had not been included in the mark–recapture study and were added to the 1979 mark–recapture estimate (Table 2). Leslie's test for non-random sampling of marked individuals did not detect non-random sampling of marked juveniles in 1979 ($T(\chi^2_{13}) = 15{\cdot}86$; $P > 0{\cdot}1$).

As noted above, the number of intermediates in the population was considered to be stable and the pooled mark–recapture estimate for this size-class over the entire study period was 40·0 ± 10·0 (Table 2). This agrees well with an estimate of 42 from home-range studies (Hutton 1984).

TABLE 3. Proportion of crocodiles seen during spotlight counts (±S.D.)

	Mean proportion seen	Range
Juveniles	0·48±0·27	0·0–(1·0)*
Intermediates	0·17±0·11	0·0–0·45
Adults	0·35±0·15	0·07–0·71
Total (*N*)	0·36±0·13	0·10–0·63

* Assuming that all juveniles were seen on at least one count in 1981 and 1982.

The number of adults at Ngezi was also considered to be stable; mortality in this size-class is low (Hutton 1984) and monitoring of migration demonstrated that one adult emigrated and one immigrated during the study period (there was no evidence of migration within smaller size-classes and the generally low migration rates are supported by the sedentary behaviour of all size-classes (Hutton, in press)). The pooled mark–recapture estimate for adults was 27·5±5·7 while a total of 27 was marked during the study period. In analysis their abundance was considered to be 28 throughout (Table 2).

Spotlight counts

Over the study period, the estimated proportion of the total population seen during spotlight counts ranged from 0·10 to 0·63, with a mean of 0·36±0·13 (S.D). In general, higher proportions of juveniles and adults were observed than intermediates (Table 3), but in each case the range was considerable.

Regression analysis

Correlations between independent variables were common (Table 4), and there were close positive correlations between the four temperature parameters (although the difference between water and air temperatures, TD, was independent of these).

TABLE 4. Correlations between environmental variables

Variable	Range	MP	ML	CL	WI	WA	MA	MW	MX	MN	TD
ML	0–1	+0·46**	·								
CL	0–1	−0·06	−0·25	·							
WI	0–1	+0·18	+0·22	+0·38**	·						
WA	0–1	+0·13	+0·32*	+0·21	+0·79**	·					
MA	7·7–26·0	+0·17	+0·19	+0·34*	+0·36*	+0·18	·				
MW	14·3–29·0	+0·20	+0·21	+0·37*	+0·28	+0·12	+0·89**	·			
MX	16–36	+0·24	+0·31*	+0·13	+0·24	+0·16	+0·71**	+0·68**	·		
MN	2–20	+0·05	+0·10	+0·41**	+0·34*	+0·16	+0·84**	+0·78**	+0·52**	·	
TD	0·2–10·8	+0·05	+0·04	+0·3	+0·19	−0·14	−0·28	+0·20	−0·10	−0·16	·
WL	−2·0–+0·02	−0·02	+0·11	−0·06	−0·20	−0·03	−0·17	−0·04	−0·36*	−0·05	+0·27

Corrections are calculated using the Pearson product–moment correlation coefficient: $*P<0·05$; $**P<0·01$.
MP = moon phase; ML = moonlight; CL = cloud cover; WI = wind; WA = waves; MA = mean air temperature during count; MW = mean water temperature during count; MX = maximum air temperature 24 h before count; MN = minimum air temperature before count; TD = difference between mean water and mean air temperatures during count; WL = water-level (see text for details).

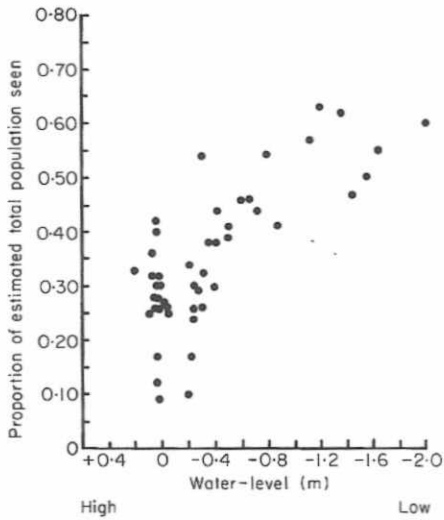

FIG. 2. Relationship between water-level and the proportion of the total population seen during spotlight counts.

In all cases, P values correlated most closely with water-level (WL). The relationship between P(*n*) and WL is illustrated in Fig. 2. A simple linear relationship provided the best fit; there was no significant non-linear relationship. Water-level alone accounted for 61% of the variation in P(*n*).

All models, except that for P(*x*), juveniles, included some temperature variable. There was no evidence for non-linear relationships with temperature. The final regression models explained between 20% and 63% of the variation in P for individual size-classes and 64% of that for all crocodiles (Table 5).

Evaluations of residuals did not suggest that any of the remaining variance in P values could be explained by seasonal effects. There was, however, a significant positive correlation between time and both P(*x*), juveniles, and P(*z*), adults. The proportion of juveniles seen during a given count increased by a factor of 2 during the course of the study (see Discussion), while the proportion of adults seen increased in the order of 10–15%.

TABLE 5. Final regression models relating proportion of crocodiles seen in a spotlight count to environmental variables. *F*-values and coefficients of determination, R^2, are given for the overall regressions. Variables are included in a given model only when the regression coefficient is significant at $P<0{\cdot}05$ (one-tailed test)

Category	Intercept	WL (m)	MA (°C)	TD (°C)	R^2	Significance
All crocodiles	+0·2303	−0·2015	—	+0·0095	0·636	$F_{2,43}=37{\cdot}5$, $P<0{\cdot}001$
Juveniles	+0·3908	−0·2320	—	—	0·213	$F_{1,44}=11{\cdot}9$, $P<0{\cdot}01$
Intermediates	+0·0087	−0·1505	+0·0058	—	0·625	$F_{2,43}=35{\cdot}8$, $P<0{\cdot}001$
Adults	+0·1991	−0·1993	—	+0·0221	0·199	$F_{2,43}=5{\cdot}3$, $P<0{\cdot}05$

WL = water-level; MA = mean air temperature during count; TD = difference between mean water and mean air temperatures during count.

The proportion of crocodiles seen but not allocated to a size class, u, was best explained as a function of TD and MA:

$$u_i = 0{\cdot}5040 - 0{\cdot}0257(\text{TD}) - 0{\cdot}0120(\text{MA})$$

$$(F_{2,43} = 5{\cdot}7;\ P < 0{\cdot}05;\ R^2 = 0{\cdot}209)$$

Residuals from this equation were significantly correlated with time. Over the course of the study, u_i decreased by *c.* 50%. The mean value was 0·18 (S.D. = 0·15), with a range of 0·0–0·64.

Applying the model: estimating the population of 1987

The results of the application of the regression equations of Table 5 to a spotlight count conducted in 1987 are presented in Table 6. Under the water-level and temperature conditions prevailing during the count, it is estimated that 90% of juveniles, 40% of intermediates and 73% of adults were observed. Inclusion of crocodiles seen but not allocated to a size-class gives an estimate of 71% of the total population observed. Summing of the size-class abundance estimates indicates a total population of sixty-one animals, while direct estimation indicates a total population of ninety animals. Both these estimates have large standard errors (Table 6) and an estimate of 64–94 for the total population is within the 95% confidence limits of both. The 1987 survey, therefore, did not demonstrate any change in overall abundance from 1982, but did suggest a shift in size structure. In 1987, juveniles, which had comprised 14% of the population in 1982, were the largest fraction of the total.

TABLE 6. Use of the regression model to estimate crocodile abundance at Ngezi 5 years after the study (July 1987); environmental variables: WL (water-level) = −2·18 m; MA (mean air temperature during count) = 10·5°C; MW (mean water temperature during count) = 14·7°C

Category	Number seen	Expected proportion* (±S.E.)	Estimated abundance	S.E. range
All crocodiles	64	0·709 ± 0·144	90	75–113
Juveniles	28	0·897 ± 0·293	31	28–46†
Intermediates	6	0·398 ± 0·126	15	11–22
Adults	11	0·726 ± 0·166	15	12–20
Summed size-classes	—	—	61	51–78‡

* Standard errors calculated by the method of Sokal & Rohlf (1981, p. 641).

† Lower limit set by the numbers of animals observed.

‡ Calculated from pooled variances of proportion seen in each size-class.

DISCUSSION

Indices vs. absolute abundance

For most management objectives, it is sufficient to monitor changes in some index of relative abundance, although harvesting programmes that seek the maximum sustained yield require the estimation of absolute population size (Caughley 1977). Even when a sustained yield is sought, it is possible to set conservative harvest quotas from changes in relative abundance. Zimbabwe's crocodile utilization follows this strategy (Child 1987).

It is well reported that uncorrected census techniques, such as aerial survey and spotlight counts, are not useful estimators of absolute crocodile abundance (Bayliss *et al.* 1986), but it is still not unusual to find wildlife managers reporting estimates of absolute crocodile abundance derived from uncorrected counts (Taylor 1988). In recent years there has been a surge in interest in the sustainable harvesting of crocodiles, and trade treaty restrictions (principally arising from the Convention on International Trade in Endangered Species of Wild Fauna and Flora) have required some form of numerical estimates to establish the status of various crocodile populations (CITES 1986). This has increased the incidence of absolute abundance estimates from inappropriate data (Tello 1986).

Where accurate estimates of crocodile numbers from spotlight counts are required, the main sources of visibility bias have to be identified and compensated for. Diving and concealment biases can only be estimated when absolute abundance is known (Bayliss 1987; Graham 1988). Observer bias can be measured through double-counting techniques (Magnusson, Caughley & Grigg 1978; Caughley & Grice 1982), but is much lower at the low speeds at which spotlight counts are conducted than in aerial survey, the most common alternative (J. M. Hutton, unpublished data).

Where no estimate is made of visibility bias, spotlight counting can only be used to give an index of abundance. Again, this is well reported, as is the fact that environmental factors affect the proportion seen (Chabreck 1966; Woodward & Marion 1978; Messel, Wells & Green 1981; Bayliss *et al.* 1986). The two main approaches to the standardization of counts have been (i) to standardize surveys by undertaking them only at certain times of the year and, as near as possible, under identical conditions (Chabreck 1966); and (ii) to measure environmental variables and derive correction factors for indices through multiple regression using spotlight counts as the dependent variable (Woodward & Marion 1978). The problem with the first approach is that there is no measure of the precision of estimates. In the second approach, either correction factors must be evaluated over a short period and, therefore, usually, a narrow range of environmental variation (otherwise the actual number of animals in the population may fluctuate), or the population being surveyed must be assumed to have a constant abundance over a long period.

Although Bayliss *et al.* (1986) used mark–recapture to correct spotlight counting techniques (and others) for absolute abundance, the time-span of the study was short and the stability of these correction factors was hard to assess. The study reported here, in which mark–recapture and spotlight counts were used concurrently to estimate and monitor the abundance of crocodiles in three size-classes over a 3-year period, is the first in which population fluctuations have been removed as a source of error in correction factors. This was the main advantage of the complicated and time-consuming mark–recapture experiment which is not likely to form part of any conventional survey method.

Mark–recapture

Estimation of crocodile numbers from mark–recapture techniques has commonly proved difficult owing to the inaccessibility of some species' habitats, the difficulty of catching large numbers of individuals, the differing behaviour of size-classes and the difficulty of satisfying the strict assumptions inherent in mark–recapture models. Murphy (1976) successfully applied mark–recapture to an American alligator population in an artificial lake. The boundaries of the population were demarcated, sampling efficiency of the species was good and size-classes were treated separately. Bayliss *et al.* (1986)

successfully used mark–recapture with estuarine crocodiles, but the assumption of equal catchability of marked and unmarked animals merited more detailed attention.

The main assumptions inherent in the mark–recapture experiment used here were: (i) that marked and unmarked animals were equally catchable and that the probability of catching an individual was the same for all individuals in each size class; (ii) that no animals were born or immigrated into the study area between marking and recapture; (iii) that marked and unmarked animals died or emigrated at the same rate; and (iv) that no marks were lost (Caughley 1977).

Unequal catchability can be due to inherent differences in individual behaviour, the result of learning or variation in the relative opportunity of capture (Caughley 1977). Inherent individual behavioural differences are obviously impossible to control. However, as an animal only had to be sighted to be 'recaptured', problems of learning were avoided and, as eye reflections could be seen from greater distances than those required for identification, it was obvious when animals were present but unapproachable; this is reflected in the number not allocated to a size-class, u. Because of the exceptional clarity of the water, even shy individuals that submerged on approach were usually identified. In support of this, Leslie's test did not detect non-random sampling within the juvenile size-class. Assumptions (ii), (iii) and (iv) were provided for in the experimental design.

The mark–recapture estimates obtained for this study were not precise; coefficients of variation for the abundance of any size-class within a year ranged from 8 to 57%. However, the good agreement of the mark–recapture results with other information on abundance increases confidence in the reliability of the acuminated population estimates used in the analysis.

Spotlight counts and visibility bias

That the proportion of the Ngezi population seen during spotlight counts ranged from 10 to 63% provides the first measure of the variation inherent in spotlight counts that have not been standardized. That only 63% of the population was seen under the most favourable conditions encountered during the study indicates that, at any time, up to 37% of crocodiles may be underwater. This is similar to the 38% reported for *C. porosus* in open rivers (Bayliss *et al*. 1986) but, as noted by Graham (1988), it is not known whether this diving statistic is widely applicable, or strongly population-specific.

Multiple regression model

The stepwise regression analysis does not guarantee that the best of the 2048 possible regression models is attained. It should, however, approach the best set of predictors of variations in proportions seen. It must be emphasized that regression models for the correction of spotlight counts at Ngezi will not be applicable to other populations.

The factor having most influence on the proportion of crocodiles seen was water-level because the animals were increasingly denied the cover of shoreline vegetation as the water-level fell. This relationship must be curvilinear overall, and appears so to the eye (Fig. 2). However, over the range measured, a linear relationship was the best statistical fit due, in part, to the large data set around zero water-level. A larger proportion of animals was also seen in warmer conditions, probably because they are more active, and also when water temperature exceeds air temperature. A lower proportion of intermediates was generally seen than of adults or juveniles. This may reflect greater wariness of this size-class and/or different habitat preferences (Hutton, in press) and demonstrates the importance of considering size-classes separately. The different relationships of proportion seen to environmental variables for different size-classes implies that the proportion of crocodiles seen, P(n), may also be a function of the size distribution of the population. This was also suggested by Bayliss (1987) for crocodile populations in Australia.

Increases in the proportion of crocodiles seen through time probably reflect improved observer efficiency. However, in the case of juvenile crocodiles, this cannot be distinguished from an effect due to a reduction in abundance; spotlight counts may be less efficient at higher crocodile population densities. A reduction in the proportion of crocodiles of unknown size seen through time also suggests an increase in observer efficiency. However, observer effects did not bias the mark–recapture abundance estimates, which are independent of sampling efficiency.

Applying the model: estimating the population in 1987

The estimates of absolute abundance derived from the application of the correction factors to a spotlight count conducted in 1987 are not precise (Table 6), but are of more value than a mere record of the numbers seen. The results indicate that there has been some successful reproduction since 1982 (this is supported by observations of nesting) and that the numbers of adults and intermediates have decreased. This is the sort of change in population structure that was predicted should the different size-classes be forced together (Hutton, in press) as occurred during the drought of 1983–84 when the lake almost dried up.

Using uncorrected spotlight counts as indices of abundance

The regression analysis shows that, if spotlight counts at Ngezi had been undertaken when the water-level was at its lowest, most of the variation in spotlight counts would have been removed and uncorrected counts would have been useful indices of abundance. However, with no formal measure of precision it would have been difficult to decide when two differing index values were reflecting a real change in abundance. Given the simple equipment required and the relative ease with which spotlight counts can usually be conducted, it is worth considering ways in which standardized, but uncorrected, spotlight surveys can give estimates of precision.

The only way to draw conclusions from the sort of simple total-count data collected at Ngezi is to undertake a series of counts to which a regression line can be fitted. Confidence limits can be calculated from the standard error of the regression coefficient. As long as counts are truly standard and there is no corresponding trend in any of the features that can affect them, a significant relationship can be taken to indicate a real trend and confidence will increase as more data is collected (Bayliss 1987). A viable alternative would have been to plan and execute the Ngezi survey as sample counts to give a population estimate together with a standard error (Jolly 1969; Graham 1988). To reduce the variance between sample counts, the area would normally be stratified into units of similar character and sample counts made within these strata (Caughley 1977; Yates 1981). Stratification and sampling usually require little additional effort and, in any case, are likely to form the basis of any survey adopted where large areas of crocodile habitat have to be covered.

We believe that carefully planned and standardized spotlight sample-counts could often be used to give wildlife managers a good indication of changes occurring in crocodile abundance.

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