Life History Parameters, Population Dynamics and the Management of Crocodilians

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During the last twenty-five years there has been an upsurge of interest in the ecology and natural history of crocodilians (Groombridge 1982). Most studies have been descriptive rather than experimental and they have emphasized management implications rather than ecological theory. The trend is not surprising. It was motivated by concern about the conservation status of a group whose natural history was poorly known, rather than by a desire to use crocodilians as an experimental model to test ecological theories. This situation is now changing and quite refined and ecologically informative experiments can and are being carried out, in well-studied crocodilian populations, without the need to consider conservation and management as primary objectives.

Nevertheless, the value of crocodilians as a renewable natural resource attracts more research funds to their study (Palmisano *et al.* 1973; Blake 1974; Blake and Loveridge 1975; Bolton and Laufa 1982; Joanen and McNease 1982; Hall 1983; Montague 1983; Cox 1984) than does the archosaurial ancestory of crocodilians *per se*, and it would seem unlikely that this will change in the immediate future. The management implications of both descriptive and experimental studies of crocodilian ecology are likely to be an integral part of crocodilian research for many years to come.

Conservation and management of most crocodilians is constrained by the fact that their ecology, particularly at the population level, is difficult to study in the field. Crocodilians often reside in the remote areas of underdeveloped countries (Groombridge 1982); many populations inhabit heavily vegetated swamps in which access is difficult (Graham 1981; Hall 1983; Webb *et al.* 1983f; Cox 1984); individuals are long-lived (Graham 1968; Webb *et al.* 1978, 1983a; Hutton 1984); the relationship between age and size is highly variable (Webb *et al.* 1978, 1983a; Hutton 1984; see Chapter 20); definitive morphological indicators of age are only just being described (see Hutton Chapter 20); the age structure of most populations is unstable as a result of commercial exploitation in the not too distant past (Nichols *et al.* 1976; Webb *et al.* 1984b; Smith and Webb 1985) [and also because annual recruitment and the sex ratio of recruits is subject to extreme environmental variation (Hutton 1984; Webb and Smith 1984)]; adults are often secretive and wary (Bustard 1968; Webb and Messel 1979; Hall 1983); they are large reptiles which are usually difficult to catch and handle (Webb and Messel 1977a; Hutton *et al.* Chapter 24; Walsh Chapter 25); and, the killing of even small samples is often difficult to justify on conservation grounds (Gans and Pooley 1976; Ogden 1978).

In addition, crocodilian management is often complicated by a need to combine different management options within the one management programme. With most species the management options available can be categorised as: *conservation*, a desire to increase densities; *control*, a desire to reduce densities; or, *harvesting*, a desire to return a sustainable yield from the populations (Caughley 1977). With crocodilians, harvesting may provide a powerful incentive for conservation, but vigorous local control may be needed simultaneously to provide positive public attitudes to conservation outside the control areas (Webb *et al.* 1984b).

Given these constraints, the present paper deals with maximizing the management value of a demographic study of a wild crocodilian population. Population size, population structure, rates of survival, rates of reproduction and rates of immigration and emigration are the six most important parameters to estimate (Caughley 1977; Nichols Chapter 17). We review the methods used to quantify them in crocodilians, and on the basis of

our own experiences, and those of Stefan Gorzula, Tommy Hines, Jon Hutton and Ted Joanen, present a generalised approach to the study of crocodilian life history parameters. Corrections and short-cuts that may be useful are discussed, along with pitfalls that we and others have encountered. By addressing such issues from hindsight, we hope to assist others embarking on similar studies for the first time.

Killing a large number of adults, or obtaining access to their bodies is clearly the quickest, most precise and least expensive way of obtaining estimates of some of these parameters (Cott 1961; Graham 1968), but for the purposes of this study we have assumed that it could not be justified (Gans and Pooley 1976). The approach we discuss is the selection of a representative population, followed by a mark-recapture study (Chabreck 1965; Chabreck and Joanen 1979; Gorzula 1978; Webb and Messel 1978a; Webb and Smith 1984; Hutton 1984) and the simultaneous investigation of specific life history parameters. The estimates obtained can be used to construct a simple population simulation model (Nichols *et al.* 1976; Graham 1976; Blomberg *et al.* 1982; Hutton 1984; Smith and Webb 1985) and this is seen as something of a natural end-point for the study. As pointed out by Nichols (Chapter 17), such models allow an overview of the population dynamics, and they can be used to direct future research at the variables which have the greatest influence on population dynamics.

LEVELS OF RESOLUTION

Within the study of population dynamics, it is possible to identify three levels of resolution, which are essentially three levels of understanding of the population processes.

First Level

The first level is aimed at determining whether the total population is stable, increasing, or decreasing. This level is normally achieved through repetitive surveys of the same population. With crocodilians, spotlight counting is the most commonly used method (Chabreck 1963, 1965, 1973, 1976; Hines *et al.* 1968; Staton and Dixon 1975; Woodward and Marion 1978; Gorzula 1978; Pernetta and Burgin 1980; Messel *et al.* 1981; Montague 1983; Webb *et al.* 1983d, 1984b; Hutton 1984; Bayliss *et al.* 1986), although the technique has limited application in heavily vegetated swamplands or in areas where crocodilians are particularly wary (Hall 1983). Size estimates made during such surveys may be subject to considerable error (Magnusson 1983; see Choquenot and Webb Chapter 21), and thus caution is needed if the estimated sizes are used to answer questions pertaining to the second level of resolution (see below). Other indices which can or have been used for the first level of resolution are: nest

counts (Graham *et al.* 1976; Graham 1981; Cox 1984; Joanen Chapter 4; Hines and Abercrombie Chapter 5), aerial counts of exposed crocodiles (Graham 1968; Cott and Pooley 1971; Parker and Watson 1970; Watson *et al.* 1971; Graham *et al.* 1976; Bayliss *et al.* 1986), tracks (Singh and Bustard 1977) and harvest statistics (Hall 1983; Taylor and Neal 1984). Choice of method depends on the nature of the habitat, the wariness of the crocodiles present, whether harvest records are available and the funds available for survey work. Bayliss (Chapter 16) has discussed theoretical and practical issues associated with quantifying parameters at this level of resolution.

Second Level

The second level of resolution is the quantification of basic population parameters: population size; population age and sex structure; rates of reproduction; rates of survival; and, rates of immigration and emigration. These permit a simple population model to be constructed (Nichols *et al.* 1976; Graham 1976; Blomberg *et al.* 1982; Hutton 1984; Smith and Webb 1985), and as discussed by Nichols (Chapter 17), such models may assume fixed rates or relationships for most parameters (deterministic models) or may include random variation in some or all parameters (stochastic models). The estimation of basic life history parameters, and thus the second level of resolution, is the primary interest of this chapter.

Third Level

The third level of resolution of population dynamics addresses the processes through which populations respond to change. These are difficult to quantify in any vertebrate species and have rarely been examined in crocodilians. Hines and Abercrombie (Chapter 5) report that when a substantial number of adult female *Alligator mississippiensis* were removed from a nesting population each year, for three consecutive years, the numbers of nests increased. A compensatory mechanism in the population appears to be operating. The survivorship of juvenile *Crocodylus porosus* in tidal rivers appears to be at least partly dependent on the density of larger animals in the river (Webb *et al.* 1984b). The identification and quantification of density-dependent processes can proceed best when the second level of resolution has been well defined, and with some species (*A. mississippiensis, C. johnstoni, C. niloticus* and *C. porosus*), that stage is now being reached.

Management oriented research can be directed at any or all of the three levels mentioned above, but difficulties arise when one attempts to answer questions within the second level of resolution from the results of studies that are primarily directed at the first; or questions in the third from studies

directed at the second. This is not to imply that valuable insights cannot be gained by such extrapolations, but rather to emphasize that if a study is aimed at second level of resolution questions, then if possible, it should be planned as such from the start.

ASSUMPTIONS

In formulating a generalized approach to population dynamic studies of crocodilians, we have made the following assumptions:

1. The population to be studied was intensively hunted in the past;

2. The population is now protected and is exhibiting a positive rate of increase;

3. Sustained yield harvesting of the resource is contemplated;

4. The population is logistically accessible and sufficiently well known that its distribution is definable within geographic bounds;

5. Logistic support for the study is available for at least a two year period; and,

6. The population dynamics are not confounded by sympatry and the differential recovery of two species which may eventually compete for resources (Medem 1971; Webb et al. 1983e).

ESTIMATING POPULATION SIZE

At the second level of resolution, an estimate of the total population size needs to be derived for subsequent subdivision into an age or size structure. Spotlight surveys are often the most convenient method of obtaining an index of the relative abundance of a population, and Murphy (1970), Hutton (1984), Bayliss et al. (1986) and Bayliss (Chapter 16) detail capture-recapture experiments which estimate total population size, and which can be used specifically to calibrate densities recorded in spotlight counts to absolute densities.

The method used by Bayliss et al. (1986) relies on harpooning a tag into wild crocodiles (capture) and subsequently reading the tag number (recapture); it avoids the logistic difficulties of physically manhandling large numbers of crocodiles. Messel et al. (1981) derived a correction from repeated surveys of C. porosus within the same stretch of river, but the correction was applicable to a population of predominantly small crocodiles and could not be adjusted for the changing size structure as the population recovered. Webb et al. (1983d) caught all C. johnstoni in a series of pools which had been spotlight surveyed and applied this correction to other pools in the same area.

Choice of method depends on the accessibility of the crocodiles and the extent of heterogeneity of the habitat. For example, separate corrections may be needed for vegetated swamps and open river channels in the one area (Hall 1983). Perhaps the biggest pitfall with spotlight counts is the extent of biases with respect to size and wariness (Bustard 1968; Webb and Messel 1979; Hutton 1984; Bayliss et al. 1986; Bayliss Chapter 16). Hutton (1984) caught crocodiles and fixed identification tags to them prior to release, but held the animals in enclosures illuminated with a spotlight in order to break the association between a spotlight and the trauma of capture; in this way he reduced "light-shyness" of captured animals (see Hutton et al. Chapter 24).

Fig. 1. Aerial counts of *Crocodylus porosus* in the N.T. are proving an efficient method of monitoring (Bayliss *et al.* 1986).

Aerial counts of exposed animals (Fig. 1) could be used in a similar fashion (Watson et al. 1971) if size-specific corrections were derived. However, the smallest size classes tend to be missed completely (Bayliss et al. 1986). Nest counts are of limited utility at the second level of resolution, because they sample only one segment of the population and hence depend on quantification of the age or size structure or an appreciation of mechanisms which may be influencing reproduction (third level of resolution).

ESTIMATING THE AGE AND SEX STRUCTURE OF THE POPULATION

1. Age

The structure of the population needs to be defined in terms of sex, age and/or size (Hutton 1984; Nichols Chapter 17). The choice of whether age, size or a combination of the two makes the "best" basic unit is unclear. Nichols (Chapter 17) feels that a size structure may be more meaningful than an age structure, as for example maturity and survivorship may be size rather than age related. Size related data are also appreciably easier to collect. We feel that if an age structure can be derived it is more informative and more easily understood. In this study we aim at an age structure, but in so doing, record the data which would allow analysis in terms of size, as discussed by Nichols.

When evaluating the strengths and weaknesses of an age structure versus a size structure analysis, it should be recognized that although some parameters are clearly related to size, it is the time period over which they operate that is important. For example, if juvenile mortality is related to size, the effect of the mortality depends upon the number of years that an individual spends in the vulnerable size classes. Similarly, although maturity is to some extent size dependent, a substantial age component is involved; in some areas, the maximum size attained by *C. johnstoni* is below the size at which maturity is reached in other areas (Webb 1985; Webb *et al.* 1983b). One must also consider that the relationship between age and size is highly variable (Webb *et al.* 1978, 1983a; Hutton 1984, Chapter 20): reduced fertility or fecundity associated with old age for example, is not necessarily associated with large size. Populations with similar size structures may have quite different age structures, reproductive potentials and consequently population dynamics.

There are two methods currently available for estimating the age of crocodilians: skeletochronology and growth rate analysis. Skeletochronology has been used with *C. siamensis* (Buffrenil 1980), *A. mississippiensis* (Ferguson 1982a) and *C. niloticus* (Hutton 1984) and growth rate analysis has been used with *C. porosus* (Webb *et al.* 1978), *C. johnstoni* (Webb *et al.* 1983a) and *C. niloticus* (Hutton 1984). Hutton (Chapter 20) discusses both methods and the problems of aging crocodilians in general.

Skeletochronology is the more precise aging method, and the best results are obtained with sections of the humerus or femur; accordingly, it is best applied to dead animals. However, Hutton (1984) found that sections of the nuchal osteoderms of *C. niloticus* contained clearly defined annual rings and in his study, a section of the nuchal osteoderm was removed from each animal captured. The extent to which osteoderm aging can be applied to other species is unknown. In *A. mississippiensis* for example, the annual rings are largely obliterated by extensive remodelling (Ferguson 1982a). If the osteoderms can be used with a particular species, then skeletochronology gives an extremely valuable age indicator.

Growth rate analysis or analysis of size-age curves has been used with *A. mississippiensis* (Chabreck and Joanen 1979), *Caiman crocodilus* (Gorzula 1978), *C. porosus* (Webb *et al.* 1978), *C. niloticus* (Hutton 1984) and *C. johnstoni* (Webb *et al.* 1983a). In general, the use of a simple size-age relationship to estimate the age of individual crocodilians is error prone, because there is extreme variation in growth rates among individuals of the same age. However, Webb *et al.* (1983a) describe a method of reducing errors if growth data on individual animals are available. The method requires some 100-200 recapture records, ideally spanning one and/or two-year periods rather than a mixture of time intervals between. Small time intervals result in large measurement errors relative to real growth and these tend to swamp the real relationship between growth and age. Nevertheless, the method has limited application to the oldest animals, which are very slow growing, unless they are particularly well represented in the sample (Hutton 1984).

Fig. 2. Mark-recapture studies on *Crocodylus johnstoni* provided an estimate of the population age structure (Webb *et al.* 1983a).

Given that growth rate analysis and skeletochronology are independent methods, they can be used in conjunction to generate two estimates of the age of each animal recaptured.

The direct method is to follow nests through from laying to hatching and measure clutch size, egg characteristics and hatching success (Cott 1961;

To derive a reasonable approximation of the population age structure the animals aged must clearly represent a random sample of animals from the population. For this reason, the size structure of the population as derived from spotlight counts should be used with caution, as there may well be size related biases in sighting probabilities (Bayliss *et al.* 1986; Bayliss Chapter 16). Capture-recapture programmes must be planned with a view to randomization. Difficulties may arise with different habitat preferences of males and females, and with seasonal sex-specific movement trends (Hutton 1984). Where recapture is necessary, capture shyness may be a problem (Hutton 1984; Bayliss *et al.* 1986).

2. *Sex*

Given that environmental sex determination appears ubiquitous among extant crocodilians (Ferguson 1985), the population sex ratio cannot be assumed to be 1:1 (males:females); nor can it be assumed to be the same for all age classes. The hatchling sex ratio in any one year depends on a variety of environmental influences and can show substantial annual variation (Ferguson and Joanen 1982, 1983; Webb and Smith 1984). It is also likely that egg survivorship and hatchling sex ratios are intimately associated with each other (Hutton 1984; Webb and Smith 1984).

Fig. 3. Crocodylus johnstoni embryos hatching; each has its sex determined by the incubation environment.

There are no simple rules for randomizing sex, size and the age of samples, as conditions vary greatly between species and within the distributional range of any one species. In areas where a severe dry season prevails, and where most animals congregate in relatively small amounts of available water for long periods, perhaps the best conditions exist for obtaining a truly representative sample.

Crocodilians larger then 30 cm snout-vent length can generally be reliably sexed by manually probing the cloaca or everting the penis (Chabreck 1963; Brazaitis 1968; Whitaker 1973; Joanen and McNease 1978). *Alligator mississippiensis* smaller than 30 cm snout-vent length cannot generally be sexed in this way because they have an undifferentiated cliteropenis (Joanen and McNease 1978), whereas the method can be used with hatchling *C. johnstoni* and *C. porosus* (Webb *et al.* 1984a), and one month old *C. niloticus* (Hutton 1984). The minimum size at which sex can be determined by inspection would therefore appear to be species specific. Methods for determining sex through gross and histological examination of the gonad are discussed by Ferguson and Joanen (1983) and Ferguson (1985).

ESTIMATING RATES OF SURVIVAL

Rates of survival are difficult to estimate for crocodilian populations. They can be expected to vary with age, size, density, weather and habitat.

We identify five primary classes of survivorship:

1. Egg survivorship (to hatching);
2. Hatchling survivorship (to one year of age);
3. Juvenile survivorship (to maturity);
4. Middle age survivorship (to a decline in reproductive output); and,
5. Old age survivorship (through senescence).

In *C. niloticus* (Hutton 1984) and *C. johnstoni* (Smith and Webb 1985), variation in egg, hatchling and juvenile survivorship rates appear to be the most important factors causing variation in population rates of increase.

1. *Estimating Egg Survivorship*

Egg survivorship can be estimated directly or indirectly, and if done in both ways, a check of consistency is provided. The indirect method is to estimate the number of mature females, the proportion of them breeding in a particular year, determine mean clutch size and estimate the number of hatchlings produced in a year. The estimate of egg survivorship provided by subtraction tells us nothing about why eggs have not produced hatchlings — information which may have a direct bearing on the type of harvest strategy employed — but it provides an holistic estimate of egg survivorship which is not confounded by biases associated with nest interference by investigators.

Joanen 1969; Webb et al. 1977, 1983b; Deitz and Hines 1980; Hall 1983; Hutton 1984). If possible, one should locate all the nests in a population under study, or if this is logistically impractical, select a sample which is random with respect to nesting in the area. Such studies are far more readily accomplished with pulse nesting species such as *A. mississippiensis* and *C. johnstoni*, which all nest within a few weeks, than with extended nesters such as *C. porosus* and *C. novaeguineae*, that nest over a few months.
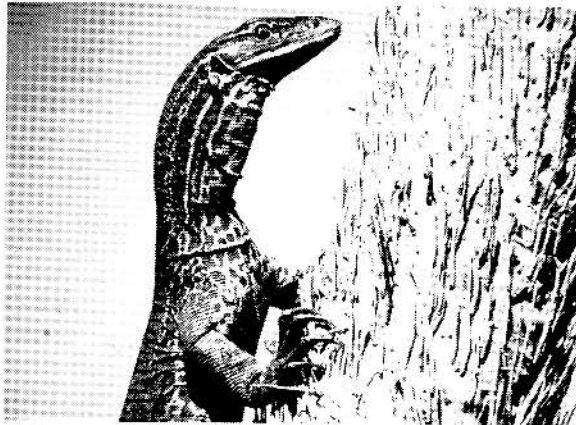

Fig. 4. Varanid lizards are a major predator on the eggs of some species of crocodilians in Australia, Asia and Africa.

If a relationship between embryonic stage of development and time can be derived (Magnusson and Taylor 1980; Webb et al. 1983c; Hall 1983; Cox 1984; Hutton 1984), a nest can be approximately "aged" on a first visit (by sacrificing one egg), and the time of hatching can be predicted for a second visit (Webb et al. 1983f; Hall 1983). As temperature has a profound effect on embryonic development rates (Webb et al. 1983b; Hutton 1984), nest temperatures need to be accounted for. Eggs that have been crushed during laying can be readily identified. The opaque banding on eggs (Ferguson 1982b; Webb et al. 1983b; Hutton 1984) can be used to distinguish eggs that were either infertile or had died prior to one day of age (they remain translucent), and can often be used to identify eggs that have ceased development at some later stage. In nests that are particularly wet the sequence of opaque banding on eggs may be disrupted, as the opacity appears to be caused by dehydration (Ferguson 1982b; Webb et al. 1986).

The extent to which predation on nests is enhanced by disturbance appears to depend on many factors. With *A. mississippiensis* (Deitz and Hines 1980) and *C. johnstoni* (Webb et al. 1983b), there seems little doubt that predators were much better able to locate eggs after the nest cavity had been opened. Alternatively, no predation was observed in large series of *C. porosus* and

C. novaeguineae nests examined in freshwater swamplands, even though nests were opened, examined and left to complete incubation in the field (Hall 1983; Webb et al. 1983f).

Estimating the number of hatchlings produced is confounded by predation at or immediately after hatching. Hatching rates can be determined by collecting eggs when the hatchlings begin to call and allowing them to hatch in captivity, but this underestimates mortality at the time of hatching. In contrast, hatchlings can be counted or collected immediately after hatching, which probably overestimates predation in the later stages of incubation. With *C. johnstoni*, some 50% of hatchlings can be taken by predators or simply die within three weeks of hatching (Smith, unpublished data). Here a separate estimate of the immediate hatchling mortality may be needed.

The survival rate of eggs can be expected to be extremely variable. In the *C. johnstoni* population within the McKinlay River, the infertility rate (which includes embryos which have died prior to one day of age) is usually around 4% (Webb et al. 1983b); but in 1983 it was 11% (Smith, unpublished data). Predation rates of *A. mississippiensis* eggs vary in relation to water levels (Nichols et al. 1976), and losses of *C. porosus* eggs to flooding vary greatly with respect to the timing of peak water levels (Webb et al. 1983f).

Whilst it is unlikely that a short-term (one season) study will allow such relationships to be quantified precisely, the data can often be used to derive reasonable first approximations. In this regard, the climate prevailing in the year of study needs to be assessed in relation to past weather records. If it was an unusually dry or wet year for example, the estimates may be substantially biased in one direction or the other. If flooding is a major cause of mortality, data on the time of nesting and height of nests above water from one year may be able to be superimposed on water height data from different years (Kushlan and Kushlan 1979; Jacobson and Kushlan 1984; Webb et al. 1983f). Such a predicted model of flood induced mortality can then be tested and refined during following seasons.

2. Estimating Hatchling Survivorship to one year of age

The most direct method of estimating hatchling survivorship is to release a large number of marked hatchlings and then attempt to capture or account for all animals of the appropriate size class the following year (Webb et al. 1983b; Hutton 1984). Where substantial hatchling movements occur, as is the case with *C. porosus* (Webb and Messel 1978a; Messel et al. 1981), that movement would need to be accounted for.

An indirect method of estimating hatchling survivorship is possible if one year olds represent a

distinct size class in the population. At the time of hatching, hatchlings can be collected continually throughout the hatching period and the numbers of one-year olds simultaneously estimated by total removal or by mark-recapture (Bayliss et al. 1986). This assumes no ecological separation, which would confound such an approach with some species in some habitats.

Fig. 5. In high density situations, juvenile crocodiles such as this *Crocodylus johnstoni*, are killed by older, larger animals.

3. Estimating Juvenile Survivorship

The most direct method for estimating juvenile survival rates is to follow particular age classes from year to year and directly examine the proportion surviving from one year to the next. However, this method assumes that movement losses do not occur, or at least can be quantified. If it can be assumed that there is no nett loss of animals of any age through movement, i.e. as many move out as move in, simply examining the number of animals in each age class will provide an estimate of survivorship. In a *C. johnstoni* population, Webb and Smith (1984) estimated the number of eggs laid for a number of years and then examined the number of animals in the population that were derived from those eggs. By assuming that there had been no nett movement (an assumption that appears valid for that population) they estimated an average survival rate for animals between one and ten years of age. In some populations of *C. porosus* (Messel et al. 1981; Webb et al. 1984b), the assumption of no nett movement losses appears not to hold and therefore an estimate of those losses must be derived to allow correction of the survival rates.

4. Estimating Middle Age Survivorship

As a very broad generalization, it can be said that crocodilians have almost 100% survivorship during their middle years. Smith and Webb (1985) assumed this to be the case with *C. johnstoni* from the age structure of the McKinlay River population and Hutton (1984) found a similar situation in the Lake Ngezi *C. niloticus* population. Nichols et al. (1976) estimated quite substantial loss rates for middle

aged *A. mississippiensis* (15% per year), but these rates would seem to result from a number of assumptions about the dynamics of the population that in hindsight may need reassessment.

In adopting the assumption of minimal loss rates of middle aged crocodilians it is vital to identify the age at which animals cease to suffer the relatively high juvenile loss rates and experience the lower middle age loss rates. This is probably obvious from the population age structure (Hutton 1984; Webb and Smith 1984).

5. Estimating Old Age Survivorship

There are few data on survival of any crocodilians beyond their middle age. The approximation used by Smith and Webb (1985) was to assume the maximum aged animals in a recovering population were five years from death, and choose a point to define the end of the middle age — high survivorship period. A constant rate of loss between these two points was then calculated. In terms of population dynamics, these assumptions had little effect on the accuracy of predicted population sizes, as the contribution of such animals to population growth is negligible when compared to annual variation in recruitment (Smith and Webb 1985).

ESTIMATING RATES OF REPRODUCTION

The reproductive rate is a summation of many different aspects of reproduction. Essentially, it is the number of females breeding in any one year. To estimate this in a meaningful way, one must determine the age at which females begin breeding, the proportion of females capable of breeding that do breed each year, how clutch size varies with age, the age at which females cease breeding, and also the proportion of females, if any, that produce two clutches in a year.

Given that the programme outlined involves the capture of crocodiles, females can be examined internally using a laparoscope (Limpus 1984; Limpus and Reed 1985). The information obtained can be used to determine whether a female is mature, has bred in the previous season, or is preparing to breed in the coming season. Similarly, plasma calcium levels (Lance Chapter 42) will indicate if a female is just about to breed. Palpating a female will indicate the presence of hard-shelled oviducal eggs (Webb et al. 1983b; Limpus 1984), and if caught immediately after nesting, the flaccidity of the cloacal region is often pronounced in females that have laid eggs. If samples of animals can be sacrificed, the reproductive rates of females taken at different times throughout the year will provide even better information (Joanen and McNease 1980). From any reasonable sample of females in which those breeding have been identified, an estimate of the minimum age of breeding can be determined.

each other can be derived (Cott 1961; Staton and Dixon 1975; Gorzula 1978, 1984; Webb and Messel 1978b; Edwards 1983; Hutton 1984; Montague 1984). Such formulae allow sizes to be estimated from remains, tracks or photographs (Gorzula 1984; Choquenot and Webb Chapter 21) and may even have utility in estimating age (Hutton 1984). However, it is usually *unnecessary* to take a large series of measurements each time an animal is caught and recaptured. Morphometric analyses will be streamlined if the detailed measurements are taken on the first ten individuals of each sex, in each 10 cm snout-vent length class encountered. The remaining animals can then be measured for growth analyses, and a much reduced set of measurements is typically all that is needed.

2. *Stomach contents.* Using the method devised by Taylor *et al.* (1978) and later modified by Webb *et al.* (1982) and Hutton (1984), the stomach contents of live crocodilians can be removed rapidly without killing the animals.

3. *Abnormalities and injuries.* As well as documenting information on the extent and nature of injuries and congenital abnormalities in surviving animals, such data can be used as an index of the extent of social interaction, a verification check if recapture data are considered suspect, a measure of the quality of wild skins that could be expected to be harvested from the population, and a source of general information on what may be causing mortality in different sized crocodilians (Cott 1961; Staton and Dixon 1975; Gorzula 1978; Webb and Messel 1977b; Webb and Manolis 1983).

4. *Habitat assessment.* A basic habitat assessment, even if subdivided into categories such as "good" and "bad" nesting habitat (Magnusson *et al.* 1978, 1980; Hutton 1984), or wetland types with "high" and "low" densities of crocodiles (Messel *et al.* 1981; Webb *et al.* 1983d), can prove invaluable when attempting to explain patterns of distribution and abundance.

SELECTION AND ESTABLISHMENT OF A STUDY SITE

The success of a study in its entirety depends on many factors, but from a practical point of view, one of the most important is choice of the best possible study site. The points listed below are some that we consider need special attention, although we clearly recognize that few if any may be attainable in some areas where crocodiles are to be studied:

1. The site should be close to a useful base and be easily and cheaply accessible from that base, to reduce logistic difficulties.

2. Hunting should not occur in the area, but if it does, then the extent of hunting should be quantifiable. Hunting returns can provide extremely useful information (Hall 1983; Taylor and Neal 1984).

3. Can a history of hunting in the area be established? It is important to know whether 50,000, 5000, 500 or 50 crocodiles were removed from the area, and equally important to know whether the original numbers present (at the time hunting started) were 10,000, 1000 or 100 crocodiles (Webb *et al.* 1984b). To simply assume that there was a pristine abundance of crocodiles everywhere is fraught with problems, as this was more than likely not the case (Webb *et al.* 1984b).

4. When the results are to be extrapolated to other areas, then the location of the site relative to the total distribution of the species needs to be considered. Unless there are specific reasons for wishing to study a marginal population (Hutton 1984), misleading general trends can come from a population at the limits of tolerance.

5. The long-term prospects of the site may be important, especially if a substantial number of animals are to be caught and marked. Long-term studies of long-lived reptiles are rare and thus consideration should be given to the availability of marked animals in ten or twenty years hence.

6. Meteorological factors are likely to be extremely important and it is thus useful to have a weather station nearby. If none is available, attempts should be made to find a station against which weather records from the study site can be calibrated. Long-term climate records, for example over the last fifty years, may be essential for interpreting the significance of trends established in a one or two-year study.

7. The study area should be already mapped or at least have aerial photographs available. A vegetation or habitat map of the area, if available, may save a considerable amount of time and effort.

8. The general distribution of crocodiles and nests within the proposed site should be known, or established on a pilot study basis. This should help determine the sampling methods to be adopted when the study begins.

9. A high proportion of the animals in the population should be accessible to researchers for capture.

10. Given that the majority of crocodiles occur in the wet-dry tropics, the effects of season are likely to be profound on many of the above points (Webb 1986). It is therefore useful to at least estimate likely changes in the study area from one season to another.

11. If the study site is too large to be included *in toto*, it may prove useful to subdivide it such that areas of intense capture are separated by and bounded with areas where no capture takes place. These areas can be sampled at a later date (if necessary), and the extent to which animals caught and marked in one area are recaught in the other can be

used to assess the general extent of movement from the first recapture period.

12. The number of crocodiles in the area should be sufficiently large to permit quantification of the target parameters. In very low density situations an inordinate amount of time and effort can be devoted to parameters that can be rapidly quantified in areas where the same species is more abundant.

13. The recapture interval most relevant to assessing population dynamics is one year. Recaptures made at varying periods throughout the year may clarify seasonal growth and movement trends, but may also confound analysis of annual trends and population dynamics. In short, two intensive recapture periods in the two years following the initial capture may provide much better population data than a year in the field with recaptures spanning various time intervals.

SUMMARY

Demographic studies of crocodilians are often aimed at supplying information useful for management. The early phases of such studies are typically confounded by many unknowns, some of which are related to the animals and their habitats and others which are related to management and the need to account for public attitudes. These realities of crocodile management demand that a high degree of flexibility be incorporated into both short- and long-term plans. The major aims of a crocodile management programme may not need to be compromised, but the route by which those aims are achieved may often need to be changed. Having an holistic view of the management processes and a clear understanding of the context within which information on crocodilian demography is required, are both important. In a somewhat idealistic situation we suggest the following sequence in a crocodile management programme:

1. Define the broad management goals that apply now, and those that may be possible when more information about the species is available;

2. Select the level of resolution that is needed and match it against the logistic support that is available or likely to be available;

3. Select a study site which has as many attractive attributes as is possible;

4. Design and carry out a study (2-3 years) which will supply realistic estimates of the most important life history parameters;

5. Incorporate those estimates into a simple population simulation model;

6. Accept the original management goals or redefine them on the basis of the information and predictions now available;

7. Activate management strategies;

8. Monitor management impact;

9. Accept the revised management goals or redefine them on the basis of monitoring results.

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