

Population Models and Crocodile Management

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IN this chapter, population models and their relationship to the management of crocodile populations are discussed. A brief conceptual framework for population management is provided, followed by a discussion of the different classes of population models, relating the different structures to relevant aspects of crocodylian biology whenever possible. As a conclusion, the potential utility of these different models for addressing questions about crocodile management is discussed, along with the research needed to supply key information "needs" of the models.

POPULATION MANAGEMENT

The goals of managing natural animal populations can generally be expressed in terms of population size and, in the case of exploited populations, harvest levels. With respect to population size, management efforts can be directed at one of three possible goals:

1. Increasing the size of desirable populations that are either declining or persisting at low numbers;
2. Maintaining the size of populations judged to be at desirable levels; or,
3. Decreasing the size of populations for which density or population growth rate are judged to be undesirably high.

For exploited populations, these goals must be considered in conjunction with the additional goal of:

4. Maintaining harvest levels consistent with commercial or recreational interests.

Effective management requires knowledge of factors that bring about changes in population size. At a very general level, all changes in population size can be expressed in terms of four fundamental demographic variables: mortality, reproduction or recruitment, immigration and emigration. A basic expression for population change can then be

written, for example, as in the following difference equation:

$$N_{t+\Delta t} = N_t - M_t + R_t - E_t + I_t \quad (1)$$

where N_t denotes the number of animals in a population at time t , M_t denotes the number of deaths occurring in the time interval $(t, t + \Delta t)$, R_t denotes the number of new animals recruited into the population via reproduction during the interval $(t, t + \Delta t)$, and I_t and E_t are the numbers of animals migrating in and out of the population, respectively, during the interval $(t, t + \Delta t)$. Any management action designed to bring about changes in population size must operate on one of these fundamental variables. Frequently, the location and geographic distribution of animals in a population of interest make it unnecessary to consider immigration and emigration, in which case the manager must accomplish his goals by influencing survival and reproduction.

POPULATION MODELS

Models can be defined as simplifications or abstractions of real systems. There are many different kinds of models, and any system can be modelled in a number of different ways. The key to the effective use of modelling is to construct a model which is consistent with the intent or goal of the modelling effort (see discussion in Conley and Nichols 1978). Because models do represent simplifications and abstractions, they cannot include all the features of the systems being modelled. However, the modeller must try to ensure that the model does contain those features of the real system that are essential to the questions being addressed by the modelling effort.

The population models to be considered here are simply equations or sets of equations that project population change over time. Equation (1) is a population model, but it is too simplistic for many uses because it includes no subdivisions of demographically distinct groups (e.g., age-sex classes) and because it utilizes numbers of deaths (M_t) and recruits (R_t) rather than treating mortality and repro-

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duction as functions of population size. We could write a potentially more useful model as follows:

$$n_{x+1,t+1} = n_{x,t} p_{x,t} \quad \text{for } 0 \leq x \leq k-1, \quad (2)$$

$$n_{0,t} = \sum_{x=1}^k n_{x,t} m_{x,t} \quad (3)$$

where $n_{x,t}$ denotes the number of females in age class x at time t , k is the number of age classes in the population or the maximum possible age, $m_{x,t}$ is the reproductive rate or the expected number of new (age 0) females produced at time t by each female of age x in the population at that time, and $p_{x,t}$ is the survival rate or the proportion of females aged x at time t that survive to enter age class $x+1$ at time $t+1$.

Standard Projection Models

Deterministic models. If we restrict equations (2) and (3) by assuming that survival and reproductive rates are constant over time (i.e., $p_{x,t} = p_x$, $m_{x,t} = m_x$), then our model is similar to those initially investigated by Leslie (1945, 1948) and, in continuous time, by Lotka (1956) and Fisher (1958). These models have now been well-studied, and synthetic summaries appear in L. Goodman (1967, 1968), Keyfitz (1968), Pollard (1973), and D. Goodman (1982). These models are very general and have been applied to problems and questions about a number of different vertebrate species (e.g., see Darwin and Williams 1964; Leslie 1966; Mertz 1971; Fowler and Smith 1973; Jensen 1974; Eberhardt and Siniff 1977; Lenarz and Conley 1980; Nichols *et al.* 1980; Eberhardt *et al.* 1982; Nelson and Peek 1982; Watts and Conley 1984).

The Lotka-Leslie modelling approach can be used to provide some general inferences of interest about crocodylian populations. These models are especially useful for examining the importance of age structure to population dynamics, a topic of special relevance to crocodiles because of their relatively long lifespans. For example, we might be interested in the following type of question: "What will be the effect on population growth rate if we bring about specified changes in the survival or reproductive rates of individuals in age-class x ?" Analytical approaches to addressing this question in the context of Lotka-Leslie models have been developed by Demetrius (1969), Goodman (1971), and Caswell (1978), and these methods may be useful for crocodile populations for which age-specific survival and reproductive rate estimates are available.

Reproductive value (Fisher 1958; Goodman 1982) is a concept which emerged from the study of Lotka-Leslie models and which is potentially useful in considering crocodile management strategies. Reproductive value can be thought of as the contribution of an individual in a particular age class to population growth, and is thus essentially a currency by which individuals in different age classes can

be evaluated. The concept is very relevant to age-specific (or size-specific; see later discussion) harvesting strategies (e.g., see MacArthur 1960). In programmes which consider rearing and restocking as a means of compensating for animals removed by egg or hatchling collection (Blake 1974; Blake and Loveridge 1975) or even harvest, reproductive value provides a currency which can be useful in establishing restocking quotas (Nichols *et al.* 1976b).

Reproductive value is also related to colonization potential (MacArthur and Wilson 1967), with colonizing individuals of high reproductive value often conferring higher probabilities of colony establishment (see Williamson and Charlesworth 1976 for a detailed treatment). This consideration would be of interest when crocodiles are introduced into new habitats or areas from which they have been eliminated. Age-specific survival and reproductive rates are needed to compute reproductive value. The computing forms of Goodman (1982) should be used because, as he pointed out, virtually all other discrete-time formulations appearing in the ecological literature are incorrect.

Stochastic models. By far the majority of the work with Lotka-Leslie models has been with the standard deterministic versions discussed above. However, two different forms of random variation or stochasticity have been introduced into these models (see Kendall 1949; Pollard 1966, 1973; Sykes 1969; Cohen 1979; Tuljapurkar and Orzack 1980). With *demographic stochasticity*, the underlying probabilities of an individual dying or giving birth to different numbers of offspring remain constant over time, but account is taken of sampling variation or variation in the actual proportions of individuals dying or giving birth to different numbers of offspring. For example, assume that 100 individuals are each exposed to an underlying mortality probability of 0.40 for a specified time interval. The actual number of individuals that die in this situation will be a random variable with a binomial distribution. Even though the expected value of the number of deaths is 40, the observed number of deaths in any specific situation will likely be some other number. *Environmental stochasticity*, on the other hand, refers to the situation in which the underlying probabilities associated with death and births vary from one time period to the next according to some probability distribution related to environmental change or something similar. For example, the underlying mortality probabilities for three different years might be 0.35, 0.43, 0.39, fluctuating about an expected value of 0.40.

Demographic and environmental stochasticity can be incorporated separately or together in Leslie-type models. When both forms of stochasticity are incorporated in the same model, environmental stochasticity is often more important (i.e., is responsible for a larger portion of the total variation; see Pollard 1973), although demographic stochasticity can also be important for small population sizes.

Stochastic Lotka-Leslie models have not received as much study as their deterministic counterparts, but they have been applied to natural animal populations in at least two instances (Wu and Botkin 1980; Cohen *et al.* 1983). These models may perhaps be of some use in obtaining crude predictions of extinction probabilities for very small crocodile populations and for generating general ideas about expected levels of variation in rates of change of crocodile populations.

Models based on size. In the Lotka-Leslie models, and their stochastic analogs, discussed above, individuals are grouped by age class. In the model of an American alligator (*Alligator mississippiensis*) population developed by Nichols *et al.* (1976a) animals were grouped by annual age class, a grouping common to many models of vertebrate populations. In retrospect, I do not believe that decision was necessarily a good one, and I now recommend that anyone developing a crocodile population model consider the use of size, rather than age, classes as state variables. There are two reasons for this suggestion:

1. Most data on crocodiles are generally collected by size class and are only converted to age class by application of growth curves which are themselves difficult to estimate. This procedure naturally introduces additional sampling error into the assignment of age classes.
2. Demographic variables of crocodiles seem more likely to be functionally dependent on size than age. Predation mortality, for example, seems very likely to be a function of size, with larger size classes being vulnerable to fewer potential predators. Reproduction may also be more closely tied to size than age in crocodilians. For example, there is evidence that sexual maturity in the American alligator is dependent on size, rather than age (see Whitworth 1971; Joanen and McNease 1975). The form of the data and the underlying biology both seem to favour the use of size-specific population models for crocodiles.

The mechanics of models based on size classes differ little from those of age-class models. If we let x denote size class, rather than age class, and define $x=0$ as the smallest size class (e.g., 0.0-0.6 m), $x=1$ as the next larger size class (e.g., 0.6-0.9 m), up to $x=k$ representing the largest possible size class, then equation (3) is still a reasonable representation for the production of young animals. According to equation (2), however, all individuals in age class $x+1$ at time $t+1$ are survivors from individuals in age class x at time t . If we construct a very general size- or stage-specific model we would replace equation (2) with:

$$n_{x,t+1} = \sum_{y=1}^k n_{y,t} r_{(y,x)t} \quad 0 < x \leq k \quad (4)$$

where $n_{x,t}$ denotes the number of individuals in size class x at time t , k is the largest size class, and $r_{(y,x)t}$ is a transition proportion representing the proportion of individuals in size class y at time t that are found in size class x at time $t+1$. Equation (4) is very general, allowing y to run from 0 to k . However, for any specific size class, x , most of the transition proportions, $r_{(y,x)t}$, would equal 0. For example, let $x=2$ denote the 0.9-1.2 m size class, and let $x=3$ denote the 1.2-1.5 m size class. For American alligators, the only non-zero transition proportions in equation (4) for $x=3$ would probably be $r_{(2,3)t}$, denoting the proportion of animals in the 0.9-1.2 m size class that grow into the 1.2-1.5 m class, and $r_{(3,3)t}$, denoting the proportion of 1.2-1.5 m animals in year t that are still in this class at time $t+1$. Note that these transition proportions incorporate both the survival rate for t to $t+1$ and the growth rate over this period.

Stage distribution models have been studied primarily by ecologists interested in plant and invertebrate population dynamics. Lefkovich (1965) generalized the Leslie matrix population model to handle organisms grouped by any identifiable stage. Examples of the use of size classes, or classes based on some other indicators of morphological stage, as state variables are found in Usher (1972), Werner and Caswell (1977), Caswell and Werner (1978), Hubbell and Werner (1979), and Hughes (1984). The concept of reproductive value is still applicable and can be computed using these models (e.g., see Caswell and Werner 1978). In addition, Caswell (1978) has developed a very general approach for quantifying the sensitivity of population growth rate to changes in demographic variables (e.g., reproductive rates and transition proportions). Stochastic versions of size-structured models could also be produced. In a stochastic model, we would think of underlying transition probabilities. These would represent the product of the survival probability and the conditional probability of being in size class x , conditioned on having been in size class y in the previous period and having survived.

Finally, it should be noted that it is possible to combine both age and size in a stage-distribution model. For example, it may be that because of parental care in many crocodilians (e.g., see review by Cott 1971), survival may be tied more closely to age than size during the first one or two years of a crocodile's life. Such a situation could be incorporated in a general stage-distribution model, with the first one or two stages corresponding to age classes and the remaining stages corresponding to size classes. The main point to remember when developing crocodile models is that we need not feel constrained by model structures that have been used in the past or for other organisms; we should instead try to tailor the model as closely as possible to the biology of the species of interest.

Incorporation of a Harvest

At first glance, the addition of a harvest to a model such as that expressed in equations (2) and (3) appears to be a simple matter. For example, let $q_{x,t}$ be the non-hunting mortality rate of individuals in age class x at time t . We define $q_{x,t}$ as the proportion of individuals in age class x at time t that would die as a result of non-hunting mortality sources during the time interval (e.g., 1 year) extending from t to $t+1$ (write this interval as $(t, t+1)$) in the complete absence of hunting mortality. Further, define $h_{x,t}$ as the harvest rate or the proportion of animals in age class x that would die as a result of hunting during $(t, t+1)$ in the complete absence of non-hunting mortality. If these two mortality sources act independently then we can write the total age-specific survival rate for a population exposed to both hunting and non-hunting mortality as:

$$p_{x,t} = (1 - q_{x,t})(1 - h_{x,t}) \quad (5)$$

Expression (5) holds true regardless of whether hunting and non-hunting mortality are temporally distinct or act at the same time, providing the two sources act independently of each other.

The inverse relationship between total survival and hunting mortality suggested by equation (5) is used in many models of harvested animal populations. However, there have been very few tests of this relationship (and therefore of the independence of hunting and non-hunting mortality) in natural animal populations. Evidence from several laboratory studies on various species (see review by Anderson and Burnham 1976) indicates that increases in hunting mortality ($h_{x,t}$) often tend to be compensated for by corresponding decreases in non-hunting mortality. In these cases, hunting and non-hunting mortality rates did not appear to be independent, with the result that changes in hunting mortality did not bring about corresponding changes in total survival.

The most comprehensive investigations of the relationship between hunting mortality and total survival in a natural animal population involve North American mallard ducks, *Anas platyrhynchos* (e.g., see Anderson and Burnham 1976; Nichols *et al.* 1984). Results indicate rejection of the kind of relationship expressed in equation (5) and suggest that historical variations in hunting mortality rates from year to year have not produced much corresponding variation in annual survival rates of mallards (Nichols *et al.* 1984).

There are several possible ways of building harvest into a population model, and selection of one will depend largely on the manner in which the relevant data and estimates are obtained. One possibility involves modelling total annual survival rate as a direct function of hunting mortality rate, thus assuming that virtually all of the variation in

total mortality is attributable to hunting. Another possibility is to model non-hunting mortality as a function of hunting mortality and, possibly, other environmental variables. For example, if the compensatory mortality hypothesis (Anderson and Burnham 1976; Nichols *et al.* 1984) holds true for crocodiles, as it appears to for some other species, then non-hunting mortality decreases as hunting mortality increases. It is also possible to model non-hunting mortality as a function of total population size (or number of individuals in particular sex, age or size classes) at a particular time of the year. For species in which the compensatory mortality hypothesis applies, it is likely that non-hunting mortality (at least during some portion of the year) acts in a density-dependent manner, with higher non-hunting mortality rates occurring when population size is high. Mechanisms might involve competition for limited resources during critical periods or even cannibalism, in the case of crocodiles. Under such a model, hunting mortality would be an important determinant of the number of animals entering the period of the year during which non-hunting mortality acts in a density-dependent manner. When hunting mortality rate is high, fewer individuals enter this period and non-hunting mortality is relatively low. When hunting mortality rate is low, density-dependent non-hunting mortality is relatively high.

In summary, it is not difficult to incorporate a harvest into a population model, but the effect of a harvest on variables of interest (e.g., population size, population rate of increase) will depend entirely on the functional relationship between either hunting and non-hunting mortality or population size and non-hunting mortality. The utility of any population model for harvested species will depend largely on how reasonable and accurately these functional relationships can be modelled.

Before leaving the topic of harvest it is important to note that reproductive rate may also be a function of population size, and that this can also mediate the effect of harvest on population size and rate of increase. There is a substantial body of evidence indicating that reproductive rate is relatively low when population size or density is relatively high for a number of vertebrate species (e.g., see Fowler 1981 a, b for a summary of evidence for large mammals; see Pospahala *et al.* 1974 for evidence in mallard ducks). In the only effort of which I am aware to examine possible density-dependent reproduction in a crocodylian, Woodward *et al.* (1984) concluded that space does not limit the number of nests within a studied American alligator population. However, if any component of reproductive rate does not act in a density-dependent manner, then it is very important to try to incorporate that relationship into a population model.

Relationship Between Environmental Conditions and Demographic Variables

In the deterministic projection models which have been described, survival and reproductive rates were assumed to be constant over time. In the stochastic projection models, random variation associated with both demographic and environmental sources was introduced into these rates. Recall that environmental stochasticity was introduced by treating the underlying probabilities of dying and producing different numbers of offspring as random variables. Generally implicit in this type of treatment is the assumption that there are direct functional relationships between environmental variables and both reproductive and survival rates. Environmental conditions are assumed to vary over time, producing corresponding variation in survival and reproductive rates. Although this treatment of environmental variation is useful for addressing some very general questions, many other questions require the direct incorporation of specific functional relationships into the model.

There is a great deal of evidence for a wide variety of taxa that variation in reproductive rate (or components of reproductive rate) is associated with variation in environmental variables (e.g., Nichols *et al.* 1976c summarize evidence for a number of vertebrates). In various crocodilians, several components of reproductive rate are thought to vary as a function of environmental variables. Breeding effort, or the proportion of sexually mature females that breed, appears to vary as a function of water levels in the American alligator (Joanen and McNease 1975; Fogarty 1974). Nest flooding also varies with water levels and is an important determinant of nesting success in a number of crocodilians (Hines *et al.* 1968; Joanen 1969; Fogarty 1974; Fleming *et al.* 1976; Webb *et al.* 1977; Kushlan and Kushlan 1980; Deitz and Hines 1980; Magnusson 1982; Webb *et al.* 1983b, d). Webb *et al.* (1983d) developed a model for simulating *Crocodylus porosus* nest flooding in a studied swamp population. Fleming *et al.* (1976) noted large between-year differences in the incidence of racoon (*Procyon lotor*) predation on American alligator nests and believed that these differences were related to water level and its influence on racoon feeding behaviour and movement patterns.

Survival rates for many vertebrates are also thought to vary as a function of environmental conditions. However, good evidence of environmentally-associated variation is not as widespread for survival rates as for reproductive rates, primarily because survival rates are often more difficult to estimate and because poor and inappropriate estimation methodologies have dominated the ecological literature (see Burnham and Anderson 1979; Anderson *et al.* 1981; Nichols and Pollock

1983). Nevertheless, some evidence of environmental influences on survival does exist for vertebrates (e.g., North and Morgan 1979; Nichols *et al.* 1982; Sauer and Boyce 1983), and it is likely that environmental conditions affect crocodilian survival rates to some extent. Hines *et al.* (1968) noted that during droughts in the Everglades, young American alligators became concentrated in remaining water and were then exposed to high predation rates. Staton and Dixon (1977:8), who worked on *Caiman crocodilus*, suggested that: "survival of the young is undoubtedly enhanced under flooded conditions".

When developing population models for many vertebrates we would be interested only in environmental effects on survival and reproductive rates. However, when dealing with crocodilians it may be important to also consider environmental effects on growth rate and hatchling sex ratio. Water levels affect growth rates in a number of crocodilians (Fogarty 1974; Gorzula 1978; Magnusson and Taylor 1981; Webb *et al.* 1983a). If a size-structured population model is developed, then environmental influences on both survival and growth would have to be considered in computing the transition proportions or probabilities of equation (4).

For most vertebrates, sex ratio at hatching or birth can be reasonably modelled as a constant. However, the recent evidence of temperature-dependent sex determination in some crocodilians (Ferguson and Joanen 1982, 1983; Webb *et al.* 1983b) provides a potential mechanism for year to year variation in hatchling sex ratio at the population level. If such variation exists and if it can be linked to an easily-measured environmental variable, then it would be extremely important to incorporate such a relationship into a population model.

DISCUSSION

As noted earlier, the key to the effective use of models is to construct or choose a model which is consistent with the goal of the modelling effort (Conley and Nichols 1978). If the goal of a modelling effort is to gain general insight into the relevance of age/size structure to crocodile population dynamics, then a Lotka-Leslie model using age- or size-specific survival and reproductive rate estimates, would be sufficient. This would permit general inferences about which age/size classes were most important to future population growth, or were the most likely to successfully found new populations in introduction experiments; what rate of increase and average age/size structure would be expected to result from the estimated survival and reproductive rates; which survival and reproductive rates were most important to population growth, etc. Several of the inferences resulting from our American alligator modelling effort (Nichols *et al.* 1976a) were sufficiently general that they could have been addressed using a

standard Leslie-type approach. This does not mean that inferences resulting from our modelling effort were incorrect or misleading; I believe that our general inferences and recommendations were appropriate. Instead I am suggesting that the level of complexity incorporated in our model was more than was required to address some of our questions (see general discussion in Pollard 1973:148-49). I thus suggest that in future efforts to model crocodile population dynamics, it may be appropriate to begin with a relatively simple model and to resort to a more complex model only when dictated by the question being addressed.

In addition to providing general population-dynamics insights such as those listed above, Lotka-Leslie models can also be useful in assessing the reliability of parameter estimates. For example, use of estimated survival and reproductive rates in a Leslie projection matrix permits computation of an asymptotic rate of increase and age/size structure, as well as a projected population trajectory. Comparison of these model outputs with independent data on population trajectory, age/size structure or rate of increase is a useful means of assessing the "reasonableness" of the estimates used in the model (e.g., see Anderson 1975a; Martin *et al.* 1979).

Despite their utility for some purposes, average estimates of survival and reproductive rates coupled with Lotka-Leslie projection models will generally not provide the information needed for a detailed programme of population management. The most critical ingredient in any management-oriented population model (indeed, in any actual management plan) is knowledge of the key functional relationships affecting the important population variables. If we are interested in harvest strategies, for example, we require knowledge of the relationship between harvest rates and subsequent survival and reproductive rates. As noted earlier, this knowledge may involve the direct relationship between annual survival rate and harvest rate or perhaps the relationship between population size at a particular time of the year (e.g., immediately following the harvest) and subsequent non-hunting mortality. The important point is that we require knowledge of such relationships and that such knowledge will not simply emerge from average estimates of harvest and survival rates (used with or without a population projection model). Instead, such knowledge can be obtained only through manipulative field experimentation accompanied by carefully planned efforts to estimate the parameters of interest.

In a recent essay suggesting ways to advance the "science" of wildlife management, McNab (1983:398) stated: "A large proportion of total effort in wildlife science is expended by managers who manipulate systems without taking advantage of the scientific opportunities provided by these

manipulations". Throughout the world there are a number of innovative management programmes underway for various crocodylian populations. These involve the harvest of young and adult animals, the taking of eggs and/or hatchlings and the reintroduction or restocking of young animals. If crocodile management is to be based on something more substantive than hunches and guesses (this is not meant in a derogatory manner — hunches and guesses have served our profession well in the past and will no doubt continue to play an important role), then it is important to plan and implement the data collection activities needed to properly evaluate these experimental manipulations.

Of course, some functional relationships relevant to crocodile population models do not lend themselves to manipulative experimentation. Potential management practices can be evaluated experimentally, but the relationships between environmental variables and demographic variables are often more difficult to ascertain. As previously noted, water level may be an important variable affecting survival and reproductive rates. In some areas it may be possible to manipulate water levels using control structures, but in large natural systems this will not be possible. Where manipulation is not possible, functional relationships can still be investigated using carefully-designed monitoring programmes which include periodic measurements of the environmental variable(s) of interest and a sampling programme designed to provide corresponding estimates of the demographic variables.

Estimating population size, survival rate and reproductive rate is perhaps the most critical and difficult aspect of investigating functional relationships. This is a topic which merits a great deal of attention, and I can do little more than list potentially-useful methods here. The size of crocodylian populations can be estimated using capture-recapture methods, night counts or nest counts (see review by Chabreck 1966). Capture-recapture models can be used to estimate the size of intensively-studied crocodylian populations (Chabreck 1966; Murphy 1977; Pollock 1982). A number of potentially-useful capture-recapture models are now available (see recent reviews by Nichols *et al.* 1981; Pollock 1981; Seber 1982), and the biologist/manager must select the class of models that is appropriate to his needs and field situation. In particular, note that a series of very flexible closed population models are now available (Otis *et al.* 1978; Pollock and Otto 1983), permitting relaxation of the assumption of equal capture probability. A heterogeneous capture probability model, permitting different animals to exhibit different capture probabilities, was found to be very useful in a study of the American alligator (Pollock 1982). Removal models are closed population models in which

captured animals are permanently removed from the population (see Otis *et al.* 1978; Pollock and Otto 1983). Catch-effort models (Seber 1982; Pollock *et al.* 1984) can be thought of as a special case of removal model. In carefully-controlled hunting situations (e.g., where all animals taken are recorded by game officers) in which animals are taken from specific areas over relatively short periods of time, removal models may provide a useful, and relatively inexpensive means of obtaining population estimates.

Night counts (e.g., see Chabreck 1966; Woodward and Marion 1978; Webb *et al.* 1983c; Taylor and Neal 1984) provide a reasonable means of sampling crocodilian populations in many areas. The major problem with estimating population size from night-count data involves estimation of the proportion of total animals which are actually seen. Because this proportion probably varies from area to area and with environmental conditions (Woodward and Marion 1978), some sort of stratified, 2-stage sampling approach is probably needed. For example, one might stratify by habitat type, and within each stratum collect night count data over a relatively large number of sampling units and attempt to estimate the proportion seen on a small number of these units by some more intensive sampling method. In an excellent example of this approach, Webb *et al.* (1983c) made intensive efforts to catch and/or account for all *Crocodylus johnstoni* in a subsample of nine pools (from a total of 962 sampled pools), and estimated that 52-90% of crocodiles present were seen on the night counts. In some areas and with some species, such intensive capture efforts will not be possible and some other means of estimating the proportion of animals seen will be needed. Radio telemetry can provide a "known" group of animals from which the proportion seen during night counts can be estimated. In any case, this need to "adjust" or "correct" count data by the proportion seen in order to estimate total population size is certainly not unique to crocodile populations. Estimation methods based on such double-sampling are presented by Jolly (1969) for large terrestrial mammals, by Martin *et al.* (1979) for migratory birds, and by Eberhardt *et al.* (1979) for marine mammals.

Nest counts have also been used to estimate population size (Chabreck 1966; Taylor and Neal 1984). In marsh habitat these counts can be conducted from the air, and extensive areas can be covered. As with the night count data, it is important to estimate the proportion of total nests actually seen. Magnusson *et al.* (1978) describe a double-survey method in which an area is sampled from the air and ground (by different observers) and nests are marked on maps. This provides data equivalent to that from a 2-sample capture-recapture experiment, with some nests being found only on one survey, some only on

the other, and some on both surveys. A capture-recapture estimator can then be used to estimate total nests (Magnusson *et al.* 1978). Although a constant sighting probability model was used by Magnusson *et al.* (1978; they explored others also), the use of four or five independent observers (this would not necessarily require four or five surveys) would permit estimation under a model assuming heterogeneous sighting probabilities (Burnham and Overton 1978; Otis *et al.* 1978). Estimates of total nests have been used, together with estimates of the proportion of sexually mature females nesting and the proportion of sexually mature females in the total population, to estimate total population size for American alligators (Chabreck 1966; Taylor and Neal 1984). These latter two proportions may be extremely difficult to estimate. Therefore, the biologist/manager should carefully consider how the resulting population estimate is to be used, as an estimate of nesting females alone may be sufficient for many purposes.

Survival rate is an especially important variable in models used to consider the effects of harvesting, and its estimation requires intensive sampling efforts. I know of no published survival estimates for crocodilians which would be considered completely satisfactory, although data collection efforts currently underway may provide such estimates for some species (e.g., the capture-recapture studies on the American alligator by the Florida Game and Fresh Water Fish Commission). Capture-recapture models for open populations (reviewed by Nichols *et al.* 1981; Pollock 1981; Seber 1982) can be used to estimate survival rate. Estimates based on such models are far superior to enumeration-type estimates which have appeared in the crocodile literature (see general discussion in Nichols and Pollock 1983). Survival rate can also be estimated in cases where crocodiles are tagged and later recovered by hunters (rather than recaptured), using the band recovery models of Brownie *et al.* (1978). Because of the intensive field effort required to conduct a good capture-recapture or band-recovery experiment, it is very important to carefully plan such experiments and ensure that sample sizes are sufficient to meet study needs (see example of such planning in Packard and Nichols 1983). As noted previously, survival rate estimates will be most useful when obtained in conjunction with an experimental manipulation or at least with an effort to carefully monitor potentially-important environmental variables. Weighted least squares can be used to test for (and estimate the parameters of) relationships between survival rates and environmental variables (e.g., Loery and Nichols 1985), and such relationships have been incorporated directly into band recovery estimation models (North and Morgan 1979; White 1983; Conroy and Williams 1984). Finally, intensive radio-telemetry studies using fairly

large numbers of animals can also be used to provide survival estimates using estimators such as those in Bart and Robson (1982).

Various components of reproductive rate have been well-estimated for a number of crocodilians and the associated estimation methods are sufficiently straightforward and well-known that they need not be mentioned here. I have not seen the Mayfield-type nesting success estimators (Mayfield 1961; Johnson 1979; Hensler and Nichols 1981; Bart and Robson 1982) used in crocodilian studies, but in many crocodilian sampling situations they may not be needed. Estimates of nesting success and estimates of total nests (from nest count surveys discussed earlier) can be combined with clutch size data to estimate total number of hatchlings produced. The proportion of sexually mature females which breed in a given year is a very important variable in any population model. It would seem that some long-term radio telemetry studies of mature females would provide useful information about the proportion breeding. Variation in this proportion with environmental variables, and perhaps even with adult sex ratio, are important research topics.

If these estimation methods are combined with field experiments to provide good estimates of important functional relationships, then these relationships can be incorporated into population models. Simulation experiments with such models have the potential to provide considerable insight into the dynamics of the modelled population and the potential effects of different management practices and/or sequences of environmental conditions. Portions of the model dealing with particular functional relationships may even be useful in predicting future population changes and thus in providing information for management decisions. For example, fall age ratio (a type of reproductive rate estimate) of North American mallard ducks for year t , is estimated using data that are not available until year $t+1$. However, in setting the hunting regulations for the fall of year t , information about the fall age ratio is important. The functional relationship between breeding population size and spring water conditions (expressed as number of ponds), and mallard reproduction is now sufficiently well-known to permit prediction of fall age ratios using estimates of population size and ponds obtained during spring (Geis *et al.* 1969; Anderson 1975a; Martin *et al.* 1979). Finally, if we become confident in our knowledge of the key functional relationships in our model, the potential exists to use the model in conjunction with optimal control methodologies to develop optimal management policies (Anderson 1975b; Walters and Hilborn 1978; Williams 1982).

It is my perception that current knowledge of most crocodilian populations does not permit the confident specification of key functional

relationships necessary to develop a completely satisfactory model for population management. If this perception is correct, then managers of crocodilian populations should be involved in experimental investigations designed to detect and estimate these key relationships. Some investigations of this type are already in progress, but crocodile management programmes throughout the world offer the potential for much additional work.

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