

## **4. Temperature-Dependent Sex Determination (TSD): Crocodilian Survivorship**

### **4.1 Biological Introduction and Historical Asides on the Crocodilia**

It is a fascinating subject why some species become extinct and others do not. Why, for example, have the three families of crocodilia (alligators, crocodiles and gavials) not become extinct during the past 100 million or so years? They have survived essentially unchanged for around 63 million years after the dinosaurs became extinct and clearly have great survival powers. As pointed out by Benton (1997), however, those that have survived are only a small group of around the 150 fossil genera of crocodilians that have been documented. Crocodiles and alligators were around in the later part of the Cretaceous (63 to 135 million years ago). As several have noted, such as Benton (1997), they were very much more widespread than they are now, with fossils found as far north as Sweden and Canada. Colbert and Morales (1991) point out that the late Cretaceous was the peak of their evolution with the largest genus being the *Deinosuchus* with the most impressive jaws of any reptiles of the period: one fossil had a skull 6 feet in length which suggests it must have had a total length of 40 to 50 feet—certainly a predator to take notice of. Carroll (1988) suggests that the decline of the genera was probably due to climatic deterioration from around the beginning of the Cenozoic (63 million years ago) era. In spite of the massive extinctions, the families that have survived are rightly viewed as living fossils. Meyer (1984) gives a general overview of them while Pooley and Gans (1976) focus on the Nile crocodile and describe, among other things, its unique biology and social behaviour which have contributed so much to its long survival.

Over the millennia the crocodilia have been vilified like no other animal and the wildest stories associated with them abound. The description of Leviathan in the Old Testament (Job 41:1–34) is just a start. It is clearly the prototype dragon. It was regularly used to scare children in the 19th century and no doubt earlier. One example is in the *Sunday School Advocate* (Volume XVII, January 22, 1888) where it is described as

‘This hideous monster. . . it is an ugly creature—a huge river dragon . . . ’

The article concludes:

‘But though this scaly monster does not haunt the rivers of the North, yet there is another great dragon ever prowling. . . It is more terrible than the alligator. . . The name of this monster is Sin!’

Unbridled prejudiced dislike of crocodiles, however, was also expressed surprisingly by some serious scientists. A well-known naturalist, Edward Topsell, in his 1607 (London) bestiary, *Historie of Foure-footed Beastes* wrote:

‘The nature of the beast is to be fearful, ravening, malicious and treacherous. The tayle of the Crocodile is his strongest part, and they never kill any beast or man, but first of all they strike him downe and astonish him with their tailles. The males of this kind do love their females above all measure, yea even to jealousy. And it is no wonder if they made much of one another, for beside themselves they have few friends in the world.’

Perhaps the most shameful, however, is the description of crocodiles by the influential Swedish naturalist Carl von Linné, better known as Linnaeus. In 1766 in a section on Reptiles-Crocodiles he wrote:

‘These foul and loathsome animals are distinguished by a heart with a single ventricle and a single auricle, doubtful lungs and a double penis. Most are abhorrent because of their cold body, pale colour, cartilagenous skeleton, filthy skin, fierce aspect, calculating eye, offensive smell, harsh voice, squalid habits and terrible venom; and so their creator has not exerted his powers to make many of them.’

Modesty was not one of Linnaeus’ traits. Describing himself, appropriately in the elevated third person, he wrote:

‘God has suffered him to peep into his secret cabinet.  
 God has permitted him to see more of his created work than any mortal before him.  
 God has bestowed upon him the greatest insight into nature-study, greater than anyone has gained . . .  
 None before him has so totally reformed a whole science and made a new epoch.  
 None before him has arranged all the products of nature with such lucidity.’

A crucial difference between the crocodilia and most other species is that their sex is determined by the incubation temperature of the egg during gestation, basically females at low temperatures and males at high temperatures. It is interesting to speculate whether this could be a possible explanation, or at least a significant contributory factor, for their incredible survivorship, and if so, how. In this chapter we discuss models to investigate this hypothesis. We first give some biological background and introduce terms used in their study. We shall frequently use the word crocodile or alligator to represent the crocodilia in general and the exact name, such as *Alligator mississippiensis* or *A. mississippiensis* when we mean the specific reptile. An excellent and comprehensive review of the reproductive biology of the crocodilians is given by Ferguson (1985).

In genetic sex determination (GSD), such as for mammals and birds, sex is fixed at conception. Environmental sex determination (ESD) is when sex is determined by environmental factors and occurs in other vertebrates and some invertebrates (see, for

example, Charnov and Bull 1977, Deeming and Ferguson 1988, 1989a,b). Temperature-dependent sex determination (TSD) is often observed in reptiles. Other than crocodiles, alligators and the rest of the crocodilia, several reptiles, such as some lizards and certain turtles, the temperature of egg incubation is the major factor determining sex. Gutzke and Crews (1988), for example, specifically studied the leopard gecko (*Eublepharis macularius*) which has a similar pattern to the crocodilia but with a lower temperature range from 26 to 32° C. With turtles it is the high temperature that gives only females, except for the snapping turtle which is like the crocodile.

The temperatures that produce all male or all female hatchlings vary little between the different species of crocodilia. Females are produced at one or both extremes of the range of viable incubation temperatures, and the intermediate temperatures produce males. For example, in *Alligator mississippiensis* artificial incubation of eggs at low temperatures, 30° C and below, produces females; 33° C produces all males; while high temperatures, 35° C, give 90% female hatchlings (but these are usually not viable). Ferguson and Joanen (1983) incubated 500 alligator eggs and found that all the young are male if the eggs are incubated in the range 32.5–33° C. Temperatures in between, that is, 32° C and from 33.5–34.5° C produce both sexes. Reproductive fitness of males and females are strongly influenced in different ways by environment. Sex starts to be determined quite early in gestation, by about the twelfth day into gestation, but is not irrevocably fixed until as late as 32 to 35 days. For *Alligator mississippiensis* the gestation is around 65 days for males and up to 75 days for females. Exact data can be found in the review by Ferguson (1985).

A key question is why has TSD evolved? It has been postulated that TSD is the ancestral form and GSD evolved from it. Deeming and Ferguson (1988, 1989a,b) have proposed an explanation of the mechanism of temperature-dependent sex determination in crocodilians. Their hypothesis is that the temperatures producing males are those that are best for the expression of the gene for the male-determining factor. In a warm nest eggs develop faster (see, for example, the graphs in Section 4.2 below and Murray et al. 1990) than in a colder one and this means the young hatch more quickly. The adults are also bigger when developed in a higher temperature; this turns out to be crucial in determining the stripe pattern in alligators (Chapter 4, Volume II). One possible explanation in the case of the crocodile is that it is better for the male to be big to fight off competitors whereas for the turtle it is better for the female to be big so that she can lay more eggs. The latter, however, could just as well apply to the crocodile. In this chapter we offer a different possible explanation, which we believe could be a significant factor in their long survival.

Observations of TSD in the natural habitat of *A. mississippiensis* in Louisiana, U.S.A., indicate there are basically three different types of nest site: wet marsh, dry marsh and levee (elevated firm ground). Broadly, levee nests are hot (34° C and hatch approximately 100% males while in the wet marsh, nests are cool (30° C) and hatch approximately 100% females. There are also temperature variations within the nest but we do not include this aspect in our models, although they could be incorporated in a more sophisticated version. Dry marsh nests have an intermediate temperature profile, the hot (34° C) top centre hatching males, and the cold (30° C) peripheries and base, hatching females (Ferguson and Joanen 1982, 1983). Since so few viable reproductive female alligators are hatched at temperatures higher than 34° C we do not include this

cohort in our modelling. Those that are incubated at these temperatures have very low relative fitness.

The female alligator (and crocodile) does not choose the sex of her offspring *per se*. However, she tries to take temperature into account when selecting her nest site since she requires a good thermal environment for herself for the three-month period she stays by the nest until the eggs are ready to hatch and she opens the nest. The female alligators take great care in selecting their nest sites, nuzzling the ground with their snouts, which contain very sensitive temperature sensors, to get it right. Good sites are frequently reused. Although the precise factors for nest site selection are not known we shall assume that a limited number of nest sites provides a density-dependent mechanism for population regulation. In particular, a limited number of marsh nest sites will prevent a totally female population from occurring although female alligators and crocodiles tend to seek a temperature environment that is as close as possible to that of their own incubation (Pooley 1977) and so the preferred habitat of females is marsh. Joanen (1969) gives some field data for the relative size of these different nest site areas; we give these at the appropriate place in the modelling below when we estimate parameter values.

The situation with alligators is not quite so simple as perhaps implied above. In fact since alligators grow faster at higher temperatures it is best for a female to be incubated near the upper end of the viable female temperature scale, which is around 32° C. It is also best for the male around this temperature, its approximate lower limit. In fact relative fitness, essentially survival times fertility, as compared with others of the same sex is highest for both males and females in the middle range of temperatures, around 32° C. In the models we develop here we focus on the principal feature of TSD, namely, the effect of temperature on sex determination. Aspects such as relative fitness could be built into a more complex model as well as other features of crocodilian development.

It is likely that skewed sex ratios, specifically spanandrous ones, that is, ratios other than 1 : 1 and biased in favour of females, occur in species which exhibit ESD as a consequence of skewed environmental types. So, natural selection favours ESD when the reproductive fitness of an individual (male or female) is strongly influenced by the environment (Charnov and Bull 1977). However, the heavily biased sex ratio, as high as 10:1 in favour of females in crocodilians (Ferguson and Joanen 1982, 1983, Smith and Webb 1985, Webb and Smith 1987), is difficult to account for in terms of traditional sex ratio theory (Deeming and Ferguson 1988, 1989b, Nichols and Chabreck 1980, Phelps 1992, Webb and Smith 1984). Webb and Smith (1984) say that from a sex ratio point of view crocodilians could be equally well if not better adapted with GSD. However, one of the selective advantages of TSD is the association of maximum potential for adult growth with sex. Male alligators and crocodiles control harems of females; large males control bigger harems, mate more often and for a longer season (Deeming and Ferguson 1989b). However, as first pointed out by Fisher (1958, 1930), under natural selection females nesting at higher temperatures and producing all male offspring would have an advantage until a 1:1 equilibrium sex ratio, the 'optimal' sex ratio as suggested by Fisher, is reached and then the two sexes would be produced in equal numbers. Selective advantages for TSD in alligators and crocodiles is possibly explained in terms of survival of the species rather than fitness of the individual which is a fundamentally different approach to that of the selfish gene.

Temperature, of course, controls more than just the sex of embryos: it affects growth and development from embryo to adulthood as mentioned above, influences pigmentation pattern, and the adult's ability to regulate its own body temperature (Deeming and Ferguson 1988, 1989b, Lang 1987, Murray et al. 1990, Webb et al. 1987). We discuss some of the implications of pigment patterning in *A. mississippiensis* in Chapter 4, Volume II. The association of TSD with potential population growth we believe can not only protect populations from environmental catastrophe but also enable them to exploit changing habitats by adjusting the metabolic requirements, growth rates and maximum size of their offspring to prevailing conditions. Deeming and Ferguson (1988, 1989a,b) postulated that this occurs by a setting of the embryonic hypothalamus. It is interesting, and perhaps highly significant, that the reptiles (crocodiles, turtles, a few lizards and others) with TSD have persisted with virtually the same morphologies for many million years of evolution (Deeming and Ferguson 1989b). They seem optimally adapted for survival not only in their present environment but also capable of survival with the changing climatic changes since the beginning of the Caenozoic era. They have other impressive and unusual characteristics (see, for example, the book of articles edited by Gans et al. 1985) which have no doubt also contributed to their survival.

Here we mainly focus on the link between temperature-dependent sex determination, sex ratio and survivorship in crocodile populations. We first describe a simple density-dependent model involving only time to highlight the ideas and motivate the more complex density-dependent age-structured model for the population dynamics of crocodilians based on the fact that sex is determined by temperature of egg incubation. In the age-structured case we follow the model of Woodward and Murray (1993). Our modelling reflects the stability of crocodilian populations in the wild, and this stability suggests selective advantages for environmental sex determination over genetic sex determination that can not be explained in terms of traditional sex ratio theory.

That population growth may be controlled by life history data was first realised by Sadler in 1830 (see Cole 1954). However it was the age-dependent linear models originally devised by Lotka (1907a,b, 1913), Sharpe and Lotka (1911), McKendrick (1926) and von Foerster (1959) that provided methods for investigating the relationships between life history parameters and population dynamics. Nichols et al. (1976) used discrete linear models to numerically simulate commercially harvested alligator populations as did Smith and Webb (1985; see also Webb and Smith 1987 and other references there) for crocodile populations in the wild. These linear models lack density-dependent mechanisms, so the population either grows or decays exponentially in a Malthusian way as we saw in Chapters 1 and 2. Nonlinearities in the birth and death processes provide a mechanism by which the population might stabilize to a nonzero equilibrium (see Gurtin and MacCamy 1974, Hoppensteadt 1975, Webb 1985). Our nonlinear age-structured model is based on life history data from studies of alligator and crocodile populations in the wild (Dietz and Hines 1980, Goodwin and Marion 1978, Joanen 1969, Joanen and McNease 1971, Metzen 1977, Nichols et al. 1976, Smith and Webb 1985, Webb and Smith 1987). We first describe the basic assumptions and a time-dependent model which demonstrates the key ideas. Even it, when compared to an equivalent GSD model, indicates some of the benefits of TSD for the crocodilia.

## 4.2 Basic Nesting Assumptions and Simple Population Model

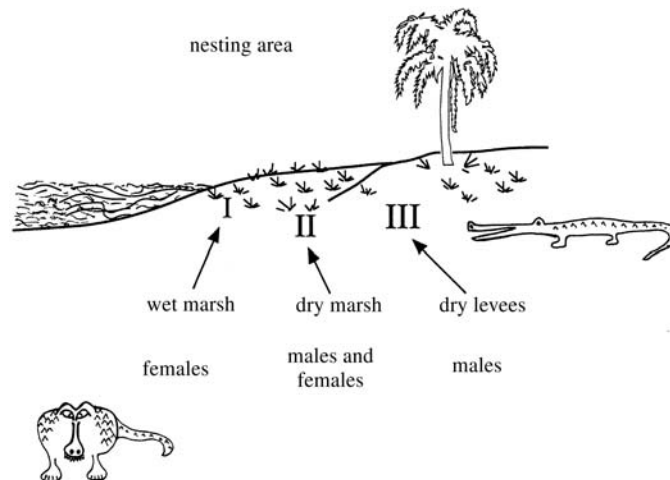
Here we describe a basic three-region model for the populations of males and females which depends only on time. We incorporate some crucial spatial elements in the model based on the observations of Ferguson and Joanen (1982, 1983). We assume that there are 3 distinct nesting regions:

- I** wet marsh, producing all female hatchlings because of low incubation temperatures in these nest sites,
- II** dry marsh, producing 50% male and 50% female hatchlings,
- III** dry levees, producing all male hatchlings because of higher incubation temperatures.

Figure 4.1 schematically illustrates what we have in mind for these three regions.

We further assume that there is a limited number of nest sites near the water which prevents a totally female population: typical figures for percentages of the total nest sites in each of these regions are given by Joanen (1969) as 79.7% for region I, 13.6% for region II and 6.7% for region III.

The population at time,  $t$ , is divided into four classes,  $f_1(t)$  and  $f_2(t)$  denoting females themselves incubated in regions I and II respectively and  $m_2(t)$  and  $m_3(t)$  denoting males incubated in II and III.

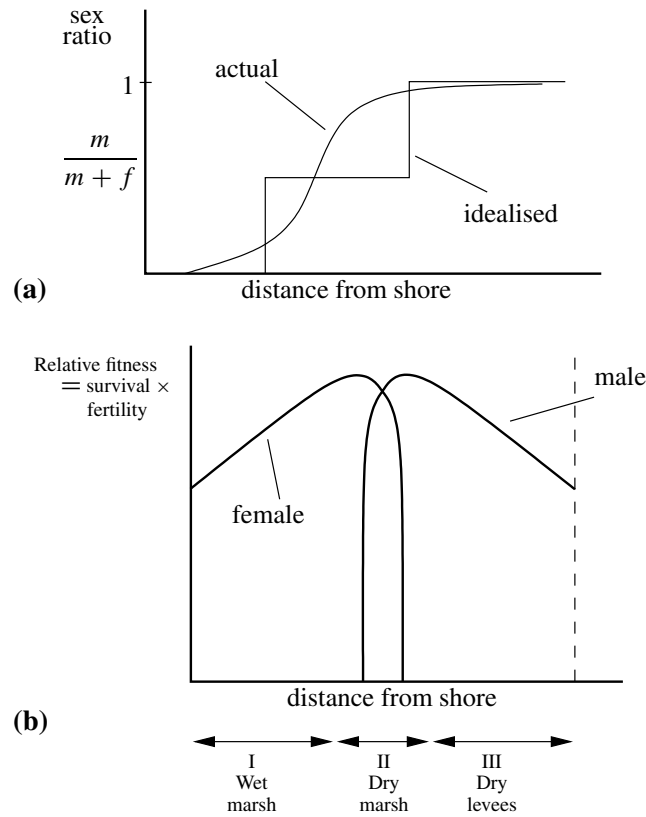


**Figure 4.1.** The three basic nesting regions, representing the environmental influence. I: The wet marsh with low temperatures giving all female hatchlings, II: the dry marsh in which half of the hatchlings are females and half males and III: the dry levees where all hatchlings are males.

- I. Wet marsh – all female hatchlings:  $f_1(t)$
  - II. Dry marsh – 50% female, 50% male hatchlings:  $f_2(t), m_2(t)$
  - III. Dry levees – all male hatchlings:  $m_3(t)$
- (4.1)
- Total female population =  $f(t) = f_1(t) + f_2(t)$ ,
- Total male population =  $m(t) = m_2(t) + m_3(t)$ .

An idealised spatial distribution of the sex ratio of males to the total population in the three-region scenario in Figure 4.1 is shown in Figure 4.2(a).

Only a fraction of females can incubate their eggs in the wet marsh region (I). Let  $k_1$  denote the carrying capacity of region I. This fraction,  $F$  say, must be a function of  $k_1$  and the female population  $f_1$  and it must satisfy certain criteria. If there are only a few females  $f_1$ ,  $F \approx 1$  since essentially all of them can nest in region I while for a very



**Figure 4.2.** (a) Idealised sex ratio of total number of males,  $m$ , to the total population of males plus females,  $m + f$  for a three-region situation schematically shown in Figure 4.1. The continuous curve is more realistic. (b) Schematic curves for relative fitness (survival times fertility) as compared with others of the same sex. Note that it is highest for both males and females in the middle range of temperatures, around 32° C.

large number of females  $f_1$ ,  $F \approx 0$  since in this situation most of them have to move away from the wet marsh region I. As an approximation to this function, the fraction

$$F = \frac{k_1}{k_1 + f_1} \quad (4.2)$$

satisfies the following,

$$F = \frac{k_1}{k_1 + f_1} \rightarrow 0 \quad \text{as} \quad f_1 \rightarrow \infty, \quad F = \frac{k_1}{k_1 + f_1} \rightarrow 1 \quad \text{as} \quad f_1 \rightarrow 0,$$

as required. It is, of course, just an approximation to the actual fraction function. Strictly  $F(f_1, k_1)$  is zero until  $f_1$  reaches the carrying capacity  $k_1$  of region I after which the extra females have to move away from the wet marsh region. The fraction (4.2) is clearly not the best approximation we could choose (for example, if the total  $f_1 = k_1$ , the carrying capacity,  $F = 0.5$  whereas it should still be zero). We use this form, (4.2), for algebraic simplicity; it broadly has the required qualitative behaviour. We use the same fraction approximation in the other regions and also in the age-dependent analysis below.

If  $b$  is the effective birth rate, that is, it includes clutch size,  $C$ , and the high mortality of hatchlings and egg predation, in other words survival,  $S$ , then, in a simple population model such as we discussed in Chapter 1, we have a dynamic equation for the population in region I (all females)

$$\frac{df_1}{dt} = b \left[ \frac{k_1}{k_1 + f_1} \right] f_1 - df_1. \quad (4.3)$$

Here we have taken the death rate as proportional to the population with  $d$  a parameter. If  $f_1$  is large the maximum reproduction is then proportional to  $k_1$  which accounts for its role as a measure of habitat capacity. The birth rate,  $b$ , is a function of the total male population,  $m$ , and is reasonably taken as

$$b = b(m) = \frac{b_0 m}{(c + m)} \rightarrow b_0, \quad \text{for small } c, \quad (4.4)$$

where  $c$  is a constant which, from field data, is indeed very small. With  $c$  small, equation (4.3) is uncoupled from the other equations in the model system below.

If we now consider region II where both females and males are produced, the fraction of females which have to move from the wet marsh region I to the dry marsh region II is simply

$$1 - \frac{k_1}{k_1 + f_1} = \frac{f_1}{k_1 + f_1}. \quad (4.5)$$

So, the total number of females who want to nest in region II is the number who like this temperature plus those that had to move from region I:



$$\frac{f_1^2}{k_1 + f_1} + f_2.$$

There is also a limited number of nest sites in region II and only a fraction of females can incubate in II, which is (cf. (4.2)):

$$\frac{k_2}{k_2 + \frac{f_1^2}{k_1 + f_1} + f_2},$$

where, in the same way as we saw for (4.2),  $k_2$  relates to the maximum number of hatchlings possible in the dry marsh region II. For algebraic simplicity we approximate this fraction by

$$\frac{k_2}{k_2 + f_1 + f_2},$$

which has roughly the same qualitative behaviour. Compared with other assumptions and approximations this approximation is minor. It can, of course, easily be included in a numerical simulation of the equations: this was done and the resulting solutions were in general qualitative agreement. Thus the equations for the females and males in region II are:

$$\begin{array}{c} \text{number of females} \\ \text{who want to} \\ \text{incubate eggs in II} \\ | \\ \frac{df_2}{dt} = \frac{b_0}{2} \left[ \frac{f_1^2}{k_1 + f_1} + f_2 \right] \left[ \frac{k_2}{k_2 + f_1 + f_2} \right] - df_2 \\ \frac{dm_2}{dt} = \frac{b_0}{2} \left[ \frac{f_1^2}{k_1 + f_1} + f_2 \right] \left[ \frac{k_2}{k_2 + f_1 + f_2} \right] - dm_2 \\ | \\ \text{fraction of} \\ \text{females able to} \\ \text{nest in region II} \end{array} \quad (4.6)$$

The factor 1/2 is because half the hatchlings are male and half are female.

Finally in region III, the dry levees, the number of females forced to move from region II to III to nest is

$$\left[ \frac{f_1^2}{k_1 + f_1} + f_2 \right] \left[ \frac{\frac{f_1^2}{k_1 + f_1} + f_2}{k_2 + \frac{f_1^2}{k_1 + f_1} + f_2} \right]$$

and the fraction able to incubate eggs in region III is

$$\frac{k_3}{k_3 + \frac{f_1^2}{k_1 + f_1} + f_2},$$

where  $k_3$  is a direct measure of the carrying capacity of III. For the same algebraic reasons as above we approximate these expressions for the two fractions respectively by

$$\left[ \frac{f_1^2}{k_1 + f_1} + f_2 \right] \left[ \frac{f_1 + f_2}{k_2 + f_1 + f_2} \right] \quad \text{and} \quad \frac{k_3}{k_3 + f_1 + f_2}.$$

The remaining females cannot nest in any suitable site. So, with these expressions the equation for males in region III (in our model there are only males here) is

$$\frac{dm_3}{dt} = b_0 \left[ \frac{k_3}{k_3 + f_1 + f_2} \right] \left[ \frac{f_1^2}{k_1 + f_1} + f_2 \right] \left[ \frac{f_1 + f_2}{k_2 + f_1 + f_2} \right] - dm_3. \quad (4.7)$$

The system of equations (4.3), (4.6) and (4.7) constitute the model for the populations in the various regions and from which we can obtain the sex ratio of the total population.

The steady state populations are given by setting the right-hand sides of (4.3), (4.6) and (4.7) equal to zero and solving the algebraic equations. Zero for all the groups is of course one solution and it is easy to see from linearising the model equations that it is always unstable (recall the analyses in Chapters 1 and 3). A little algebra gives the positive steady states, denoted by asterisks, as

$$\begin{aligned} f_1^* &= \left( \frac{b_0}{d} - 1 \right) k_1, \quad m_2^* = f_2^* = \frac{1}{2} \left[ -A + (A^2 + C)^{1/2} \right], \\ m_3^* &= \frac{2k_3 f_2^* (f_1^* + f_2^*)}{k_2(k_3 + f_1^* + f_2^*)}, \quad A = f_1^* - k_2 \left( \frac{b_0}{2d} - 1 \right), \quad C = \frac{2k_2 f_1^{*2}}{k_1}. \end{aligned} \quad (4.8)$$

Since, from field studies,  $b_0/d$ , the effective births over the lifetime of an alligator, or other crocodilia, is of the order of 100 to 300, we can approximate these steady states by

$$f_1^* \approx \frac{b_0 k_1}{d}, \quad m_2^* = f_2^* \approx \frac{b_0}{d} F_2(k_1, k_2), \quad m_3^* \approx \frac{b_0}{d} F_3(k_1, k_2, k_3), \quad (4.9)$$

where  $F_2(k_1, k_2)$  and  $F_3(k_1, k_2, k_3)$  are obtained from (4.8).

We are particularly interested in the sex ratio,  $R$ . This is given by (4.9) for large  $b_0/d$  as

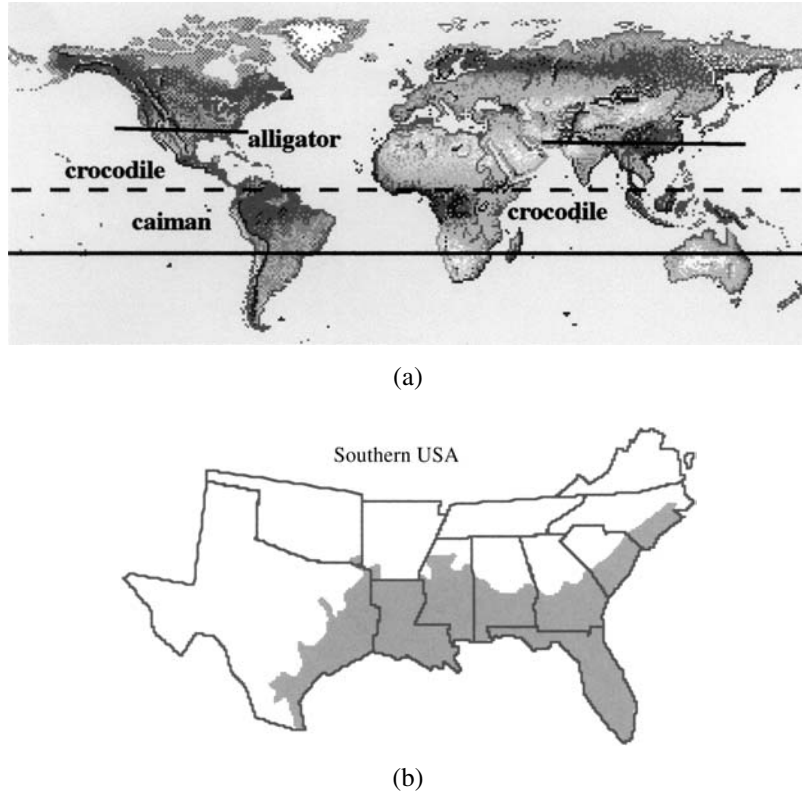
$$R = \frac{m_2^* + m_3^*}{f_1^* + f_2^* + m_2^* + m_3^*} \approx \frac{F_2(k_1, k_2) + F_3(k_1, k_2, k_3)}{k_1 + 2F_2(k_1, k_2) + F_3(k_1, k_2, k_3)} = \phi(k_1, k_2, k_3), \quad (4.10)$$

where  $\phi$  is defined by (4.10). In this asymptotic case the sex ratio is independent of  $b_0/d$ , and so the parameters,  $k_i$  with  $i = 1, 2$  and  $3$ , that is, those parameters proportional to the carrying capacities in the various regions I–III, are the key parameters. The environment is clearly seen to have a crucial influence on the sex ratio. With the estimates for the percentage carrying capacity in the three regions given by Joanen (1969) above, namely,  $79.7 : 13.6 : 6.7$ , the sex ratio of males to the total population is given by (4.10) as approximately 0.13 which means there are roughly 7 to 8 females to 1 male. Although we do not do it here, it is possible to carry out a stability analysis of these steady states with the methods we described earlier in the book but it is algebraically complex. Interestingly, such an analysis shows that there can be no periodic solutions: the positive steady state is always stable. Using the equations we can also investigate the effect of some catastrophe which greatly reduced the populations and obtain estimates for the recovery time to their steady states: this has to be done numerically except for small perturbations about the steady states where linear theory could apply. If the equations are to be studied in depth numerically then more appropriate fractional functions could be used but the general results would not be qualitatively different.

It is intuitively clear how the crocodilia, because of TSD, can recover from a catastrophic reduction in their population. Following a major reduction, all the female crocodiles will be able to build their nests in region I and hence produce only females; this then allows the remaining males to have larger harems. The skewed sex ratio in the crocodilia thus maintains a large breeding population which provides the mechanism for rapid repopulation after a disaster. What is certainly not in doubt is that TSD has been a very effective reproductive mechanism in view of the remarkable survivorship of the crocodilia.

Catastrophes, natural or otherwise, raise the question of extinction. If we consider extinction this would certainly happen if we have, from (4.3),  $b < d$ . With  $b = b_0 m / (c + m)$  this implies that  $m < cd / (b_0 - d) = O(1/b_0)$  for  $c$  small and  $b_0$  large, which implies that essentially all the males have to be eliminated. The natural habitat of males is in the water where it is virtually impossible to kill them all which, in turn, implies the almost impossibility of extinction except through the elimination of all the nest sites, that is, by completely destroying their habitat. With the increasing encroachment of their habitat by human population pressures it is certainly possible that alligators could disappear at least from the southern U.S. Figure 4.3(b) shows the approximate area in the U.S. where they are currently found.

The survival of alligators in the U.S. could depend on alligator farms which are already on the increase in these states. These, however, must be commercially viable and so the sale of alligator skins for shoes, belts, or whatever products appeal to consumers, is perhaps to be encouraged. Conservation takes on a different hue in these circumstances. Bustard (1984) discusses one such conservation strategy for the captive breeding of the gharial (*Gavialis gangeticus*) in India. After an extensive survey of the situation in India he made a strong case for captive breeding programmes. He also discussed the crocodile situation in Australia. It is clear we have to redefine what we mean by ‘conservation’ and survival of a species if it means only managed survival. It is a subject which already gives rise to heated discussion—and not only between conservationists and evolutionary biologists.

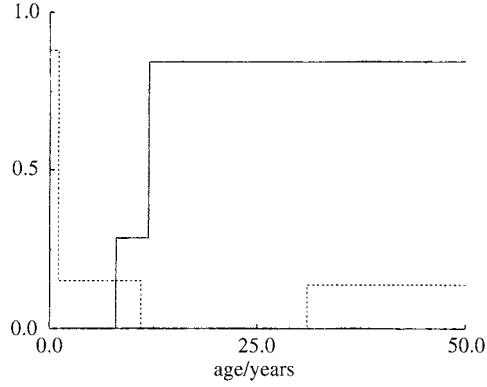


**Figure 4.3.** (a) Approximate areas around the equator where crocodilia are found. (b) Approximate region in the U.S. where alligators are currently found.

### 4.3 Age-Structured Population Model for the Crocodilia

The problem with population models which involve only time is that if age,  $a$ , plays an important role in survival or reproduction, it should be taken into account. In the case of the crocodilia it is important since both reproductive maturity and death rates vary significantly with age; Figure 4.4 shows typical averaged forms of the death rate,  $d(a)$ , and the birth rate,  $b(a)$  taken from the literature (Smith and Webb 1985, Webb and Smith 1987). Since we are ultimately interested in survivorship we must develop an age-structured model using the ideas in Sections 4.1 and 4.2. We introduced age-structure in population models in Chapter 1 and developed the techniques necessary to investigate the solutions. It would be helpful for the reader to briefly review that section prior to continuing with what follows.

We consider the nesting region to be divided into the three regions I, II and III as in Section 4.2 and analogously denote the four population classes by  $f_1(a, t)$  and  $f_2(a, t)$  denoting females themselves incubated in regions I and II, and  $m_2(a, t)$ , and  $m_3(a, t)$  denoting males incubated in regions II and III where  $a$  refers to age, and  $a_M$  is the maximum attainable age; they can live a long time, of the order of 70 years. So, for



**Figure 4.4.** Typical averaged birth,  $b(a)$  (solid line), and death,  $d(a)$  (dotted line), rates as a function of age, for the Australian freshwater crocodile (*Crocodylus johnstoni*). (Drawn from Smith and Webb 1985)

example,  $f_1(a, t)$  denotes the population density at time  $t$  in the age range  $a$  to  $a + da$ . We get the total time-dependent population,  $F_1(t)$ , by integrating over all ages from  $a = 0$  to  $a = a_M$ ,

$$F_1(t) = \int_0^{a_M} f_1(a, t) da.$$

We assume, as we tacitly did above, that the population is ‘closed,’ that is, it changes in size only through the processes of birth and death. The extensive radiotelemetric studies of Joanen and McNease (1970, 1972) show this is a biologically reasonable assumption if we consider fairly large home ranges. The death rate,  $d(a)$ , and birth rate,  $b(a)$ , are assumed to be only functions of age and typically as illustrated in Figure 4.4. Since differential sexual mortality is unknown we assume it is independent of sex. The birth processes are more complicated to describe as we shall show.

Just as described above, we consider sex is allocated to newborn alligators according to the availability of male and female producing nest sites. We further assume that all female alligators themselves incubated in wet marsh areas prefer to nest in region I since they seek a temperature environment that is as close as possible to that of their own incubation. Also, because of the limited number of nest sites in region I, only a fraction of females are able to incubate their eggs in wet marsh areas. Following (4.2) (and for similar algebraic reasons) we take that fraction to be  $k_1/(k_1 + Q_1)$ , where  $k_1$  is the maximum number of nests that can be built in the wet marsh.  $Q_1(t)$  denotes the total number of sexually mature (reproducing) females themselves incubated in region I; that is,

$$Q_1(t) = \int_0^{a_M} q_1(a) f_1(a, t) da. \quad (4.11)$$

Here  $q_1(a)$  is a weight function which reflects the effect of age: for example, older females cease to be reproductive.  $Q_1(t)$  is a weighted average with respect to age of the age density distribution of females in region I. The fraction of females who stay in the wet marsh has the same properties as in Section 4.2. For the reasons given there we take

the approximate fraction with the properties

$$\frac{k_1}{k_1 + Q_1} \rightarrow 1 \quad \text{as} \quad Q_1 \rightarrow 0, \quad \frac{k_1}{k_1 + Q_1} \rightarrow 0 \quad \text{as} \quad Q_1 \rightarrow \infty,$$

which again is as we want, namely, when  $Q_1$  is small nearly all the females themselves incubated in region I can nest there and when  $Q_1$  is large the vast majority have to move away from the wet marsh and nest elsewhere in regions II or III. As we pointed out above this fraction is an approximation to a more complicated but more accurate form for the fraction of females that can nest in region I. The arguments for using the approximate forms for the various fractions used in the age-independent model carry over to those used here and below.

Eggs incubated in region I produce all female,  $f_1$ , hatchlings because of low incubation temperatures. The density-dependent age-specific *maternity function*  $b_{11}(a, Q_1(t))$ , where  $b_{11}$  is the average number of offspring (per unit time) successfully hatched from eggs laid in region I by a female of age  $a$  who was herself incubated in region I, is given by

$$b_{11}(a, Q_1(t)) = CSb(a) \frac{k_1}{k_1 + Q_1}, \quad (4.12)$$

where  $C$  is the clutch size,  $S$  is the survival rate of eggs and hatchlings and  $b(a)$  is the age-dependent birth rate. The clutch size may be anything up to 70 eggs with an average around 40, but their survival is extremely small; there are many predators for the eggs as well as the hatchlings.

We assume that those females who cannot build nests in region I move to region II. Female alligators themselves incubated in dry marsh areas prefer to construct nests in region II. However in region II there is also a limited number of nest sites so that only a fraction  $k_2/(k_2 + [Q_1(t) + Q_2(t)])$ , is successful. Here  $k_2$  is the maximum number of nests that can be built in the dry marsh, and  $Q_2(t)$  is the total number of sexually mature females themselves incubated in region II. As before we consider eggs incubated in region II produce 50% female,  $f_2$ , and 50% male,  $m_2$ , hatchlings. For  $i = 1, 2$ , the density-dependent age-specific maternity functions  $b_{i2}(a, Q_1(t), Q_2(t))$  are the average number of offspring (per unit time) successfully hatched from eggs laid in region II by a female of age  $a$  who was herself incubated in region  $i$ , so

$$\begin{aligned} b_{12}(a, Q_1(t), Q_2(t)) &= CSb(a) \left[ \frac{k_2}{k_2 + Q_1(t) + Q_2(t)} \right] \left[ \frac{Q_1(t)}{k_1 + Q_1(t)} \right], \\ b_{22}(a, Q_1(t), Q_2(t)) &= CSb(a) \left[ \frac{k_2}{k_2 + Q_1(t) + Q_2(t)} \right]. \end{aligned} \quad (4.13)$$

The remaining females are forced to move to region III where the approximate fraction able to incubate eggs is  $k_3/(k_3 + [Q_1(t) + Q_2(t)])$  where  $k_3$ , as before, relates to the maximum number of nests that can be built in the levees. Eggs incubated in region III produce all male,  $m_3$ , hatchlings because of higher incubation temperatures. For  $i = 1, 2$ , the density-dependent age-specific maternity function  $b_{i3}(a, Q_1(t), Q_2(t))$  is

the average number of offspring (per unit time) successfully hatched from eggs laid in region III by a female of age  $a$  who was herself incubated in region  $i$ ,  $i = 1, 2$ ,

$$\begin{aligned} b_{13}(a, Q_1(t), Q_2(t)) &= CSb(a) \left[ \frac{k_3}{k_3 + Q_1(t) + Q_2(t)} \right] \left[ \frac{Q_1(t) + Q_2(t)}{k_2 + Q_1(t) + Q_2(t)} \right] \\ &\quad \times \left[ \frac{Q_1(t)}{k_1 + Q_1(t)} \right], \\ b_{23}(a, Q_1(t), Q_2(t)) &= CSb(a) \left[ \frac{k_3}{k_3 + Q_1(t) + Q_2(t)} \right] \left[ \frac{Q_1(t) + Q_2(t)}{k_2 + Q_1(t) + Q_2(t)} \right]. \end{aligned} \quad (4.14)$$

Indications from available data suggest that even though there are fewer males than females in alligator and crocodile populations, the male population size is rarely if ever a limiting factor in reproduction (Webb and Smith 1987, Nichols et al. 1976). For this reason the maternity functions (4.14) depend only on  $f_1$ , and  $f_2$  (via  $Q_1(t)$ , and  $Q_2(t)$ ) and the model is said to be *female dominant* (Keyfitz 1968, Sowunmi 1976).

The life history data given by the clutch size,  $C$ , the egg and hatchling survival,  $S$ , the death rate  $d(a)$ , the reproduction rate  $b(a)$  and the carrying capacity parameters  $k_1$ ,  $k_2$ ,  $k_3$ , contain a great deal of information about the potentialities of the population and its relationship to the environment (Cole 1954, Stearns 1976). The clutch size,  $C$ , ranges from 1 to 68 for *A. mississippiensis* (Ferguson 1985). There are five primary classes of survivorship: (i) egg survivorship (to hatchling), (ii) hatchling survivorship (to one year of age), (iii) juvenile survivorship (to maturity), (iv) middle age survivorship (to a decline in reproductive output) and (v) old age survivorship (through senescence). Egg and hatchling survivorship is extremely low due to predation, flooding, cannibalism, desiccation and freeze mortalities, as well as eggs cracking during laying and the failure of the nest to open. Juveniles are also at risk, mainly due to predation, but middle age survivorship is high (crocodilia have almost 100% survivorship during their middle years), declining again in old age. Averaging over each of these classes gives the age-specific death rate,  $d(a)$ . Typically the reproduction rate,  $b(a)$ , is constant in middle age, and zero for both immature and senescent crocodilia. It is obtained by averaging estimates of the age at which females begin breeding (approximately 9 to 12 years old), the proportion of females capable of breeding that do breed each year (between 33 and 84%), and the age at which females cease breeding. Typical averaged forms of  $d(a)$  and  $b(a)$  from Smith and Webb (1985) are shown in Figure 4.4. As before  $k_1$ ,  $k_2$ ,  $k_3$  are proportional to the size of the wet marsh, dry marsh and levees carrying capacities respectively.

#### 4.4 Density-Dependent Age-Structured Model Equations

We can now write down the model equations for the several populations  $f_1(a, t)$ ,  $f_2(a, t)$ ,  $m_2(a, t)$  and  $m_3(a, t)$  respectively females themselves incubated in regions I and II and males incubated in regions II and III as described above.

Here  $a$  refers to age, and  $a_M$  is the maximum attainable age. We now write down the conservation equations as we did in Chapter 1, Section 1.7 remembering that  $a$  is

chronological age and  $t$  is time. The equations are

$$\frac{\partial}{\partial t} f_i(a, t) + \frac{\partial}{\partial a} f_i(a, t) = -d(a) f_i(a, t), \quad \text{for } i = 1, 2 \quad (4.15)$$

$$\frac{\partial}{\partial t} m_i(a, t) + \frac{\partial}{\partial a} m_i(a, t) = -d(a) m_i(a, t), \quad \text{for } i = 2, 3, \quad (4.16)$$

where  $d(a)$  is the age-specific *death rate* and typically as in Figure 4.4. As above we assume a female alligator seeks a nesting region which provides her with a temperature as close as possible to that at which she was incubated. Then the birth processes by which individuals are introduced into the population are the usual *renewal*-type equations. Hatchlings are born at age  $a = 0$  and so

$$\begin{aligned} f_1(0, t) &= \int_0^{a_M} f_1(a, t) b_{11}(a, Q_1(t)) da, \\ f_2(0, t) &= \frac{1}{2} \int_0^{a_M} f_1(a, t) b_{12}(a, Q_1(t), Q_2(t)) da \\ &\quad + \frac{1}{2} \int_0^{a_M} f_2(a, t) b_{22}(a, Q_1(t), Q_2(t)) da, \\ m_2(0, t) &= \frac{1}{2} \int_0^{a_M} f_1(a, t) b_{12}(a, Q_1(t), Q_2(t)) da \\ &\quad + \frac{1}{2} \int_0^{a_M} f_2(a, t) b_{22}(a, Q_1(t), Q_2(t)) da, \\ m_3(0, t) &= \int_0^{a_M} f_1(a, t) b_{13}(a, Q_1(t), Q_2(t)) da \\ &\quad + \int_0^{a_M} f_2(a, t) b_{23}(a, Q_1(t), Q_2(t)) da, \end{aligned} \quad (4.17)$$

where from (4.11) and the equivalent for  $Q_2(t)$

$$Q_1(t) = \int_0^{a_M} q_1(a) f_1(a, t) da, \quad Q_2(t) = \int_0^{a_M} q_2(a) f_2(a, t) da. \quad (4.18)$$

For  $i = 1, 2$ ,  $j = 1, 3$ , the density-dependent age-specific *maternity functions*  $b_{ij}(a, Q_1(t), Q_2(t))$  are given in (4.12) through (4.14) which are the average number of offspring (per unit time) successfully hatched from eggs laid in region  $j$  by a female of age  $a$  who was herself incubated in region  $i$ . We assume that density-dependent constraints act on births in the form of a limited number of nest sites. Remember that the ‘sizes’  $Q_1(t)$  and  $Q_2(t)$  are weighted averages, with respect to age, of the age-density distributions of the females in regions I and II respectively.

To complete the model equation formulation we finally must assume some known initial age-structure of the populations,

$$f_i(a, 0) = \phi_i(a), \quad i = 1, 2, \quad m_i(a, 0) = \phi_i(a), \quad i = 2, 3. \quad (4.19)$$

Biologically, of course,  $\phi_i(a)$ ,  $d(a)$  and  $b_{ij}(a, Q_1(t), Q_2(t))$  are all nonnegative.



### Birth and Death Data

We use the (smoothed) data from Smith and Webb (1985) to construct the reproduction,  $b(a)$ , death,  $d(a)$ , rates and the initial population  $\phi(a)$ ; see Figure 4.4.

The effective birth rate is  $CSb(a)$  where  $C = 13.2$  is average clutch size,  $S = 0.295 \times 0.12$  is survival rate of eggs and hatchlings, and the age-structured reproduction function and age-structured death function are given by

$$b(a) = \begin{cases} 0.000 & 0 < a \leq 8 \\ 0.286 & 8 < a < 12 \\ 0.844 & 12 \leq a < a_M \end{cases} \quad d(a) = \begin{cases} 0.151 & 1 < a < 11 \\ 0.000 & 11 \leq a < 31 \\ 0.139 & 31 \leq a < a_M \end{cases} . \quad (4.20)$$

To be specific we assume that the initial population,  $\phi(a)$ , has a simple exponential dependence on age,  $a$ ,

$$\phi(a) = c_1 + (c_2 - c_1)e^{-c_3 a}, \quad \text{where} \quad \begin{cases} c_1 = 3.376, \\ c_2 = 135.970, \\ c_3 = 0.155, \end{cases} \quad (4.21)$$

where the  $c_i$  were determined from a nonlinear least squares regression fit to the initial (smoothed) data of Smith and Webb (1985).

It is not possible to solve the above model system of equations analytically as we were able to do in Chapter 1, Section 1.7, but we can solve them numerically if the initial age distribution of the population is given and the pertinent life history parameters,  $C$ ,  $S$ ,  $d(a)$ ,  $b(a)$ ,  $k_1$ ,  $k_2$ ,  $k_3$  are constant (with respect to time). In this way we can compute the future populations. Intuitively with fixed life history features there must ultimately be a stable age distribution and hence a fixed sex ratio (Cole 1954).

## 4.5 Stability of the Female Population in the Wet Marsh Region I

The females in region I can be considered as a single isolated species since the birth and death processes depend only on age,  $a$ , and the size of the sexually mature female population in region I,  $Q_1(t)$ . For a species to survive it must possess reproductive capacities sufficient to replace the existing generation by the time it has disappeared. We define the *net reproductive rate*,  $R_1$ , to be the expected number of female offspring born to an individual female during her lifetime when the population size is  $Q_1(t)$ . The number of female offspring born to a female between age  $a$  and  $a + da$  is  $b_{11}(a, Q_1(t))da$ , so if we sum over  $a$ , we have

$$\begin{array}{ll} \text{net reproductive} & \text{expected number of female offspring born} \\ \text{rate in region I} & \text{to an individual female during her lifetime} \end{array} \quad (4.22)$$

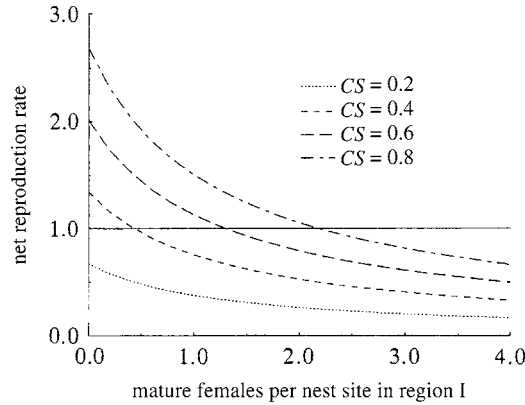
$$R_1[Q_1(t)] = \int_0^{a_M} b_{11}(a, Q_1(t))\pi(a) da,$$

where  $\pi(a)$  is the probability that an individual will survive to age  $a$ ; that is,

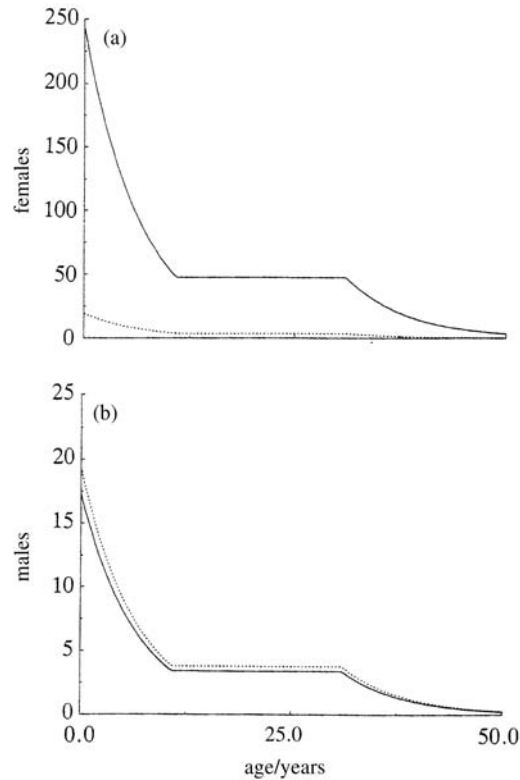
$$\pi(a) = e^{-\int_0^a d(s) ds}. \quad (4.23)$$

The female population in region I will either be increasing or decreasing, or it will remain constant, depending on whether  $R_1 > 1$ ,  $R_1 < 1$  or  $R_1 = 1$ . As long ago as 1760, Euler investigated the mortality and survivorship of humans, in effect using the idea of a net reproductive rate (see the translation of his article in Euler 1970 (1760)). So, for there to be a stable age distribution it is necessary and sufficient that  $R_1(Q_1^*) = 1$  has a nonzero solution,  $Q_1^*$ ; that is, *for each female member throughout her life, the expected number of female births is 1*. Gurtin and MacCamy (1974), Sowunmi (1976) and Webb (1985) point out that in classical (linear) theory  $R_1$  is independent of  $Q_1$ . It would be fortuitous if this were to be the case; however, in most problems of interest here there is at least one value of  $Q_1^*$  for which  $R_1(Q_1^*) = 1$  as we see in Figure 4.5. This figure shows, for several clutch sizes and survival rates, the numerical simulations for the net reproductive rate as a function of the number of sexually mature females in region I as a function of the number of mature females in region I relative to the available nesting space in region I, namely,  $Q_1/k_1$ .

We have assumed throughout that the environment is stable (that is,  $k_1$ ,  $k_2$  and  $k_3$  are constants) whereas, in reality, annual recruitment (and the sex ratio of recruits) is subject to extreme environmental variation (Webb and Smith 1984, 1987). However Gurney and Nisbet (1980a) showed that in age- and density-dependent populations, environmental fluctuations are not significant if the members of the population have a long reproductively active stage, with or without an immature phase and a period of senescence. This agrees with the observation of Deeming and Ferguson (1989b) that only if the skew is consistently toward males for at least the entire reproductive life span of a whole generation, does a species run into serious problems.



**Figure 4.5.** Numerically calculated net reproduction rate,  $R_1$ , as a function of the number of sexually mature females in region I relative to the space,  $k_1$ , available for nesting in region I,  $Q_1/k_1$ . This graph shows that provided the number of eggs producing surviving hatchlings, that is, the product  $CS$  with  $C$  and  $S$  the clutch size and survival respectively, is sufficiently large there is a value  $Q_1^*$  for which the  $R_1(Q_1^*) = 1$ ; that is, a stable age distribution exists. A biologically realistic value of the parameter  $CS$  is approximately 0.5. (From Woodward and Murray 1993)



**Figure 4.6.** Numerical solution of the three-region model showing the equilibrium age distributions of (a) females incubated in regions I (solid line) and II (dotted line), and (b) males incubated in regions II (solid line) and III (dotted line). The sex ratio at the steady state is  $(m_2 + m_3)/(f_1 + f_2) = 0.122$  or, in other words, 12.2% of the population are males. (From Woodward and Murray 1993)

A stable solution of the equations for the female population in region I inevitably gives a stable solution of both the male and female populations in regions II and III. The three-region density-dependent age-structured model was solved numerically (Woodward and Murray 1993) by replacing the derivatives by finite differences and the integrals by quadrature formulae (Kostova 1990). Figure 4.6 shows the female and male stable age distributions,  $f_1$ ,  $f_2 = m_2$ , and  $m_3$  in the case  $k_1 : k_2 : k_3 = 79.7 : 13.6 : 6.7$  (Joanen 1969). The population is flat for  $11 < a < 31$  because we assumed 100% survivorship during the middle years. At equilibrium, the sex ratio,  $(m_2 + m_3)/(f_1 + f_2)$ , expressed as percentage of the population that is male, is 12.2%, roughly one male to every eight females.

## 4.6 Sex Ratio and Survivorship

In view of the analytical complexity of the full model we simplify by assuming that  $f_2 = 0$ , which is biologically fairly realistic since, compared to the number of females

nesting in region I, only a small fraction of females nest in region II (Joanen 1969); see also Figure 4.6. We now use this simpler model to investigate the effects of the life history phenomena on sex ratio.

The model system we consider in this situation consists of two populations  $f_1(a, t)$ : namely, females incubated in region I and  $m_3(a, t)$ , males incubated in region III. We have no region II, in effect, in this scenario. The equations, boundary and initial conditions are, from (4.15) through (4.17) and (4.19),

$$\begin{aligned}\frac{\partial}{\partial t} f_1(a, t) + \frac{\partial}{\partial a} f_1(a, t) &= -d(a) f_1(a, t), \\ \frac{\partial}{\partial t} m_3(a, t) + \frac{\partial}{\partial a} m_3(a, t) &= -d(a) m_3(a, t),\end{aligned}\tag{4.24}$$

with

$$\begin{aligned}f_1(0, t) &= \int_0^{a_M} f_1(a, t) b_{11}(a, Q_1(t)) da, \\ m_3(0, t) &= \int_0^{a_M} f_1(a, t) b_{13}(a, Q_1(t), Q_2(t)) da\end{aligned}\tag{4.25}$$

with initial conditions

$$f_1(a, 0) = \phi_1(a), \quad m_3(a, 0) = \phi_3(a).\tag{4.26}$$

The equation for  $f_1(a, t)$  in (4.24) with the boundary and initial conditions in (4.25) and (4.26) is the same as the population equation in Chapter 1, equations (1.54) to (1.56). We could not write down an analytical solution exactly (we ended up with an integral equation), but we were able to carry out some relevant similarity analysis. Here we solve the equation numerically.

Since the death rate is assumed independent of sex, the sex ratio does not depend on age and, at equilibrium, the sex ratio of the population density equals the primary (at hatching) sex ratio. Defining the *net reproductive rate*,  $R_3$ , to be the expected number of male offspring born to an individual female during her lifetime when the population size is  $Q_1(t)$ , we have

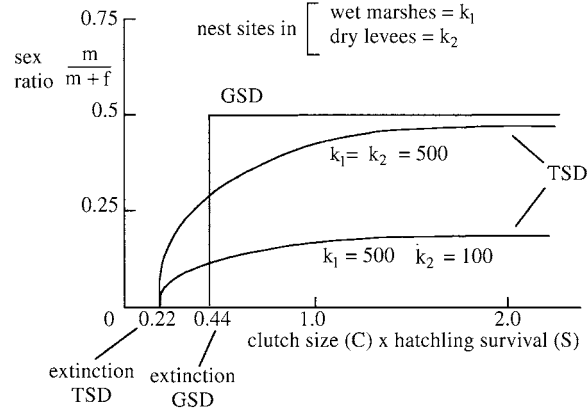
$$\begin{array}{ll}\text{net reproductive} & \text{expected number of male offspring born} \\ \text{rate in region III} & \text{to an individual female during her lifetime}\end{array}\tag{4.27}$$

$$R_3[Q_1(t)] = \int_0^{a_M} b_{13}(a, Q_1(t)) \pi(a) da,$$

where the maternity function  $b_{13}(a, Q_1(t))$  is given by (4.14) with  $Q_2 \equiv 0$ , and  $k_2 \equiv 0$ , and  $\pi(a)$  given by (4.23), namely,

$$b_{13}(a, Q_1(t)) = C S b(a) \left[ \frac{k_3}{k_3 + Q_1(t)} \right] \left[ \frac{Q_1(t)}{k_2 + Q_1(t)} \right] \left[ \frac{Q_1(t)}{k_1 + Q_1(t)} \right].$$

At equilibrium,  $Q_1(t) \equiv Q_1^*$ , and the ratio of the expected number of male offspring to the expected number of female offspring is given by



**Figure 4.7.** Numerically calculated sex ratio for the two-region model as a function of clutch size,  $C$ , and hatchling and egg survival,  $S$ , for various carrying capacities: (i)  $k_1 = 500, k_3 = 100$ , and (ii)  $k_1 = k_3 = 500$ . Here  $k_1$  and  $k_3$  are directly related to the maximum number of nests that can be constructed in the wet marsh and the levees, respectively. The minimum value of  $CS$  for a nonzero stable age distribution of the TSD model is 0.22 which is half that for the minimum necessary for the existence of a nonzero equilibrium in the GSD model, which is 0.44. (Redrawn from Woodward and Murray 1993 who give the accurate quantitative forms plus another case in which the carrying capacities  $k_1 = 500, k_3 = \infty$ )

$$\frac{R_3(Q_1^*)}{R_1(Q_1^*)} = \int_0^{a_M} b_{13}(a, Q_1^*) \pi(a) da, \quad (4.28)$$

since from Figure 4.5,  $R_1(Q_1^*) = 1$ . Hence, for a stable age distribution, it is necessary that *the expected number of male births equals the neonatal male/female sex ratio* (Sowunmi 1976).

For a given reproduction rate,  $b(a)$ , and a given death rate,  $d(a)$ , the sex ratio will be skewed depending on the number of eggs producing surviving hatchlings,  $CS$ , and on  $k_1$  and  $k_3$ . Numerical simulations of the two-region model illustrate this result and are represented in Figure 4.7. There is a range of values of  $CS$ ,  $m < CS < M$ , for which the TSD model has a nonzero stable age distribution, but the only equilibrium of the corresponding GSD model is the zero solution as we show in Section 4.7 below.

#### 4.7 Temperature-Dependent Sex Determination (TSD) Versus Genetic Sex Determination (GSD)

At the most basic level the easiest way to compare the two methods of sex determination is to consider a two-region model without age-dependence. We showed in the last section how the sex ratio and survival depended on the product of the clutch size and hatchling survival. To get some idea of how these play a role in genetic sex determination and for ease of comparison we consider here a particularly simple model in which the populations depend only on time. As in the previous section we again consider only a two-region model, region I where only females are incubated and a region III where

only males are incubated. This is a simplified version of the model in Section 4.2 and is the age-independent equivalent of the model in Section 4.4.

With these assumptions the birth rate,  $b$ , and death rate,  $d$ , are constant parameters. Let the clutch size,  $C$ , and the survival,  $S$ , be as before. The female and male populations are denoted by  $f_1(t)$  and  $m_3(t)$  respectively.

The equation for the female population is then (cf. (4.3))

$$\frac{df_1}{dt} = CSb \left[ \frac{k_1}{k_1 + f_1} \right] f_1 - df_1 \quad (4.29)$$

but where here we have included  $CS$  explicitly in the birth rate for ease of comparison with the previous section. The equation for the male population is (4.7) but with  $f_2 = k_2 = 0$ , namely,

$$\frac{dm_3}{dt} = CSb \left[ \frac{k_3}{k_3 + f_1} \right] \left[ \frac{f_1^2}{k_1 + f_1} \right] - dm_3 \quad (4.30)$$

with initial conditions  $f_1(0) = f_0$  and  $m_3(0) = m_0$ .

The steady state populations are

$$f_1^* = k_1 \left( \frac{CSb}{d} - 1 \right), \quad m_3^* = \frac{CSb}{d} \left( \frac{k_3}{k_3 + f_1^*} \right) \left( \frac{f_1^{*2}}{k_1 + f_1^*} \right) \quad (4.31)$$

which are nonnegative if  $CSb > d$ . The sex ratio, male to female offspring, is given by

$$R = \frac{m_3^*}{f_1^*} = \frac{k_3(CSb - d)}{k_3d + k_1(CS - d)}. \quad (4.32)$$

If we now suppose that the crocodile sex was genetically determined there is no region variation in sex but there is the equivalent limitation of nest sites; here  $k_1 + k_3$  is the available carrying capacity. The corresponding equations for females  $f(t)$  and males  $m(t)$  are then

$$\begin{aligned} \frac{df_1}{dt} &= \frac{CSb}{2} \left[ \frac{k_1 + k_3}{k_1 + k_3 + f_1} \right] f_1 - df_1 \\ \frac{dm_3}{dt} &= \frac{CSb}{2} \left[ \frac{k_1 + k_3}{k_1 + k_3 + f_1} \right] f_1 - dm_3 \end{aligned} \quad (4.33)$$

with initial conditions  $f_1(0) = f_0$ ,  $m_3(0) = m_0$  and where again we have included  $CS$  explicitly in the birth rate. There is symmetry between males and females in this case, with half the births being female and the other half male. The steady state populations are given by

$$m_3^* = f_1^* = (k_1 + k_3) \left( \frac{CSb}{2d} - 1 \right), \quad (4.34)$$

which are nonnegative only if  $CSb > 2d$ . The sex ratio of males to females is always 1 : 1.

Even with the steady state solutions (4.31) and (4.34) we can see the advantages of TSD over GSD for the crocodilia. From (4.31), that is, with TSD, a positive steady state exists if  $CSb/d > 1$  whereas for GSD it requires  $CSb/d > 2$ . To be more specific, from Figure 4.7 we see that in the age-dependent situation the sex ratio under TSD tends to zero when  $CS = m = 0.22$ , that is, the value when the species becomes extinct. To relate that to the analysis here means we have  $CSb/d = 1$  corresponding to  $CS = 0.22$  and so the critical  $CS$  for GSD is simply  $CS = M = 0.44$ ; this is the value we used in Figure 4.7 for comparison. With GSD there is extinction therefore for  $CS < M = 0.44$ .

The minimum value of  $CS$ , namely,  $M$ , for a nonzero equilibrium solution of the GSD model is approximately twice the minimum,  $m$ , necessary for the existence of a nonzero stable age distribution of the TSD model. In this range, the smaller the value of  $CS$ , the larger the skew in favour of females. Outside this range, both the TSD and GSD model have nonzero stable age distributions. For large values of  $CS$ , the sex ratio of the TSD model tends to  $k_1 : k_3$ , whereas for the GSD model it is 1 : 1. These comparisons of theoretical and empirical population phenomena suggest that survival of the species is much more important than an optimal sex ratio.

The modelling and analysis in this chapter on an age-structured model for crocodilia populations are based on parameter values obtained as far as possible from field data. The model demonstrates a selective evolutionary advantage for temperature-dependent sex determination in crocodilian populations even though the probability that any one female will successfully reproduce herself is low. In this case, it is the population as a whole that is benefited, not a particular individual as in traditional sex ratio theory.

Animals whose sex is determined genetically maintain a 1 : 1 sex ratio. So, if a species exhibits GSD it is necessary for each female to produce two (one male, one female) net offspring for the population density to be stable and survive. Actually the figure is closer to 2.1 offspring per female. However, if a species exhibits temperature-dependent sex determination, or more generally environmental sex determination, ESD, it is likely that a skewed sex ratio will occur as a consequence of skewed environmental types. If the sex ratio is spanandrous (biased in favour of females), as is the case for the crocodilia, a stable population density can be maintained with fewer net offspring. In the wild, each female alligator or crocodile will lay approximately 600 to 800 eggs per lifetime but, on average, less than two of these (as few as 1.1 in a population that has a sex ratio of 10 : 1 in favour of females) will survive to successfully reproduce themselves. Thus, as a result of evolving TSD, alligator and crocodile populations are extremely stable despite the high mortality of eggs, hatchlings and immatures.

In addition to the advantage of producing more females than males, the crocodilia have evolved life history tactics (namely, early maturity, many small young, reduced parental care and multiple broods) that minimize the probability of leaving no young at all (Stearns 1976). Temperature-dependent sex determination may also be important in enabling populations to survive environmental changes and catastrophes as mentioned above. Not only is a rapid expansion of the population associated with the production of large numbers of females but also different incubation temperatures produce a population adapted to a range of environments after they hatch, independent of sex (Deeming

and Ferguson 1989b). Another plus is that male- and female-producing nests are located near the natural habitat of the adults.

## 4.8 Related Aspects on Sex Determination

An interesting and fundamental question not addressed in the models in this chapter, is how a single temperature can operate to give hatchlings of both sexes such as in region II, or more specifically at an incubation temperature of around 32° C. There clearly cannot be a simple switch that is the trigger for determining sex. There has been considerable interest in the molecular mechanism of TSD (Deeming and Ferguson 1988, 1989a, Johnston et al. 1995) and it is on it that temperature almost certainly operates. Also, in the wild the temperature of eggs in the nest fluctuates over a 24-hour period and even during the breeding season. Changes in the average incubation affect the ability of a member of the species to develop as a male or female. This is also a feature for many turtles. Georges (1989) suggested that, in the natural nests of fresh water turtles with TSD, it is perhaps the duration of time during incubation, or proportion of development at given temperatures which are crucial. Georges (1989) put forward an interesting basic model (see the exercise) to explore this idea. Georges et al. (1994), using this model, present experimental data (in a controlled experimental situation) on the marine turtle (*Caretta caretta*) that it could indeed be the proportion of development at a temperature rather than the daily duration of exposure that is the determining factor in sex selection. The work of Rhen and Lang (1995) on the snapping turtle is particularly relevant.

In the case of *A. mississippiensis* Deeming and Ferguson (1988, 1989b) hypothesised that the effect of temperature appears to be cumulative rather than at a particular developmental stage. They suggested that the development of the testes depends on the production of some male determining factor (MDF) during a critical period of development. There could be an optimal temperature to produce this factor, such as 33° C, but that it can also be produced at lower temperatures on either side of the optimal temperatures for a male, namely, around 32° C. If the threshold of MDF in the embryo does not reach the threshold level for a male it develops as a female. This hypothesis would explain why some temperatures can produce either males or females.

An interesting application (Ferguson, personal communication 1993) of their hypothesis is based on the belief that the basic molecular mechanism of sex determination in alligators is the same as for chickens even though they have GSD. The prediction is that it should be possible to manipulate the sex of birds by environmental manipulation, such as temperature pulses, early in incubation. He found that a specific temperature pulse early on did indeed affect sex determination: 10% of the chickens had a reversal in their sex.

It seems to be generally accepted that the default body plan in mammals, including humans, is female. A fetus becomes male if it is exposed to sufficient testosterone at an appropriate time or times in development. The gene which triggers the production of testosterone comes from the Y chromosome, which is inherited from the father. Women usually have two X chromosomes; the fetus inherits the X chromosomes from the mother. In the U.S. about 2% of men and 1% of women are attracted to their own sex. Recent interesting research by McFadden and Pasanen (1998) suggests that



lesbianism could be a result of a female's fetus being subjected to male hormones at specific times in development and hence acquire characteristics more associated with males. They based their tentative conclusions on the study of what are called click-evoked otoacoustic emissions (CEOAES) which are noises the ear makes in response to clicks: these emissions seem to be related to cochlear amplification which is how very low sounds can be heard. The experiments consisted of examining the strength of CEOAES of 237 people, homosexual, bisexual and heterosexual men and women. They found that homosexual and bisexual women had more malelike responses than heterosexuals. Of course there are many caveats and questions concerning the tentative conclusions. One is where the testosterone comes from. Women produce testosterone as well as men (who also produce small amounts of estrogen) but at a greatly reduced level. It is possible that a surge in the mother's testosterone at a crucial period in development could account for the results of McFadden and Pasanen (1998).

Hormone levels have an effect on the human sex ratio; see for example, James (1996, 1999) who suggests that parental hormone levels at the time of conception play a role in the sex of the offspring. James (2000) presents further data to support the influence of hormones on sex determination. Among other things James (2000) cites the fact that schizophrenic women have significantly more daughters while epileptics have significantly more male siblings. Steroid hormones affect neurotransmitters in the brain so he suggests that these abnormal sex ratios support the hypothesis that hormone levels at conception in part control the sex of the offspring. Poisons also possibly affect sex ratios and certainly fertility. James (1995) implicates dioxin in reduced levels of testosterone in workers exposed to the poison. This affects fertility as do sodium borates (Whorton et al. 1994).

As we have seen, the sex ratio plays a crucial role in alligator population dynamics and survival. In an interesting article Johnson (1994) puts forward a simple, but, as he shows, a highly informative model to investigate the effect of male to female sex ratio on the per capita growth rate in a population (not involving temperature in a TSD way). He suggests that the model could be useful in investigating how the sex ratio could be exploited by a population to ensure survival. The paper is a nice example of how a simple model based on some basic biological hypotheses can give rise to some interesting implications and pose some highly relevant questions. Since female age has an important effect on the per capita birth rate it would be interesting to put age distribution into Johnson's (1994) model. Although the world average human male to female sex ratio has been fairly constant (slightly more female to male births) there is increasingly convincing evidence of some shift in the sex ratio in humans; see, for example, Alpert (1998) who asks where all the boys have gone. This is very different to the situation which still exists in rural China where the ratio of boys to girls is very much higher than the world norm due to external interference before and after birth.

Johnston et al. (1995) review the various molecular mechanisms which have been proposed and suggest what is required to get a fuller understanding. They make the case for also considering a possible female determining factor (FDF) and its accumulation and how either a MDF or FDF may be temperature-dependent. There is a temperature-sensitive period (TSP) in the development of sex. They hypothesise that if a threshold level of FDF to result in a female is not reached by the beginning of the TSP then the embryo has the potential to develop into a male. If it has reached the threshold

for a female by the start of the TSP then it will develop into a female whatever the subsequent temperature of incubation. From their experiments Johnston et al. (1995) suggest that a particular type of protein—an SRY-type protein—could play a role in male sex determination.

Various experiments have been carried out on alligator embryos (Lang and Andrews 1994) to investigate the effect of moving the egg from one temperature to another, both single-shift and double-shift experiments. The results are consistent with the hypothesis that temperature controls the production of some sex-determining factors whether MDF, FDF, hormones or whatever. If these are produced at a sufficient rate over a long enough time they result in what is referred to as a sex determination cascade (Wibbels et al. 1991). Wibbels et al. (1994) describe a mechanistic approach to sex determination but ‘mechanistic’ in a different sense to what we understand by a mechanism used in this book.

The phenomenon of TSD is still far from understood. The above discussion of the possible molecular mechanism involved in sex determination and the results of incubation at different temperatures during gestation seems ripe for further modelling which could highlight implications of various scenarios and suggest further enlightening experiments.

There are many aspects of modelling TSD that have not been discussed in this chapter and several alternative and modified versions that would be interesting to study. An age-independent model with delay representing the time to maturity would be of interest to see how the results from it compared with the age-dependent model. It would certainly be much easier to study various scenarios of control and so on with such a model since it would be possible to carry out some preliminary analysis. A comparison of models would be informative, even with only two regions. As we learn more about TSD (not only with regard to the crocodilia), development and temperature, the effect of environmental fluctuations and so on, the more closely models will be able to reflect the biology and ecology of these remarkable creatures and give pointers as to their future survival.

## Exercise

- 1 Certain turtles have temperature-dependent sex determination with females incubated at high temperatures and males at low temperatures. Since the temperature fluctuates during the day an egg spends only a fraction of its time in a high temperature. Assume that a threshold temperature  $T_0$  exists below which no development takes place and that the development rate is approximated by

$$\frac{dS}{dt} = k(T - T_0),$$

where  $k$  is a positive constant. Suppose that the temperature varies daily according to

$$T = R \cos t + M, \quad 0 \leq R < M,$$

where  $R$  is the amplitude and  $M$  is the mean with  $M > T_0$ . Here  $t = 2\pi$  corresponds to 24 hours. The condition on  $M$ ,  $R$  and  $T_0$  is that the nest temperature is always greater than or equal to the threshold temperature.

Suppose that females are produced if more than half of embryonic development occurs above an effective nest temperature  $T_1$ . Show that  $T_1$  is given by

$$T_1 = R \cos t_1 + M, \quad t_1 = \frac{\pi}{2} - \frac{R}{M - T_0} \sin t_1.$$

Show graphically how to determine  $t_1$  and discuss how  $T_0$  varies with the ratio of the daily temperature amplitude,  $R$ , to the difference between the mean temperature,  $M$ , and the threshold  $T_0$ . What are the implications for the sex ratio outcome as the parameters vary?



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