

POPULATION DYNAMICS OF THE AMERICAN ALLIGATOR

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Vanity of vanities, saith the Preacher, vanity of vanities, all is vanity.

Ecclesiastics I:2.

INTRODUCTION

The necessary title of this chapter suggests more vanity than I would prefer to confess. To begin with, I am not familiar with "the American Alligator". Indeed, modern research indicates that despite relative genetic homogeneity (Adams et al. 1980), the beast varies in demographically important ways from place to place--and perhaps from year to year. That is to say, alligators strongly reinforce the natural historian's fear of generalizations. To make matter worse, I am not particularly confident even about any single-frame "snapshot" of an alligator population at time t ; therefore, to project a dynamic "movie" over t , $t+1$, ..., $t+n$ seems indeed the height of vanity. In other words, most of what I personally know about alligators focuses rather narrowly on Florida animals. And I admit that even for these populations I cannot offer decent life tables, much less expressions of density dependence. Nevertheless, scientific ignorance about alligators is not unbounded. Some facts are known quite well enough, and these facts necessarily entail general demographic consequences. I shall review these facts, and I shall even venture in some instances to speculate beyond the confines of available data. Still, I hate to promise more than I can deliver, and in an age of longer titles, I would have called this chapter "Alligator Life History: Meditations from a Demographic Perspective." Thus my general strategy is rather simple. I shall examine the alligator literature for relevant life-history data. Supplementing this information with observations recently conducted in Florida, I shall attempt to establish broad ranges for values of several important demographic parameters. This will permit semi-informed guesses about what manner of demographic beast the alligator must be. In other words, my essay's objective is to employ what is known about alligators while speculating on matters which are not yet understood. In particular, I have in the back of my mind three presently unanswered questions, all of considerable scientific and managerial significance: What are alligator survival rates? How do alligators respond to alterations in density? And how are alligators populations affected by demographic catastrophes? Again I admit at the outset that I can do little more than merely raise these interesting questions. But I want to start you readers thinking about them because you all will be the folks eventually to work out the solid answers.

Actually I would have been unwilling to attempt even this modest task without considerable assistance, but, fortunately, alligator biologists have been very willing to share their time and insights. Colleagues that come readily to mind are Tommy Hines, Terri Jacobsen, Mike Jennings, Wayne King, Wendell Neal, Jim Nichols, Jane Packard, Franklin Percival, David Scott, Dave Taylor, Phil Wilkinson, and Allan Woodward. The most creative advice came, of course, from Paul Moler--when he could tear himself away from his eternal pursuit of the noble *Pseudobranchius*. The writing of this essay was partially supported by a faculty research grant from Wofford College. And, finally, I need publicly to thank the Spartanburg, South Carolina, K-Mart for selling a word processor that even I could afford.

DEFINING RANGES OF DEMOGRAPHIC PARAMETERS

The traditional first cut at alligator population dynamics has been to establish a population size structure and to interpret that structure by way of growth rates into a life table (Nichols et al. 1976b). In Florida we have been deterred from that approach by two basic difficulties. It is, to begin with, exceedingly hard to determine a population's size structure. The general problems in night-light counts are well known (Woodward 1978, Magnusson 1983, Wood et al. 1983), and even if those problems were entirely solved, the counts could provide no information on the demographically crucial sex ratios. Understandably leary of night counts, alligator managers have focused instead on harvest structures. Unfortunately, however, harvests are generally biased against some size classes (Hines 1979, Taylor and Neal 1984). Furthermore, Florida observations suggest that harvest is also seriously biased by sex, a point amplified by Ferguson and Joanen (1983).

The saddest note it, of course, that determining a size structure is the easier half of the life-table battle. Within the next few years histological techniques for alligator age determine will probably be developed, but presently it is no fun at all to figure growth rates. In Florida, for example, we have learned that growth rates vary from area to area. Within a given area, they vary from year to year. Within a single area-year, they vary from microhabitat to microhabitat. And when all obvious space, time, and habitat variables are controlled, growth rates appear to vary stochastically from gator to gator!

All of this reinforces my reluctance to inflict an empirical growth curve upon an observed population structure (though you really should take a look at Taylor and Neal [1984]). Nevertheless, there is a very real sense in which limited, certain knowledge about growth tells us a great deal concerning the demographic nature of alligators. A newly-hatched alligator is approximately 25 cm in length and weighs about 50 g. If it is a male, a hatchling can eventually grow to be over 4 m long and may increase its weight by 7,000%. Females are significantly smaller; nevertheless, they seldom attain reproductive maturity at much less than 2 m (about 35 kg). This extraordinary increase from hatchling to adult size, a well-known fact, provides a reasonably firm jumping-off point for an analysis of alligator demography.

Let us consider a hypothetical alligator from north-central Florida, where climate dictates a 6.5-month (about 200 day) growing season. Investigations in Florida indicate that age at maturity is not necessarily constant across a given population, and it certainly is not the same throughout the alligators entire range. McIlhenny (1935) speculated that females might mature in 6-7 years. Although a specially fed captive gator was observed to lay eggs at under 5 years of age (Whitworth 1971), I am reluctant to believe that wild animals successfully nest at ages less than the 9-10 years suggested by Chabreck and Joanen (1979). At the other extreme is the 18-plus years given by Fuller (1981) for North Carolina animals, a figure echoed by Jacobsen (pers. comm.) for alligators

in nutritionally impoverished portions of the Florida Everglades. I shall eventually return to this age-at-maturity question, but for now let us simply assume that a hypothetical female alligator in north-central Florida has, at around age 12 (length about 1.9 m), just reached reproductive adulthood. If we grant her membership in a numerically stationary population, then she can do her part in maintaining the population's stationary size if she produces in her lifetime exactly one daughter that lives long enough to begin her own reproductive career. To see how she might do this, let us consider a simple model of our newly matured female's lifetime production. If D is the expected number of daughters that will survive to begin their own reproductive careers, then

$$(1) \quad D = (Y) (N) (P),$$

where Y is the expected number of years before our newly-matured female dies or becomes reproductively senile; N is the expected number of hatchling daughters our female will produce annually across all Y year; and P is the probability that a given hatchling daughter will survive to begin her own reproductive career. (Demographers will note that what I call D would in conventional notation be $R[0]$, the net reproductive rate, calculated in terms of new reproductive-age females rather than hatchling females. Furthermore, I have chosen the nonstandard approach of analyzing the net reproductive rate rather than the finite rate of increase, because the former is calculable in a more easily explained manner from the alligator data we possess).

Each factor in this simplistic equation is actually a combination of many demographic parameters. Let us therefore dissect Equation (1) and indicate apparently reasonable ranges for parameters values.

Y : Expected Years between Maturity and Senescence or Death

Let L represent the probability that a reproductively mature female lives from one year to the next. (Technically the demographer would prefer to talk about $L[t]$, which would represent age-specific survivorship between age t and age $t+1$. Fortunately, such precision is probably not practically important. Gibbons and Semlitsch (1982) have demonstrated that mortality in large emydid turtles remains approximately constant over time, and examination of Florida harvest size-class ratios suggests that the same may be true female alligators, at least over the first 10-15 years of maturity. In any case, the current alligator literature does not suggest important deviations from constant adult survivorship, so I shall simplify the demographic equations and replace $L[t]$ with the single parameter L). Convincing estimates for L do not abound. Nichols et al. (1976a, b) suggest an approximate value of 0.89. Taylor and Neal (1984) believe that survivorship among adult male gators is about 0.775; these authors recognize that female mortality would be lower. Informal observations on radio-telemetered animals suggest to Wilkinson (pers. comm.) that adult female survivorship may be in the neighborhood of 0.95. Given this admittedly sketchy information, it may not be unreasonable to assume initially that adult survivorship is in the 0.85- 0.95 range among female alligators.

To calculate an alligator's potential reproductive years, one must consider not only mortality but also senescence. The time of onset doubtless varies across individuals, and in any case senescent effects are not necessarily sudden (Ferguson and Joanen 1983). Webb et al. (1983b) suggest that female alligator senescence occurs between 40 and 50 years of age. Table 1 gives expected reproductive lifetimes (Y in the equation above) for newly matured female alligators with various fixed survivorship, ages to maturity, and ages at senescence. From this table it is clear that unless annual survivorship is very high, the number of years between expected maturity and expected senescence is relatively much less important than mortality in determining Y . Furthermore, it also appears that Y is likely to lie between about 6 and 18 years.

Table 1. Expected Reproductive Lifetimes

Annual survivorship	Age at maturity	Age at senescence	Expected years as adult (Y)
0.85	16	40	6.03
0.85	12	45	6.12
0.85	9	50	6.15
0.85	--	infinity	6.15
0.90	16	40	8.73
0.90	12	45	9.20
0.90	9	50	9.36
0.90	--	infinity	9.49
0.95	16	40	13.80
0.95	12	45	15.91
0.95	9	50	17.21
0.95	--	infinity	19.50

N: Expected Annual Production of Hatchling Daughters per Mature Female

To avoid getting fancy, I shall express the complex parameter N as

$$(2) \quad N = (R) (E) (H) (F),$$

where the various equation components are as defined below.

R: Annual Nesting Probability. R expresses the probability that a reproductive-aged female nests in any given year. Field research in Louisiana suggests values ranging between 0.48 and 0.68 (Chabreck 1966, Joanen and McNease 1971, 1973, 1975, 1976). Working with animals in a thermally altered reservoir (Par Pond, South Carolina), Murphy (1981) believed the proportion of females nesting was less than 34%. Wilkinson (1983) reports about 27.5% for the South Carolina coastal plain. All these values are considerably lower than estimates reported for *Crocodylus niloticus* (87.6%; Graham 1968) and *C. johnstoni* (90%; Webb et al. 1983a). Perhaps this interspecific variation is a function of differing energy budgets and of more rigorous metabolic requirements in the alligator's temperate range. In that connection it would be particularly interesting to ascertain the percent of adult female gators that nest in certain subtropical Florida habitats. But for the present let us simply agree that, for alligators in general, the proportion of adult females nesting is probably between 0.2 and 0.7.

E: Probability of Nest Success. E is the probability that any given nest escapes predation, flooding, etc. and hatches. Again, field research presents a bewildering array of values. Metzen (1977) reports nest success of 10%. This occurred, however, in area of heavy black bear infestation and is probably about as unusual as the 90% success which can be observed some places, some

years, in Florida. Presumably more typical are the 48.3% and 74.2% success rates reported by Ruckel and Steele (1984) for two Georgia locations. Dietz and Hines (1980) give 67.9% for Orange Lake, Florida. The rate at Rockefeller Refuge, Louisiana, is about 68.3% (Joanen 1969), in South Carolina it is approximately 70% (Wilkinson 1983; this source reports the proportion of nests from which at least one egg hatched). Discounting the somewhat aberrant findings of Metzner (1977), one might conclude that values for E typically lie between 0.3 and 0.7.

H: Hatchlings per Nest. H is the expected number of living young that a nest will produce, given that the nest is not destroyed. Over the years, a great deal of information has been collected on alligator clutch size and fertility. Representative data on these factors are reported in Table 2 below. Where possible, information from geographically proximate areas was combined; I had to calculate some of the figures below from other types of statistics presented in the cited works.

Even in "successful" nests, there are various reasons that not all fertile eggs hatch, and therefore calculations based on percent fertility overestimate the number of actual hatchlings. On the other hand, difficulties in field observation usually mean that reports of hatchlings actually seen tend to underestimate production. I shall largely neglect these factors and assume that H, production per successful nest, is somewhere between 20 and 40.

F: Proportion of Hatch Female. F is the proportion of living hatchlings that are female. Most information on alligator sex ratios seems to focus on animals beyond the hatchling stage (Forbes 1940, Chabreck 1966, Nichols and Chabreck 1980, Murphy 1981, Murphy and Wilkinson 1982, Wilkinson 1983). Earlier, Ferguson and Joanen (1983) reported a reasonable sample of Louisiana marsh hatchling production as 80% female. On the other hand, Taylor (pers. comm.) believed the sex ratio in a north Louisiana system was close to 50-50. In Florida we have observed individual pods with nearly all imaginable sex ratios. My subjective evaluation is that our population-wide hatchling cohorts are no more than 60% female--and may be significantly less. Since alligator gender is determined by early incubation temperatures, it is entirely possible that hatchling sex ratios may differ substantially by geographical area. Nevertheless, by microhabitat nest-site selection, laying females can exercise some "choice" over the gender of their offspring, and arguments have been presented (Ferguson and Joanen 1983) for the likelihood of female-skewed hatchling production in numerous habitats. Therefore, despite field suggestions that gender ratios may not be so definitely skewed, I shall bow to Ferguson's greater expertise and state that F probably lies between 0.6 and 0.8.

P: Probability that a hatchling Daughter Survives to Reproductive Age.

Even in simplest form, this parameter must involve the growth and survival rates of immature animals. We shall model it as

$$(3) \quad P = S^{**}M$$

where the equation components are as defined below.

M: Time of Maturity. M is the expected number of years between hatchling and attainment of reproductive maturity by female alligators. This parameter has already been briefly discussed above; indications are that in most alligators it lies between 8 and 16 years.

S: Average Immature Survival. S is the "average" (geometric mean) annual survival probability for immature female alligators between ages 0 and M years. (Recall that the geometric mean is necessarily equal to or less than the arithmetic mean.) Our field work in central Florida suggests that appropriate values probably lie between 0.55 and 0.70. This very rough range

Table 2. Nest Production.

Location	Number of nests	Average clutch size	Percent fertile	Percent Reported hatched per successful nest	Estimated Production (clutch size times % fertile, or % hatch)	Source
North Carolina	--	35.3 (minimum)				Fuller, 1981
South Carolina	--	40.6				Bara, 1972
South Carolina	203	44.2	93.85%		41.5	Wilkinson, 1983
Georgia (2 areas)	60	39.4	84.6%		33.3	Rockland Steele, 1984
Okefenokee Georgia	55	30		70%	21.0	Metzen, 1977
N. Central Florida (2 areas)	67	37.5		67.9%	25.5	Deitz and Hines, 1980
N. Central Florida (2 areas)	21	34.6	87.6%		30.3	Woodward, pers. comm.
Central Florida (2 areas)	78	45.7	89.5%		40.9	pers. obs.
Lk. Apopka, FL	20	44.8	45.8%		20.5	pers. obs.
Okeechobee Florida	63	43.6	77.9%		34.0	Woodward pers. comm.
Rockefeller Ref., LA	--	39.5		58.2%	23.0	Joanen, 1969

matches reasonably well with the S-value of 0.61-0.62 derivable from the alligator population model of Nichols et al. (1976b). One should note that S incorporates hatchling-year survival, which under some circumstances may be extremely low.

Summary of Suggested Parameter Values.

At this point we can express D, the expected lifetime production of daughters that reach reproductive age, as a function of the 7 parameters defined above:

$$(4) \quad D = (Y) (R) (E) (H) (F) (S^{**}M).$$

If we restrict our analysis to a stationary population (in which D is 1.0 by definition), then we can fix any 6 parameters and observe what value the seventh, "free" parameter, must take. In Table 3 I list previously suggested ranges and range midpoints for all parameters. I also indicate the value each parameter would take if it were left free and all other parameters were fixed at their mid-range values.

GROWTH AND SURVIVAL: THE DEMOGRAPHIC POWER OF PARTICULAR PARAMETERS

We should note that when "freed", all parameter values fall outside suggested ranges. Some (e.g., Y and H) seem biologically unrealistic, and others (R, E, F) are logically impossible. This indicates that we have in a sense "underestimated" the dynamics of a stable alligator population: the varminths survive better, mature faster, lay more eggs, or produce more females than we had thought. But our simple model tells us more than this: it can also point out which parameters are demographically most important. To address this matter of importance, we should inquire how each parameter affects the value of D when all other parameters are held constant. We can see from Equation (4) that the effects of Y, R, E, H, and F are linear: changes in the values of these parameters will produce only proportional changes in D. Table 3 (above) clearly shows that none of these parameters, considered alone, can be realistically expected to have a value high enough to offset the values estimated for other parameters--and thereby maintain a viable alligator population. Furthermore, even when all these parameters are taken together, the situation is not greatly improved. For example, hold S and M at their suggested mid-range values, but allow Y, R, E, H, and F simultaneously to assume their maximum values suggested as plausible by Table 3. D is then calculated to be 1.00. This means, of course, that the expected lifetime production of maturing daughters has just reached the bare maintenance level. Furthermore, in real gator populations, it is certainly not sufficient to run during normal years at mere maintenance! As we shall eventually discover, demographic catastrophes (such as complete one-year nesting wipeouts) are not uncommon. Therefore (since years with surplus production high enough to balance such catastrophes appear to be very rare and perhaps physiologically impossible), long-term demographic success would require D to stand at a cushioned level substantially above 1.0 during typical years.

Now, for contrast, set all the linear parameters (Y, R, E, H, and F) at midrange and alter only S and M, the nonlinear parameters, to their most favorable suggested values. D is then calculated to be 3.27, a figure greatly exceeding the production required for population maintenance.

The major demographic point of this tedious exercise concerns growth and survival. If female alligators indeed require a substantial number of years of mature (evidence is strong that they do), then in a stable or increasing population, the average survival of even the immature age classes

Table 3. Parameter Ranges.

Parameter and Abbreviated definition	Suggested range	Mid-range value	Value if left free
Y, expected repro. lifetime	6-18	12	60
R, probability of nesting	0.2-0.7	0.45	2.23
E, probability nest hatches	0.3-0.7	0.50	2.48
H, number of hatchlings	20-40	30	124
F, proportion of hatch female	0.6-0.8	0.7	2.61
S, average immature survival	0.55-0.70	0.625	0.723
M, years to reach maturity	8-16	12	7.6

must be quite high (Woodward et al. 1987). Furthermore, this requirement for high survival cannot be obviated by increases in clutch size, nest survival, or percent female: these parameters simply do not have the "punch" to make up the alligator demographic deficit.

ALLIGATOR INSTARS: FURTHER RAMIFICATIONS OF GROWTH AND SIZE

Knowledge about alligator size and growth rates has thus led us indirectly to the conclusion that survival, even among juveniles, must be rather high. Furthermore, there is another demographic lesson to be learned from this matter of size. A newly hatched alligator is one of the smaller vertebrate predators in a Florida wetlands system; after it matures, it will be the largest. Thus it may be unreasonable to represent alligators of all sizes by one simplistic demographic model. Consider, for example, the question of population response to changes in density. Simple patterns of density-dependent population growth have often been modeled by the familiar Verhulst-Pearl logistic curve:

$$(5) \quad dN/dt = N(1 - N/K)$$

According to this equation, the rate of per capita population increase decreases linearly as density approaches a "carrying capacity"; the operative mechanism is usually assumed to be some form of intraspecific competition. Even the intro wildlife textbooks admit that the model will require a few minor patches before it can be applied to any actual population. But with gators the problems are more than cosmetic: one might in fact ask whether it makes sense to use this model at all when talking about alligators. How, for example, should one express the density of a natural alligator population? Number of animals per hectare? Meters of animals per hectare? Kilograms of animals per hectare? All of these suggestions sound rather foolish, since it is not realistic to think that hatchlings and adults compete directly for any important, limiting resource.

Of course it is possible to rework Equation (5) for alligators. One would begin by redefining density (and thereby the units of K) as some sort of effective size-structured competition density (call it ED):

$$(6) \text{ ED} = \frac{\text{BIG old gator size}}{\text{hatchling size}} \int a(x,y) f(x) dx dy,$$

where ED is that weird effective density, $a(x,y)$ is the effect of an animal of size x on an animal of size y , and $f(x)$ is the density of animals of size x . Unfortunately, Equation (6) is mostly a play-like-you-know-calculus expression, largely useless for at least two reasons. First, the purist gator biologists will demand integration over at least one more variable since effects doubtless differ by sex. And second, realists will point out that we do not have any idea about what numbers to plug into the relatively simple equation already offered.

Nevertheless, practical problems and pseudo-mathematics aside, there is a point, of sorts, to Equation (6). It reminds us that alligators of different sizes have different eco-demographic effects upon--and are differently affected by--other alligators of various different sizes: as alligators grow, they change their ecological status. Fortunately, there is a stylistically elegant (and calculus-free) way to state all this. As some of the old-time Florida crackers say, "At some point they got to stop being big lizards and start being little gators." The simplicity of this expression is appealing, and I believe the basic idea is not inaccurate. Growth rates of young Orange Lake alligators decline until the animals are about 3.5 year old and 85 cm long. Then there occurs a noticeable, statistically significant upturn in growth once more. Webb et al. (1978) discovered a similar situation in young estuarine crocodiles (*Crocodylus porosus*), and it is tempting to speculate on the life-history significance of these upturns. Many predators exploit prey of basically constant size throughout their lives. On the other hand, general isometry of head-to-body length ratios in crocodylians suggests that they are adapted to take increasingly large prey as they themselves grow longer (Dodson 1975). Such adaptations could have at least two consequences. First, as an alligator matures, it becomes able to exploit new food resources unavailable to one-time competitors. Perhaps this is the case with our Orange Lake gators. As youngsters they may compete to some degree with fish, otters, herons, watersnakes, etc. But when the gators get big enough (perhaps this begins around the growth flex point of 85 cm), the former competitors are no longer so important--except perhaps as occasional sources of food!

Second, the exploitation of different sized prey by different sized alligators presumably serves to partition food resources. While we need not agree with Murphy (1981) that such partitioning is the factor which directly permits high alligator densities, we should at least recognize that intraspecific gator competition is structured to a degree by size. Consequently, the next section of this essay will consider the relationship between structured competition and demographic events such as the more or less complete loss of a year's hatchling production.

ONE-YEAR NESTING WIPEOUTS

My discussion of alligator density dependence will necessarily begin by considering what (if anything) happens when the density of young animals is altered. I talk about juvenile gators because in some Florida systems we have been able to count accurately the number of nests constructed; thus we have a decent idea about the size of a hatchling cohort. I do not think we can

do as well with adult animals; rather, I believe that study populations are likely to contain far more alligators than conventional night-count investigations may indicate. For example, experimental harvest on Orange Lake, Florida, has removed substantially more 3-m plus animals than we believed were present--and has not appreciably altered the night-count structure. Therefore, let us descend ever so briefly from the rarefied heights of speculation and consider nests and hatchlings, subjects we actually know something about. Authorities agree, for example, that flooding can be a very real problem (Hines et al. 1968, Joanen 1969, Joanen et al. 1977). At construction time, the center of the egg chamber in Florida gator nests is characteristically less than 70 cm above the water level. The incubation period (about 65 days) runs very approximately from 1 July through 31 August. Thus a 1-m rise in water levels during these months (some of Florida's rainiest) can drown most of the year's egg production in a given wetlands system. Nesting effort has been carefully monitored on lakes Jessup (central Florida; a comparatively unmanaged water system) and Okeechobee, a few floating nests and levee nests hatched, but most of the year's production was destroyed. On Lake Jessup (where 50-150 nests are usually constructed) absolutely no hatchlings were produced. Furthermore, high water is not the gator's only potential weather problem, for in some years, in certain habitats, extremely dry conditions may also cause the near-entire loss of a hatchling cohort (Hines et al. 1968, Hines pers. comm.). Like floods, droughts appear particularly to affect the younger age classes.

We do not know how often flood, drought, or other population-extrinsic factors induce such catastrophic mortality, but examination of Florida weather data suggests that one-year wipeouts are not extremely uncommon. Thus we may wonder how an alligator population might respond to such events. To begin with, we must admit that it is largely metaphorical to talk about "population response"--as if the population per se possessed a homeostatic adjustment mechanism independent of the biology of its individual members. Rather, we should inquire how a particular hypothetical alligator might be affected by the absence of, say, a year's hatchling cohort. Recall my statement above that some resources are partitioned by alligator size. To the degree that this position is strictly valid, the absence of one cohort size class should exert relatively little effect upon animals of other sizes--and the population would not respond in any dramatic way to a one-year wipeout.

Of course any statement of absolute size-class independence would be simplistic, and I can imagine two (by no means mutually exclusive) ways in which alligators might respond to a one-year wipeout. First, it is possible that nest failure in year t leaves mature females more capable of reproduction in year $t+1$. This could occur for many reasons. If, for example, all nesting sites are flooded before laying begins, it is possible that a female might resorb her eggs. Furthermore, even if completed nests were destroyed, females would expend less energy in nest attendance and hatchling protection. Presently I have no evidence that these phenomena actually occur; it is uncertain that energy savings would be very significant, and in any case it is reasonably clear that clutch size (at least) does not increase in Florida wetland systems in the year following a wipeout. But there is also another possibility. A given female might be on a "physiological schedule" to nest in year t and to be quiescent the next year. In that case, energy recouped--because of nest failure in year t might increase the probability that the female would reproduce in year $t+1$. Indeed it does appear that the percentage of females nesting increases somewhat after a year of catastrophic nest mortality. But I do not have the data to test this possibility statistically.

A second possible response to catastrophic mortality would be increased growth rates among animals in age classes adjacent to the one that was destroyed. Let me simplify just a little. Suppose that no alligators were hatched in year t . Then hatchlings produced in year $t+1$ would enter a system vacant of yearlings that might have competed with them for scarce resources. Thus they might grow faster, and some could attain reproductive size ahead of "schedule".

Five rather sticky comments should be offered about this second proposed scenario. First, if compensatory growth actually occurs, it would probably affect most directly those animals hatched the year after the wipeout. However, one would expect the "benefits" to be passed in diluted quantity on down (and possibly up) the age pyramid.

Second, if he/she were not careful, a systems theorist might look at our compensatory scenario and say, "The number of animals was reduced at year t . Even if you mature the $t+1$ hatchlings a whole year faster than normal, you still won't get any compensatory reproduction for at least 10 to 12 years. For technical reasons, feedback delayed that long (proportional to generation time) doesn't do you much good; it is highly likely to destabilize the system". This catchy little objection is defeated by the simple fact that feedback is not delayed very much at all. Consider the population's reproductive capacity. The first impact (on the total number of breeding-size females) of a year- t wipeout might be expected at, say, year $t+12$. However, that is just about the same time that one might expect fast-growing $t+1$ animals to begin their accelerated reproductive years.

Third, although considerable time and money have been expended in Florida to test experimentally the possibility of compensatory growth among wild hatchlings, the results have been inconclusive (Hines and Abercrombie 1987). This is not surprising. For one thing, it is extremely difficult in Florida wetlands systems to achieve reasonable control over environmental variation: extraneous variables eat up one's degrees of freedom! More important, the growth experiment may not have run long enough yet. Most of the Florida gator folks believe that compensatory growth (if it occurs) would be least important in the first years after hatchling. Animals hatched in year "wipeout + 1" would always have a "vacant" size class just above them--unless they grew into it! (Here for sake of argument we neglect intra-cohort growth-rate variability, which renders the idea of precisely separate size classes something of an abstraction.) That asset would not be particularly valuable to small alligators, which compete for food with fish, watersnakes, and what have you. Rather it would become significant after the young alligators had grown to the size at which their only important competitors would be other gators. In other words, there are sound ecological reasons to suspect that most compensatory growth would be delayed beyond the first year or two of an alligator's life.

Fourth, you will note that I have dealt exclusively with compensatory growth and have not mentioned compensatory survival. That is because I believe that direct compensatory survival is unlikely to occur in any important degree (and see Webb et al. 1983b). This is not because field research has failed to demonstrate compensatory survival (of course it has failed, but given the difficulties in estimating wild crocodilian survival rates, who would have expected otherwise?). Instead, it is because at this point I cannot even guess how the presence or absence of year- t hatchlings would directly affect the survival probability of other alligators. For young alligators in typical Florida habitats, food is the only demonstrably important resource that is mediated by density (note that some authorities-- Thorbjarnarson, pers. comm.--would deny that even food resources are meaningfully related to wild alligator densities). The absence of an otherwise adjacent year-class might allow more food--but how many young alligators would die of causes related to lack of food in any case? It is my opinion (admittedly subjective, but based on some experience with wild and captive animals) that the response of young crocodilians to moderate food deprivation is stunting, not starvation or even ill health. Furthermore, it seems to me that the chief response to more severe food deprivation is-- more stunting. Of course it is important to note that compensatory growth has demographic effects on reproduction somewhat similar to those caused by compensatory survival. Suppose a set of animals grows rapidly and attains reproductive maturity in $M - 1$ years instead of the usual M years. Then the population receives reproductive benefit from those animals expected to die between $M - 1$ and M years. Considering the problem a bit more expansively, we might say that the effective reproductive lifetime is

extended by one year. (At this particular point, demographers might question my easy decision to examine "D" rather than If the above speculations are correct, then one effect of a nesting wipe-out might be the temporary reduction of generation-time. The population-wide consequences of this would extend somewhat beyond the addition of one reproductive year to a cohort of females.)

Fifth, I would like to point out that all my speculation on compensatory growth is basically unencumbered by statistically valid data (Hines and Abercrombie 1987). And I could also be bad wrong about the survival business.

CONTINUING, MORE BLATANT, SPECULATIONS ON DENSITY DEPENDENCE

Since I have already stretched the available gator data painfully thin, there seems little reason why at this point I should not openly break entirely the fetters of real information and just plain guess about alligators. First, I do not believe that growth or survival is significantly dependent on density for animals much under 1 meter (Webb et al. 1983b; however, density alterations that concentrate mixed size classes into close proximity may result in cannibalism [Delaney and Abercrombie 1986]). Nor am I convinced that density alterations (at levels induced by moderate harvest or routinely observed under natural conditions in the field) affect large adult alligators in any important way (Hines and Abercrombie 1987). For animals of intermediate size, however, the situation may be very different: in a long-term stable population, there may be a survival and/or growth bottleneck for older juveniles and subadults. I have reported the growth slowdown above. And, furthermore, preliminary Florida studies (Delaney and Abercrombie 1986) indicate that (Nichols et al. 1976b notwithstanding) this may be the size class most severely affected by cannibalism.

I do not know how such a subadult bottleneck might impact male alligators. On the one hand, it is possible to argue that any effects would be demographically irrelevant. Research has indicated that some individual males may have very long reproductive lifespans (Ferguson and Joanen 1983). If, year after year, one or two of these long-lived males can breed a large number of females, then the presence of many males will not be critical to population maintenance. Thus, if even a few subadult males occasionally make the transition to maturity, that could be sufficient; or at least such is the assumption of male reproductive value under which we in Florida have generally operated. On the other hand, the proportion of successfully maturing males could be more important than our Florida research has usually assumed. Alligator precopulatory pairing behavior is often quite protracted. Since in certain climates there is only a restricted time period during which ovulation and spermatogenesis coincide, a single male may be able to breed only a very limited number of females: thus a shortage of adult males could result in reduced reproduction (Wilkinson, pers. comm.).

Whatever the reproductive importance of males, the fate of maturing females is certainly a significant demographic question. I believe that near-adult females may be limited from breeding by the presence of dense age/size cohorts above them--and that the removal of older females may increase the percentage of the younger animals that nest. For example, over four years, 122 female alligators larger than 1.8 m were removed from Orange Lake (about 5000 ha; north-central Florida). Although this number exceeds by about 25% the maximum number of nests observed in any pre-test year (and nest observation is known to approach 100%), to date absolutely no decrease in number of nests has occurred (Hines and Abercrombie 1987, Woodward, pers. comm.). Florida researchers are uncertain at this point how density alterations may have affected nesting, though we are reasonably sure that the limiting factor is not physical nesting sites

(Woodward et al. 1984). Perhaps density reduction breaks the growth bottleneck and allows pre-adult females to reach mature size more rapidly. Could such a mechanism operate fast enough to explain the maintenance of nesting effort throughout the Orange Lake experimental harvest? Intuitively, at least, this seems unlikely. Perhaps, then it is possible that removal of large females frees up some sort of "social space", thereby allowing smaller animals to breed and nest (see Ferguson and Joanen 1983). If this latter scenario were correct, then while nesting per se might be maintained, actual hatchling production would be expected to decrease. After all, Ferguson and Joanen (1983) show that younger alligators often produce only small numbers of eggs; these authors also state that smaller females may not even be reproductively synchronized with the males' sperm production. On Orange Lake case neither mean clutch size nor fertility showed any decline following 1981, 1982, or 1983 harvests (over which a total of 93 adult females were taken). However, in the summer of 1985 (after the 1984 harvest), very modest reductions in clutch size and percent fertility were noted.

All these observations tempt one to believe that the initial response to reduced female density is an increase in the breeding percentage of large adults. Continued removal of fully mature females may eventually result in early recruitment of smaller animals to the reproductive ranks. At the present time, however, I would counsel against uncritical acceptance of such assumptions since the Orange Lake experiment is far from complete. Furthermore, the 1985 data should be received with particular caution since they were gathered after a siege of very dry spring weather--which may have affected clutch size and fertility quite independently of density or harvest. In other words, it's all hard to figure. And like other bits of information on alligator density dependence, the Orange Lake insight must remain for now just one more tantalizing clue that something must be going on.

CONCLUSION

From McIlhenny (1935) into the sixties, zoologists seemed confident that they knew about the biology of the alligator. But, as additional hard data were collected, the realization of ignorance grew. Despite much valuable research (particularly the field observations of Joanen and the laboratory studies of Ferguson), alligator population dynamics remains a mystery, very partially unraveled. Furthermore, it is highly probable that over the coming decades, alligators (like other crocodylians) will be subjected to increasing commercial exploitation. This will present both problems and opportunities. Even in our ignorance we know that alligators are slow-maturing, long-lived animals. As such, they cannot be expected to recover rapidly from serious overharvest like white-tail deer (or possibly fast-maturing spectacled caiman [Staton and Dixon 1977, Rebelo and Magnusson 1983]), and gator exploitation should therefore be conducted with considerable caution. On the other hand, some relatively safe harvest strategies have been suggested, and revenues generated by these harvests can help finance long-term, if modest, research (Hines and Abercrombie 1987). In the present essay I have tried to indicate areas in which investigation would be especially important. Particularly, I believe we need to know more about the growth and survival of female alligators between 1 and 2 meters. We should also determine more about the percentages of various sized females that successfully nest, and we need to discover how all these factors vary with density. Except for one or two potential technological breakthroughs (such as a precise histological technique for age determination), these next steps will be slow and expensive. Fortunately--and on this, I believe virtually all alligator researchers will agree--the work will also be fun.

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