Journal of Herpetology, Vol. 24, No. 2, pp. 176–184, 1990

Environmental Variability and the Reproductive Success of Everglades Alligators

JAMES A. KUSHLAN[1] AND TERRI JACOBSEN[2]

[1]*Department of Biology, University of Mississippi, University, Mississippi 38677, USA*
[2]*Institute of Ecology, University of Georgia, Athens, Georgia 30602, USA*

ABSTRACT.—**The reproductive success of the American alligator in the Everglades is constrained primarily by egg mortality, due to flooding by seasonally fluctuating water levels. The timing of nesting is positively correlated with spring air temperatures, and nesting during the summer rainy season places eggs at risk to flooding. Water level at the time of nesting is positively correlated with the elevation at which eggs are deposited above the marsh bottom, which involves nest size, egg placement, and site elevation. Alligators respond and to some extent accommodate to higher water levels at the time of nesting. The percent of nests lost to flooding depended on clutch elevation and on the maximum water depth during the incubation period. Clutch elevation frequencies were normally distributed. Regression models permit estimation of the extent of nest flooding over a 30-yr period. Flooding has increased in recent years, coincident with the institution of water management in the southern Everglades. Prior to water management, the increment of water level rise during the incubation period was predictably correlated with water level at the time of nest construction. This predictability disappeared during the current period of water management, thereby altering the pattern of environmental variation. These results suggest that conservation of alligators in the Everglades, and by extension of the Everglades wetland ecosystem, depends on restoration of more predictable hydrological fluctuations.**

A primary factor regulating tropical and subtropical wetlands is the seasonal fluctuation of water depth caused by variation in rainfall and upland runoff (Lowe-McConnell, 1975; Sarmiento, 1983; Kushlan et al., 1985; Kushlan, in press *a*, *b*). We have studied the responses of animals to fluctuating hydrological conditions in the Florida Everglades (Kushlan, 1976*a*, 1986, and in press *b*), to determine the adaptations and the extent of the ability of aquatic organisms to accommodate, or adjust, to fluctuating hydrological conditions. The American alligator (*Alligator mississippiensis*) was chosen as a study animal because its reproductive success depends on the survival of eggs during a prolonged incubation period, during which rising water levels may flood the nest and asphyxiate the embryos (Joanen, 1969; Joanen et al., 1977; Joanen and McNease, 1979). We specifically address: (1) whether alligators can accommodate to fluctuating water levels during their nesting season; (2) whether hydrological predictability exists in a fluctuating water marshland; and (3) whether man-caused changes in hydrological predictability can affect alligator nesting success.

METHODS

Nesting success was studied in a 10 km² study site in the southern Everglades, located in Everglades National Park, Florida. Some additional data were gathered in four similar areas. Water levels were recorded weekly at 37 stations and continuously at one station within the study area. The latter was used for analysis because water levels there were highly correlated with the other stations throughout the study site ($r > 0.997$, $P < 0.05$, for 37 stations). The continuous recording station also provided comparable information on water stage over a 30 yr period. Water level is recorded in m above mean sea level (MSL) and transformed to water depth (average elevation being 1.55 m MSL, $N = 840$ measuring sites in the study area). Air temperature and rainfall were recorded continuously at three sites in the study area and at a NOAA climatological station, 15 km NW of the study area. Daily air temperature (taken as the midpoint between high and low) at the NOAA station was highly correlated with the mean temperature in the study area ($r = 0.986$, $P < 0.001$, $N = 354$) and so was used in calculations.

Alligators deposit a clutch of eggs in a nest they construct of nearby vegetation. We determined the number of nests constructed in the study area each year through aerial and ground searches. We counted the eggs, determined their viability (Ferguson, 1982), and measured the heights of the clutch top and bottom (m MSL) in 71 nests. Other nest measurements and clutch counts were taken in other study areas and used for summary descriptive statistics. The age of the eggs was determined according to embryonic stages found (C. Grabowski, pers. comm.), and the laying date was estimated. The success of each nesting effort was determined by mon-

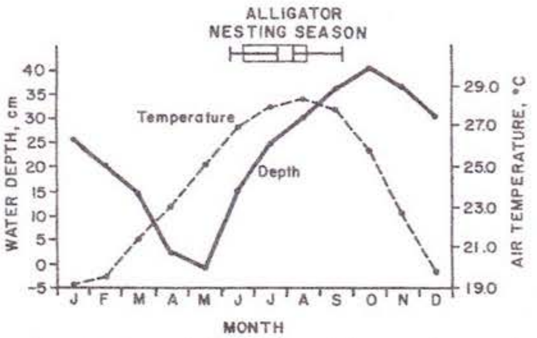

FIG. 1. Annual fluctuation of temperature and water depth in the Everglades in relation to the timing of alligator nesting. The box encompasses the average period of incubation with the ranges of nesting and hatching dates shown as bars. Water depths and air temperature are monthly means (1952–1982).

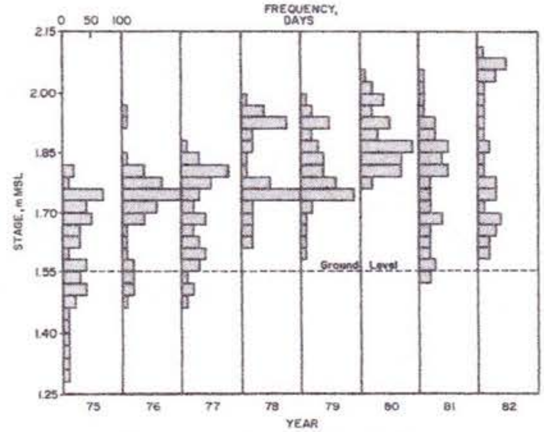

FIG. 2. Frequency distribution in days of daily water level for each year during the study period, 1975–1982.

itoring the nest throughout the incubation period.

Data are given as mean ± standard deviation; N = number of samples. Analyses were performed using SPSS version 9 (Hull and Nie, 1981) and BMDP (UCLA, 1981). In multivariate linear regressions we used 24 hydrological and temperature variables to derive the best sets of predictor variables using Mallow's C and tolerance criteria of 0.001 (UCLA, 1983). ANOVAs were followed by SNK (Student-Newman-Keuls) range tests (Hull and Nie, 1981). Range, median and quartiles of some data sets are displayed as described by Tukey (1977).

RESULTS

Hydrology.—Water levels and temperature fluctuate seasonally, and hydrological conditions vary annually (Figs. 1, 2). Figure 3 illustrates the pattern of water level fluctuation, rainfall, and discharge into Everglades National Park in three years showing extensive egg flooding. Water depth in the study area is determined by a combination of local rainfall and by the downstream flow of water from higher marshes to the north. This flow historically was the result of the timing and extent of upstream rainfall. Since the institution of flood control structures, especially after the construction of a cross-drainage levee in 1962, 14 km N of our study site (see Blake, 1980; and Leach et al., 1972, for details). The effect of water management on water depths in the study area can be observed in Fig. 3, by comparing the timing and extent of summer rainfall, discharge, and water depth during several high water years of the study.

In 1978, water levels rose slowly through the early summer. Although rainfall was heavy during this period, exceeding 5 cm on several days, discharge into the study area did not respond and remained low until mid July, when it increased dramatically in response to opening the water management gates. A second rapid increase followed a single 6 cm episode of rainfall. Since water depth rose 25 cm in response to the 6 cm rain, most of the rise was caused by an increase in discharge permitted by a further opening of the gates. The timing and extent of these discharge events were the proximal result of water management actions. Essentially, water from the heavy rainfall of June and July, which should have resulted in gradually increased discharge in June and early July, was withheld, forcing a larger release in late summer.

In 1981, following a wet season having relatively low discharge and water levels, an extraordinary rainfall event of 13 cm resulted in a rapid rise in water levels. Note, however, that even with this exceptional event, discharge into the study area was retarded by two weeks owing to delayed opening of the flood control gates.

In 1982, water levels rose rapidly due to rainfall from a tropical storm that occurred in June, prior to the alligator nesting season. As in 1981, a two-week retardation of increased discharge was caused by a delay in opening the flood control gates. A second, greater rise in water level in late June and early July was not accompanied by a concurrent series of high rainfall events, and can be attributed primarily to discharge that had been delayed upstream, now occurring during alligator nesting.

Thus in each year, rainwater was retained in reservoirs and when released caused a rapid increase in water levels in the study area. These increased water levels were delayed in timing from the rainfall events that ultimately caused them; we suggest that they may have been implicated to some degree in flooding of alligator nests in two of the three years of high mortality.

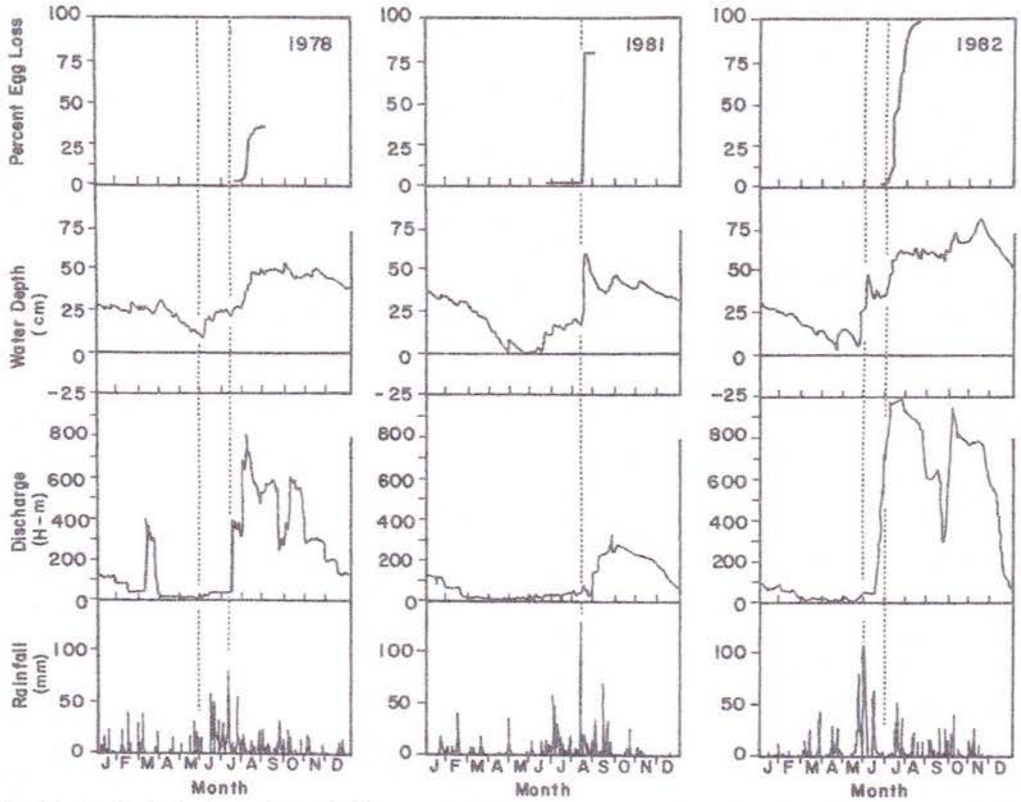

FIG. 3. Hydrological correlates of alligator nest flooding in 1978, 1981, and 1982. Shown are the cumulative percent egg loss, water depth in the study area (in cm depth), daily discharge across the northern boundary of Everglades National Park (in ha-m), and daily rainfall (in mm).

Nest Characteristics.—Alligators built nests in the Everglades less than one meter high (65.0 ± 13.1 cm; N = 213). The average clutch is located centrally within the nest mound, 19.3 ± 6.1 cm (N = 184) from the top of the nest. The eggs form layers, 16.9 ± 4.9 cm thick (N = 181).

Female alligators often remain in attendance at the nest (Kushlan and Kushlan, 1979). However, after egg deposition the female does not alter the elevation of the eggs relative to the ground, although additional nesting material is sometimes added on top. Compaction and dispersion of nest material occurred only in 1982 (average compaction = 17.8 ± 12.29 cm (N = 9), after embryo death had already occurred in those nests.

Time of Nesting.—Egg deposition occurred from late June to early July (Fig. 1). In 1975–1982, the average date of egg-laying was 26 June (±10.7 days, N = 71 nests; range, 9 June–27 July). The mean laying date differed significantly among years (F = 8.86, df = 8,175, $P < 0.05$). Nesting occurred later in 1976, 1977, 1979, and 1981 than in the other three years of the study (SNK, $P < 0.05$).

Alligators nested earlier following warmer springs and delayed nesting following colder springs. Based on evaluation of all combinations of monthly air temperature and stage level data from March through June using all nests, we found that two spring air temperature variables yielded the best correlation to nesting timing ($C_p = 0.03$, multiple $r = 0.479$, F = 8.80, df = 2,59, $P < 0.001$). Annual mean laying date (which weighs each year equally) was highly correlated with April through June air temperatures ($Y = 241.62 - 5.45 X_1 - 2.18 X_2$, multiple $r = 0.930$, $P < 0.001$, df = 7, where Y = mean laying date, X_1 = mean April air temperature (C), and X_2 = mean May-June air temperature). Thus, the nesting season occurred during the period of relatively warm temperatures (Fig. 1).

Nesting Success.—The average clutch size was 30 eggs ($\bar{x} = 29.7 \pm 7.54$, $N = 197$ nests). The numbers of nests constructed in the study area differed annually. Based upon our knowledge of the activities of individual females, we found that an average of 29% of mature females nested each year (range 16 to 58%).

Overall average loss of eggs was 40.5%; me-

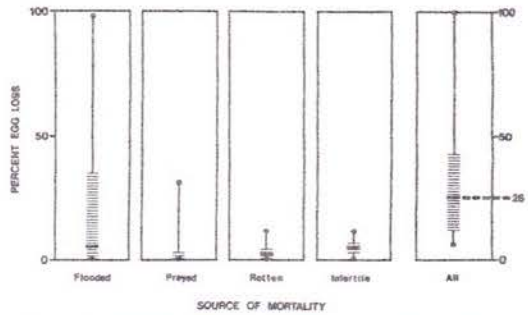

FIG. 4. Annual variation in alligator egg mortality. Shown are the range, quartile, and median of percent loss of eggs derived from observations of 71 alligator nests in 1975–1982. The overall median loss is noted.

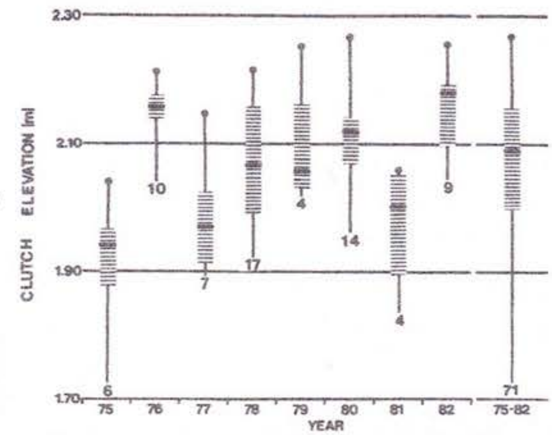

FIG. 5. Variation in clutch elevation in 71 alligator nests in 1975–1982. Shown are range, quartile, and median of measured clutch heights (m MSL). Numbers of nests measured each year are indicated.

dian loss was 26.2% (Fig. 4). Flooding was the single most important cause of nest failure. On average 27.9% of all eggs laid were killed by flooding annually. The mean and median infertility rate was only 4.7% of eggs laid. Predation was similarly low, averaging 6.6%.

Flooding losses are caused naturally by heavy rainfall and its concurrent increase in water flow, but can be exaggerated by management manipulations that result in higher flows and increased water levels, especially when these are postponed into the incubation period. In 1978, flooding resulted in a mortality of 35.2% of all eggs; in 1981, 75%; and in 1982, 97.9%. The 1981 flooding was caused primarily by heavy rainfall on site, upstream discharge being delayed by two weeks (Fig. 3). In 1978 and 1982, however, the flooding was caused not by the rainfall itself but primarily by increased discharge, the timing of which had been delayed from antecedent rainfall events (Fig. 3), by water management decisions upstream of the study area. Thus in two of three years of high nest flooding, delayed and therefore enhanced discharge events led to the elevated water levels. In the absence of such discharge retardation, water flows would have occurred as rainfall events took place, resulting in a more gradual rise and lower ultimate water level.

Clutch Elevation.—Clutch elevation above the ground varied significantly among years ($F = 7.11$, df = 6,63, $P < 0.05$; Fig. 5). The average deviation among years was 0.087 m. To evaluate this variation, a bivariate regression analysis of clutch elevation against temperature and hydrology variables was performed. The most significant relationship was between clutch elevation and average water level during the last two weeks of June, at the time of nest construction. Thus, the annual mean clutch elevation was correlated with average water levels for 15–30 June ($Y = 0.663X + 0.889$, $r = 0.951$, $P < 0.001$, $N = 8$ yr, where Y is the mean annual clutch elevation in m and X is the mean water level in m MSL). Using partial correlation, we also evaluated the response to water level of the several components of clutch elevation. Change of clutch elevation at the time of nesting primarily involved the height of the nest mound (partial $r^2 = 0.46$) and height of egg placement within the mound (partial $r^2 = 0.43$), and to a lesser extent the height of the nest site used (partial $r^2 = 0.02$).

The frequency distribution of standardized nest heights is normally distributed (Fig. 6). A normal probability plot of the standardized deviations of observed clutch heights against the standardized deviations expected from a normal curve for a sample of 71 was linear, indicating no significant deviation of the observed distribution from normality (Daniel and Wood, 1980).

Nest Flooding and Clutch Height.—We examined the relationship between clutch loss and the various environmental variables using multiple regression. The percent of nests that flooded was most strongly correlated with a single variable, the maximum height water levels reached during the incubation period ($Y = 216.5X - 302.6$, $r = 0.906$, $P < 0.05$, $N = 8$, where Y is the percent of nests flooding and X is the maximum water level [m MSL] in the 59 days following egg laying). Thus, the rise in water level during incubation is the cause of nest flooding.

Despite finding a significant linear relationship between water level and nest flooding, we can expect upper and lower limits of nest flooding. A natural lower limit is set by ground level. An upper limit might be set by the physical ability of alligators to build nest mounds, and

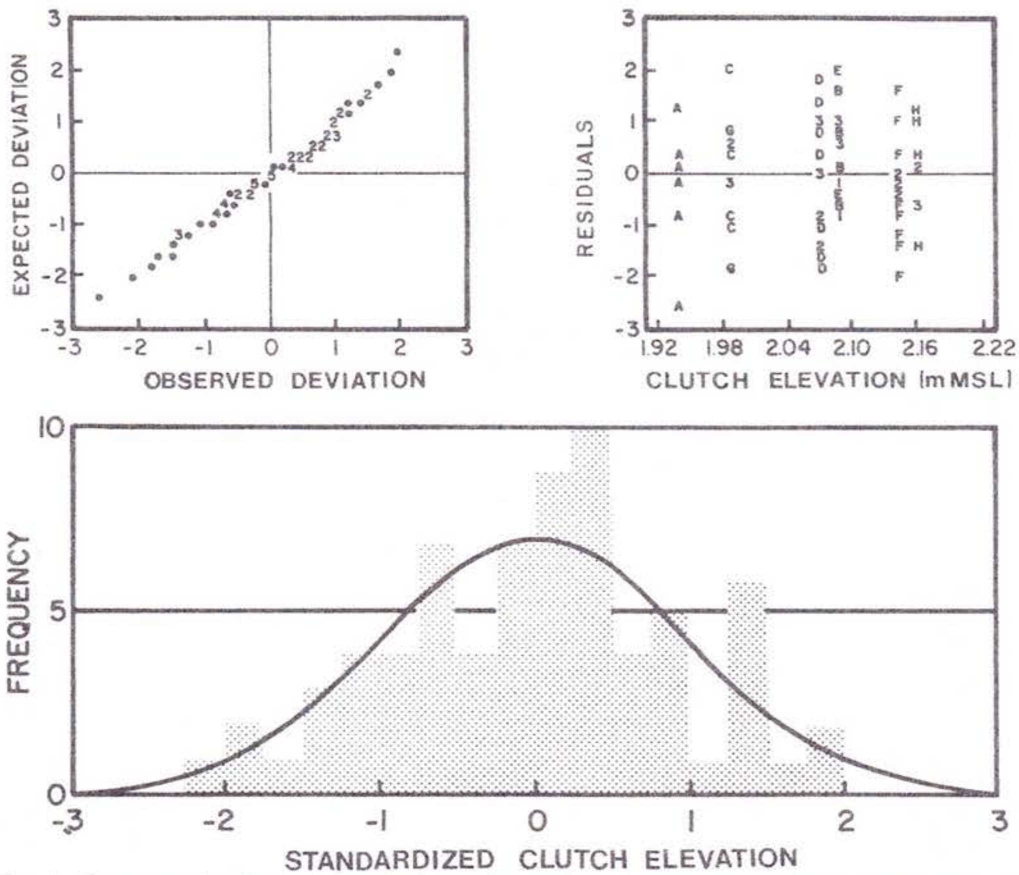

FIG. 6. Frequency distribution of standardized alligator clutch elevations, 1975–1982; N = 71 nests. The distribution is not significantly different from the superimposed standard normal distribution for N = 71, as is shown by the left insert which is the relationship between expected deviations of clutch height taken from a normal curve and the observed standarized deviations. Right insert shows the stability of the variation of clutch heights among years. Letters indicate years from 1975 (A) to 1982 (H), and numbers indicate overlapping values.

perhaps by desiccation and sex imbalances due to warm temperatures in high nests (Ferguson and Joanen, 1982). Thus, the appropriate model to describe the relationship between nest flooding and water level may be a sigmoid curve with asymptotes at high and low nest elevations.

The cumulative normal distribution of standardized nest heights, derived from Fig. 6, provides an appropriate sigmoid model. Here, the percentage of nests below a certain water depth is also the proportion of clutches that would flood if water reached that level. The percentage of nests that flood is estimated by converting the difference between maximum water level (W) and the mean annual clutch height (Y) to an appropriate normal deviate (using $Z = (W - Y)/SD$, where Z is the approximate standard normal deviate and SD is the standard deviation). The percentage of the area under the normal curve lying left of the standard normal deviate (Z) is the estimated proportion of nests flooding at that water level.

Effect on Age Structure.—Nest flooding resulted in a change in the size distribution of juvenile alligators over the course of the study (Fig. 7). Note especially the reduction in the smallest size classes in 1979, and the loss of the smallest size classes in 1981 and 1982 following two years of extensive flooding. These data indicate that the mortality caused by nest flooding can be an important determinant of population age structure over a number of years of repeated flooding.

Historical Perspective.—Using the regression models and historical information on spring temperatures and water levels, it is possible to estimate past nest flooding in the study area. The time of nesting is calculated from spring air temperatures; elevation of the clutch above

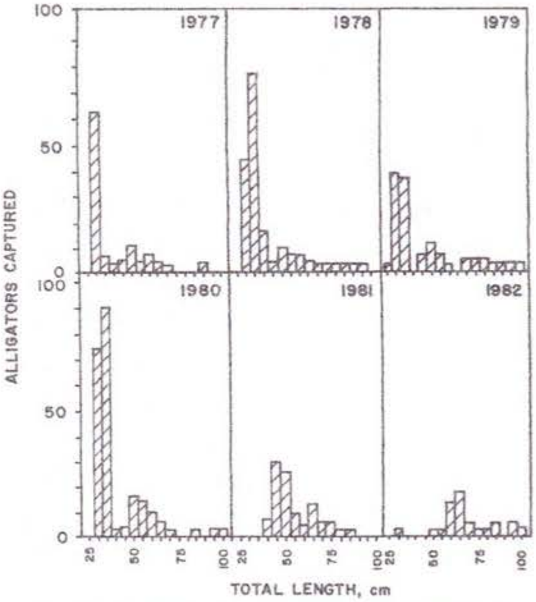

FIG. 7. Reduction in the frequency of small size classes due to nest flooding in 1977–1982. Shown are the size frequency distributions of alligators <1 m total length captured in October of each year.

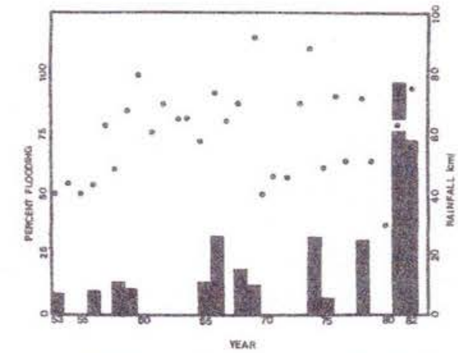

FIG. 8. Percent of alligator nests estimated to have been flooded in the southern Everglades, 1953–1982. Also shown (dots) is the total rainfall during the summer nesting season in each year.

the ground is estimated based on water levels in the last two weeks in June; and the loss of nests is estimated from the maximum water level achieved during the incubation period relative to clutch elevation. The results (Fig. 8) suggest that recent high losses of eggs due to flooding are unprecedented in the 30 yr record. The figure also shows that the extensive flooding of recent years was not associated with extraordinary rainfall during the nesting season.

Based on these estimates, we can calculate that from 1953 to 1962 nests flooded in 40% of the years at a mean annual loss of 4 ± 4.5%. From 1963–1970, water management operations varied too greatly to evaluate their effect. From 1971 to 1982, the current period of water management in the southern Everglades, some flooding occurred at about the same rate as previously (33% of years), but annual losses and the variability of the losses to flooding increased five fold (20 ± 32.8% loss). Thus the pattern and impact of flooding differed historically from that experienced under recent water management policies.

Hydrological Predictability.—To determine whether hydrological predictability exists at a scale meaningful to alligators, we investigated the relationship between the maximum water levels occurring during the incubation period and antecedent hydrological conditions. We found that, prior to the current period of water management, 86% (r^2) of the variation in the maximum water levels achieved during the incubation period is explained by water level during the period of nest construction (Fig. 9). The relationship broke down after 1971, in the current period of water management.

DISCUSSION

Reproductive Success.—Given the importance of temperature in setting the annual cycle of poikilotherms, it is reasonable to suspect that the correlation of alligator egg laying with spring air temperatures is a deterministic one. Similar relationships have been found elsewhere (Joanen and McNease, 1979). Specific temperatures during the nesting season also determine the sex of alligator embryos (Ferguson and Joanen, 1982).

Congruent with the dependence of nesting timing on warm air temperatures, nesting occurs in the summer and coincides with season-

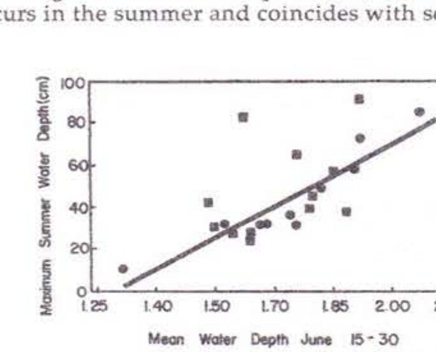

FIG. 9. Relation of maximum water depth during the alligator incubation period to mean water level (m MSL), 15–30 June. The relationship is fitted to the black dots, for 1953–1962 ($r = 0.928$, $P < 0.05$, N = 10), prior to the current period of water management. There is no relationship in the current period of water management (1971–1982), shown by black squares. shown by black squares.

ally rising water levels (Fig. 1). On average, the annual rainy season begins one month before the average date of egg deposition; because Everglades alligators have an incubation period averaging 59 days, hatching generally occurs before the maximum annual water level is reached. Nonetheless, these results indicate that the timing of alligator nesting season, driven by thermal considerations, occurs at a time when eggs can be at risk from flooding should water levels rise too high.

Flooding of nests is the principal source of nesting mortality of the American alligator in the Everglades. Other mortality rates are relatively low. The minor role of predation in nest mortality appears to be somewhat atypical, since it is usually substantially higher in other populations, ranging from 16.5% in Louisiana and 56.3% in north Florida, to 86.4% in Georgia (Joanen, 1969; Dietz and Hines, 1980; Metzen, 1977). Low predation rates in the Everglades appear to be due to the isolated locations of nests and, perhaps, to a high frequency of nest guarding exhibited by females there (Kushlan and Kushlan, 1979). In the frequency of these sources of nesting failure, the alligator differs markedly from the sympatric American crocodile (*Crocodylus acutus*) (Kushlan and Mazzotti, 1989).

Total reproductive output also depends on clutch size and nesting effort. The average clutch size in the Everglades is substantially smaller than in other populations. Clutches in Louisiana average 38.9 eggs (Joanen, 1969), 25% larger than in the Everglades; the clutch sizes of two north Florida populations, 38.7 and 36.1, were 18% and 23% larger (both significantly so: $T = 6.75$, $P < 0.05$, $df = 233$; $T = 4.22$, $P < 0.05$, $df = 226$; Dietz and Hines, 1980). Also, the nesting effort (percent of females nesting) in the Everglades is substantially less than the 67% reported for Louisiana (Joanen and McNease, 1973).

Because of their relatively small clutch size and reduced nesting effort, Everglades alligators have a lower baseline reproductive potential per breeding episode than do other populations studied. Given a 25% lower clutch size and a 50% lower nesting effort, an Everglades alligator produces on average one-third as many eggs per mature female per year than do alligators in Louisiana (5.0 vs. 15.9 viable eggs; Joanen, 1969). This low initial reproductive output means that a proportional reduction due to mortality would leave fewer eggs hatching in the Everglades than in other populations.

Mortality of young age classes (such as eggs, hatchlings, or juveniles) is an important aspect of population stability of alligators. Crocodilian population models have demonstrated that the factors detrimental to the survival of young have a greater effect on long-term population sizes and stability than do mortality factors affecting adults (Nichols et al., 1979; Blomberg et al., 1982). Nest flooding clearly can affect age structure in the Everglades, at least in the short term (Fig. 7).

Although there is no evidence of long-term impact of nest flooding (which would require a study even longer than our seven years). There is some evidence that the high levels of flooding mortality is not normal for the alligator in the Everglades. The model results suggest that the recent episodes of high nest flooding were not typical of the past 30 years, the extent of the historic hydrological record in the Everglades.

Environmental Variability.—Variability in the physical environment can be expected to constrain the adaptive strategies of organisms, and it has been argued that such variation plays a major role in organismal adaptation and resulting community organization (Wiens, 1974; Harrison, 1979; Chesson and Warner, 1981; Grossman et al., 1982). Reproductive adaptations especially may be expected to show correlations with evolutionarily significant characteristics of the environment (Giesel, 1976). Changeable environments, such as fluctuating marshlands, presumably demand specific adaptations for organisms to be able to accommodate to the seasonal and annual changes. The adaptations and accommodations to hydrological fluctuations in the Everglades and similar marshes have been demonstrated in fishes, birds, and invertebrates (Kahl, 1965; Lowe-McConnell, 1975; Kushlan, 1975, 1976*a*, *b*, in press *b*; Kushlan et al., 1985; Beissinger, 1986).

However, the extent to which environmental variation is predictable in a statistical sense or the extent to which organisms can use this predictability is little understood (Colwell, 1974; Stearns, 1981). In southern Florida annual and multiyear rainfall cycles provide some long-term and intermediate-term repeatability in hydrological conditions (Thomas, 1974; Beissinger, 1986). The ability of individuals to respond in a predictive manner to cycles of 5–7 yr is unlikely, given the relatively short life spans of the organisms. Our finding of a correlation between the maximum water levels that flood nests and water conditions weeks earlier when nests were being built (the many presumably stochastic vagaries of intervening rainfall and natural surface water flow notwithstanding) provides evidence that fluctuating environmental factors have short-term deterministic components. Organisms such as alligators can potentially use these predictable aspects of the hydrological regime.

Historically, entraining on spring air temperatures and water levels at the time of nest building apparently provided sufficient information for the alligator to accommodate to ambient and future conditions. In response, the alligator can vary time of nesting, nest mound size, placement of the clutch within the mound, and to a lesser extent the location of the nest, thereby providing mechanisms to compensate to some extent for variable water levels.

The increase in nest flooding in recent years has corresponded to a period in which the natural predictability of the hydrologic regime in the southern Everglades has broken down in some years (Fig. 9). Historically, water levels at the time alligators constructed their nests were a good predictor of the maximum water levels that would later occur during the incubation period. In fact at the time of egg laying, alligators had available an environmental cue that would, in a statistical sense, explain or predict 86% of the variation in succeeding hydrological conditions. The coincidence of increased nesting failure with loss of hydrological predictability suggests that water level fluctuations (in this case resulting from current water management practices) can exceed the alligator's accommodative ability.

Reduced correspondence between environmental cues and future events would inhibit appropriate responses, and has changed the life-history ground rules under which alligators have previously survived in the hydrologically fluctuating Everglades environment. Historically, egg mortality due to flooding was consistently low (4 + 4.5%), but recently mortality has become high (20%) and highly variable (SD = 32.8%). The adaptations of an organism would differ under these two mortality regimes (Charnov and Schaffer, 1973; Stearns, 1976; Congdon et al., 1982). In a variable environment with high juvenile and low adult mortality, an organism might be expected to use a bet-hedging strategy, having a small clutch size, intermittent breeding, and high parental investment toward surviving young (Stearns, 1976). This appears to be the historic situation for Everglades alligators. However, when egg mortality is variably high, the more appropriate strategy is a high degree of iteroparity and reduced parental investment (compare, for example, the strategy of the American crocodile in estuarine areas of southern Florida; Kushlan and Mazzotti, 1989). The life history adaptations and the accommodative ability of alligators may be increasingly inappropriate to the new set of environmental conditions in the Everglades.

The destruction of the predictability of operant environmental cues by natural catastrophic events (such as tropical storms) or unnatural environmental manipulations (such as water management) can apparently dramatically affect the ability of organisms to accommodate to a fluctuating wetland ecosystem. Our studies have demonstrated that intrusive water management practices have affected a wide range of animal populations in the Everglades (Kushlan, 1986, 1987, 1988; Kushlan and Frohring, 1986; Mazzotti et al., 1988).

The identification of statistically predictable hydrological and biological relationships within a fluctuating ecosystem and the further identification of limits on the ability of a species to accommodate to disruption of these relationships have implications not only for the understanding of how organisms adapt to fluctuating environments but also for conservation. Reduction in hydrological predictability is caused by water management practices involving the discharge of surface water into the southern Everglades of Everglades National Park. The conservation of Everglades alligators, in addition to specific management measures (Jacobsen and Kushlan, 1988), requires the reestablishment of the natural predictability of seasonal water level fluctuation. It is likely that similar deterministic relationships exit for other species in other hydrologically variable ecosystems, and that these may be of interest in both theory and conservation practice.

Acknowledgments.—We are pleased to be able to acknowledge our collaborator in this study, Duane Meeter of Florida State University, for his crucial advice and guidance on statistical analyses. We also thank D. Peck, B. Lawson, A. Muller, M. Salzburg, M. Spalding and P. Stine, who provided important assistance in the field and laboratory. Analyses were conducted at Florida International University, South East Regional Data Center, and we thank D. Hall, R. Holley, and P. Frohring for assistance. T. MacVicar of the South Florida Water Management District supplied hydrological information. We thank F. Golley, D. Meeter, T. Murphy, and E. Odum, and anonymous referees for their valuable suggestions. The study was supported by the U.S. Department of Interior, National Park Service. We would especially like to acknowledge the encouragement and collaboration of former Park Superintendent, John Good, in the execution of this study.

Literature Cited

Beissinger, S. R. 1986. Demography, environmental uncertainty, and the evolution of mate desertion in the snail kite. Ecology 67(5):1445–1459.

Blake, N. M. 1980. Land into water—water into land. Univ. Press Florida, Tallahassee, Florida. 344 pp.

Blomberg, G. E. D., C. St. Pierre, K. D. Smith, S. M. Caddell, and S. R. Pett. 1982. Simulated population dynamics of crocodiles in the Okavango River, Botswana. *In* D. Dietz and F. W. King (eds.), Crocodiles: Proc. Fifth Working Meeting Crocodile Specialists Group. IUCN, Morges, Switzerland.

CHARNOV, E. L., AND W. M. SCHAFFER. 1973. Life history consequences of natural selection: Cole's result revisited. Amer. Natur. 107(951):791–793.

CHESSON, P. L., AND R. R. WARNER. 1981. Environmental variability promotes coexistence in lottery competitive systems. Amer. Natur. 117(6):923–943.

COLWELL, R. K. 1974. Predictability, constancy, and contingency of periodic phenomena. Ecology 55(5): 1148–1153.

CONGDON, J. D., A. E. DUNHAM, AND D. W. TINKLE. 1982. Energy budgets and life histories of reptiles. *In* C. Gans (ed.), Biology of the reptilia, Vol. 13, pp. 233–271. Academic Press, New York.

DANIEL, C., AND F. S. WOOD. 1981. Fitting equations to data. John Wiley and Sons, New York. 458 pp.

DIETZ, D. C. AND T. C. HINES. 1980. Alligator nesting in north-central Florida. Copeia 1980(2):249–258.

FERGUSON, W. M. J. 1982. The structure and composition of the eggshell and membranes of *Alligator mississippiensis*. Trans. Zool. Soc. London 36(1): 99–152.

———, AND T. JOANEN. 1982. Temperature of egg incubation determines sex in *Alligator mississippiensis*. Nature 296(5860):850–853.

GIESEL, J. L. 1976. Reproductive strategies as adaptations to life in temporally heterogeneous environments. Ann. Rev. Ecol. Syst. 7:57–79.

GROSSMAN, G. D., P. B. MOYLE, AND J. O. WHITAKER, JR. 1982. Stochasticity in structural and functional characteristics of an Indiana stream fish assemblage: a test of community theory. Amer. Natur. 120(4):423–454.

HARRISON, G. W. 1979. Stability under environmental stress: resistance, resilience, persistence, and variability. Amer. Natur. 113(5):659–669.

HULL, C. H., AND N. H. NIE. 1981. SPSS update 7–9. McGraw-Hill, New York. 402 pp.

JACOBSEN, T., AND J. A. KUSHLAN. 1986. Alligators in natural areas: choosing conservation policies consistent with local objectives. Biol. Cons. 36(2):181–196.

JOANEN, T. 1969. Nesting ecology of alligators in Louisiana. Proc. Ann. Conf. SE Assoc. Fish Game Comm. 23:141–151.

———, AND L. MCNEASE. 1973. Developments in alligator research in Louisiana since 1968. Presented at Symposium of the American Alligator Council. Winter Park, Florida. (Mimeo.)

———, AND ———. 1979. Time of egg deposition for the American alligator. Proc. Ann. Conf. SE Assoc. Fish Wildl. Agencies 33:15–19.

———, ———, AND G. PERRY. 1977. Effects of simulated flooding on alligator eggs. Proc. Ann. Conf. SE Assoc. Fish Wildl. Agencies 31:33–35.

KAHL, M. P. 1965. Food ecology of the wood stork (*Mycteria americana*) in Florida. Ecol. Monogr. 34(1): 97–117.

KUSHLAN, J. A. 1975. Population changes of the apple snail (*Pomacea paludosa*) in the southern Everglades. Nautilus 89(1):21–23.

———. 1976*a*. Environmental stability and fish community diversity. Ecology 57(4):821–825.

———. 1976*b*. Wading bird predation in a seasonally-fluctuating pond. Auk 93(3):464–476.

———. 1986. Responses of wading birds to seasonally fluctuating water levels: strategies and their limits. Colonial Waterbirds 9(2):249–251.

———. 1987. External threats and internal management: the hydrologic regulation of the Everglades. Environ. Manag. 11(1):109–119.

———. 1988. The conservation and management of the American crocodile. Environ. Manag. 12(6): 777–790.

———. *In press a*. Avian use of fluctuating wetlands. *In* R. R. Sharitz and J. W. Gibbons (eds.), Freshwater wetlands and wildlife. DOE Symposium Series 61, Oak Ridge, Tennessee.

———. *In press b*. Wetlands and wildlife: the Everglades perspective. *In* R. R. Sharitz and J. W. Gibbons (eds.), Freshwater wetlands and wildlife. DOE Symposium Series 61, Oak Ridge, Tennessee.

———, AND P. C. FROHRING. 1986. History of the southern Florida Wood Stork population. Wilson Bull. 98(3):368–386.

———, AND M. S. KUSHLAN. 1979. Function of nest attendance in the American alligator. Herpetologica 36(1):27–32.

———, AND F. MAZZOTTI. 1989. Population biology of the American crocodile. J. Herpetol. 23(1):7–21.

———, L. G. MORALES, AND P. C. FROHRING. 1985. Foraging niche relationships of wading birds in tropical wet savannas. Neotropical Ornithology. Amer. Ornith. Union Monogr. 36:663–682.

LEACH, S. D., H. KLEIN, AND E. R. HAMPTON. 1972. Hydrological effects of water control and management of southeastern Florida. Florida Bur. Geol., Rept. Invest. 60. Tallahassee, Florida.

LOWE-MCCONNELL, R. 1975. Fish communities in tropical fresh waters. Longman, New York. 237 pp.

MAZZOTTI, F., J. A. KUSHLAN, AND A. DUNBAR-COOPER. 1988. Desiccation and cryptic nest flooding as causes of nest mortality in the American crocodile (*Crocodylus acutus*) in Everglades National Park. Florida Sci. 51(1):65–72.

METZEN, W. D. 1977. Nesting ecology of alligators on the Okefenokee National Wildlife Refuge. Proc. Ann. Conf. SE Assoc. Fish Wildl. Agencies 31:29–32.

NICHOLS, J. D., L. VIEHMAN, R. H. CHABRECK, AND B. FENDERSON. 1979. Simulation of a commercially harvested alligator population in Louisiana. Louisiana State Univ. Center Agr. Sci. Rural Dev. Baton Rouge, Louisiana. 59 pp.

SARMIENTO, G. 1983. The savannas of tropical America. *In* F. Bourliere (ed.), Ecosystems of the world, Vol. 13, pp. 245–288. Elsevier, New York.

STEARNS, S. C. 1976. Life-history tactics: a review of the ideas. Quart. Rev. Biol. 51(1):3–47.

———. 1981. On measuring fluctuating environments: predictability, constancy, and contingency. Ecology 62(1):185–199.

THOMAS, T. M. 1974. A detailed analysis of climatological and hydrological records of south Florida with reference to man's influence upon ecosystem evolution. *In* P. J. Gleason (ed.), Environments of south Florida: present and past, pp. 82–122. Miami Geol. Soc., Memoir 2. Coral Gables, Florida.

TUKEY, J. W. 1977. Exploratory data analysis. John Wiley and Sons, New York. 688 pp.

UCLA. 1983. BMDP statistical software. Univ. California Press, Los Angeles, California. 880 pp.

WIENS, J. A. 1974. On competition and variable environments. Amer. Sci. 65(5):590–597.

Accepted: 15 September 1989.