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In the Everglades, the American alligator nests in the high water period of summer and fall. Nesting success is tied to prevailing water conditions, in part determined by water management procedures. Alligators placed eggs higher in years when water levels were high at nesting time. Generally, 5% of the eggs deposited are lost to flooding, but in 1978, 35% were lost. Loss of 3% of the eggs laid was due to rainfall, and 32% were lost because of management discharge of water into the park determined by conditions in upstream water storage areas. Several options exist to reduce impact of discharge on nesting alligators, but effects on other components of the Everglades system must also be considered.

The American alligator (Alligator mississippiensis) is the dominant animal of the Everglades. Its activities shape plant communities and determine pathways of energy flow among animal populations (Craighead 1968, Kushlan 1974). Ponds, which alligators maintain, are dry season refugia for aquatic animals and so are important feeding sites for wading birds (Kushlan 1976a). Because of this, maintenance of a viable alligator population is essential for preserving natural ecological processes in the Everglades.

The subtropical climatologic pattern of alternating wet and dry seasons appears to be an important factor controlling the composition and functional relationships of Everglades animal communities (Kushlan 1976b, Kushlan et al. 1975). Patterns of water level fluctuation in the Everglades have been altered by water management procedures, which consequently affect animal populations within Everglades National Park (Kushlan et al. 1975, Kushlan 1979). Presently the remaining Everglades north of the park has been broken into water management units in which water storage is controlled by levees, canals and regulated discharges (Leach et al. 1972).

Everglades National Park encompasses the downstream tip of the Everglades (Fig. 1). Historically, surface water moved into this area as sheet flow across the entire width of the Everglades. Now surface water is discharged from a water conservation area into the park through 5 or fewer spillways, most located west of the true Everglades drainage (Fig. 1). A minimal monthly flow is mandated by Congress and discharge in excess of this amount occurs when water in the conservation areas exceeds a predetermined level. The established schedule of minimal discharge into the park is based approximately on historic mean flows. Present water management procedures, including the delivery schedule, have served to prevent excessive drying of the southern Everglades, such as occurred when the water management system was completed in the early 1960's, and all surface water flow was eliminated. However, these procedures fail to take into account year-to-year differences in hydrologic conditions. In wet years, temporary storage of water and its subsequent release into the park can result in unnaturally rapid elevation of the water level there.

The ecological effect of water management procedures is the subject of a coordinated series of studies of Everglades hydrology and of the basic biological components of the Everglades food web (fishes, wading birds and alligators) being undertaken at the South Florida Research Center. Understanding the effects of water level fluctuations on the alligator population is particularly critical because of the dominant role of this species in the system, and because its ecology, especially nesting biology, is intimately tied to water conditions. Alligators deposit their eggs in nest mounds constructed of marsh vegetation (Fig. 2) at the beginning of the usual rainy season in June. Subsequently, eggs are susceptible to flooding from rises in water level during the 60-65 day incubation period. Such rises can be caused either by rainfall or by management discharge. Thus the biological management of surface flow into the park requires understanding the role of water level fluctuations on alligator nesting success.

METHODS

The study was conducted in the Everglades marsh of Everglades National Park from 1975 through 1978. The data reported in this paper were from within and near a 10 km^2 study area (Fig. 1). Nests within this area were located by searching from fixed-wing aircraft and helicopters and on the ground. At each nest site, we measured the height of the nest and the height of the eggs above ground level, and we counted the clutch. Rainfall and water level fluctuations were measured by a continuously recording Landsat gauging station located within the study area. Nests were monitored throughout incubation to determine their fate and the time of hatching. The number of eggs lost to rising water level in each nest was estimated from the percentage of the nest cavity that flooded. Depending on stage of development, alligator eggs are adversely affected by more than 2 hours of submersion, and 48 hours of submergence produces total mortality of all eggs (Joanen et al. 1978).

RESULTS

The usual annual pattern of water level fluctuation is for water levels to begin falling in December-January with the beginning of the dry season. Levels fall faster in spring and usually reach their lowest point in late May. Water rises at the beginning of the summer wet season, reaching highest levels for the year in the fall.

This generalized pattern of water level fluctuation varies somewhat from year-to-year (Fig. 3) depending on rainfall and discharge. The spring dry period was driest in 1975 and wettest in 1978. The early fall wet season was drier in 1975 and 1977 than in 1976 and 1978. Alligator nesting phenology corresponded to the water cycle. Courtship occurred during the drying period or early wet season in April and May, nest building and egg laying during rising water periods of June and July, hatching during the relatively high water period of August and September. Because of this phenology prevailing water conditions can influence nesting in various ways.

Although it might be expected that alligators would choose higher nesting locations in wetter years, the elevation of nest sites selected by alligators did not vary in different years. However, the elevation of the lowest egg was positively correlated with water levels at the time of laying ($r = .47$, $p \quad .01$, $n = 36$). That is, the higher the water level at the time of nest building, the higher the eggs were placed (Fig. 4).

Alligator eggs were adversely affected by water level rises in 3 of the 4 years of the study (Table 1). In 1975, an exceptionally small nest was completely flooded and another nest was partially affected. In 1977, two nests were partially flooded. Over the first 3 years only 3.6% of the nests completely flooded and 14% of the nests were in some way adversely affected by rising water levels during the incubation period.

In 1978, flooding was much more severe. Twenty-six percent of the nests completely flooded, and 63% of the nests were affected by flooding (Table 1). Flooding of alligator eggs becan on 2 August and through the end of hatching, 35% of the eggs were lost because of flooding (Fig. 5).

Part of this flooding of eggs in 1978 was caused by release of surface water into Everglades National Park. The amount and distribution of discharge changes somewhat from year-to-year (Fig. 6), although usually discharges are relatively low in early summer and increase in fall. In 1978, late summer discharge was exceptionally high (Fig. 6). This high discharge was first released in late July 1978 when all discharge structures were simultaneously opened, eventually to full capacity. P. C. Rosendahl (in prep.) has analyzed the hydrologic consequences of this event. Immediately south of the discharge structure water levels rose .38 m between 17 July and 20 July. This wave-like pulse of water progressed south and westward at a rate of about 1.6 km/day, reaching the study area on 30 July 1978 (Fig. 3). The water level increase caused by the flood discharge began to stabilize by 8 August. Water levels around the nests rose 15.2 cm (Fig. 3) from 30 July to 8 August.

On 12 August, 6.1 mm rain fell and other rain also fell throughout the period. The effect of rain events after 30 July was to aggravate the impact of the flood water by further increasing levels. To determine whether these rainfall events could have flooded eggs in the absence of the 15.2 cm rise in water from the discharge pulse, we plotted the water levels that would have occurred assuming that water level rises equaled the rainfall, and that water loss from evapotranspiration equaled 6 mm per day. (This was the water level decline that occurred without rain in July 1978). Without the discharge event, 15 eggs or about 3% of the total would have been lost to flooding. Thus the discharge pulse accounted for the loss of about 32% of the eggs.

In 1975-77, an average of 14 eggs were lost to flooding. In 1978, 166 eggs were lost (Table 1). It is not possible to determine the number of eggs that hatched since nearly all eggs, hatching or not, are usually removed by the alligator. However we can estimate the number of unflooded eggs. In 1975-77, an average of 273 eggs were not flooded. Because of the greater number of animals nesting in 1978, more eggs survived. However on a per capita basis, potential productivity was much reduced from an average of nearly 30 eggs to 17 eggs per female attempting to nest.

DISCUSSION

The nesting tactics of the alligator exhibits some flexibility in response to water conditions. The alligator can respond to year-to-year differences in water levels at the time of nesting by placing eggs higher above the marsh bottom in wet years. This would have the effect of requiring higher water levels to flood eggs. The upper limits of egg placement may be determined by nest geometry or by humidity factors higher above the water. Placing eggs higher in wet years appears to result in low egg loss in years when water levels fluctuate in a normal manner.

Hydrologic management can adversely affect alligator nesting success in two ways. Surface water discharge early in the wet season is usually kept at minimum scheduled levels in order to restore storage in the water conservation areas. As a result, water in Everglades National Park may be held at lower levels at the time of nest construction, and thus result in lower egg placement, than would otherwise have occurred. Later in nesting, discharge is generally held to a set schedule unless water in the conservation area rises above scheduled levels. When this happens, water is vented into the park causing immediate water level rises near the discharge points. This wave of water progresses down the Everglades causing instantaneous water rises at alligator nests, in addition to any rises caused by local rainfall. From August 1 to 18, 1978, this discharge amounted to 63,500 acre feet, nearly 25% of the total minimal annual delivery to Everglades National Park. A delay of several weeks in releasing discharge would have protected all but 3% of the alligator eggs in the study area. Alternatively, this same total discharge, if it had been spread over the entire period when the rain actually fell, would have had less of a cumulative impact because incrementally increased runoff would have led to less of a rise in water levels.

The latter consideration suggests a foundation for a biologically meaningful management strategy. Impact on alligator nesting occurs not only because of the massive discharge itself, but more fundamentally, because holding water deliveries until flood conditions occur in the conservation area requires releases to be massive and relatively instantaneous. An alternate policy would be to allow wet season discharge to more closely correspond to what they would have been under natural conditions, given a specific set of rainfall and hydrologic conditions. In wet years, this might mean delivery of more water than scheduled; in dry years, less water. From the perspective of the alligator population, management in wet years would be particularly important since potential production is greater in wet years and a wet early summer would result in higher egg placement.

It is important to realize that restoration of more historic amounts of water discharge is not completely sufficient, because the location of the present discharge structures do not correspond to the areas where sheet flow occurred naturally. Thus a natural amount of discharge through these structures would not necessarily result in natural patterns of water level rises downstream. Since it is the downstream effect rather than discharge amount per se that is crucial, the relationships must be determined between water level rises within the slough and possible quantity and distribution of discharge.

It is also important to remember that alligators are only part of the Everglades system. No viable management strategy should consider only the effect on alligators. The effects of discharge on other components of the system, such as on fishes and wading birds must also be determined. Thus additional understandings of water level relations are required before comprehensive recommendations can be made. Nonetheless, the effects of water level rises on alligator nesting success illustrate both the potentially serious impact of discharge events on animal populations and suggest some insights for the development of future management options.

ACKNOWLEDGEMENTS

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Table 1. Effects of water level rises on alligator nests in the Everglades

Year	Number of nests	Number of nests that failed because of flooding	Number of nests affected by flooding	Egg loss from flooding	Number of unflooded eggs	Number of unflooded eggs per nest
		# (%)	# (%)	# (%)		
1975	9	1 (11%)	2 (22%)	31 (11.1%)	248	27.5
1976	12	0	0	0	345	28.7
1977	7	0	2 (29%)	11 (4.6%)	228	32.6
1978	19	5 (26%)	12 (63%)	166 (35.2%)	305	16.6

FIGURE CAPTIONS

Figure 1. Map of southern Florida.

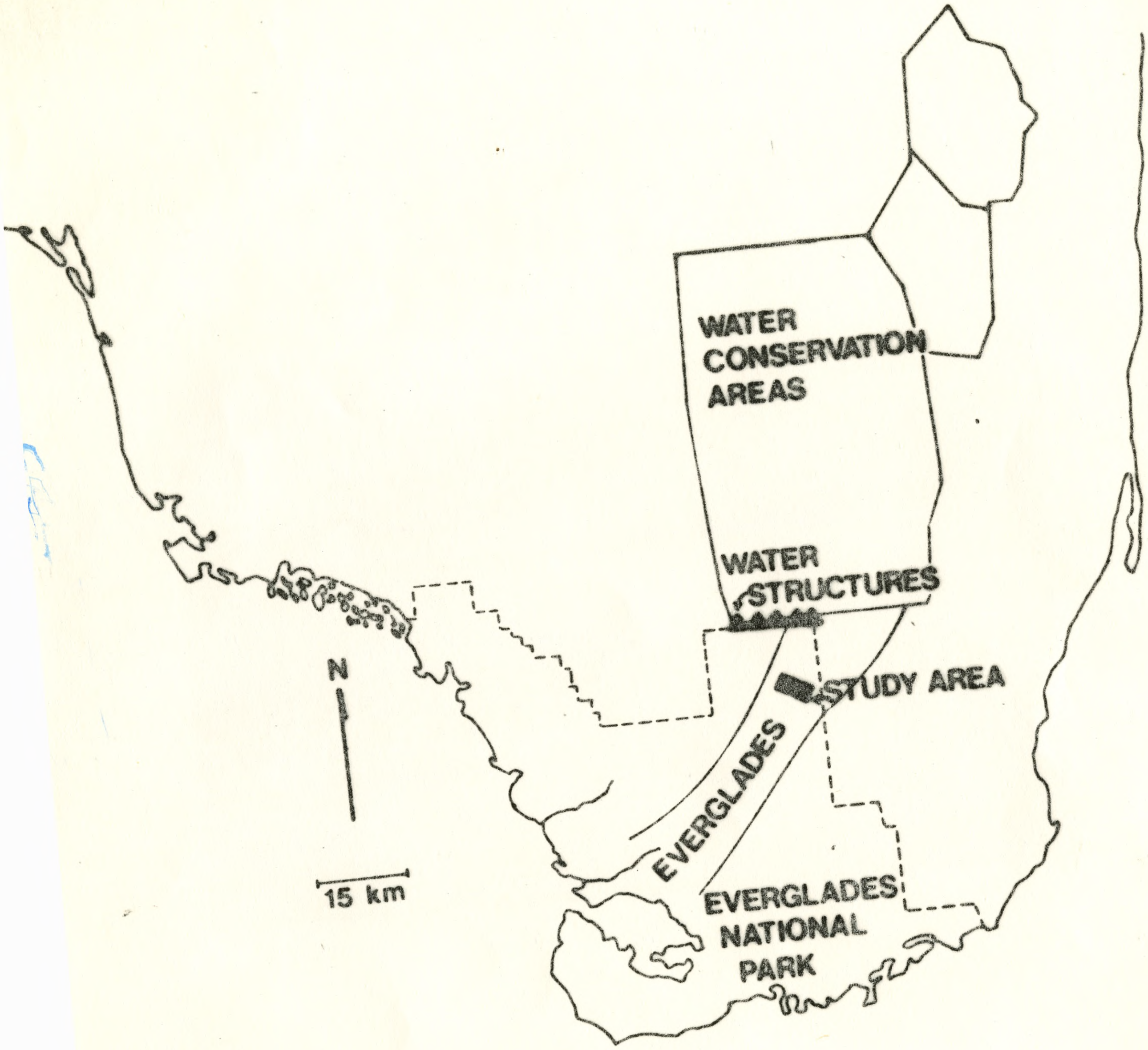
Figure 2. Alligator nest mound in the Everglades.

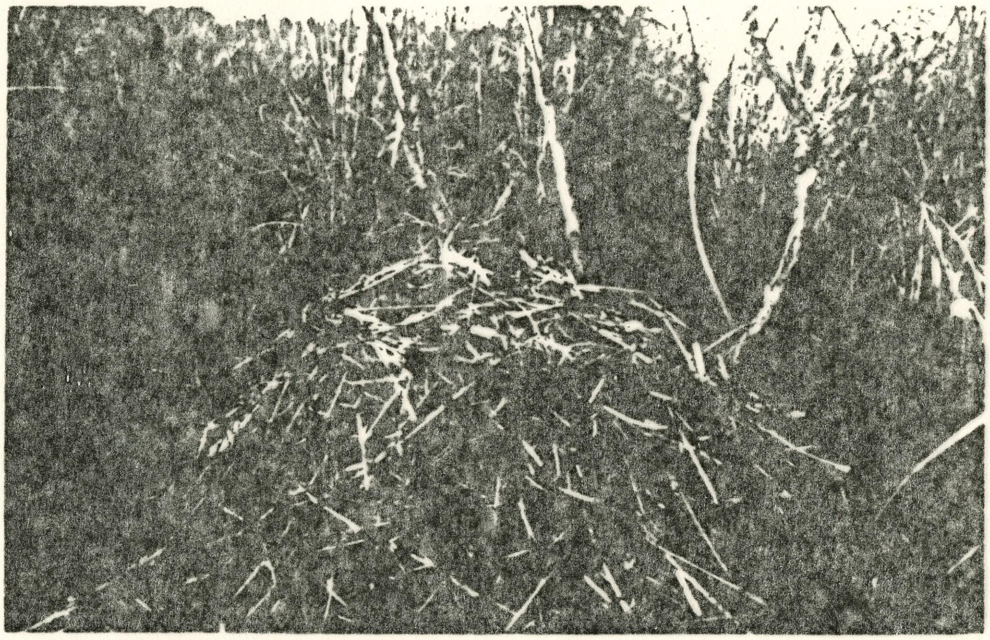
Figure 3. Fluctuation of water levels in the Everglades during April-September in 4 years, 1975-78.

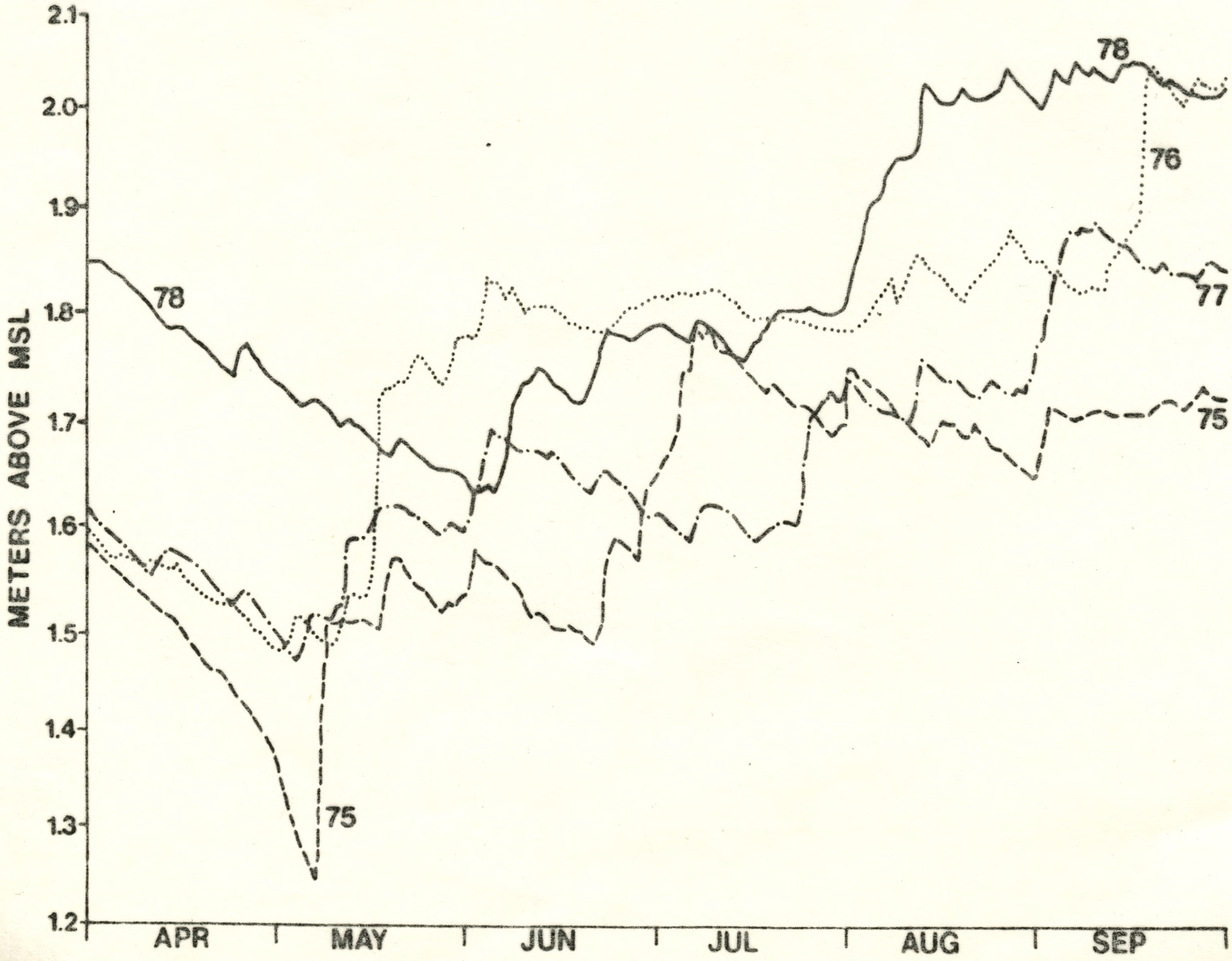
Figure 4. Relationship between elevation of the lowest egg in alligator nests and water level on the date of laying, 1975-78. Regression line based on 32 nests. The marsh bottom is 1.42 m above mean sea level.

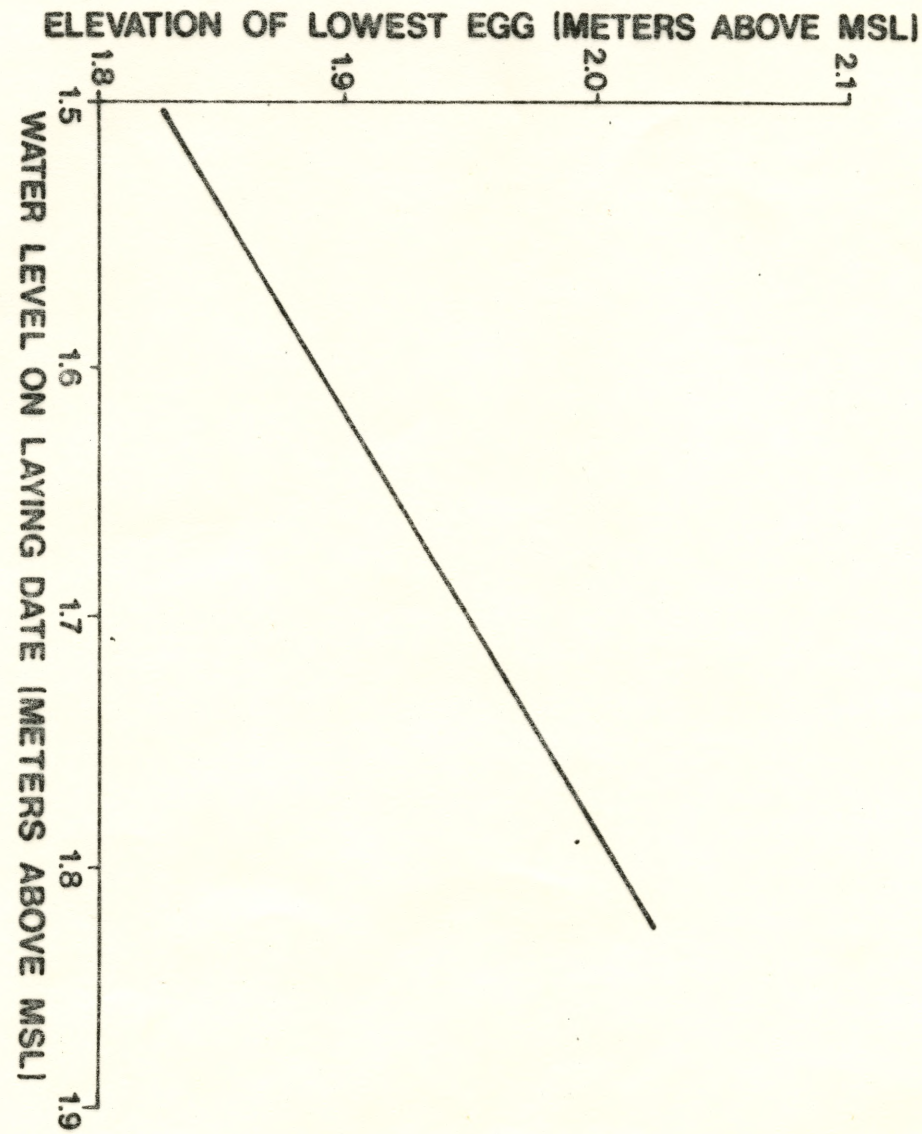
Figure 5. Cumulative egg loss from flooding in August 1978.

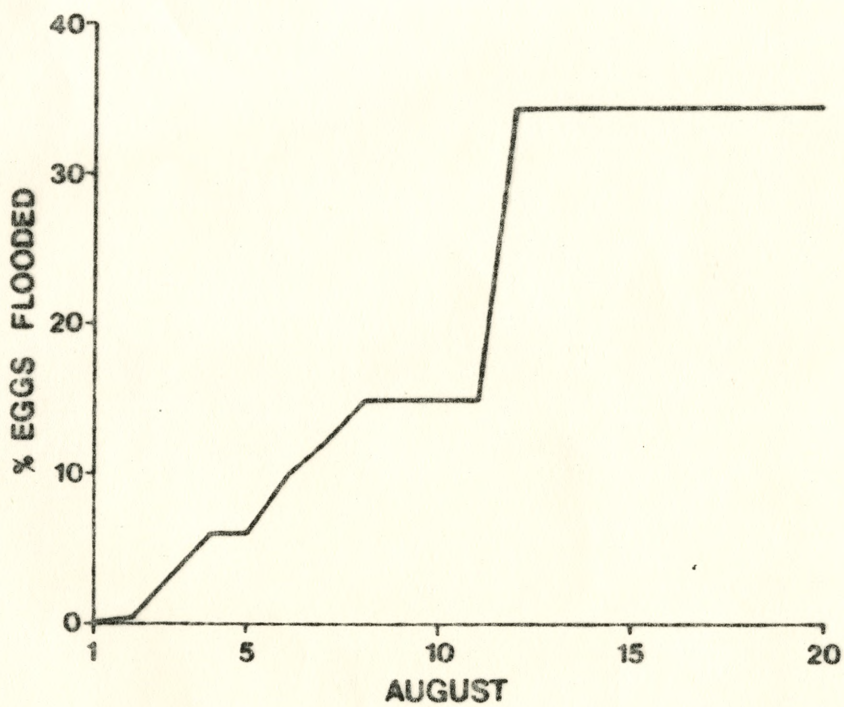
Figure 6. Monthly discharge of surface water into the southern Everglades of Everglades National Park, 1975-1978.


WATER
CONSERVATION
AREAS
WATER
STRUCTURES
STUDY AREA
N
15 km
EVERGLADES
EVERGLADES
NATIONAL
PARK




METERS ABOVE MSL
2.1
2.0
1.9
1.8
1.7
1.6
1.5
1.4
1.3
1.2
APR
MAY
JUN
JUL
AUG
SEP
78
76
77
75
78
75


ELEVATION OF LOWEST EGG (METERS ABOVE MSL)
1.8
1.9
2.0
2.1
WATER LEVEL ON LAYING DATE (METERS ABOVE MSL)
1.5
1.6
1.7
1.8
1.9



% EGGS FLOODED
40
30
20
10
0
1
5
10
15
20
AUGUST