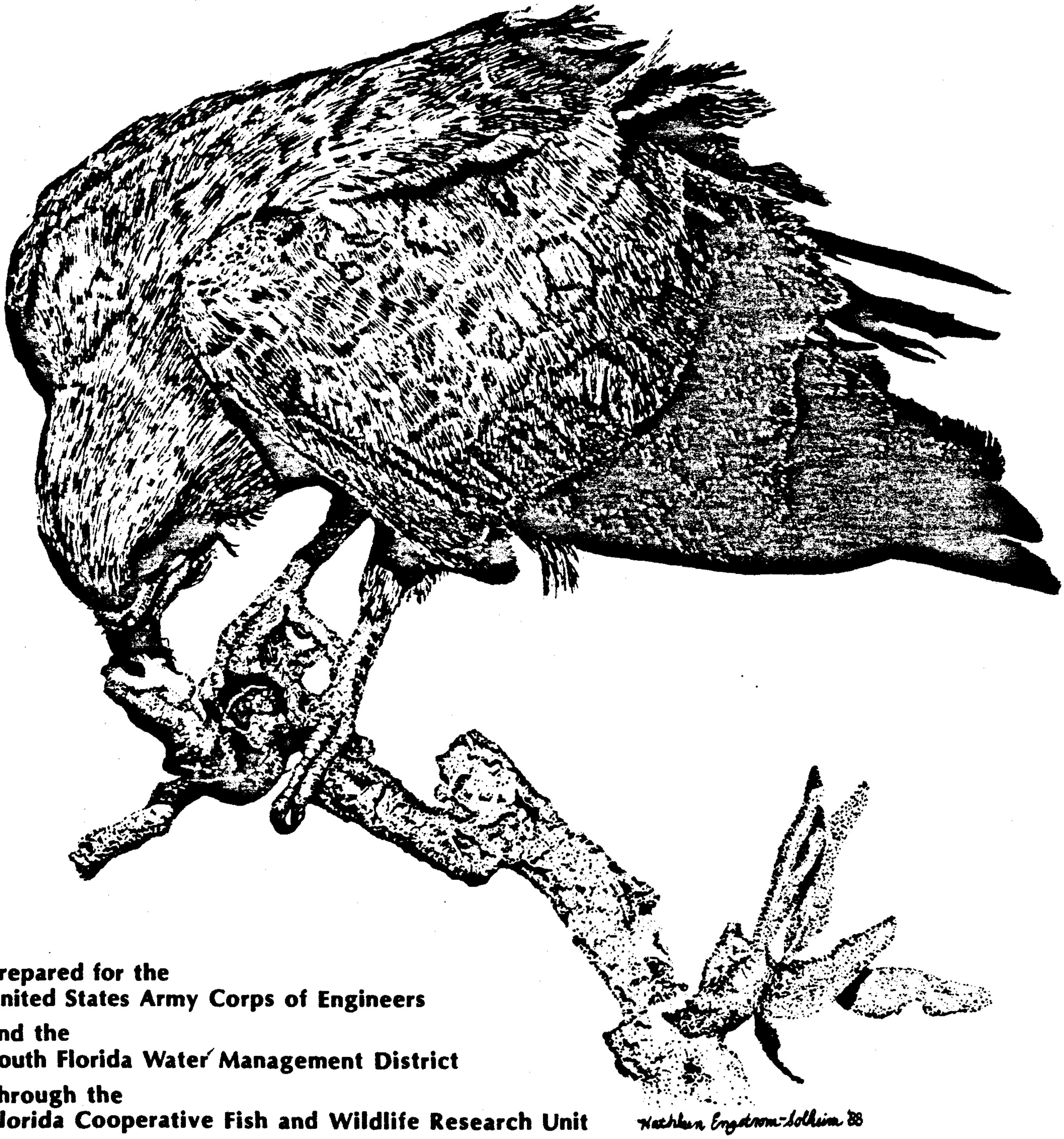
Nesting Ecology of Snail Kites in Water Conservation Area 3A

**Robert E. Bennetts, Michael W. Collopy
and Steven R. Beissinger**



**Prepared for the
United States Army Corps of Engineers
and the
South Florida Water Management District
through the
Florida Cooperative Fish and Wildlife Research Unit**

NESTING ECOLOGY OF SNAIL KITES IN WATER CONSERVATION AREA 3A

Final Report

by

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SUMMARY

During 1986 and 1987, we studied the nesting success and nest-site selection of Snail Kites (Rostrhamus sociabilis) in Water Conservation Area 3A (WCA-3A) of the Florida Everglades. Particular emphasis was placed on evaluating the influence of hydrologic conditions. Water conditions in both 1986 and 1987 were higher than the long-term average during the primary nesting season (January through July). A lack of rainfall resulted in drier than average conditions by mid-June of 1987; however, most nesting efforts had been completed by this time.

We monitored 148 active nests (i.e. nests in which at least one egg was laid) during 1986 and 227 during 1987. The distribution of nesting kites in WCA-3A during both years was restricted to a relatively narrow range of ground elevations. These elevations corresponded to areas in which hydrologic conditions were suitable for nesting. Most nests (94%) were initiated at sites where water depths ranged from 20 to 80 cm. Water depths at adjacent foraging areas (open sloughs) generally were 10 cm or more deeper than at nest sites. The areas in WCA-3A where nesting occurred on average dried out once every 1.9 to 3.8 years (for the 19-year period of record). A large portion of WCA-3A dries out more frequently than once every 1.9 years and was not used by nesting kites. A smaller portion of WCA-3A dries out less frequently than every 3.8 years. No extensive nesting occurred in this region during this study; however, it may be important to kites during drier years. Areas where Snail Kites nested had a greater ratio of open water to sawgrass than did regions that were not used for nesting. Snail Kites tended to select nest substrates that offered sturdy structural support and were located over water. Willow was the most commonly used nest substrate but was used less than expected based on its high availability. Pond apple and melaleuca were selected in higher proportion to their availability. Dry hammocks contained numerous sturdy substrates, but were avoided, presumably because of high predator densities.

The environmental correlates of nesting success were not consistent between 1986 and 1987. Our results indicate that the relative importance of factors influencing nesting success varies among years and that predictability of nesting success, based on environmental conditions above or below threshold levels may be low. Step-wise logistic regression indicated that the date of nest initiation was the most important correlate of nesting success in 1986 and 1987; although previous studies found no such relationship. Nesting success was not influenced by water levels, which were relatively high, during this study; however, previous studies have shown clearly that success often decreases to zero when areas dry out completely. This suggests that the influence of water level is a threshold response.

ACKNOWLEDGMENTS

This project could not have been accomplished without the help of the many individuals who contributed greatly to its success. It is with our deepest appreciation that we acknowledge their contributions.

Our field assistants, Elaine Caton, Hugh Dinkler, and Nancy Dwyer worked many long hours under conditions that were often well beyond what is normally expected of a field assistant, and did so willingly, cheerfully, and without hesitation. Elaine Caton was an integral part of the initial project design and her suggestions undoubtedly contributed to the quality of the research. Nancy Dwyer provided relentless assistance with the data entry, analyses, and all phases of this report. Their efforts are sincerely appreciated.

Peter Frederick and his assistants, Reed Bowman and Susan Fitzgerald, often provided assistance in the field, and were a constant source of logistic support, stimulating discussions, and friendship. Peter also came to the rescue on numerous occasions, with tools in hand, when we were stranded by broken boats or trucks.

We appreciate the helpful comments on drafts of this report provided by Walt Dineen, Nancy Dwyer, Lewis Hornung, Jon Moulding, Jim Rodgers, and Noel Snyder. We carefully considered all criticisms; however not surprisingly for a report of this magnitude, we are not in complete agreement on all interpretations. We have tried wherever possible to identify alternative viewpoints to our interpretations.

Many people assisted with various aspects of the field work. Alan Gillespie, Patrick Railey, and Paul Stone contributed numerous hours of effort dredging the marsh in search of apple snails. We thank them for their efforts and for keeping their sense of humor in spite of being stranded more than once in the Everglades. For assisting with foraging observations we thank Mike Green, Rose-Marie Etemad-Green, and Dave Westneat. We also thank Irma Caton for assisting us with our nest searches and checks. Marilyn Spaulding helped us to identify nest parasites.

We are deeply indebted to James Wyatt for keeping our airboats running. Without his help we would have lost many hours of field work. We greatly appreciated his expertise and the numerous repairs that frequently extended well into the night and weekends.

Ken Portier provided considerable statistical advice. Ken Portier and Lori Pfahler also set up and ran the logistic regression analyses. We received additional advice on statistical analyses and/or applications of the Mayfield Method from Barbara Black, Tom Edwards, Doug Johnson, Jim Nichols, and Karen Steenhof. We appreciate their help. We thank Reed Bowman and Peter Frederick for the many thought provoking discussions of Mayfield analyses and survivorship.

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For sharing their knowledge of apple snails and use of the suction dredge, we thank Earl Rich and Oscar Owre. For sharing their knowledge of snake lore we thank George Dalrymple, Dick Franz, and Paul Andreatis. George Dalrymple spent several hours in the field with us an generously shared his knowledge of the Everglades herpetofauna. For their insight of the Everglades and for providing us with living conditions which greatly enhanced our experience in South Florida we are indebted to Fred and Sandy Dayhoff. We also thank Fred Dayhoff for his emergency welding which kept our airboat going.

Joyce Kleen kept us informed of Snail Kite sightings through the sighting program at Loxahatchee National Wildlife Refuge. Betty Wargo and Noel Chandler informed us of kite nesting activity on Lakes Kissimmee and Okeechobee during 1986. James Rodgers, Jr. kept us informed of nesting activity and assisted in banding throughout South Florida during 1987.

Mark Spier kept us informed of kite activity in Everglades National Park and helped us obtain weather data. Mike Brown of the Florida Game and Fresh Water Fish Commission informed us of several nests in WCA-3 that we had missed.

We thank the Florida Game and Fresh Water Fish Commission, particularly James Rodgers, Jr., for allowing us to use unpublished data from the annual Snail Kite Surveys. The Florida State Division of Forestry generously allowed us to park our airboats at their Trail Glades facility.

For their secretarial support, forwarding mail, and assisting in numerous other ways, we are grateful to Barbara Fesler, Cathy Ritchie, and Lonell Segars. We thank Kathy Engstrom-Solheim for the cover artwork and Margy Summers for the cover design. We are grateful to Adele Karolik and Rick Yates for their help during the frantic final hours of preparing this report.

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INTRODUCTION

The Snail Kite (Rostrhamus sociabilis) is a medium-sized raptor of the Neotropics. Although Snail Kites may be locally common in South and Central America, Mexico, and Cuba (Sykes 1984), the Florida Snail Kite (R. s. plumbeus) is listed as endangered both federally and by the State of Florida (U.S. Fish and Wildlife Service 1986).

Historically, the numbers of Snail Kites in Florida have not been well documented (Nichols et al. 1980), and estimates prior to the early 1900's are lacking. Howell (1932) gives a general indication of kite numbers during the early 1900's by describing that "scattered flocks of a hundred or more birds" were frequently found within a limited area. It is impossible to assess, however, whether these flocks were widespread or local concentrations during times of food shortage. As recently as 1985, over 350 Snail Kites have been reported using a single roost during a period when Water Conservation Area 3A had dried out (J. Takekawa, pers. comm.). At any rate, we can reasonably assume that kite numbers in Florida, up until the 1930's, were at least 100 and probably numbered in the hundreds or even thousands. During the mid-1900's, estimates of the Snail Kite population in Florida were consistently under 100 (see Sprunt 1954, Steiglitz and Thompson 1967, Sykes 1979). In recent years (1970's-1980's), Snail Kite numbers generally have been increasing with population estimates of at least 668 birds during 1984 (Florida Game and Fresh Water Fish Commission, unpubl. data).

Declines in the kite population from the early to mid 1900's generally have been attributed to widespread drainage of Florida's marsh habitats (e.g. the Everglades) (see Bent 1937, Steiglitz and Thompson 1967, Sykes 1979, 1983b, Beissinger 1986). There seems little doubt that Snail Kite populations are influenced by the hydrologic conditions (see Sykes 1983b, 1987b, Beissinger and Takekawa 1983, Beissinger 1986).

Although it is impossible at this point to determine cause and effect, the kite population increase beginning in the 1970's is likely, in part, a response to the impounding of WCA-3A. The impounding of WCA-3A lengthened the hydroperiod, which resulted in increased apple snail populations (Kushlan 1975) and vegetation changes (e.g. opening of sawgrass stands) that enhanced Snail Kite habitat (see Sykes 1987b). WCA-3A was completed in 1962 (Zaffke 1983). There was a subsequent period of over 10 years before Snail Kite populations began increasing. This lag period probably was related to the time it took for WCA-3A to fill, snail populations and vegetation to respond to the increased hydroperiod, and kites to colonize the area. After this lag period, however, Snail Kite populations began increasing and closely tracked the hydrologic conditions (Fig. 1).

Most of Florida's Snail Kites currently are found in WCA-3A (FGFWFC, unpubl. data) and the relative importance of WCA-3A to the total Florida Snail Kite population has been increasing since kite populations first began increasing in WCA-3A (Fig. 2). The proportion of the total population (from annual surveys) of Snail Kites in WCA-3A has reached as high as 92.2% during 1983 (J. Rodgers, pers. comm.). There is little question that WCA-3A has become an increasingly important area for the Snail Kite in Florida.

PURPOSE AND OBJECTIVES OF THE STUDY

In 1983, the U.S. Army Corps of Engineers was authorized by Congress to conduct an experimental program of water deliveries to Everglades National Park (ENP) (U.S. Army Corps of Engineers 1985). This experimental program was in response to requests from ENP for water deliveries that were more timely and better suited to their management needs. In 1983, a "flow-through" system was employed which left three of the four S-12 structures (gates which allow water to flow from WCA-3A to ENP) open. This system resulted in very low water levels in WCA-3A and reduced the water supply storage function of WCA-3A. Beginning with the resumption of the summer wet season in 1985, a "rainfall-driven" system was employed which incorporated current rainfall into a formula for determining flow rates (see U.S. Army Corps of Engineers 1985 for details of plan).

The potential for hydrologic changes resulting from this phase of the experimental release program led the Corps of Engineers and the South Florida Water Management District

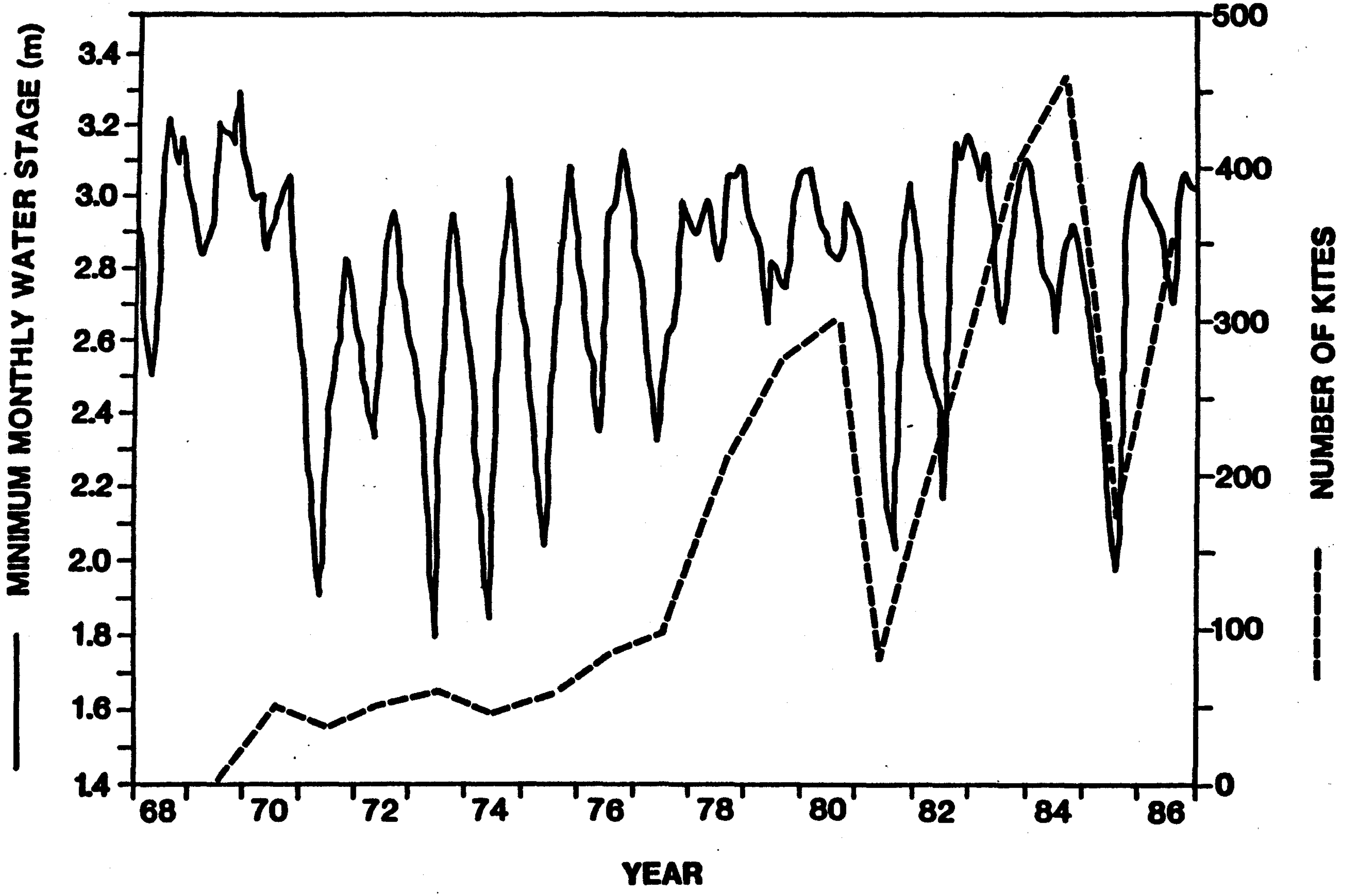


Figure 1. Minimum monthly water stage in WCA-3A (average of 3-4 and 3-28 stations) from 1968 - 1986 shown in relation to annual Snail Kite surveys from WCA-3A for the same time period. Surveys from 1968 - 1980 were conducted by the USFWS (Sykes 1983a, 1983b), and surveys from 1981 - 1986 were conducted by FGFWFC (FGFWFC unpubl. data).

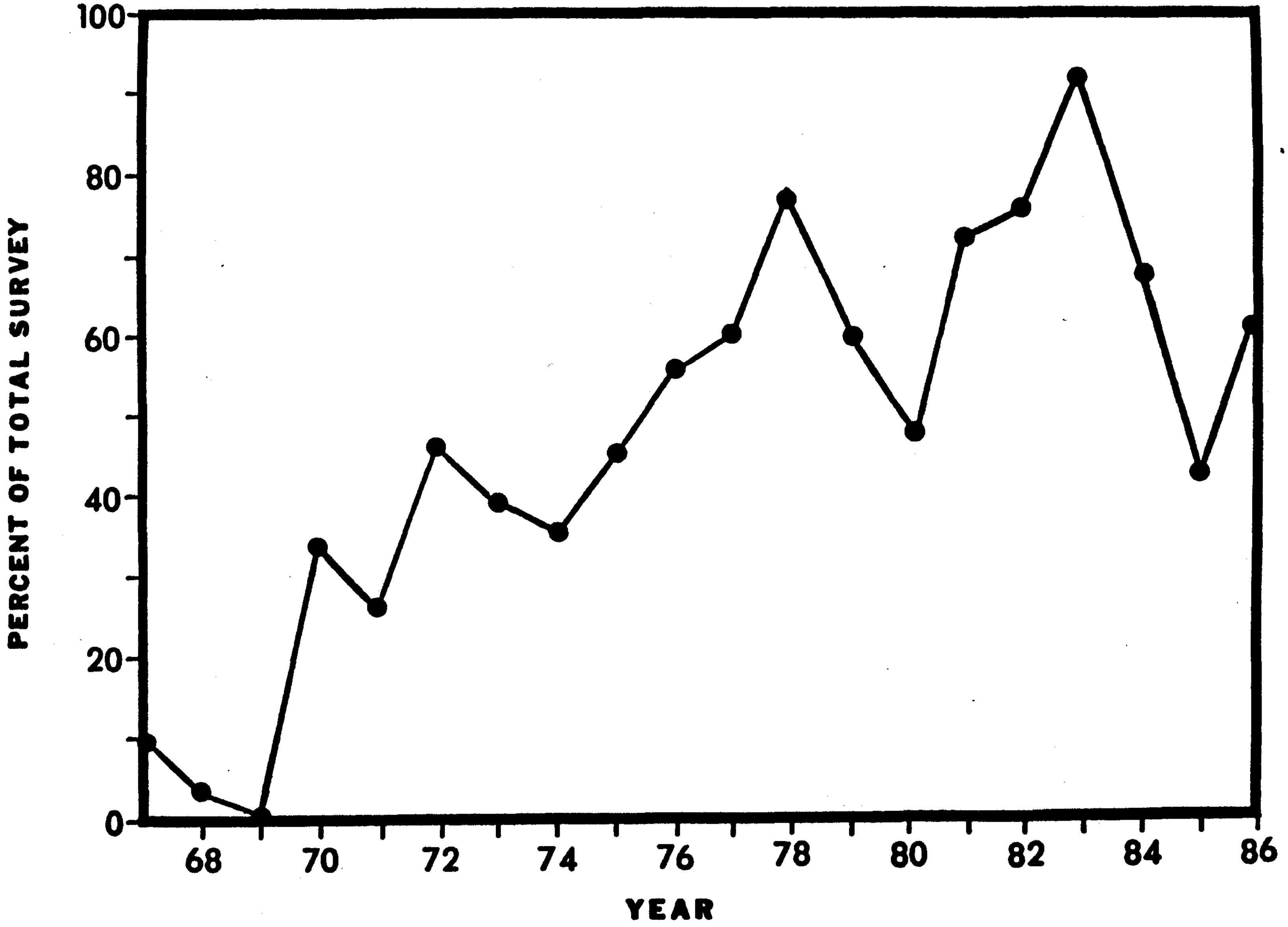


Figure 2. Percent of the total annual Snail Kite Surveys that are accounted for by kites in WCA-3A. Surveys from 1968 - 1980 were conducted by the USFWS (Sykes 1983a, 1983b) and surveys from 1981 - 1986 were conducted by FGFWFC (FGFWFC unpubl. data).

to fund this study to determine the influence of these changes on nesting Snail Kites. This report summarizes the results from that study.

The objectives of this study were to evaluate the nesting success and nest-site selection of Snail Kites during the experimental "rain-driven" water release program and to evaluate the potential impacts of the water delivery program on future nesting populations. Emphasis was placed on the effects of hydrologic conditions in an effort to evaluate the influence of the experimental release program; however, the scope of the project included examining several potential influences on the reproductive ecology of Snail Kites. We also intended for this project to provide a comprehensive data base that would assist in future management decisions related to the Snail Kite within the Everglades.

STUDY AREA

Water Conservation Area 3A is an approximately 237,000 ha impoundment that lies 25 km west of Miami and immediately north of Everglades National Park. Our primary study area was located in the portion of WCA-3A that lies south of Alligator Alley (Hwy 84) (Fig. 3) because most Snail Kite use in WCA-3A in recent years has occurred in this region (Sykes 1984).

The primary study area is dissected by the Dade and Broward County lines; the northern portion is in Broward County and the southern portion is in Dade County. The primary study area was bordered on the north by Alligator Alley, the south by Tamiami Trail (Hwy 41), the west by the L-28 levee, and on the east by the L-67A (southeast) and L-68A (northeast) levees (Fig. 4). The area slopes gradually from the northwest to southeast and ranges in elevation from approximately 2.0 m (6.7 ft) to 3.0 m (11 ft).

Vegetation

The vegetative communities of WCA-3A have been described in considerable detail by Loveless (1959), McPherson (1973), Zaffke (1983), and Tanner et al. (1987). The southern

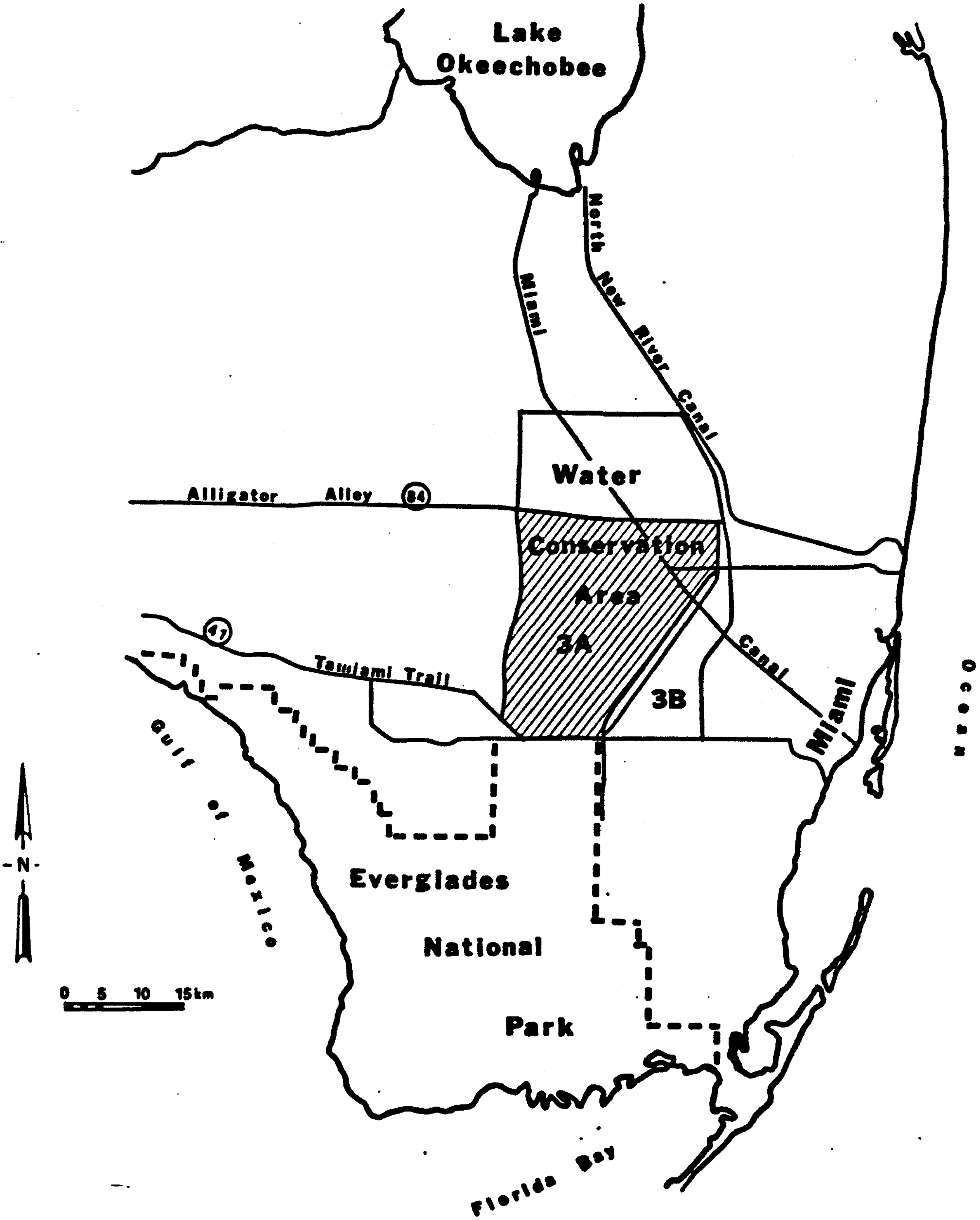


Figure 3. Location of primary study area (shaded) within WCA-3A.

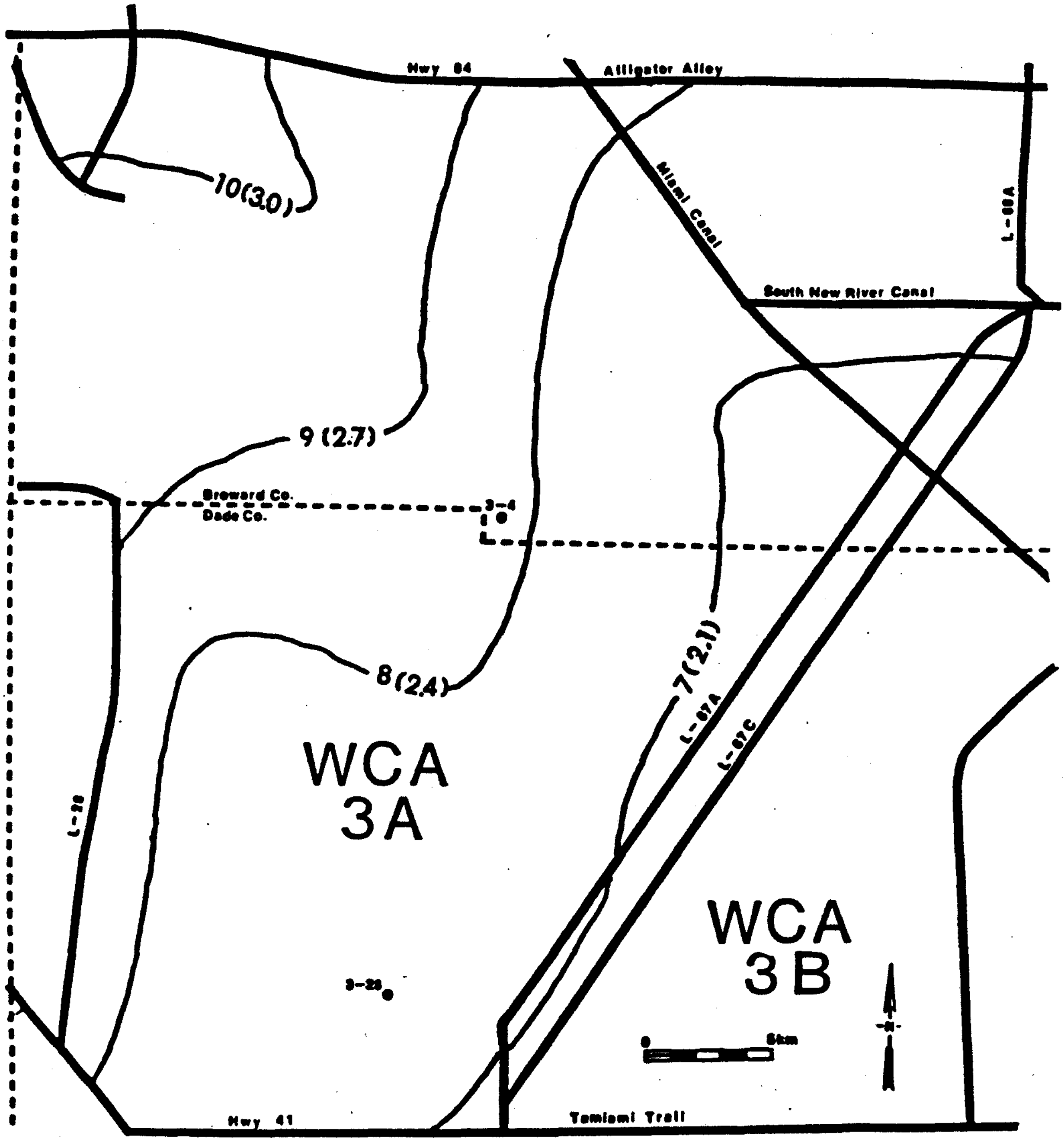


Figure 4. Water Conservation Area 3A showing levees, continuous water recording stations (3-4 and 3-28) and elevation in feet (m).

portion (Dade Co.) of the WCA-3A, except for the extreme western edge, is comprised of open sloughs (see Loveless 1959) interspersed with stands of sawgrass (Cladium jamaicensis). Tree islands of all size classes are relatively common throughout the area. Tree islands in this region are comprised predominantly of willow (Salix caroliniana), but the relatively dry northern ends of the larger islands often were of mixed species. Single shrubs of willow and pond apple (Annona glabra) are common throughout the area, but a variety of other species also occurred.

Coco Plum (Chrysobalanus icaco) and cypress (Taxodium spp) become increasingly abundant in the tree islands along western edge of southern WCA-3A; with an approximately 0.5 - 1.0 km wide strip of predominately cypress occurring along the L-28 levee. The slough communities along this western portion are largely replaced by wet prairie (see Loveless 1959) with spikerush (Eleocharis spp) becoming the predominate emergent graminoid.

Cattail (Typha latifolia) interspersed with sawgrass and open sloughs occur throughout the northeast region and the wet prairie communities are largely absent. The northeastern portion of the study area has relatively few tree islands; those few tree islands present are predominantly willow. The northwest region of the study area has relatively high proportion of wet prairie communities and numerous tree islands of mixed species.

Hydrologic and Weather Conditions

Site specific water levels may vary greatly with local features (e.g. local topography and vegetation); however, the general trend in WCA-3A is for water depths in WCA-3A to increase from northwest to southeast following the topographic contours.

The general hydrologic trend in WCA-3A is for water levels to decrease through the spring months and to increase again with the onset of daily thunderstorms, usually beginning in late May or early June (Fig. 5). The nesting seasons of 1986 and 1987 can be characterized as relatively wet compared to the long-term average.

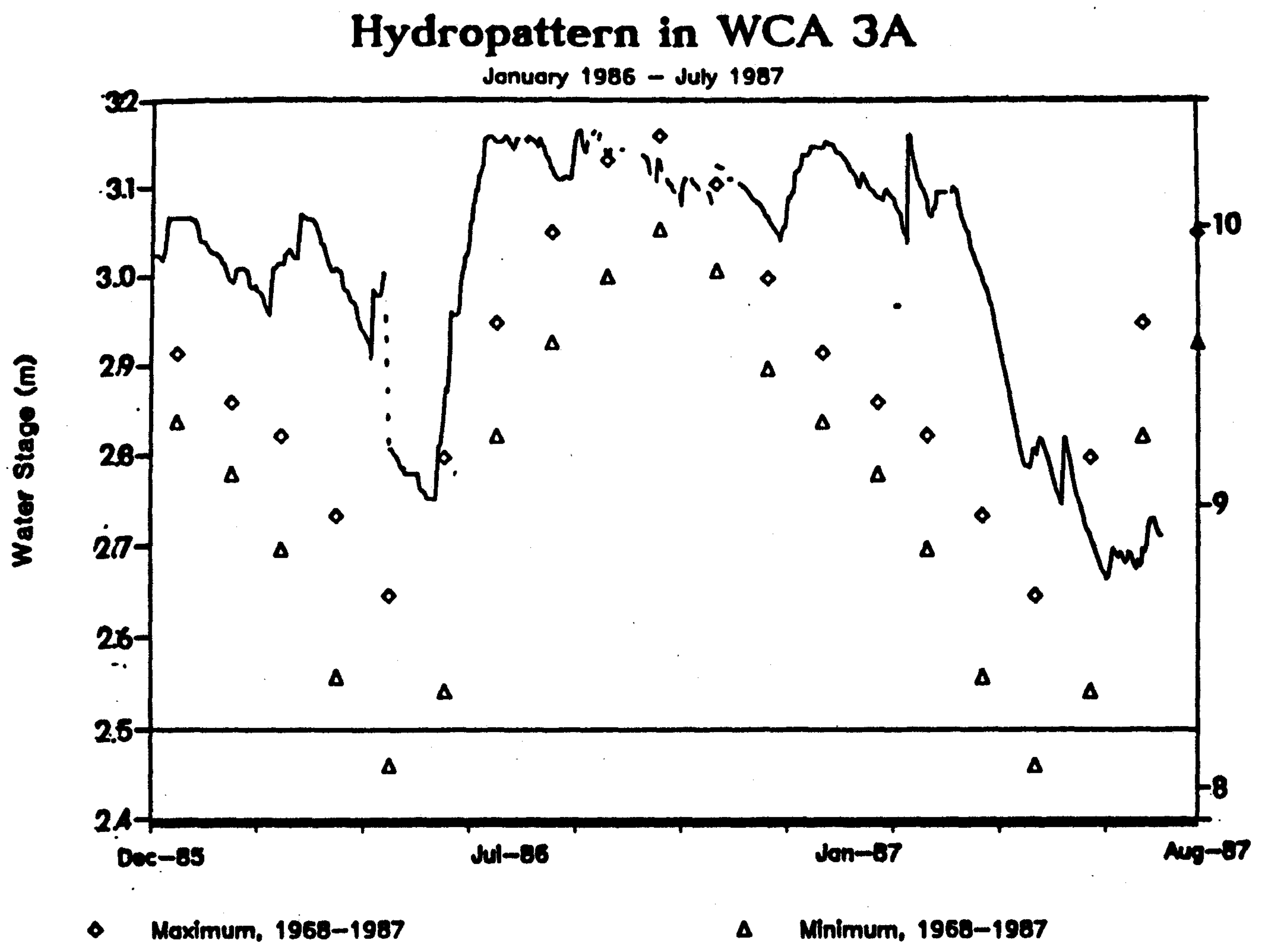


Figure 5. Stage at 3-4 water gauging station from December 1985 through August 1987, comparing actual stage with mean monthly maximums and minimums, calculated for the period of record at gauge 3-4.

During 1986 and 1987, water levels in WCA-3A declined rapidly beginning in mid-March (Fig. 6). Water levels during both years reached their lowest levels in June. As expected, water levels during 1986 increased sharply in late June and July with the onset of daily thunderstorms. In 1987, however, below normal rainfall in May and June resulted in low water levels persisting through July.

The rainfall pattern in WCA-3A generally consists of periodic storm systems through the winter and spring followed by near daily localized thunderstorms. The most notable deviation from the normal rainfall pattern (i.e. long-term average) was a storm system in March 1987 (see Fig. 7) which contributed to the month of March having over 300% more rain than the long-term average (Fig. 8).

The 1986 nesting season in general was slightly cooler than 1987, with a greater number of cold fronts occurring in March when nesting was being initiated (Fig. 9). Wind patterns generally were similar in 1986 and 1987, but a few storm systems resulted in relatively high winds in January and early February 1987 (Fig. 10).

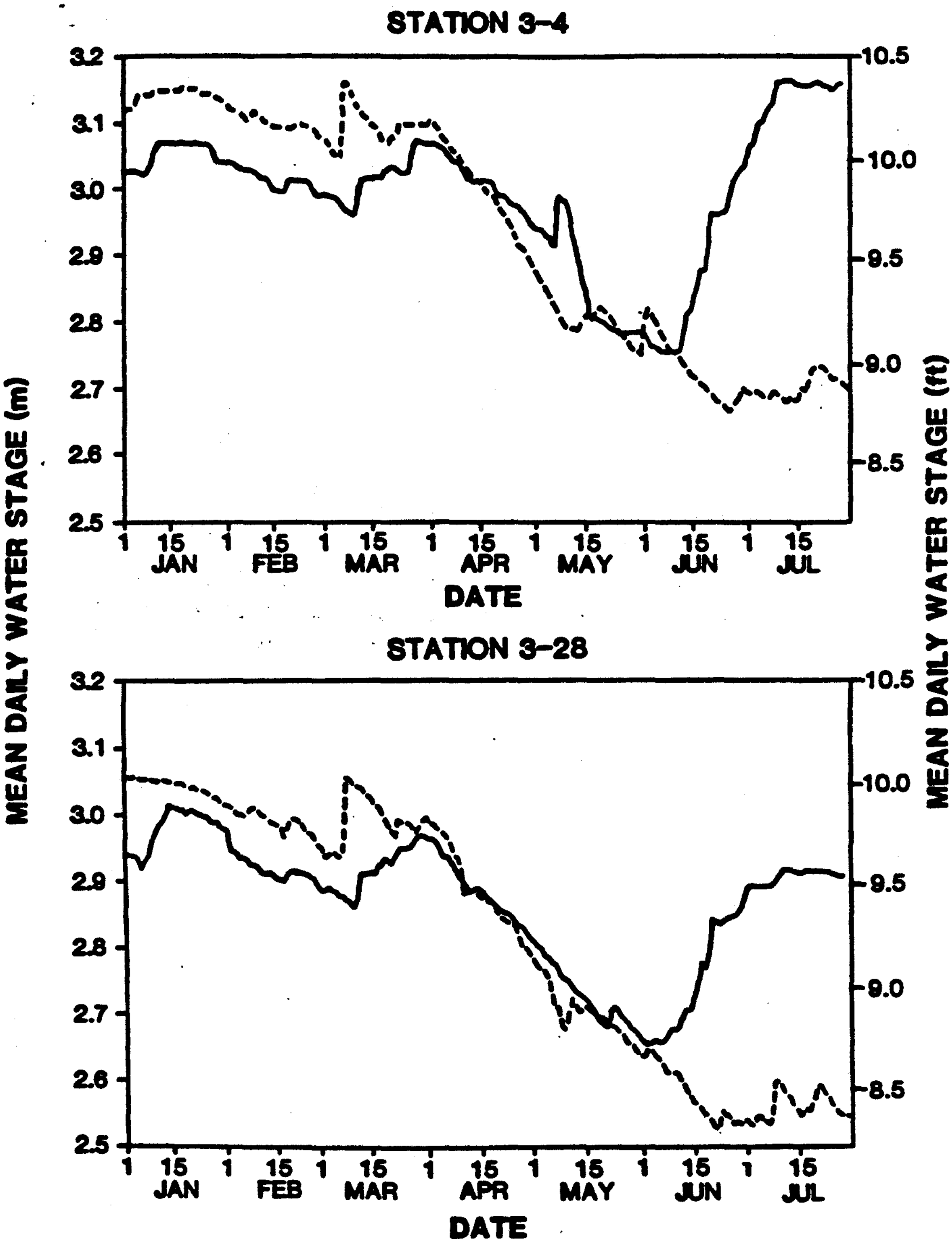


Figure 6. Mean daily water stage at 3-4 and 3-28 stations for 1 January through 31 July 1986 (—) and 1987 (--).

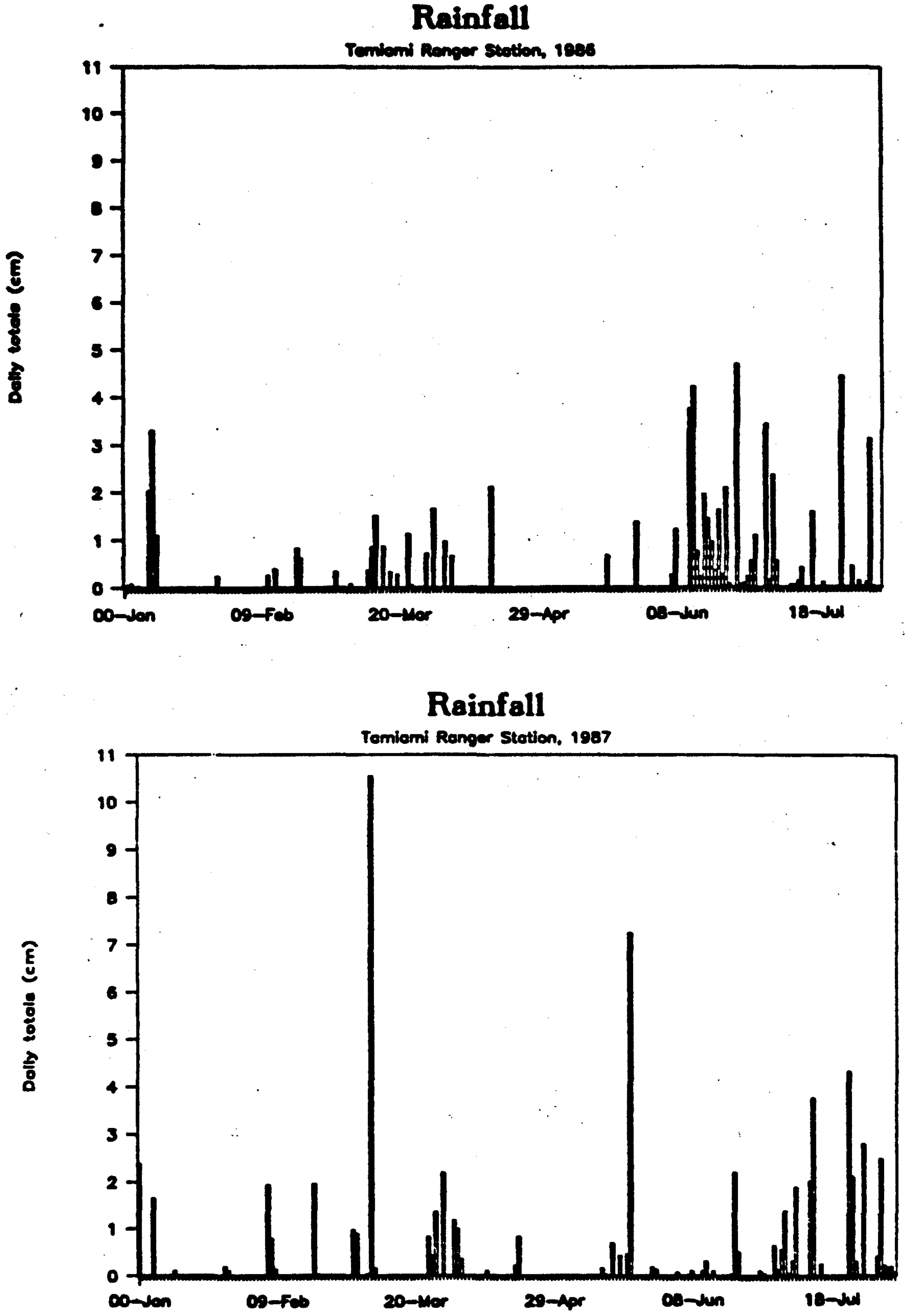


Figure 7. Daily rainfall totals at Tamiami Ranger Station in 1986 and 1987 winter/spring seasons.

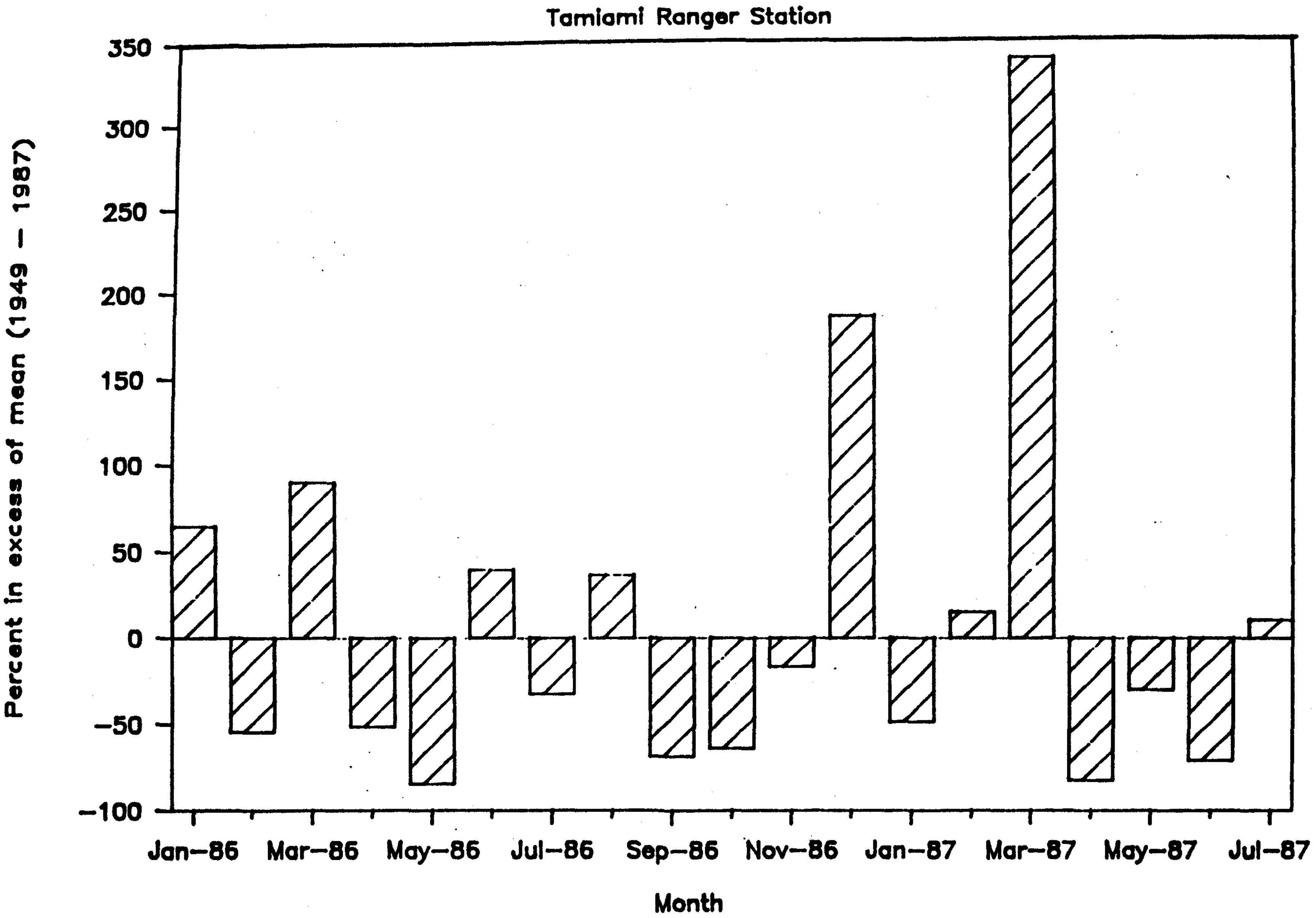
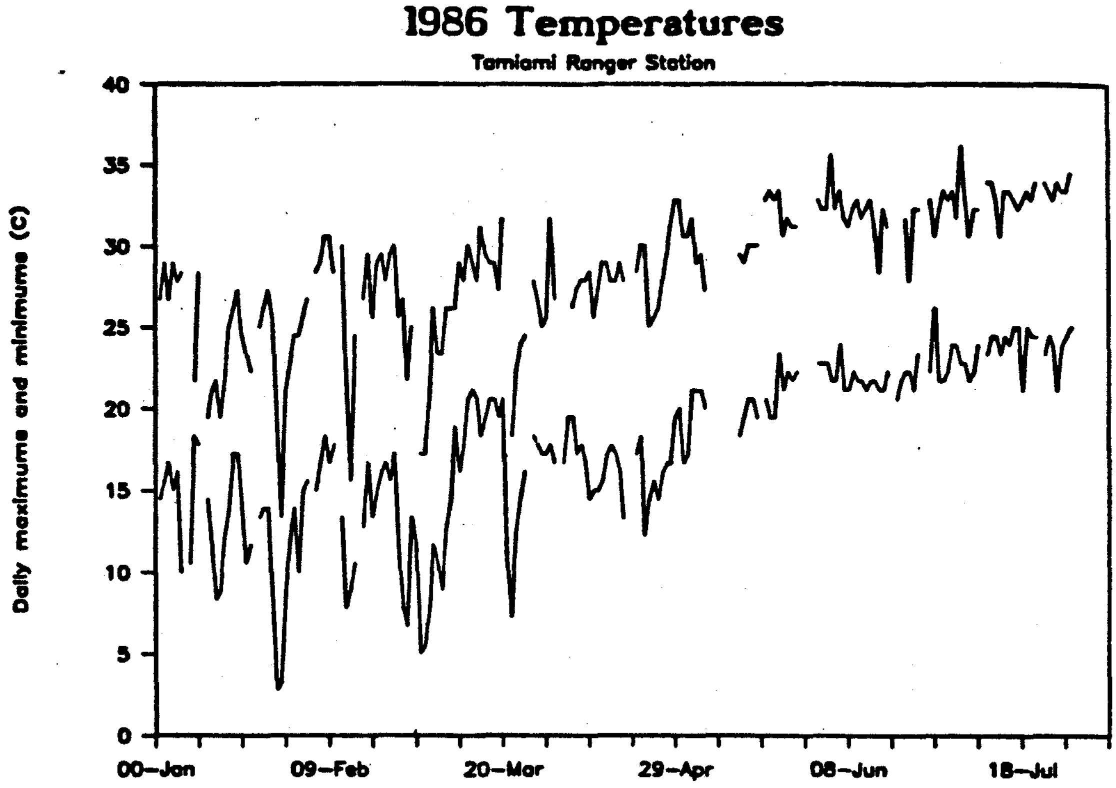


Figure 8. Monthly rainfall totals at Tamiami Ranger Station, expressed as a percent deviation from the monthly average, calculated for the period of record (1949 - 1987).



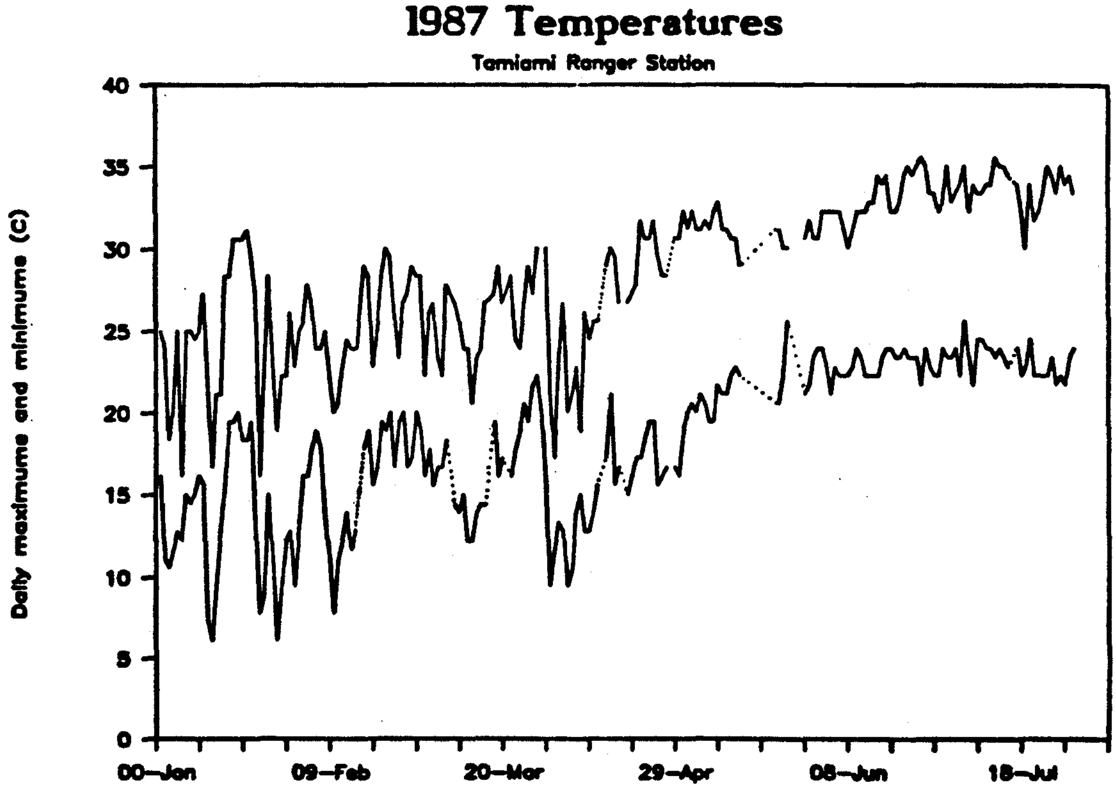
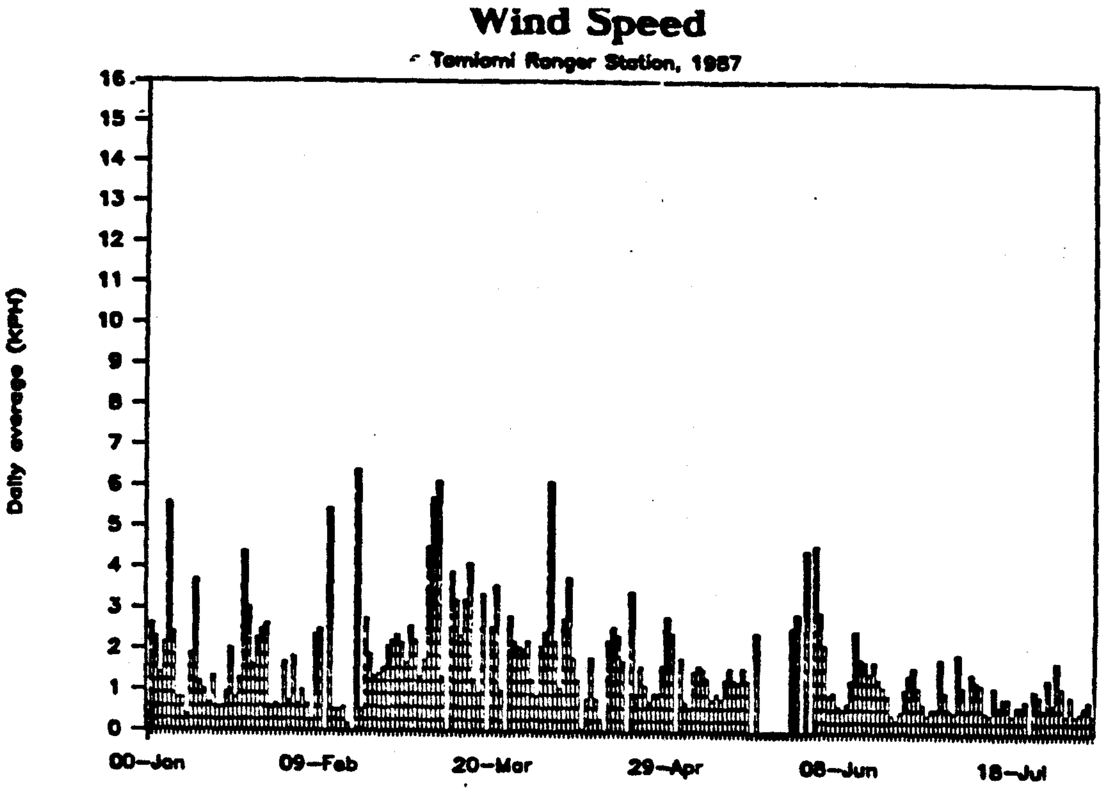
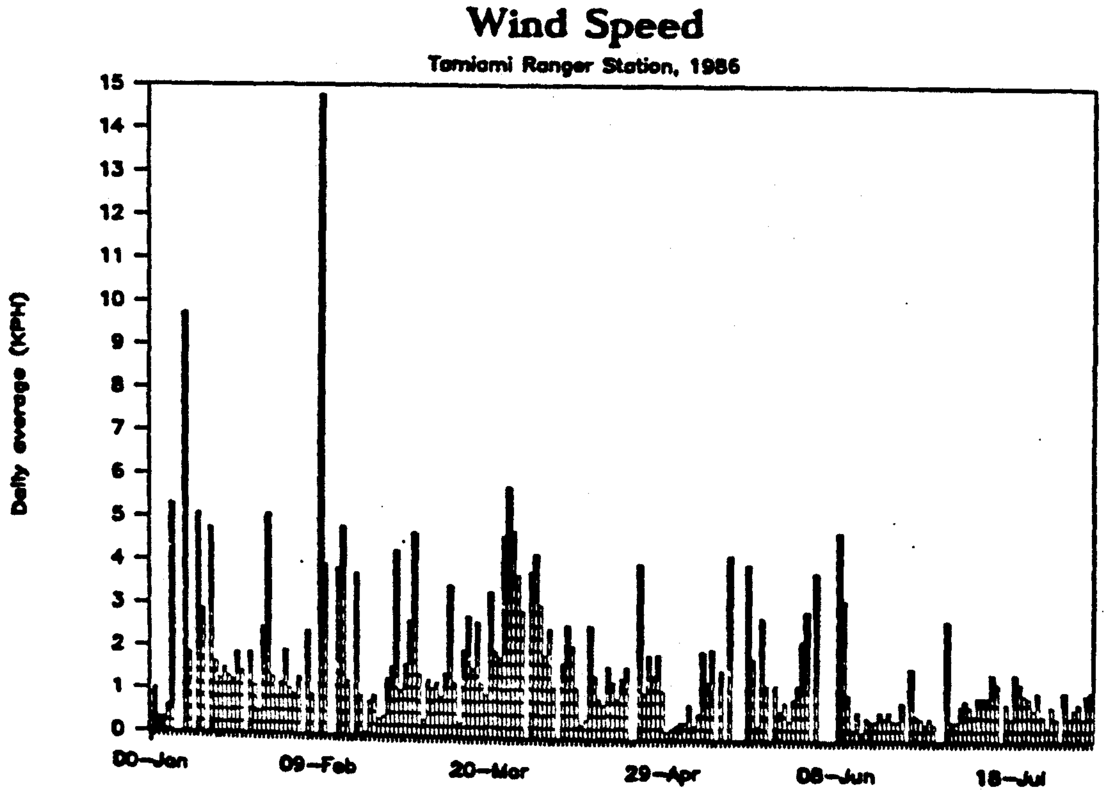


Figure 9. Daily maximum and minimum temperatures during winter/spring of 1986 and 1987, measured at Tamiami Ranger Station.





nd 1987,

Figure 10. Daily mean wind speed during spring of 1986 and 1987, measured at Tamiami Ranger Station.

METHODS

Nest Searches and Monitoring

We searched the primary study area for Snail Kite nests by systematically traversing four regions (Fig. 11). The regions were based on the location of access points and our ability to search the area within a 12-hour day. The western half of the north region dried out for much of each nesting season, and was consequently not accessible during these periods. Because of the relatively few nests found, we decreased our search effort in the entire north region during 1987 to periodic searches intended to determine any major changes in distribution.

We located nests primarily through the behavior of adult Snail Kites. When adult kites were flushed from a nest they tended to circle upward, whereas non-nesting birds that were flushed, flew more horizontally away from the boat. This behavior allowed us to find nests with relative ease by intensively searching the area from which birds exhibiting this flight pattern had departed. In addition to this flight pattern we also were able to find nests by: 1) observation of kites carrying sticks; 2) adult kites bringing apple snails to females (courtship) or young; 3) aerial courtship displays (see Steiglitz and Thompson 1967, Sykes 1987b, Beissinger 1988); 4) vocalizations of the adults or begging calls of the young (see Beissinger 1988); and 5) nest searches after repeated observations of adult birds at the same location.

The latitude and longitude of nest locations were recorded using a LORAN-C navigational unit. We found through repeated visits to the same locations that the unit was consistently accurate to within 20-30 m; however, this precision may not extend to the actual latitude and longitude values. Locations were entered into a geographical information system (GIS) data base and overlaid on to a geo-referenced satellite image from SPOT Image Corporation using the ERDAS computer system (ERDAS Inc. 1987).

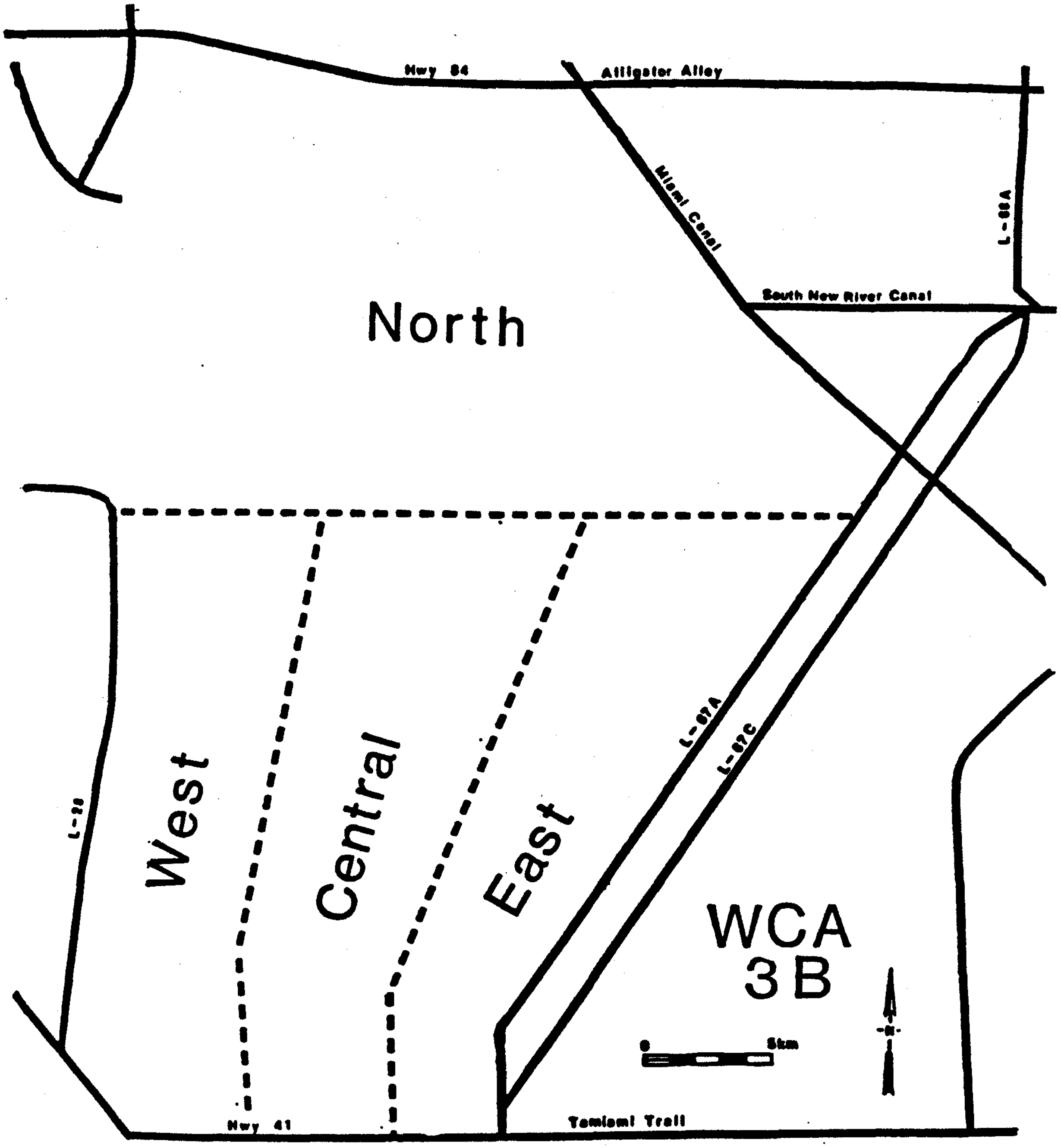


Figure 11. Diagram of the four regions of WCA-3A that we systematically searched for Snail Kite nests.

Nesting Terminology

For the purposes of this report, we generally followed the terminology suggested by Steenhof (1987). A breeding attempt was considered to begin with the laying of the first egg. An occupied nest was any nest which was actively being attended by adult Snail Kites, regardless of whether breeding had been initiated. A breeding pair was a mated pair of Snail Kites in which the female had laid at least one egg. Because Snail Kites are sequentially polygamous (Beissinger and Snyder 1987) and iteroparous (Beissinger 1986), an individual adult kite may have been a member of more than one breeding pair during one nesting season. When referring to a nest (rather than the breeding pair), we considered a nest active if breeding had been initiated (i.e. at least one egg had been laid) (Postupalsky 1974).

Nesting success was defined as the proportion of active nests from which at least one young survived to fledging age. Because of the difficulties in determining if a nest was successful after the young began flight, we considered fledging age to be 80% of the average age at first flight (Steenhof and Kochert 1982). Although the reported age of first flight is variable (see Nicholson 1926, Steiglitz and Thompson 1967, Chandler and Anderson 1974, Beissinger 1988) we found that Snail Kites generally were capable of first flight and often left the nest at 30 days. We therefore considered a nest successful when at least one young reached 24 days old (80% of 30 days). This approach assumes that nestling mortality between 24 and 30 days is negligible, but reduces the potential to mistakenly identify a nest that fledged young as having failed. We made no attempt to assess nesting success prior to the laying of the first egg or after the young reached fledging age.

Habitat Selection

At each nest site we placed a water gauge which was read on each subsequent visit to the nest (approximately every 7 to 10 days). Estimates of nest-site water depth at the time breeding was initiated was obtained directly from nests located during that period; nest-site water depths for those nests found after breeding had been initiated were estimated using a regression equation relating water depths at the nest-site and the nearest continuous gauging station. P. Frederick (pers. comm.) used this method and found that the correlation between sites in southern WCA-3A and these continuous recording stations usually had r^2 values greater than 0.90. We made no attempt to estimate the water depth at time of breeding initiation for nests that we could not estimate the time that the first egg was laid.

The average frequency at which nesting areas dry out was estimated by the number of years that the minimum water stage recorded at gauges 3-4 and 3-28 fell below the elevation range within which we found Snail Kite nests. This provided an average interval between dry downs expressed in years. A similar approach was used to estimated the dry down interval of other areas within the Everglades. In these other areas, however, we estimated the elevation range from reported nesting distributions and used the closest continuous water recording station to determine an approximate dry down interval.

The proportion of open water in areas that were used and not used for nesting was determined using a satellite image from SPOT Image Corporation. The image used was a composite of multi-spectral and panchromatic bands with pixel resolution of 10 m^2. The image was classified using training fields of known habitat types (Jansen 1986) and compared with low level (300 m) aerial photographs of known areas for accuracy. We concentrated our classification on distinguishing sawgrass from open water. Habitats that that were functionally similar to Snail Kites (e.g. sloughs with different species of floating vegetation) were combined in the final classification. We did not attempt to distinguish the species composition of tree islands.

Due to available imagery and our current computer capabilities we were able to classify only a portion of WCA-3A (Fig. 12). The portion we classified, however, contained

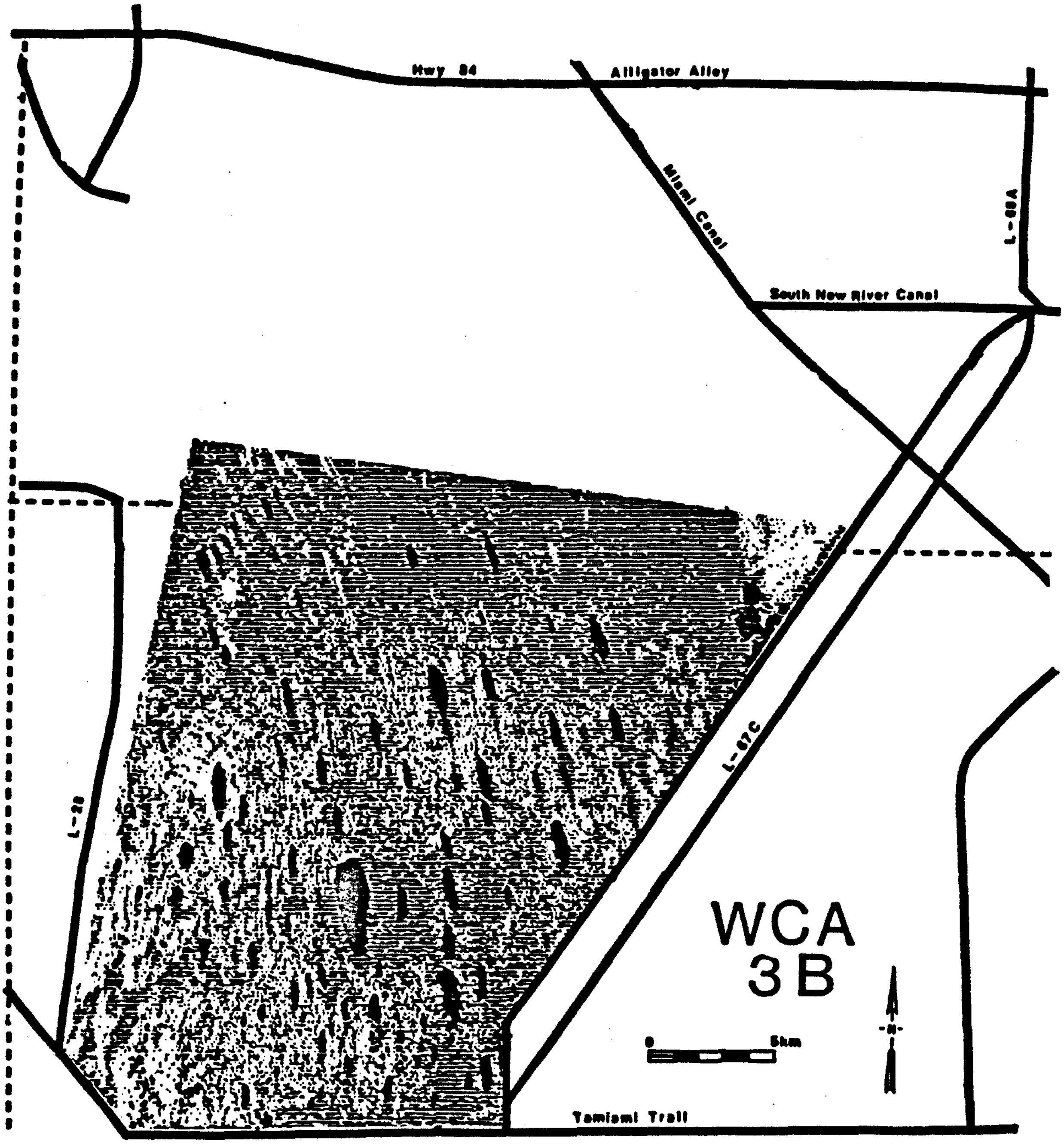


Figure 12. Boundaries of WCA-3A, showing the portion which we classified using satellite imagery for habitat analyses.

approximately 80% of the nest locations in WCA-3A. We therefore believe it reasonably represents the nesting habitat of kites in WCA-3A.

Based on approximately 105 hrs of observation including 184 prey captures by nesting Snail Kites, we estimated the average foraging range extended 1 km from each nest site. We used the search function of the ERDAS computer system (ERDAS 1987) to delineate a 1 km radius around each nest site. The proportion of open water to sawgrass was then assessed using the BSTATS function of ERDAS (ERDAS 1987) within polygons of areas that were used and not used by nesting kites. Areas of overlapping (i.e. < 2 km from the closest nest) use were included within each polygon. Nesting areas that were a minimum of 2 km from the closest nest (i.e. did not overlap) were considered a separate polygon. The proportion of open water to sawgrass was compared between areas that were used for nesting (i.e. use polygons) and continuous areas that were not used for nesting by Snail Kites (non-use polygons), but were within the overall distribution of kites in WCA-3A. We also compared the proportion of open water to sawgrass between areas that were used for nesting and areas that were outside of the distribution (i.e. above the elevation range within which we found all nesting kites) of nesting kites.

We estimated apple snail abundance during 1987 using three separate measures. We used two indices (capture time and egg cluster counts) at each of eight nesting areas with a 1 km radius that were centered around nests or colonies; four in areas of high kite nesting density and four in areas of low nesting density (Fig. 13). An area was considered high nesting density if it had an accumulative total of at least 10 occupied Snail Kite nests for the season. An area was considered low nesting density if it had an accumulative total of no more than 5 occupied nests for the season. Some nests in these areas probably went undetected; however, because our search effort and observation time in these areas was extensive, it was unlikely that we had overlooked enough nests to mis-classify an area.

One area of high and low nesting density each were observed simultaneously by two observers over a three to four-day period. These simultaneous observations were intended

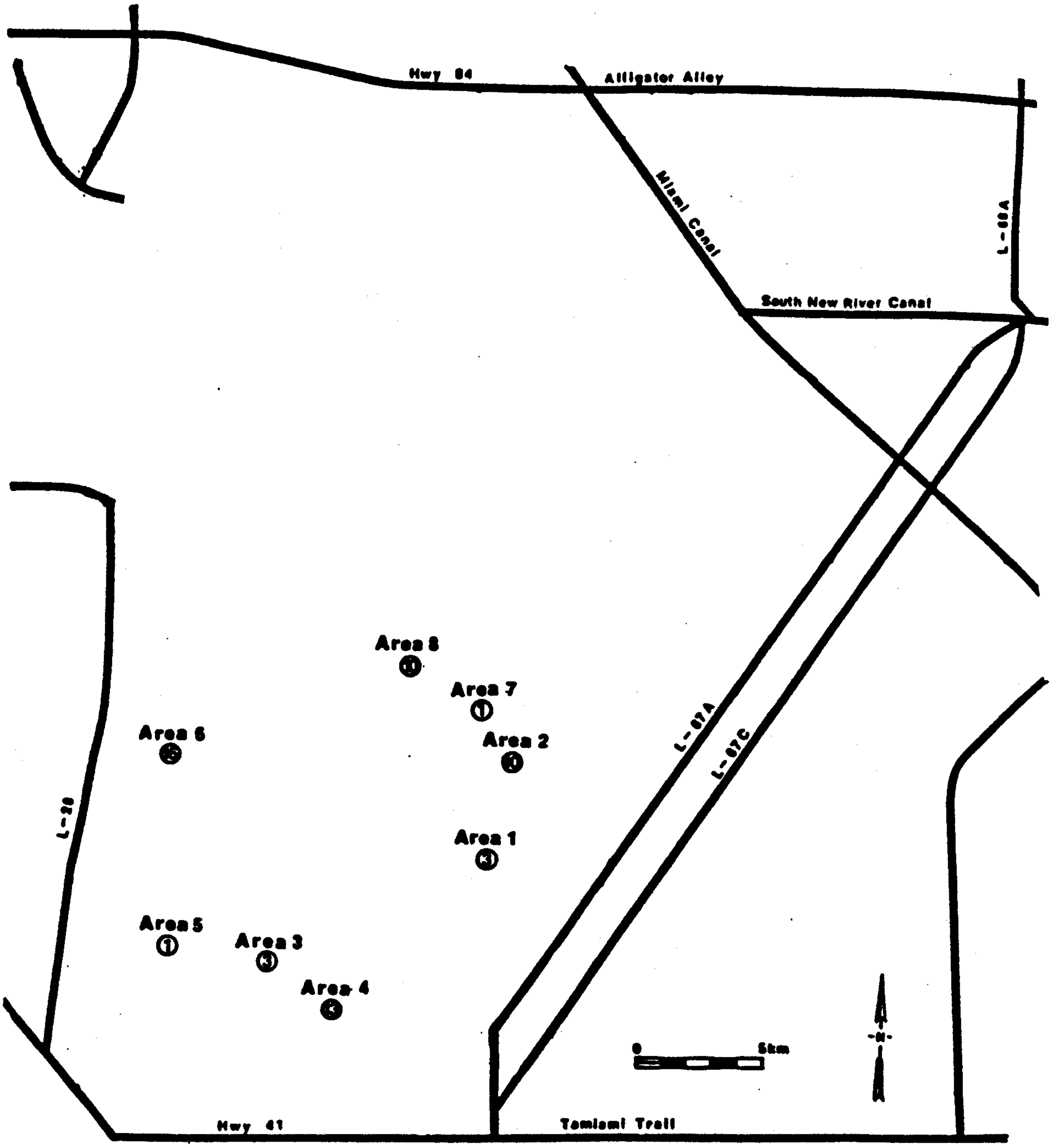


Figure 13. Location of nesting areas in WCA-3A in which we sampled apple snails. Shown within the circles are the estimated number of Snail Kite nests that occurred in the area during 1987.

to minimize the influence of seasonal environmental changes that could influence kite foraging behavior or egg laying by apple snails. Foraging observations were conducted between the hours of 0900 and 1200 to minimize the influence of daily temperature changes on foraging behavior.

Capture time was measured as the interval (in seconds) from when a Snail Kite left a perch and commenced foraging until a snail was captured. In order to maintain comparable samples, we did not sample any areas in cypress habitat where still-hunting was a common foraging method. In all of the areas we sampled, kites primarily foraged by flying low over the marsh until apple snails were detected (see Sykes 1987a, Beissinger in press). Consequently, only actual flight time was included in the total time to capture a snail. In the event that a kite perched before capturing a snail, the time was stopped and continued when the kite resumed foraging.

Egg cluster counts were conducted by traversing the high and low density nesting areas along east/west transects. The first transect began approximately 1 km north of the nest or colony. At the end of each transect, we looked at the second hand of our watch and moved to the south 10 times the number of seconds displayed by the second hand to begin our next transect. We repeated this procedure until the nesting area had been completely traversed. Because the slough systems are oriented north/south, our transects frequently crossed sawgrass/open water edges. Each time we crossed a sawgrass/open water edge we counted the number of egg clusters using a 1 x 2.5 m PVC frame that was flipped end over end four times. This resulted in sampling a strip that was 1 x 10 m. Because we suspected that the number of egg clusters present was influenced by the proximity to the sawgrass edge, at each edge we sampled a strip on the edge, 7.5 m into the sawgrass from the edge, and 15 m into the sawgrass from the edge.

We developed an egg cluster index based on the number of egg clusters on the edge and within the interior sawgrass that accounted for how much edge habitat was within the nesting area. Based on the distribution of egg clusters in relation to the sawgrass edge

(Fig. 14), we calculated an egg cluster index as:

$$ECI = C_eP_e + C_iP_i$$

where C_e is the mean number of egg clusters per 10 m from the edge samples, P_e is the proportion of the sawgrass area that is along a sawgrass/open water edge, C_i is the mean egg cluster count for the interior sawgrass samples, and P_i is the proportion of the sawgrass area that is not along an open water edge. This procedure weights the egg cluster counts by the amount of edge habitat within each nesting area. Our sampling showed that the number of egg clusters was higher along the sawgrass/open water edge, but that there was little difference between the samples taken at 7.5 m and 15 m from the edge.

We estimated the proportion of edge to interior sawgrass from satellite imagery using the BOUNDRY program of the ERDAS computer system (ERDAS Inc. 1987). This program identifies when pixels classified as sawgrass are adjacent to pixels of open water. The relative areas could then be calculated using the BSTATS program (ERDAS Inc 1987). Because of the resolution of the image, only areas of sawgrass or open water of at least 10 m^2 would have been included in this analysis. We believe this level of resolution was acceptable since most kite foraging occurred in sloughs considerably larger than 10 m^2.

In addition to the two indices of snail abundance we used one direct measure of snail abundance. This method was a modified version of a technique described in detail by Brook (1979) and adapted for sampling apple snails by Owre and Rich (1987). The technique involves the use of a portable suction dredge which was powered by a Honda 3.5 hp pump (see Owre and Rich 1987 for details of the pump and its operation). Water and the substrate (e.g. peat) are sucked via a probe into a large (6mm) meshed collecting bag. Snails were then sorted from the substrate and counted.

Whereas Owre and Rich (1987) estimated that 100 probes into the substrate covered an area of 0.5 m (based on the diameter of the probe), we used a 1 m^2 wire mesh frame that extended vertically to above the water surface and had steel prongs (made from a barbecue grill) that extended approximately 10 cm into the substrate. This enabled us to sample a

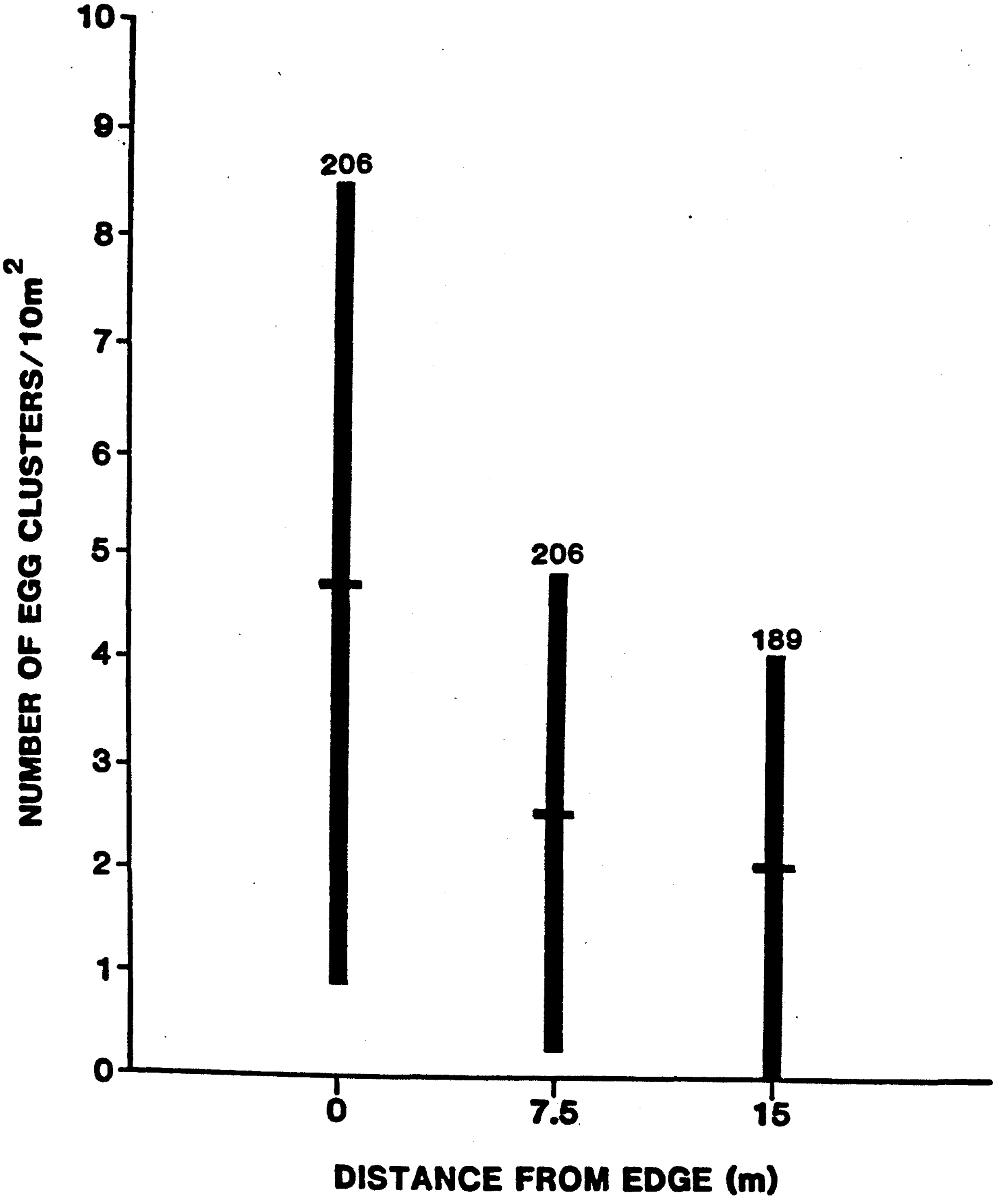


Figure 14. Mean apple snail egg cluster counts (± SD) along the sawgrass/open water edge and within the interior c the sawgrass stand. Sample sizes (i.e. no. of plots) are shown.

completely contained 1 m vertical column, which we sampled down to a depth of 8 cm into the substrate. The emergent vegetation within the 1 m column was first removed and searched by hand. This enabled us to suck the entire substrate down to 8 cm without interference from vegetation.

Because this method is relatively labor intensive (a 3-person crew could sample a maximum of approximately twenty, 1 m^2 plots per day), we only were able to sample one area of high nesting density (area 6) and one of low nesting density (area 5). In order to control for the influence of vegetation, all of our samples were take approximately 1 m into the slough from the sawgrass edge. The plot locations were selected randomly within the nesting area by observing the second hand on a watch and traveling along the sawgrass edge via airboat for 10 times the number of seconds shown on the watch.

Nest Site Selection

We compared the relative use of nesting substrates to their availability for nest sites in stands smaller than 100 m^2. We hope to include larger stands in this analyses at a later date using satellite imagery; however, without extensive ground-truthing, we are currently unable to classify tree islands by species. We measured nest site availability of stands smaller than 100 m^2 in southern WCA-3A below 25.9^o latitude. This area includes approximately 60% of the nests we observed. We did not measure availability in the entire area because of the extensive sampling time required and because much of northern WCA-3A was dry (i.e. inaccessible) at the time of our sampling.

Using a LORAN C navigational unit, we traversed southern WCA-3A and counted the number of stands less than 100 m^2 of each species within a 100 m radius of the intersection of each minute of latitude and longitude. We estimated the 100 m radius using a Leitz rangefinder. We did not attempt to measure surface area of the nesting stands. Consequently, the availability of species occurring in larger stands (e.g. willow) would be under represented.

Nest Success and Productivity

The Mayfield Method (Mayfield 1961, 1975, Miller and Johnson 1978, Johnson 1979, Hensler and Nichols 1981, Hensler 1985) was used to calculate nest success because it has several advantages over traditional measures (i.e. no. successful nests/no. nests observed). Essentially we chose this method for two reasons; first, unless all nests are found on the first day of the nesting period, traditional success estimates are biased (Hensler 1985) and tend to overestimate success (Mayfield 1975). Secondly, the Mayfield estimate of success is better suited to statistical comparisons than traditional methods (Miller and Johnson 1978).

The Mayfield Method requires that nests be checked at intervals throughout the nesting cycle. We visited nests at approximately 7 to 10 day intervals. The failure date for nests that failed between intervals was assumed to be the midpoint between the last two nest visits. Johnson (1979) found this assumption was reasonable when intervals between nest visits did not exceed 15 days.

An inherent assumption of the Mayfield Method is that nests fail at a constant rate throughout the nesting period (Hensler and Nichols 1981, Hensler 1985). This assumption may not always be valid (Green 1977). We assessed the assumption of constant failure in two ways. The first was to test for differences in the failure rate of nests between the egg and nestling stages during each year. The second method of assessing the assumption of constant failure was to construct survivorship curves from nests found during egg laying. These curves were calculated as the proportion of observed nests surviving each day. As with our Mayfield calculations, the midpoint between the last visit when the nest was viable and the first visit after the nest had failed was assumed to be the day of failure.

number

Based on our results, we used separate estimates for the incubation and nestling stages, but believed that differences within stages were slight and did not warrant further separation. Our overall success estimates were derived by combining the separate incubation and nestling estimates in accordance with the procedures described by Hensler (1985).

Hensler and Nichols (1981) demonstrated that the Mayfield estimate is a maximum likelihood estimator (m.l.e.) for which statistical analyses for the asymptotic distribution are appropriate. Formulae for calculating nest success and the corresponding statistical analyses are provided in Appendix 1. Tests of significance between groups were performed using a standard normal test.

We compared nest success in relation to several environmental and nest-site variables. Nest success for the entire nesting period (overall success) was used for comparisons among variables having one value per nest (e.g. nest substrate and nest height). We used daily nest survivorship in comparisons of nest success among variables having values that changed throughout the season (e.g. water level and weather).

We partitioned the nesting season into three equal 36-day periods (early, middle, and late season) based on the range of dates in which nests were initiated. We then compared nesting success between nests in which the first egg was laid within each of these 36-day periods. The early period was from 31 January through 6 March. The middle period was from 7 March through 12 April. The late period was from 13 April through 19 May. Nests for which we could not estimate the date of initiation were excluded from these analyses.

We also compared nesting success between nests that were located in each of the four major substrates (willow, pond apple, cypress, and melaleuca) and of varying nest height and distance to land. Sample sizes were insufficient for analyses among the lesser-used nest substrates.

We compared daily nest survivorship of nests while they were in each of three water level classes (< 25.0 cm, 25.1-50.0 cm, 50.1-75.0 cm). We considered a nest to have been in a given water level class for an observation interval if the water depth at the nest remained within that class on the nest visits at the beginning and end of the observation interval and if the continuous water recording stations did not show water level changes that would indicate that the water depth could have crossed into a different depth class. Observation intervals in which water depth crossed from one depth class to another were not used in the analyses. This approached eliminated the possibility that a given observation interval was arbitrarily assigned to a depth class at the cost of a reduction in sample size.

Because we did not have weather instruments at each nest site, the influence of weather variables was compared based on averages recorded at the nearest continuous station (an average of gauges 3-4 and 3-28 for rainfall, and Tamiami Ranger Station for temperature and wind). We compared daily survival of nests based on daily averages (e.g. of rainfall) recorded between each nest visit.

The relative importance of how environmental and nest-site characteristics influenced nest success was assessed using stepwise logistic regression. We used the LOGIST procedure of SAS (Harrell 1980) to develop a model for each year (and one for combined years) that best discriminated successful from unsuccessful nests. The variables that were entered into the analyses are summarized in Appendix 2, and those having an initial Chi-square value of < 0.05 were entered stepwise into the model by order of highest initial Chi-square value (Harrell 1980).

Comparisons between years of clutch size and the number of young fledged were made using Chi-square contingency tests. Hatchability within clutch sizes was compared using Mann-Whitney tests.

We considered a clutch complete only after the maximum number of eggs observed was maintained for at least one nest visit after the maximum number was reached (i.e. no egg loss was observed). Nests in which we detected egg loss before our second visit, regardless of the number of eggs, were not presumed to have been complete.

RESULTS

Distribution of Nesting Snail Kites

Snail Kites were distributed throughout the south and western portions of WCA-3A (Fig. 15). The overall nesting range in WCA-3A did not markedly differ between 1986 and 1987; however, the distribution of nests within that range was patchy and varied between years. Some areas where kites nested in 1987 were not used in 1986 and some areas used in 1986 were not used in 1987. The most notable area that was used in 1986 but not 1987 was a large willow head along the northern portion of the L-67 levee. We monitored six nests in this area during 1986 and we suspect that several more were undetected. During 1987, we observed one kite in the area, but found no indication of nesting activity. Several areas, particularly within the south-central portion of WCA-3A were used in 1987, but not in 1986. Because we traversed the entire area searching for nests (see methods) during both years, we do not believe that differences in distribution were attributable to sampling bias.

The range of nesting within WCA-3A tended to occur within 2.1 m (6.8 ft) and 2.5 m (8.2 ft) elevation (Fig. 16). Steiglitz and Thompson (1967) also reported that Snail Kite nesting distribution corresponded with an elevational gradient at Loxahatchee National Wildlife Refuge. The nesting range tended to extend toward slightly lower elevations (i.e. deeper water) in 1986 and slightly higher elevations (i.e. shallower water) in 1987.

The distribution of nesting Snail Kites during 1986 and 1987 differed from the historic distribution reported by Sykes (1984) for 1968 through 1980 and the more recent distribution of successful nests reported by Beissinger (1983a) for 1983 (Fig. 17). We found considerably more nesting activity in the south-western and south-central regions of WCA-3A than has previously been reported.

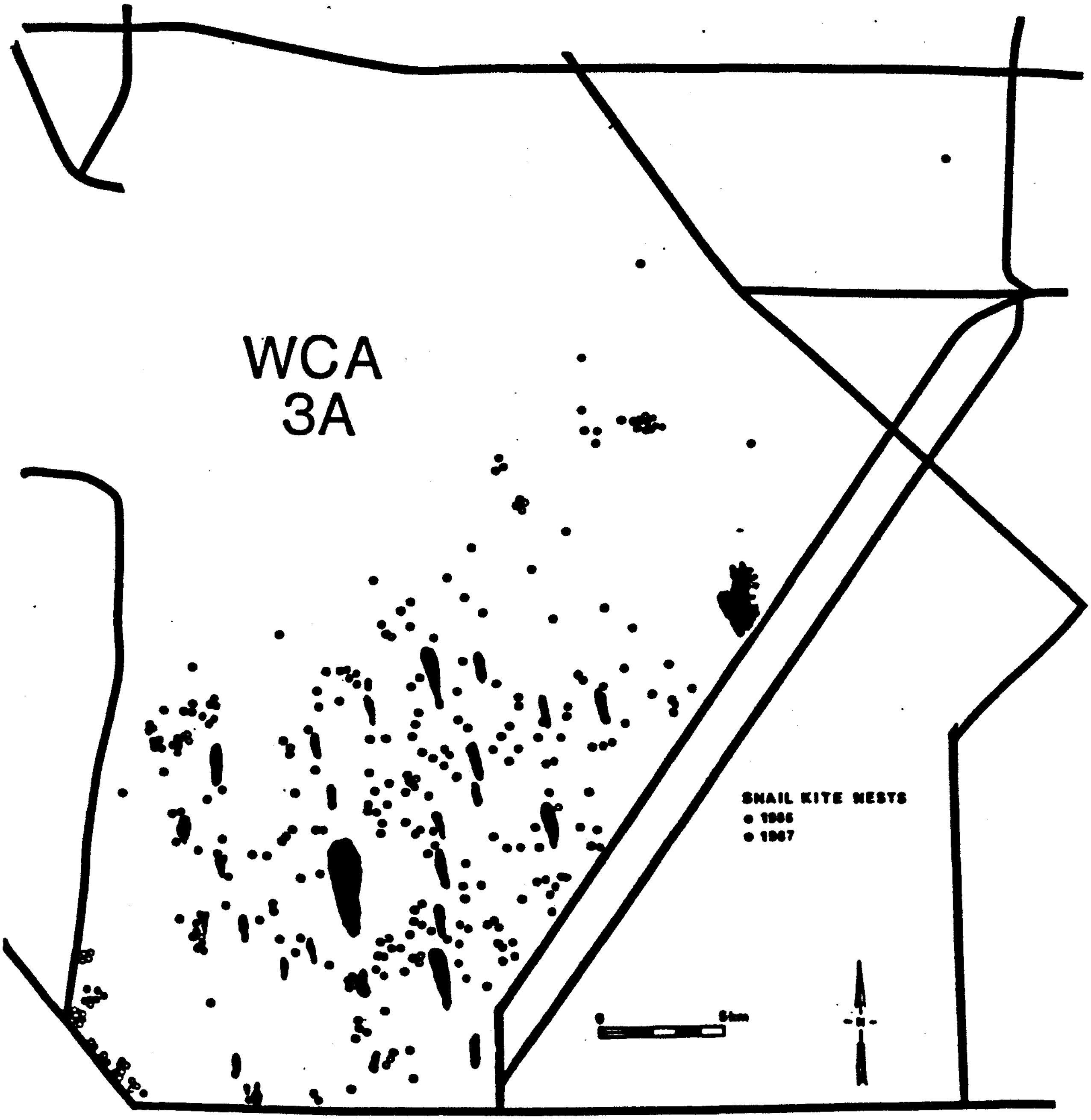


Figure 15. Distribution of nesting Snail Kites in WCA-3A during 1986 (N=148) and 1987 (N=227). Major tree islands within the nesting distribution are shown for reference.

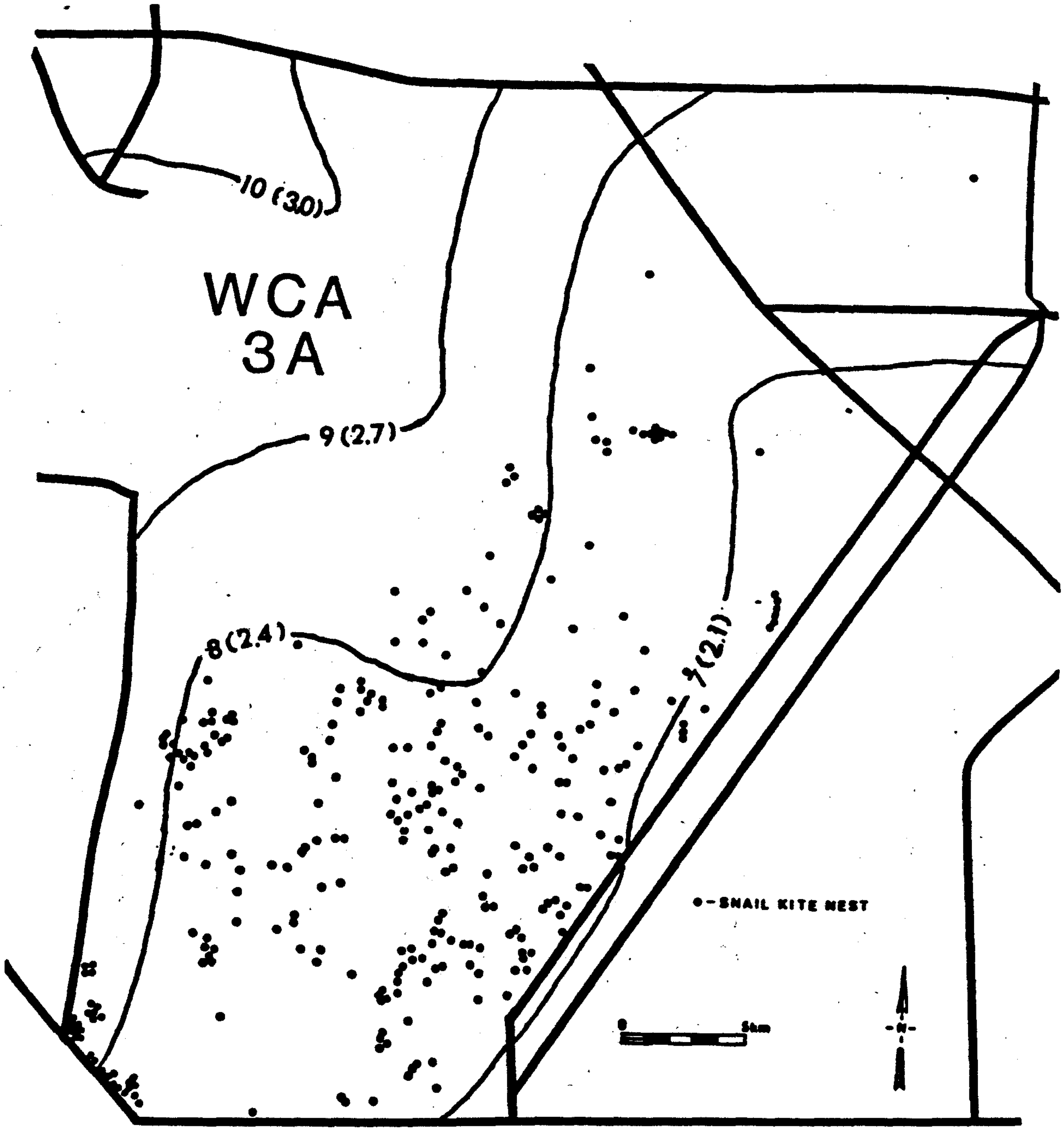


Figure 16. Distribution of nesting Snail Kites in WCA-3A during 1986 and 1987 in relation to topography (1 ft [m] contour intervals).

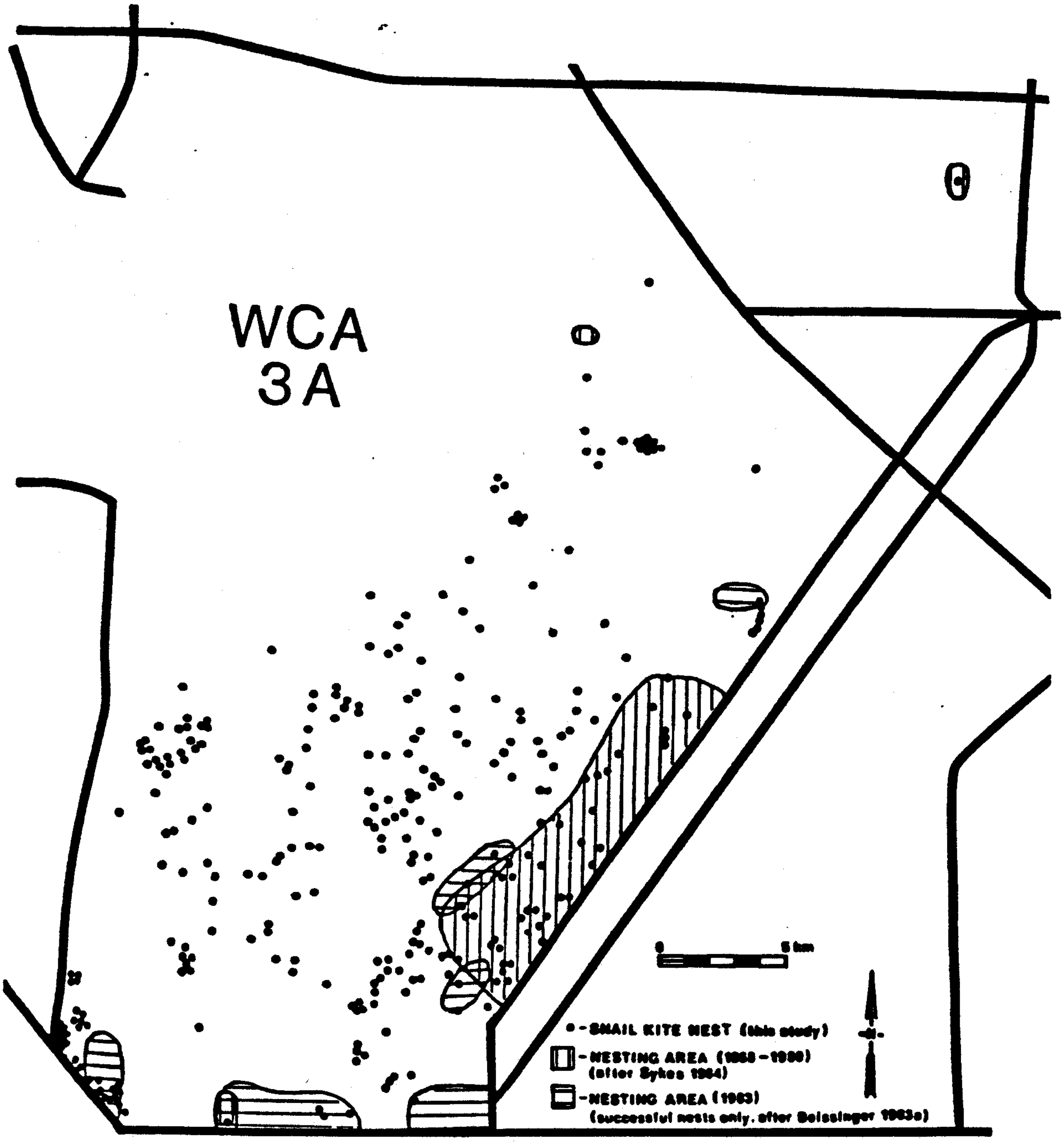


Figure 17. Distribution of nesting Snail Kites in WCA-3A during 1986 and 1987 in relation to the nesting areas reported by Sykes (1984) and Beissinger (1983a, successful nests only).

ation

Habitat Selection

Water depth.-- We were able to estimate the water depth for the time that breeding was initiated (i.e. when the first egg was laid) for 281 nests. At this stage of breeding, almost all nests were over water (280 of 281 nests), and most sites (94% of 281 nests) had water depths ranging from 20 - 80 cm. In only one case during 1986 and 1987 did we encounter a nest that was built over dry land. This nest was built within an ongoing kite colony that recently had dried out directly under the nest trees. The surrounding sloughs of this colony, however, were completely inundated. Water depth at nest sites during the initiation of breeding ranged from 0 to 75 cm in 1986 and from 21 to 105 cm in 1987 (Fig. 18). Mean depth at the time of initiation was lower in 1986 ($x = 41.22$, $n = 96$) than in 1987 ($x = 49.63$, $n = 185$) ($t = 4.69$, $P < 0.01$).

Although most nests were initiated in areas with water depths ranging from 20 - 80 cm, considerable fluctuation in depth occurred throughout the season. A prolonged drying trend occurred during both years from March through May (Fig. 19). A strong increase in water depth resulting from daily thunderstorms occurred in June of 1986. In 1987, however, below normal rainfall during early summer resulted in low water levels persisting through July.

Water depths at nest sites usually were shallower, by 10 cm or more, than depths in the surrounding open water sloughs where the kites often foraged. This resulted from kites nesting within inundated tree islands or sawgrass stands which often were 10 cm or more higher elevation than the surrounding sloughs (see also U.S.D.I. 1972, McPherson 1973, Worth 1983). As a consequence of higher elevation, some nest sites dried out (i.e. nests that were built initially over water); as the seasons progressed; however, we did not observe any nests in which the surrounding sloughs dried completely.

The permanent water gauging stations in this region (i.e. 3-4 and 3-28) are located in open sloughs. These gauges therefore indicated depths of the foraging habitat as opposed to nest sites. Although we had water depth gauges at each nest site, some general trends are illustrated (see Fig. 19) by these continuous water depth recording stations. It should be

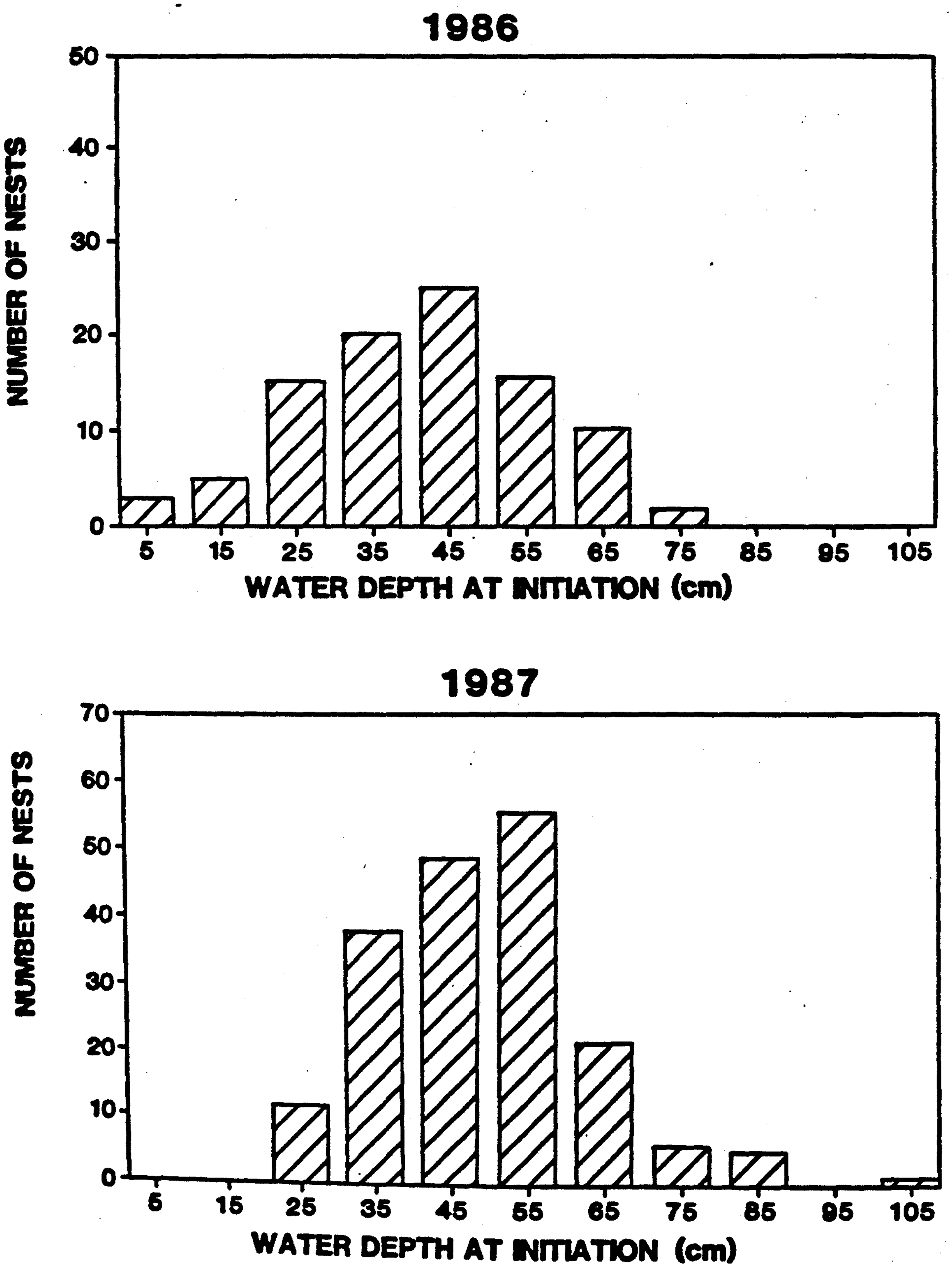


Figure 18. Frequency distribution of the number of nests found in each water depth class (10 cm intervals) at the time of breeding initiation . The depth value shown is the midpoint of the 10 cm class (e.g. 15 cm represents water depths ranging from 10.1 to 20.0 cm inclusive).

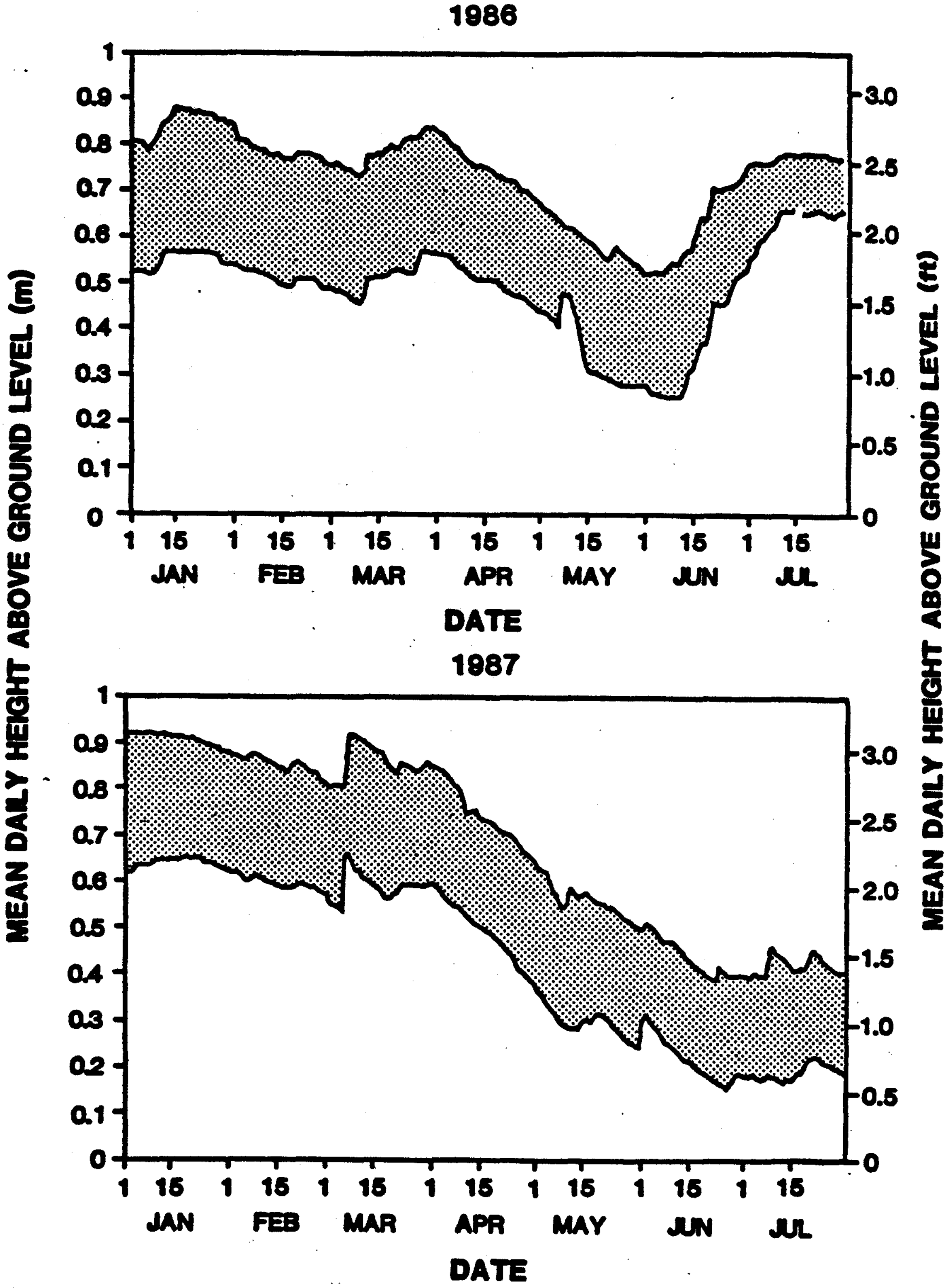


Figure 19. Mean daily water depths within the elevation range used by nesting Snail Kites (shaded). Values were derived by subtracting the ground elevation (i.e. 2.1 - 2.5 m) from the mean daily water stage at gauges 3-4 (higher elevation) and 3-26 (lower elevation). Note that these gauges are located within open slough communities and therefore represent depths of 10 cm or deeper than would be expected at actual nest sites.

noted therefore that these gauges often indicate depths of 10 cm or more than would be expected at nest sites.

Dry-down interval.-- Snail Kites in WCA-3A were distributed throughout the area between 2.1 m and 2.5 m elevation (see Distribution of Nesting Snail Kites). Based on the minimum water levels recorded at gauges 3-4 and 3-28 this elevation range dries out to ground level or below approximately every 1.9 to 3.8 years (Fig. 20).

A large portion of WCA-3A dries out more frequently than the areas in which we found nesting kites (i.e. areas above 2.5 m elevation). We observed Snail Kites foraging in the wet prairie communities of these higher elevation areas during times of high water, but found no indication (e.g. courtship displays and stick carrying) that any nesting occurred in these areas.

A region of elevation lower than 2.1 m (i.e. an area that dries out less frequently than every 3.8 years) occurs along the northern portion of the L-67 levee, but relatively few kites were observed in this area. Snail Kites nested in one large willow head ($N = 6$) on the edge of this wetter area during 1986, but only one kite was observed in the area during 1987 and no nests were found.

Proportion of open water.-- The habitat in which Snail Kites nested had a ratio of open water to sawgrass ranging from 12 - 67% ($x = 32.4 \pm 0.13$ (SD) for nesting areas of 1986 and 1987 combined). Within the general area of nesting distribution (i.e. between 2.1 and 2.5 m elevation) the ratio of open water to sawgrass in areas used and not used by nesting kites did not differ significantly in either 1986 or 1987 (Mann-Whitney Tests, $P > 0.05$) (Fig. 21). Differences in the proportion of open water of areas used for nesting also did not differ significantly between 1986 and 1987 (Mann-Whitney Test, $P > 0.05$).

Systematically sampled areas sampled above 2.5 m elevation (where we found no nesting kites) had a significantly lower proportion of open water than areas below 2.5 m that were used for nesting in 1986 (Mann-Whitney Test, $P < 0.05$) or 1987 (Mann-Whitney Test, $P < 0.05$) (Fig. 22).

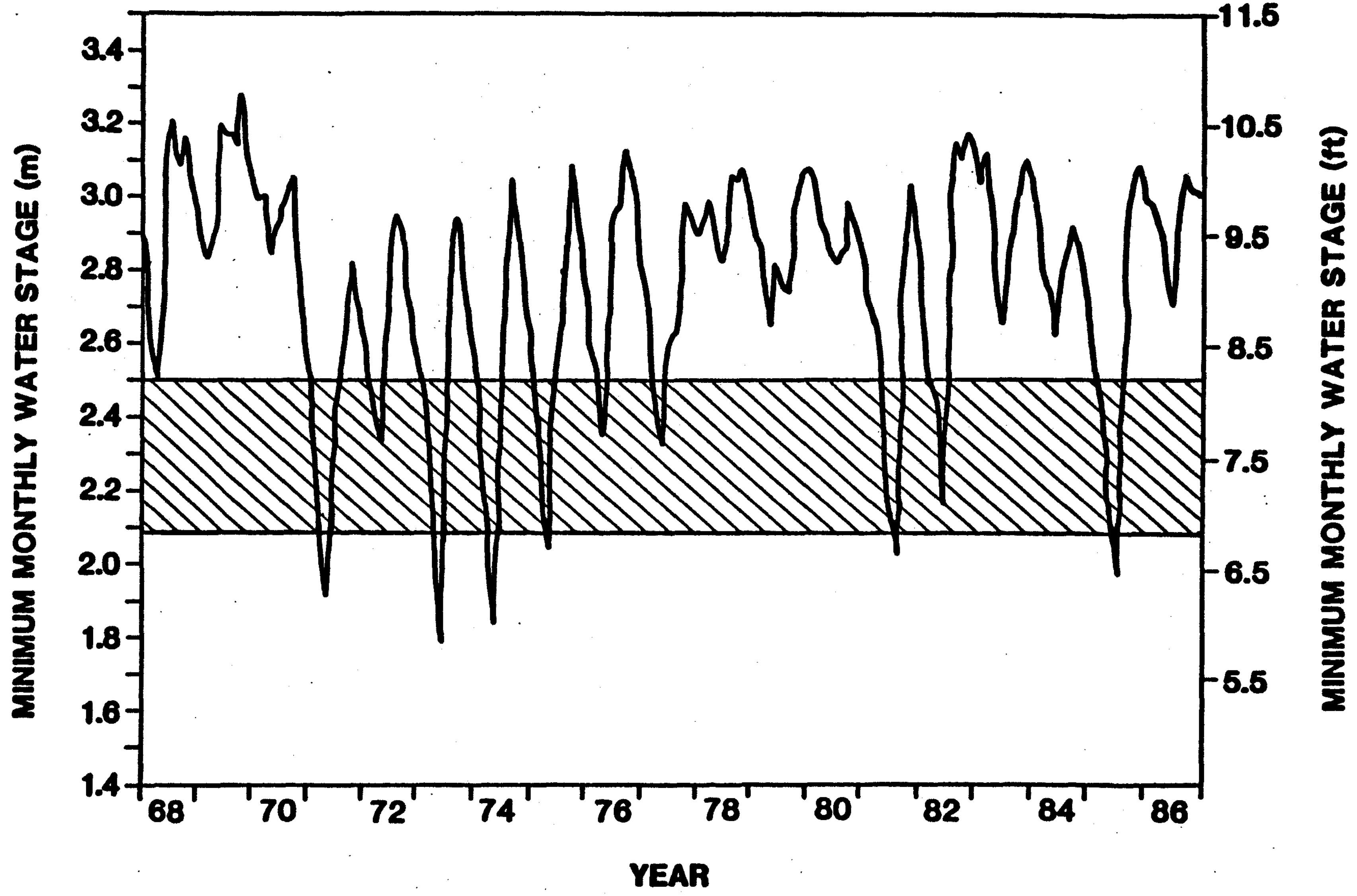


Figure 20. Minimum monthly water stage in WCA-3A (average of gauges 3-4 and 2-28) from *1968 - 1986*. The shaded area represents the elevation range for which we found breeding *Snail Kites*.

The shaded area represents the elevation range for which we found breeding Snail Kites.

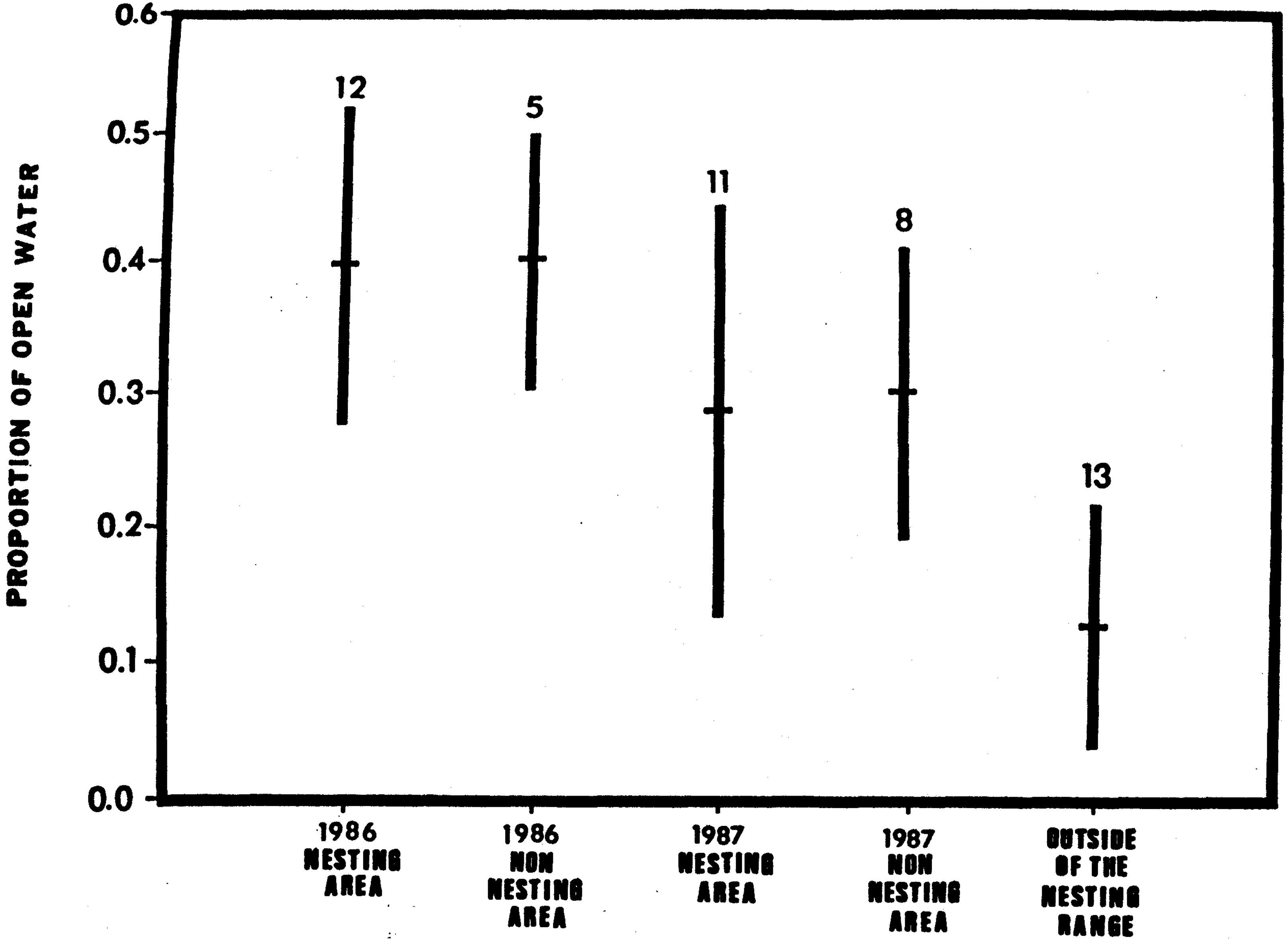


Figure 21. Proportion of open water to sawgrass for areas within the nesting range of Snail Kites in WCA-3A that were used and not used for nesting. Also shown is the proportion of open water from systematically sampled areas outside of the nesting range (i.e. above 2.5 m elevation).

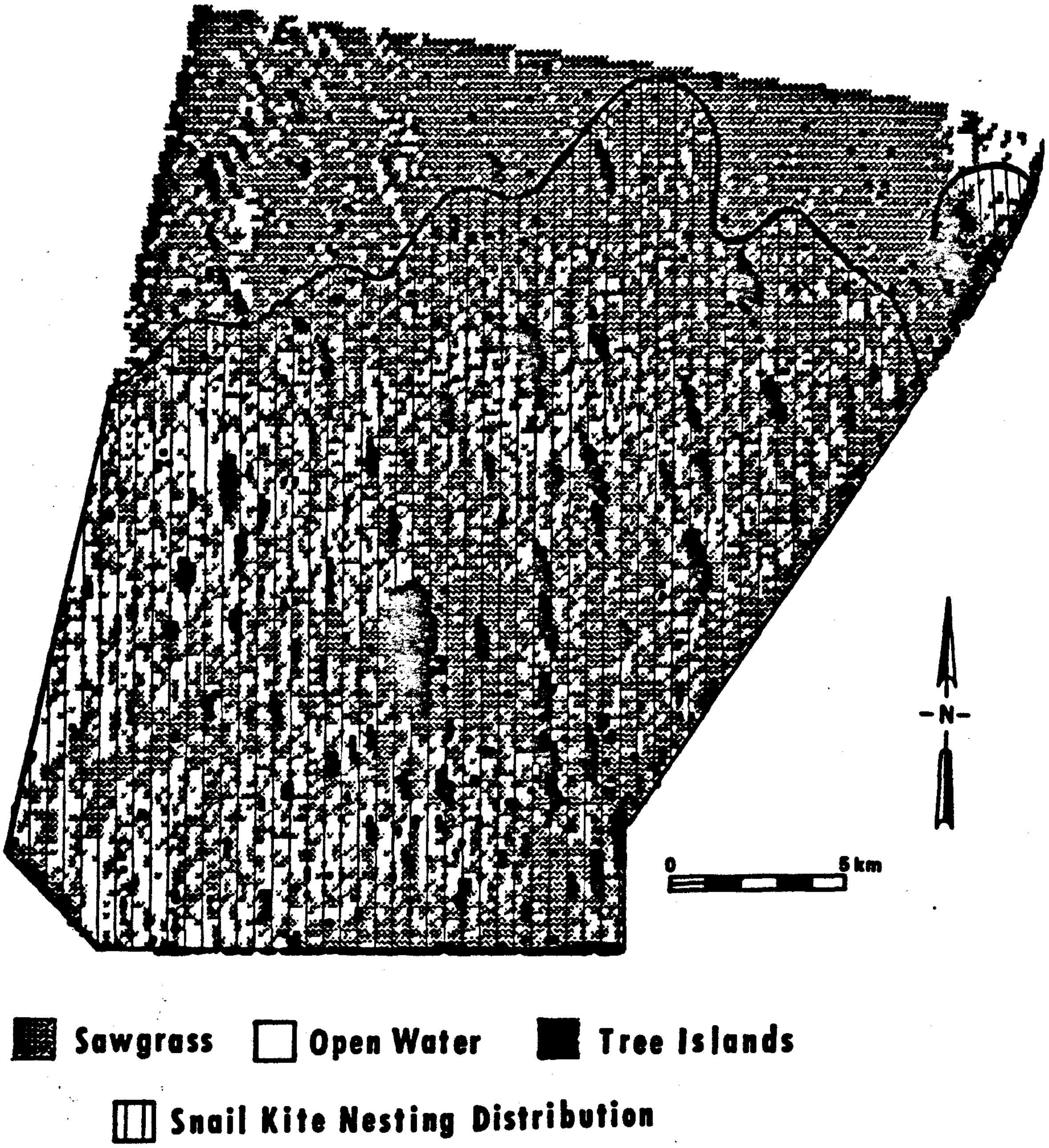


Figure 22. Classified GIS Map of southern WCA-3A showing distribution of nesting Snail Kites (shaded). Note the amount of open water within the distribution compared with outside the nesting distribution.

Apple snail abundance.-- If snail abundance is an important determinant of habitat selection for Snail Kites, then it should be greater in areas of higher nesting density. We hypothesized therefore that areas of higher nesting density would have lower capture times, higher apple snail egg cluster indices, and higher snail counts from suction dredging.

There was no significant difference in the time that it took foraging birds to capture snails in areas of high nesting density compared with areas of low nesting density (Wilcoxon paired-sample test, $P = 0.43$); however, in three of four paired comparisons capture time was greater in areas of high nesting density (Fig. 23). This result was not consistent with our prediction that capture times would be lower in areas of high nesting density.

In contrast, apple snail egg cluster densities and the egg cluster indices were significantly higher in areas of higher kite nesting density for all of the paired samples (Wilcoxon paired-sample test, $P = 0.05$) (Figs. 24 and 25). These results were consistent with our predictions.

Because of time and logistical constraints we were only able to sample two areas using the portable suction dredge (one each of high and low nesting density). Twenty plots each were dredged at areas 5 and 6. We found no significant difference in snail abundance between the two areas (Mann-Whitney test, $P = 0.46$); however, our snail density estimates were higher in the area of high nesting density ($x = 0.65$ per $m^2 \pm 1.04$ [SD]) than in the area of low nesting density ($x = 0.45$ per $m^2 \pm 0.60$ [SD]).

Capture time and snail egg cluster indices were not significantly correlated ($r^2 = 0.18$, $P > 0.05$) (Fig. 26). We did not have a sufficiently large sample size to statistically assess the correlation between suction dredging and the two snail abundance indices; however, results were consistent between the suction dredging and egg cluster counts, but not between suction dredging and capture times.

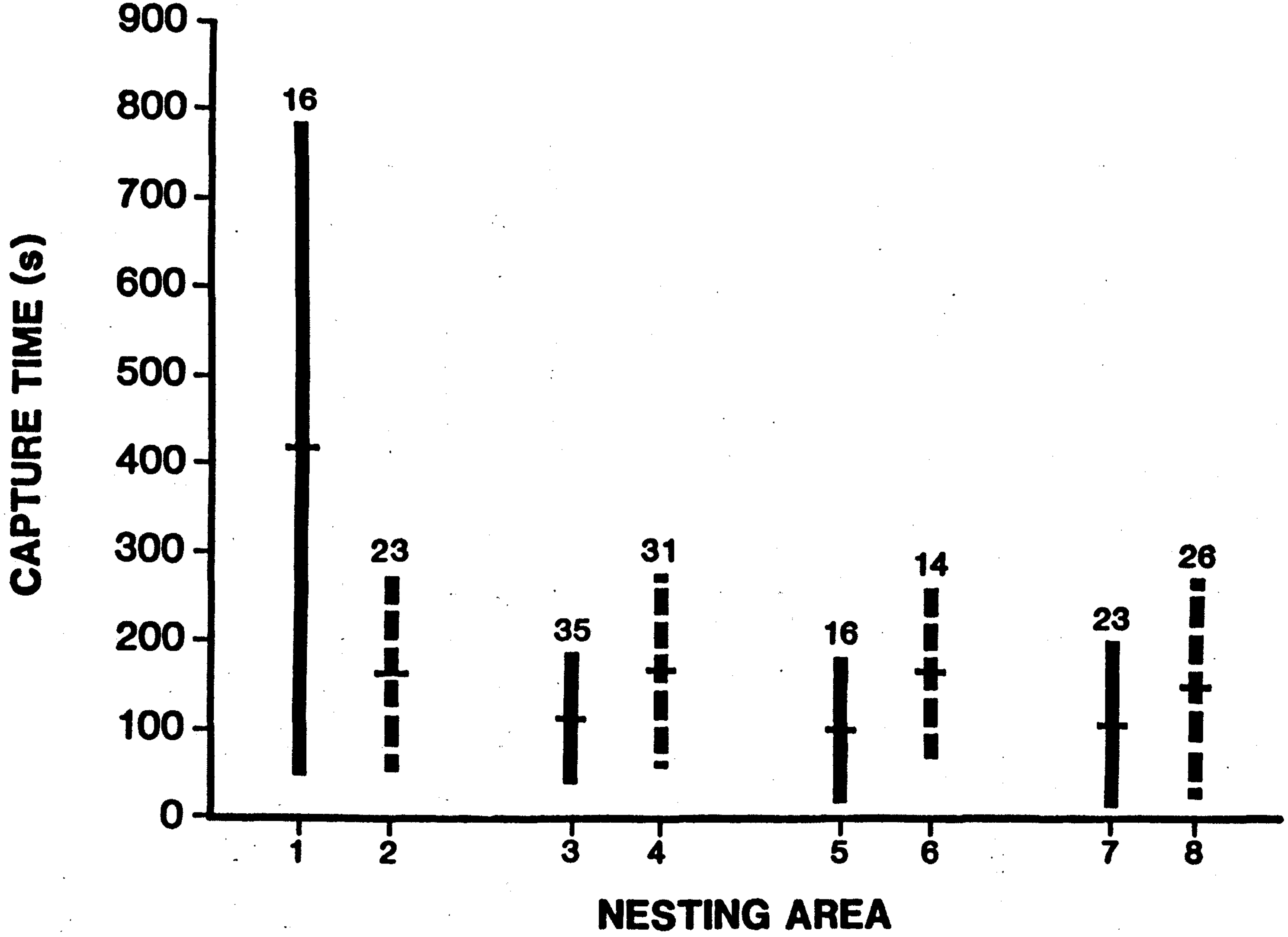


Figure 23. Mean capture times (± SD) of foraging Snail Kites in areas of low (—) and high (--) nesting densities. Areas 1-2, 3-4, 5-6, and 7-8 were paired samples observed observed during approximately the period of time.

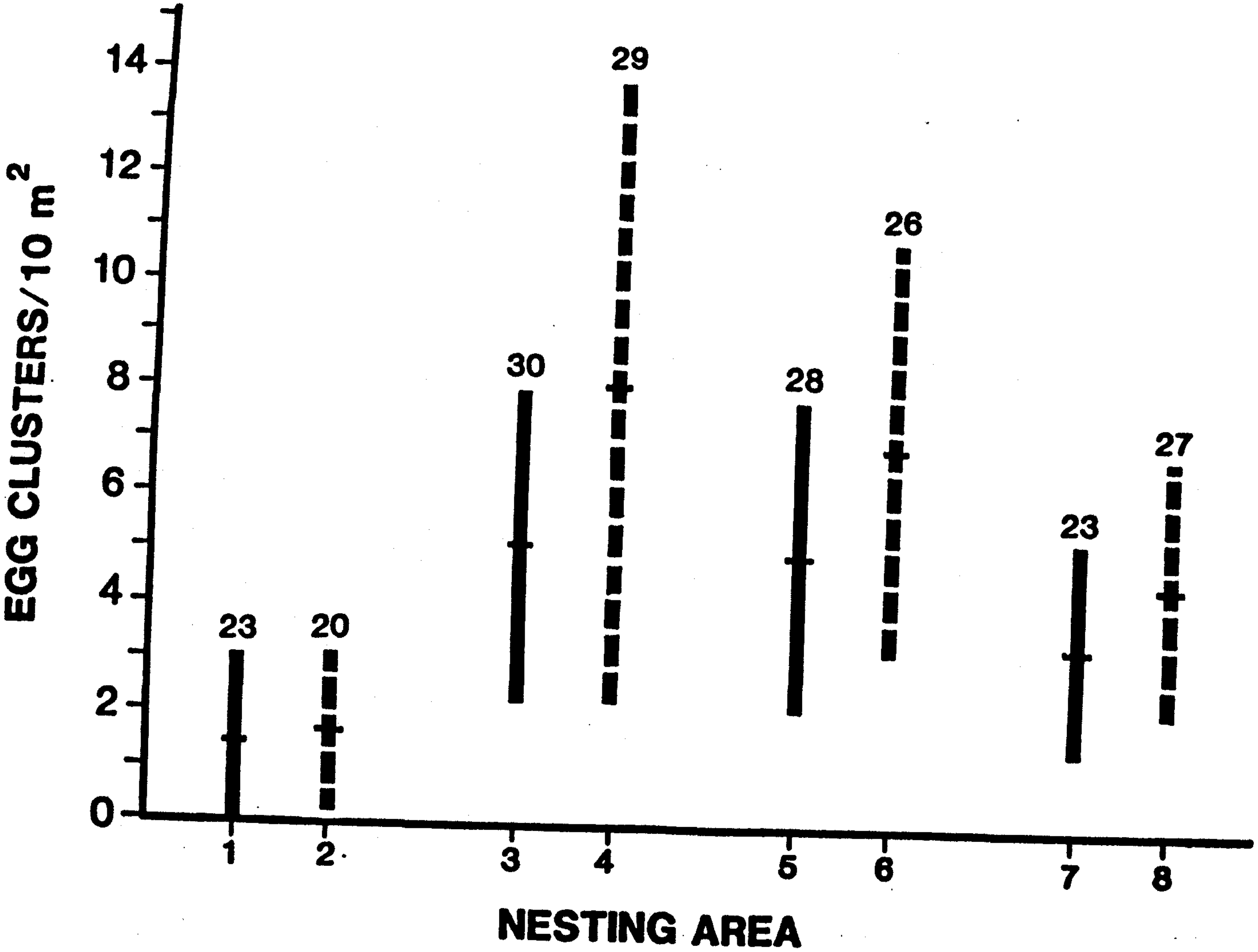


Figure 24. Egg clusters/10 m^2 in areas of low (—) and high (--) nesting densities. Areas 1-2, 3-4, 5-6 and 7-8 were paired samples observed during approximately the same period of time.

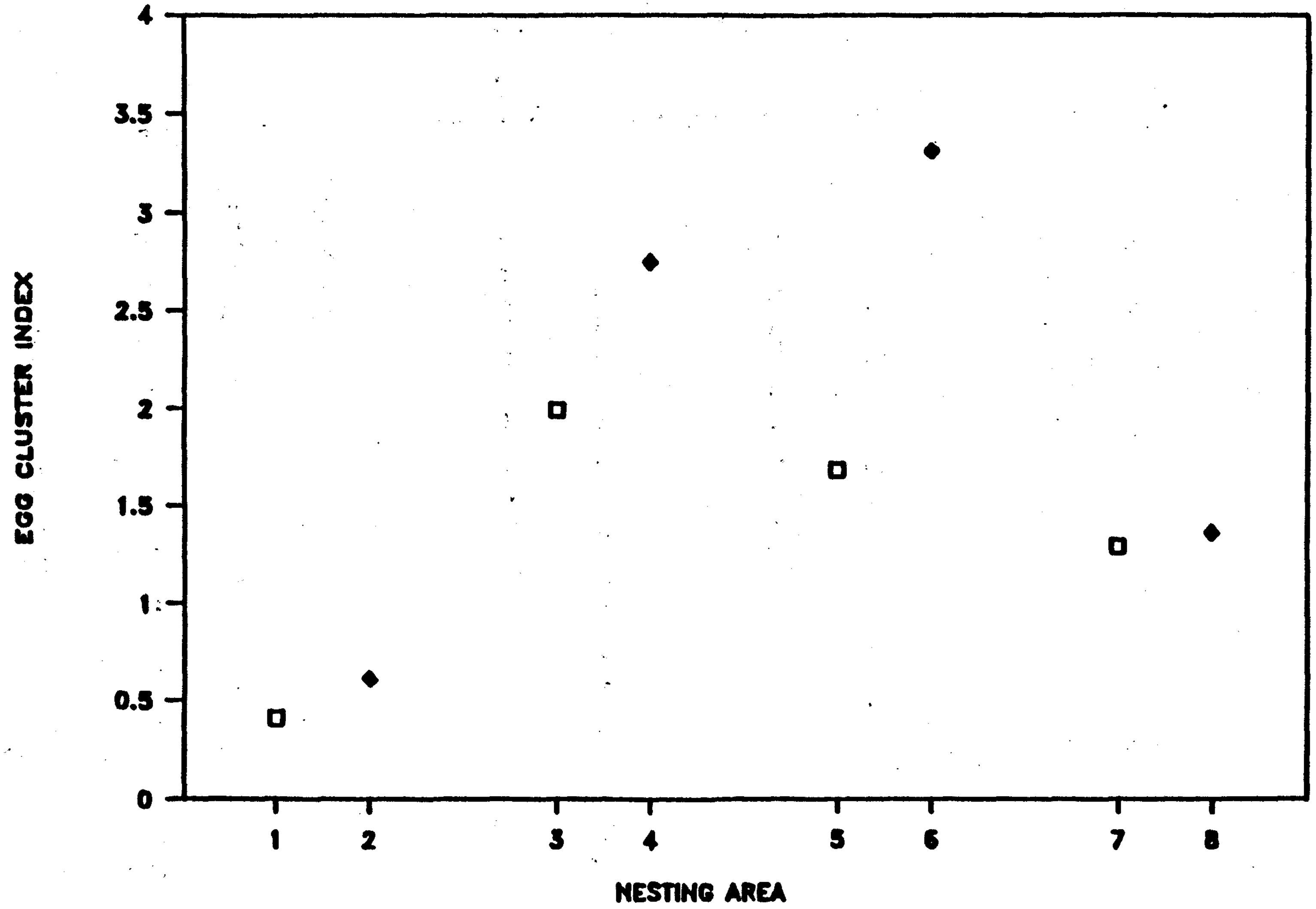


Figure 25. Egg cluster indices (see methods) in areas of low (□) and high (◆) nesting densities. Areas 1-2, 3-4, 5-6, and 7-8 were paired samples observed during approximately the same period of time.

Figure 25. Egg cluster indices (see methods) in areas of low (□) and high (◆) nesting densities. Areas 1-2, 3-4, 5-6, and 7-8 were paired samples observed during approximately the same period of time.

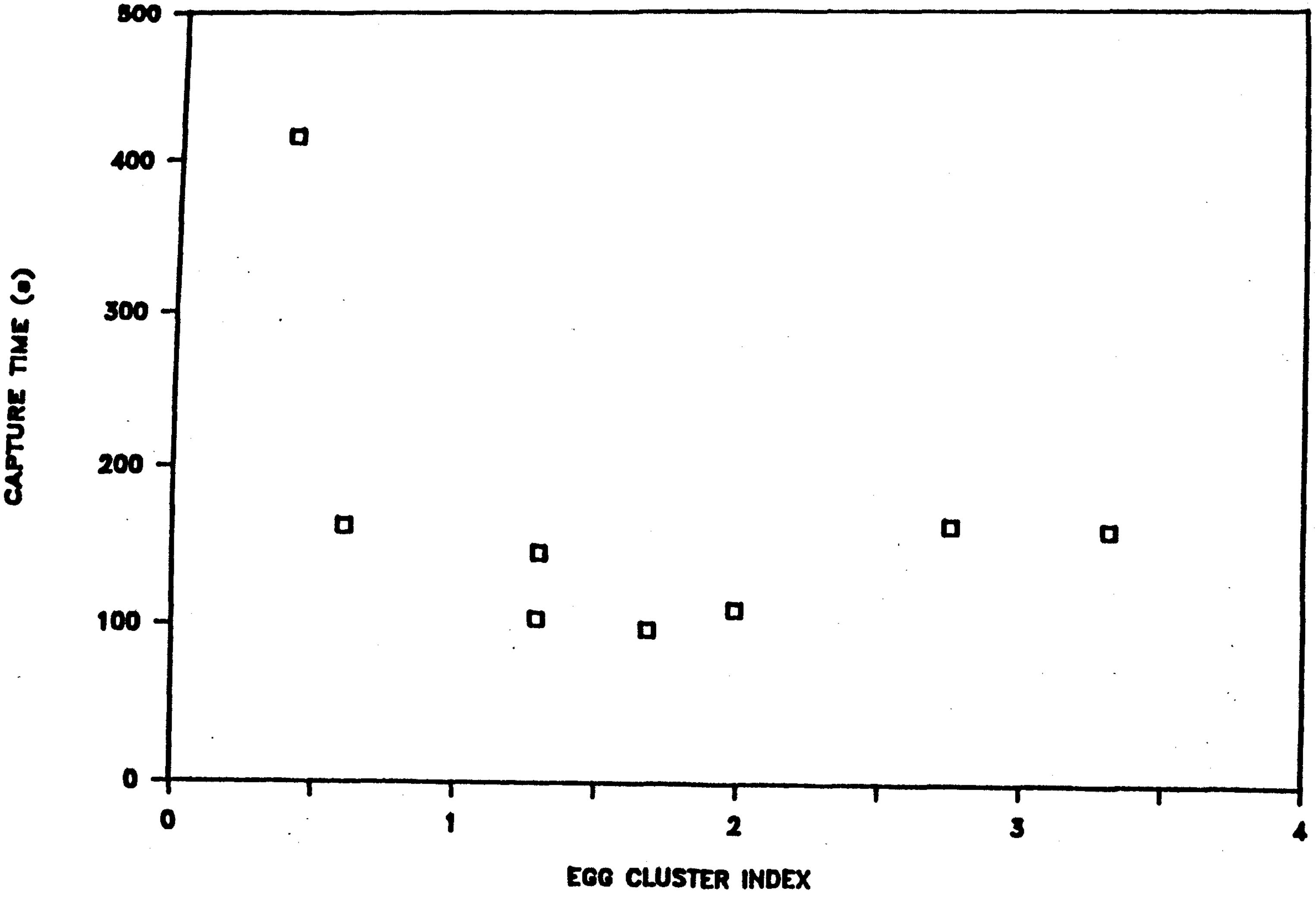


Figure 26. Scattergram showing the relationship between capture times and egg cluster indices for the eight nesting areas sampled.

Nest-site Selection

Nest substrate.-- The relative use of nest substrates did not differ between 1986 and 1987 ($X^2 = 6.58$, $P > 0.25$, df = 5); however, the use of nest substrates did differ from what was available ($X^2 = 79.21$, $P < 0.001$, df = 6). Willow was the most frequently used substrate in both 1986 and 1987, followed in decreasing order of use by pond apple, cypress, melaleuca, and wax myrtle (Fig. 27). Snail Kites also rarely used coco plum (< 4%), sweetbay (< 2%), sawgrass (< 2%), buttonbush (< 1%), and cattail (< 1%) as nest substrates.

Although willow was the most frequently used substrate, it was used less than expected compared to its relative abundance in WCA-3A (Fig. 28). Sweet bay also was used less than expected from its relative abundance, but the departure from expected was not as pronounced. Pond apple was used considerably more than expected based on its relative abundance. Because we measured the availability of nest substrates by the number of available clumps < 100 m^2, rather than by total area (see methods), we did not assess the use of sawgrass or cattail compared to their relative abundance; however, because sawgrass was extremely abundant and cattail common, both were undoubtedly used less than would have been expected. The remaining substrates were used at nearly expected frequencies.

Nest height.-- Nests ranged in height from 0.9 m (3 ft) to 12.4 m (41 ft) above ground level in 1986, and from 0.9 m to 8.6 m (28 ft) in 1987. Nest height in 1986 ($x = 2.24$ m [7 ft], SE = 0.06; outliers removed [Sokal and Rohlf 1969]) did not differ significantly from 1987 ($x = 2.36$ m [8 ft], SE = 0.08; outliers removed) ($t = 1.10$, $P = 0.27$) (Fig. 29).

Although we did not measure what heights were potentially availability to nesting kites, the heights selected appeared to correspond with the height of the stand (or part of the stand) within which the birds were nesting. Higher nest sites were potentially available at sites that were not selected for nesting (e.g. hardwood hammocks).

Stand size.-- Although we estimated the stand size within which each kite nest was located, we did not measure each stand. There were, however, no obvious preferences shown

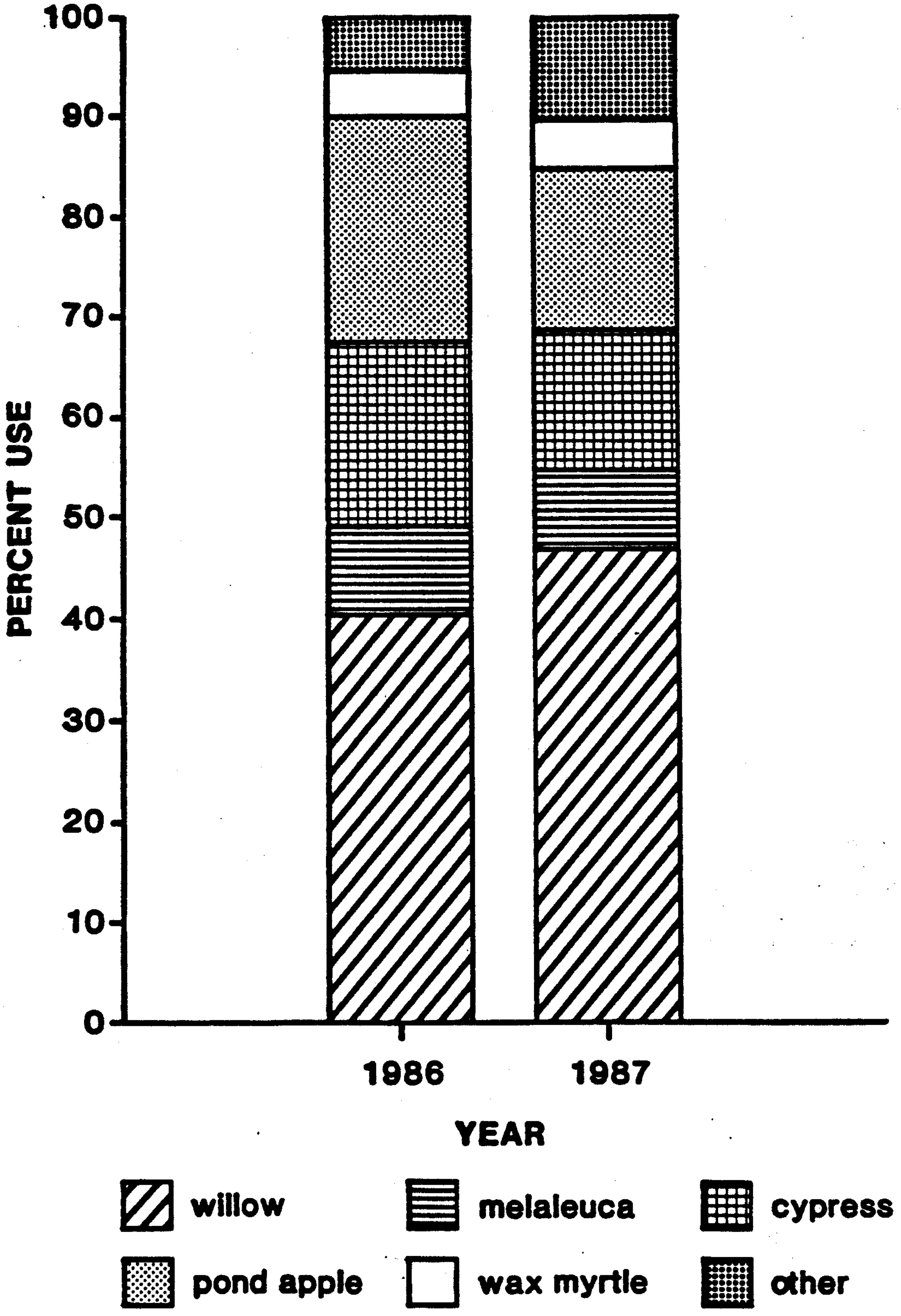


Figure 27. The relative use of nest substrates in WCA-3A during 1986 and 1987.

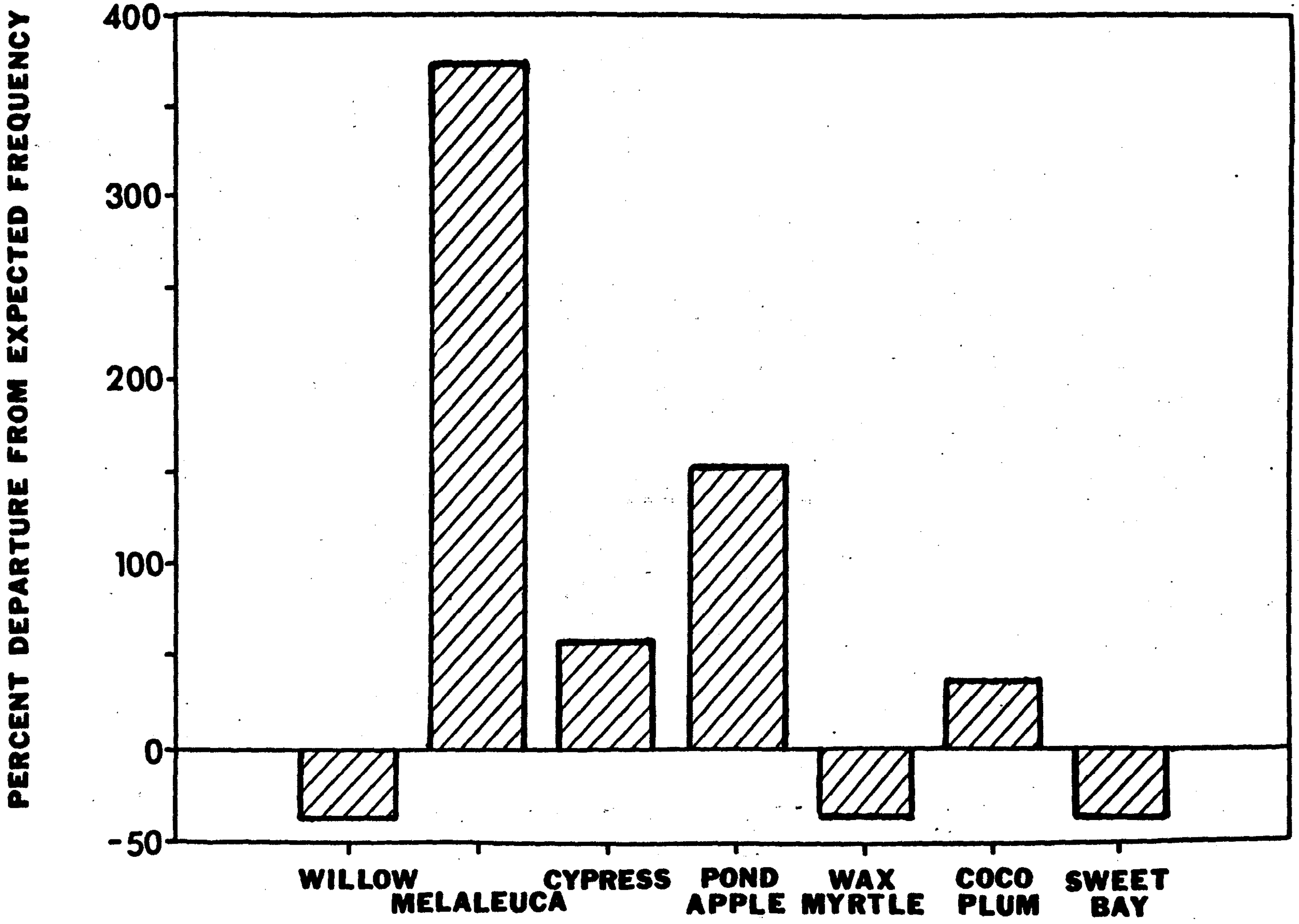


Figure 28. Percent departures from expected frequencies of use of nesting substrates compared with their abundance in WCA-3A.

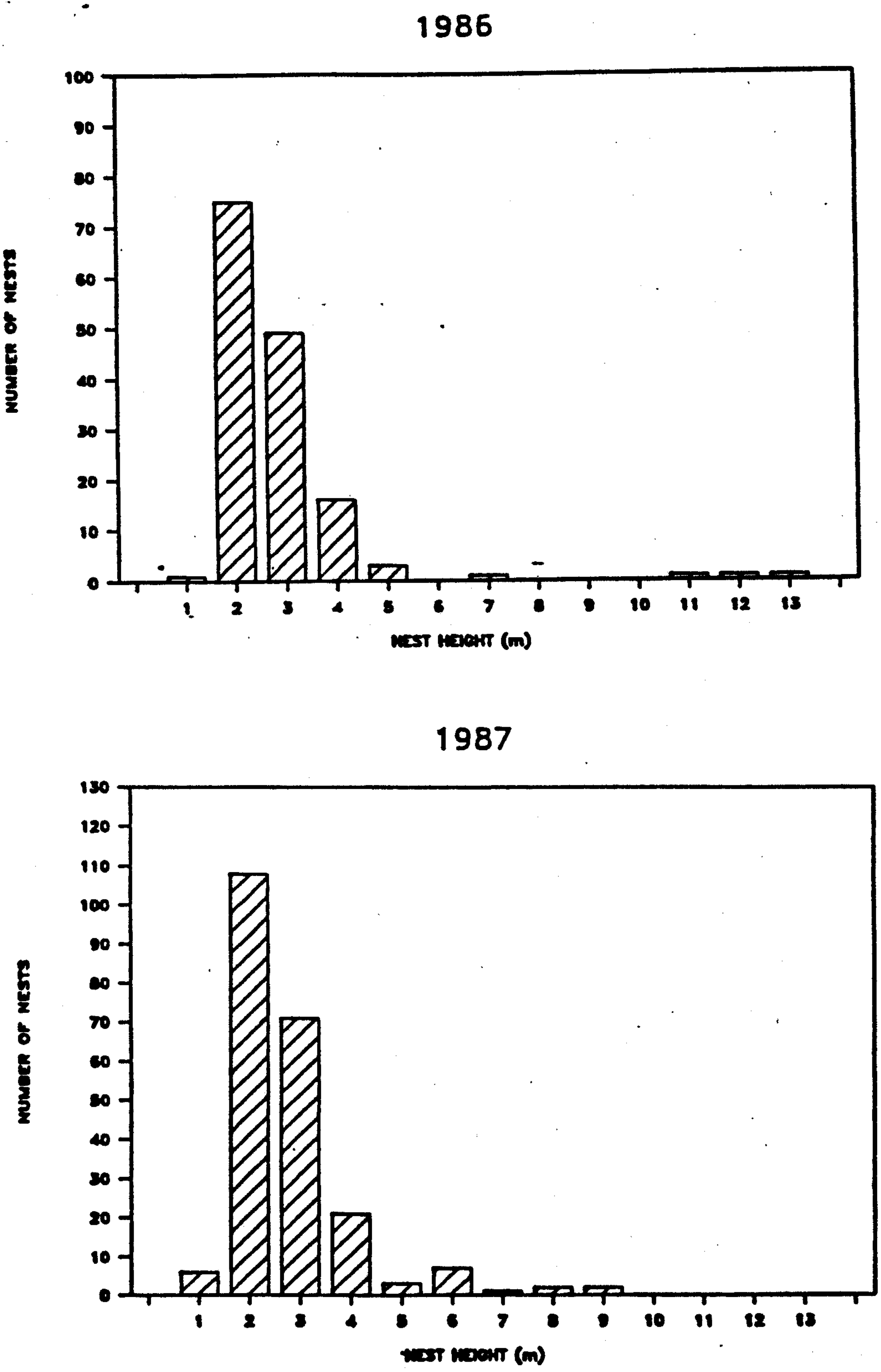


Figure 29. Frequency distribution of Snail Kite nests in WCA-3A during 1986 and 1987 by nest height (1 m increment).

for any particular stand size, with the possible exception of a slight tendency towards the use of single shrubs or small patches of woody vegetation.

There were, however, obvious preferences for the placement of nests within stands. For example, even though nests frequently were located in large tree islands, we never found a nest within the dry hammock portion of any tree island. Nests within large tree islands usually were located within the trailing southern portion that was in deeper water (Fig. 30). These trailing portions usually were comprised predominantly of willow, but kites frequently selected single pond apples or other species as nest substrates when they were available.

When nests were located in larger tree islands they also were usually placed in isolated shrubs adjacent to the main body of the stand or in the outermost edges of the canopy (Fig. 31). Unlike many of the wading birds (with which kites often nested), nests seldom were placed far within a dense canopy.

Size of the Breeding Population

We found 148 nests in which breeding (i.e. at least 1 egg was laid) occurred in 1986; 227 nests were found in 1987. An improved estimate of the number of breeding attempts in the area was obtained by calculating the number of breeding attempts that would have to have had been initiated in order to observe the number of successful nests that were found, given the probability that a nest would be successful (Miller and Johnson 1978). This calculation yielded an estimate of 196 and 284 breeding attempts during 1986 and 1987, respectively (based on our Mayfield estimates of nesting success). These estimates also may be low because of the assumption that all successful nests are found, a condition probably not true for this study. In several cases we felt that the time required to locate all nests within a colony could have been detrimental to the eggs or young of those adults that were kept off their nest during the search. In such cases we restricted the time of our search, regardless of whether all nests had been found. We also did not study

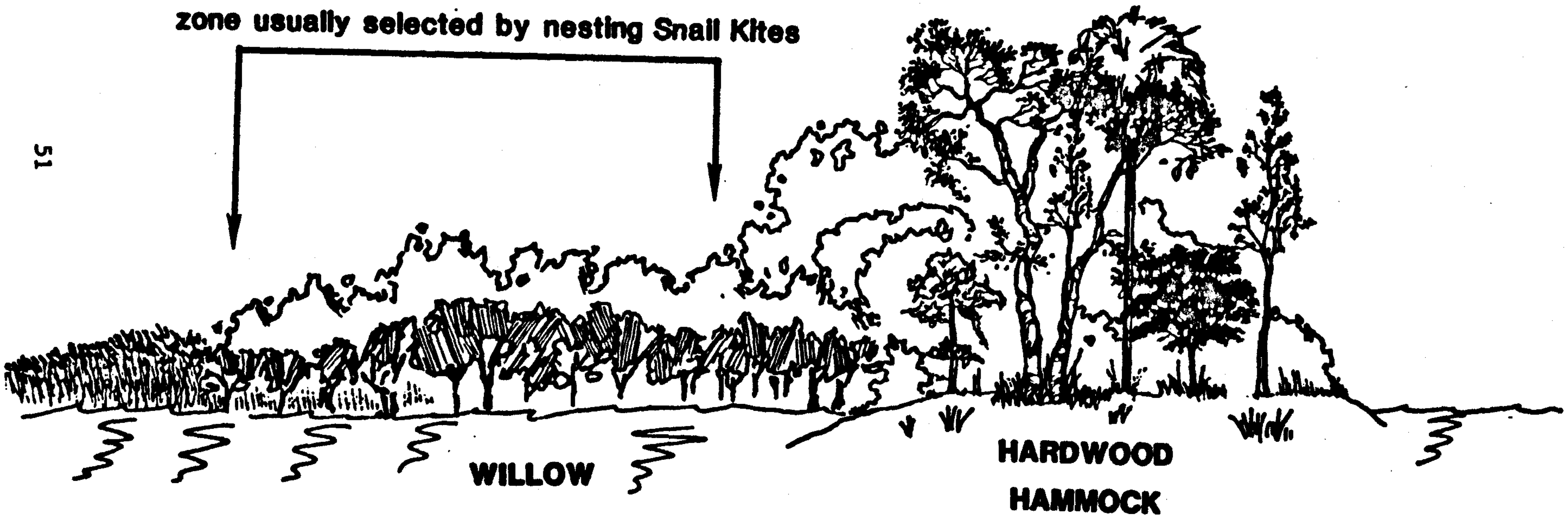


Figure 30. Lengthwise cross section of typical tree island in WCA-3A showing the zone usually selected by nesting Snail Kites. The hardwood hammock portion is usually on the northern end of the islands.

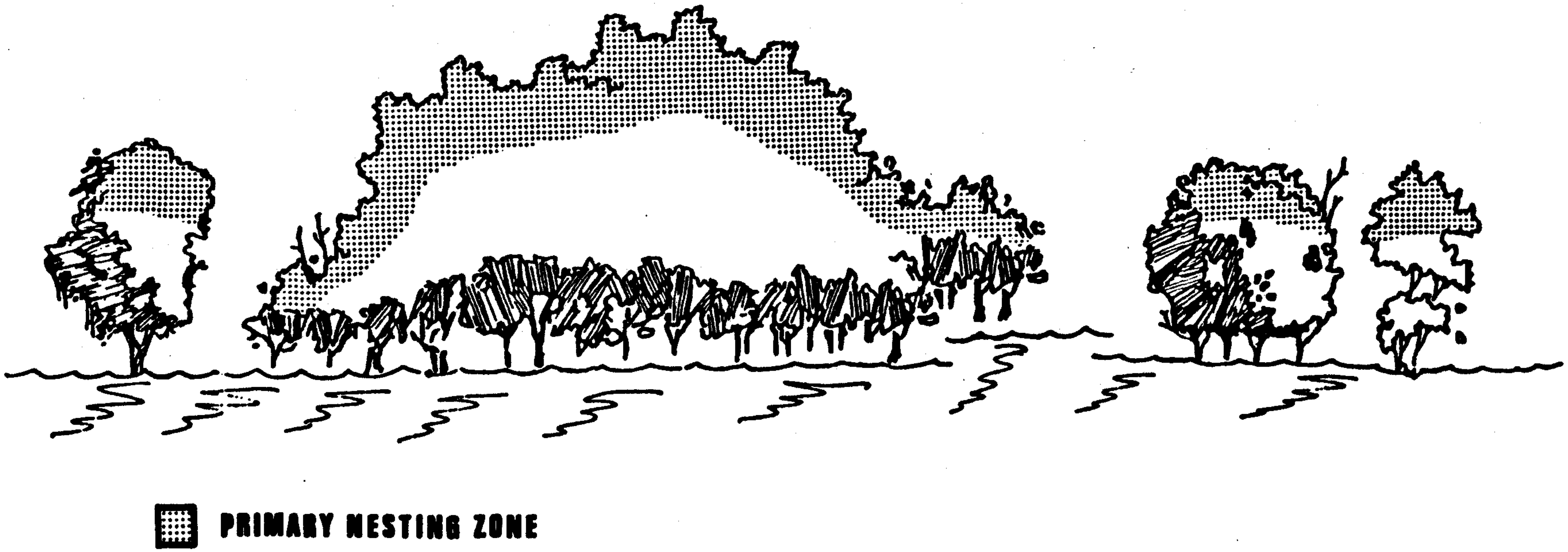


Figure 31. Cross section of typical small (< 500 m^2) willow head showing the zone usually selected by nesting Snail Kites.

one colony (Miccosukee) of nesting kites because it was regularly under observation by the public. We suggest that reasonable adjusted estimates of the number of breeding attempts in WCA-3A are 200-250 during 1986 and 300-350 during 1987. These estimates, however, would not include nest initiation in which breeding (i.e. eggs laid) did not occur.

We found 167 occupied nests (i.e. nests with actively attending adults but not necessarily having initiated breeding) in 1986, and 237 in 1987. This estimate, however, is undoubtedly low because most nests were found after breeding had been initiated and many failures before eggs laying were probably missed in our surveys.

Nesting Success

Our overall estimates (Mayfield) of nesting success in WCA-3A was 23% in 1986, and 36% in 1987 (Appendices 3). Success was significantly greater in 1987 than in 1986 ($Z = 2.86$, $P < 0.05$) (Fig. 32).

Survivorship and Age-Specific Nest Failure

Daily nest survival differed significantly between the egg and nestling stages during 1986 ($Z = 3.40$, $P < 0.001$), but not during 1987 ($Z = 1.53$, $P = 0.13$). Contrary to the findings of Beissinger (1986) and Sykes (1987b), daily nest survival during the nestling stage of 1986 was lower than during the egg stage. This may in part result from our inclusion of nests that failed after the predicted hatch date (i.e. day 27) in the nestling stage. Except in cases of hatching failure or when we had evidence that the eggs had not hatched, we included nests that failed after day 27 to have failed in the nestling stage (i.e. we assumed that they had hatched). There was no significant difference in overall success between the incubation periods of 1986 and 1987 ($Z = 0.73$, $P = 0.23$) (Fig. 33); however, success through the nestling period was significantly greater ($Z = 4.38$, $P < 0.001$) in 1987 than in 1986.

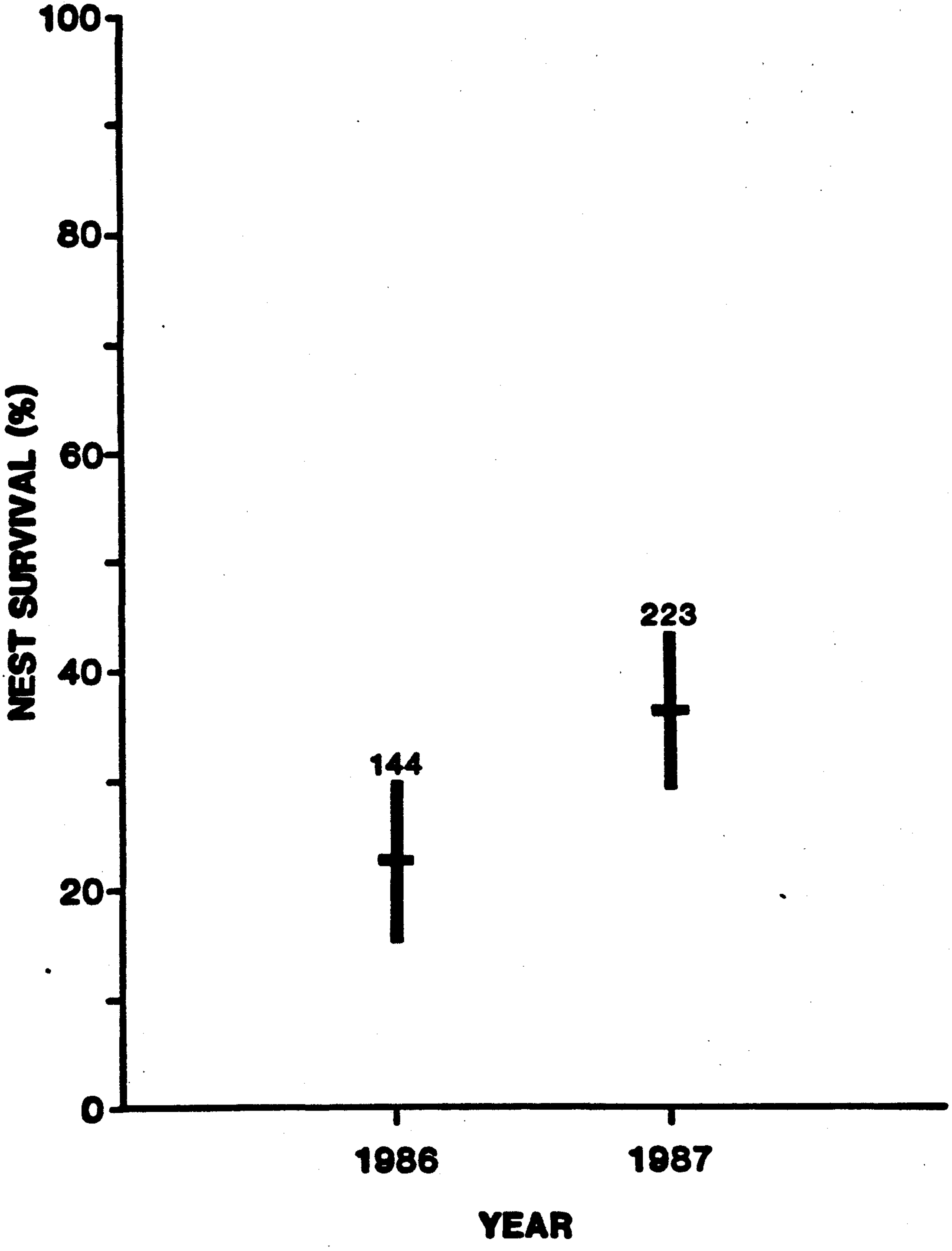


Figure 32. Mayfield estimates of overall nesting success of Snail Kite nests in WCA-3A during 1986 and 1987. Ninety-five percent confidence intervals about the estimate and sample sizes are shown.

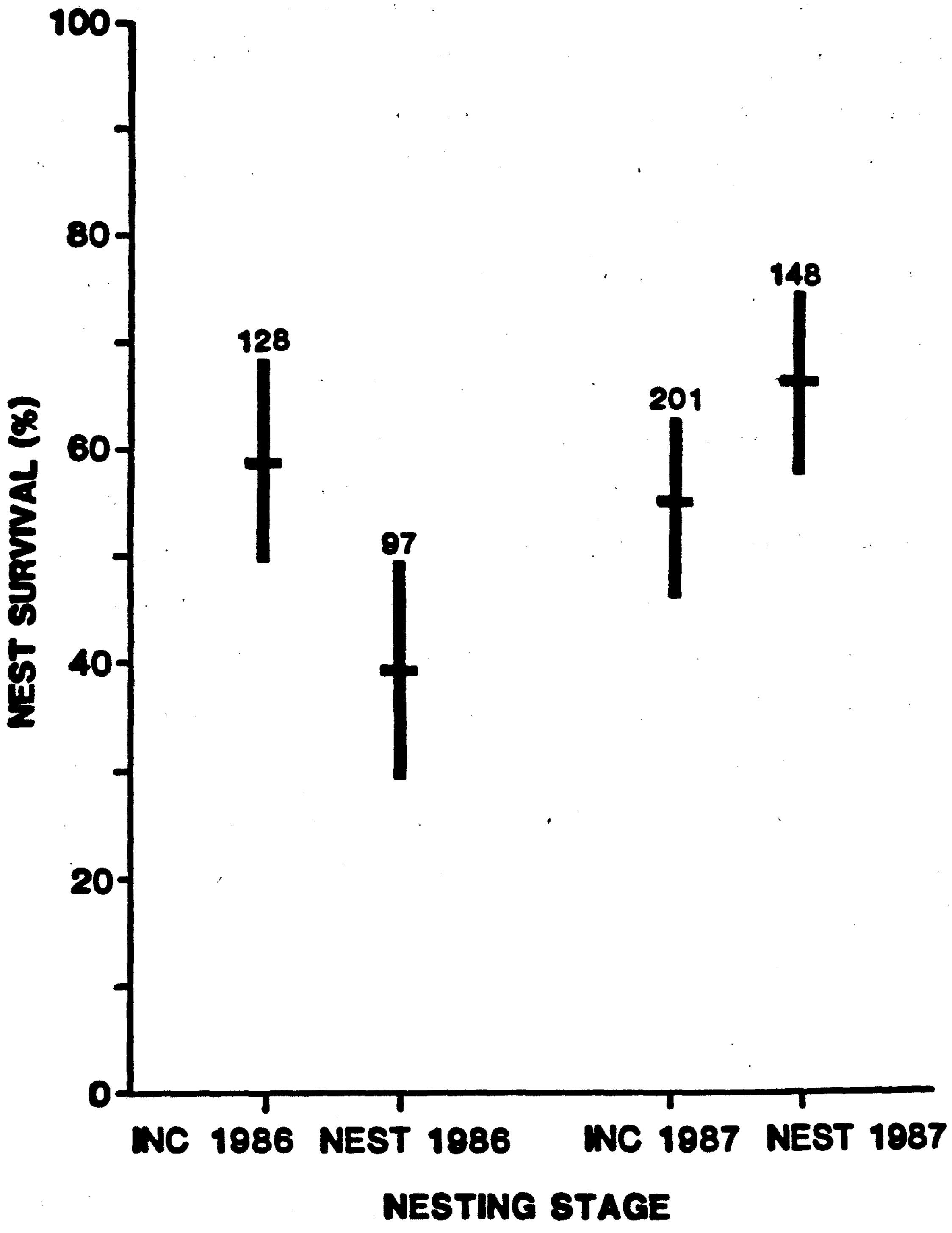


Figure 33. Mayfield estimates of nesting success during the incubation and nestling stages of Snail Kite nests in WCA-3A during 1986 and 1987. Ninety-five percent confidence intervals about the estimate and sample sizes are shown.

Mayfield estimates of daily survival during successive 6-day intervals after hatching showed that survival was lowest during the first 6-day interval after hatching for both 1986 and 1987 (Fig. 34). There was a significant difference ($Z = 2.93$, $P = 0.002$) in 1986 between the first and last 6-day interval after hatching (Appendix 4); the first interval also was significantly different from the third ($Z = 3.10$, $P = 0.001$) and fourth ($Z = 2.09$, $P = 0.18$) 6-day periods during 1987.

Another method for illustrating age-specific survivorship is plotting the proportion of nests with a known date of initiation that survive each day. This approach revealed that failure during the egg stage of 1986 tended to occur late (Fig. 35). This result probably was due both to hatching failure (11 cases in 1986) and to nests that might have failed after hatching but were mis-classified as egg-stage failures. This latter result arises from our procedure of estimating the failure date as the midpoint between the last nest visit when the nest was viable and the first visit after failure. This pattern of late failure during the egg stage was not as dramatic during 1987. Although not as pronounced as the Mayfield comparison using 6-day intervals, this approach to age-specific survivorship also showed a tendency for failure during the nestling stage to occur earlier (i.e. concave curve between day 27 and day 51). The less pronounced change in survivorship shown from this method probably is the result of presenting failures on a daily basis rather than lumping by 6-day intervals.

Productivity

The frequency distributions of different-sized clutches were not different between 1986 and 1987 ($X^2 = 2.62$, $P > 0.95$, $df = 3$) (Table 1). Clutch sizes ranged from one to three in 1986, and from one to four in 1987; modal clutch size was three during both years.

The mean (± S.D.) clutch sizes of 2.59 (± 0.61) and 2.53 (± 0.64) for 1986 and 1987, respectively, were slightly lower than those reported by Beissinger (1986) or Sykes

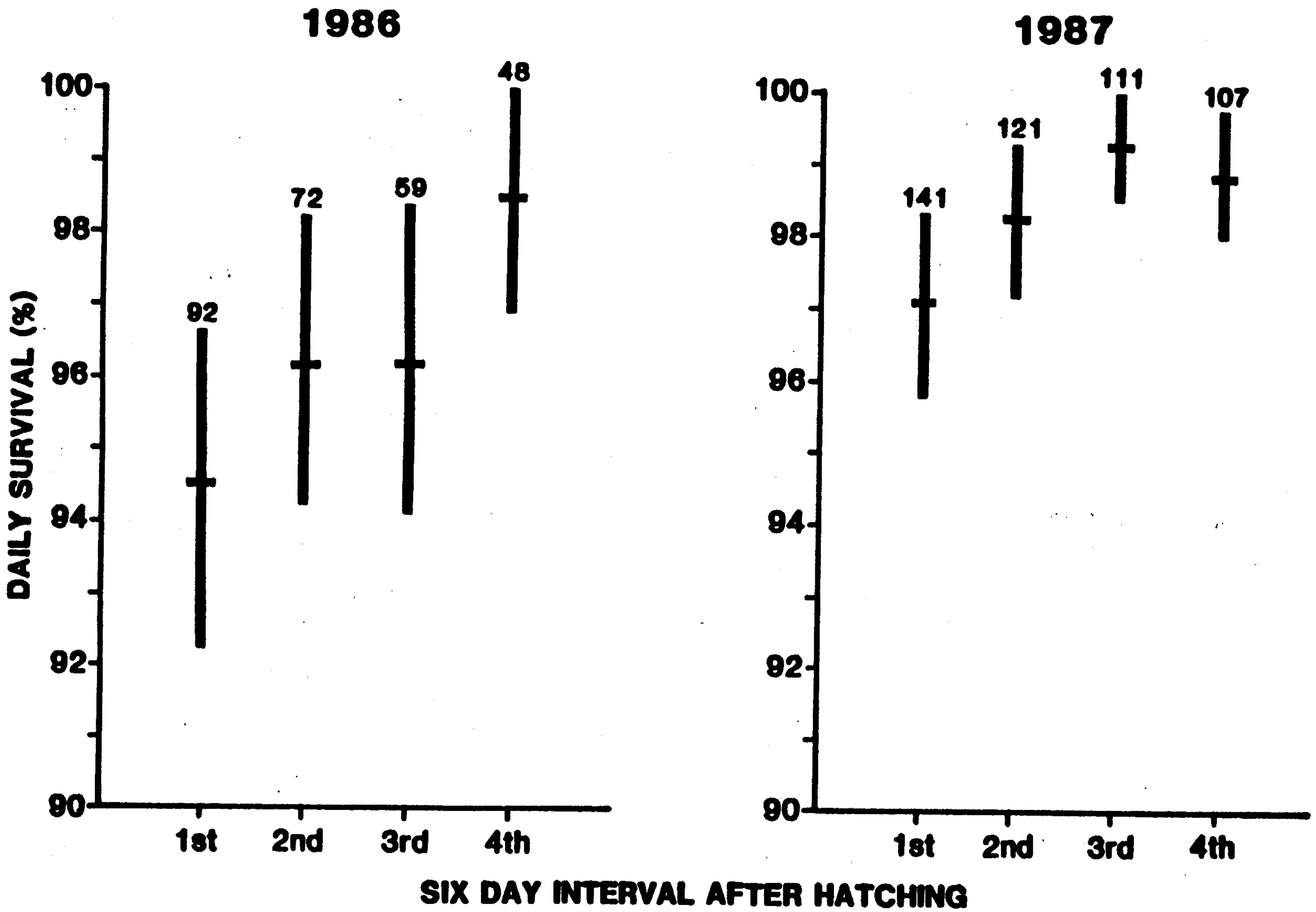


Figure 34. Daily survival of Snail Kite nests in WCA-3A of four consecutive 6-day nestling periods during 1986 and 1987. Ninety-five percent confidence intervals about the estimates and sample sizes are shown.

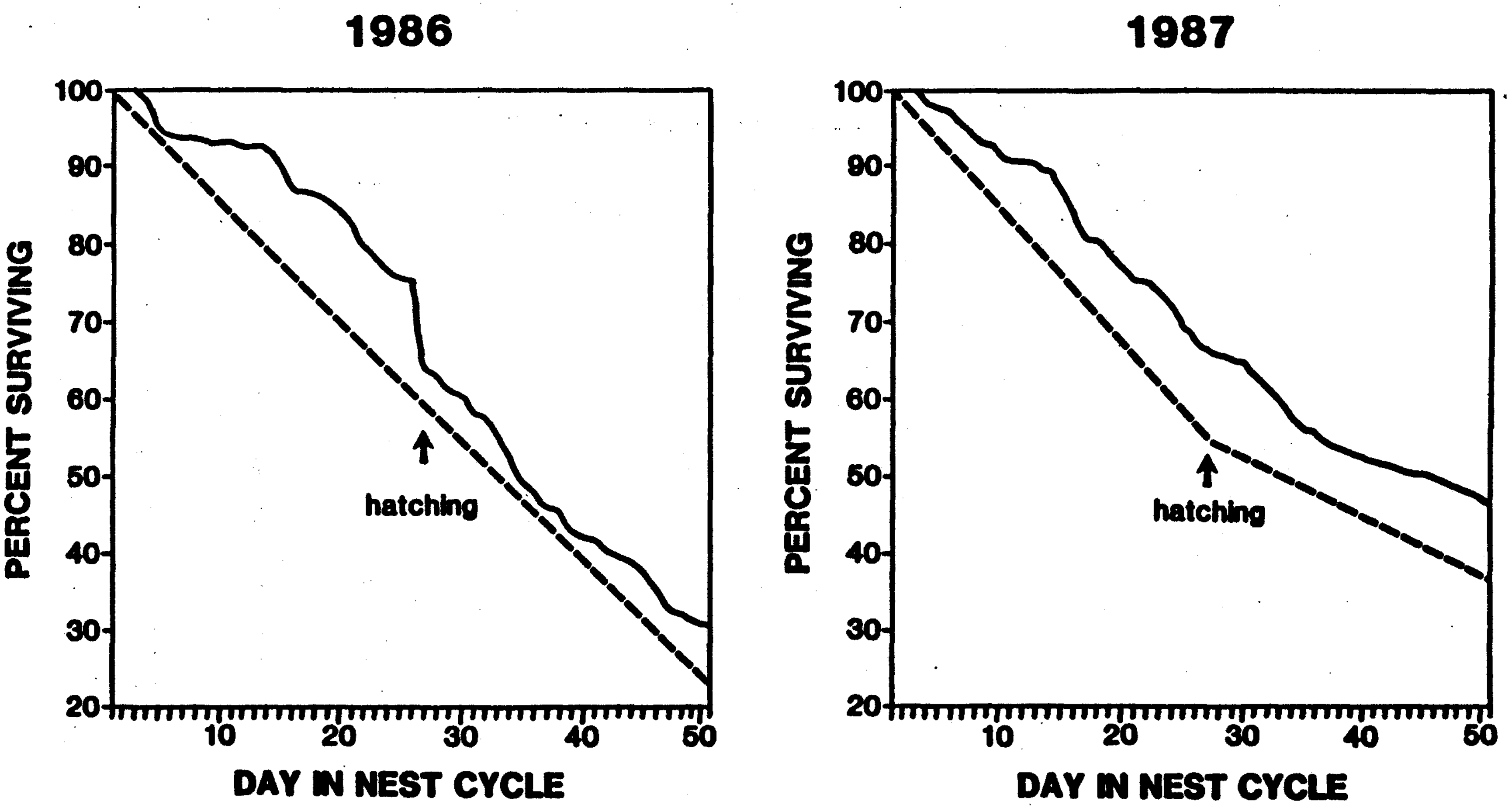


Figure 35. Survivorship of Snail Kite nests through the nesting cycle, calculated as the percent of nests found that survived daily (—). Survivorship from Mayfield estimates (--) are shown for comparison.

Table 1. Clutch sizes reported in Florida since 1880.

			1-Egg[a] Clutches		2-Egg Clutches		3-Egg Clutches		4-Egg Clutches		5-Egg Clutches		6-Egg Clutches		
Year(s)	N	$\bar{X}$	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%	Source
1880-1925	91	3.23[a]	--	--	12	13	54	59	17	19	8	9	0	0	Beissinger (1986)
1925-1959	57	2.96[a]	--	--	9	16	43	75	4	7	0	0	1	2	Beissinger (1986)
1968-1978	---	---	2	2	23	17	101	80	1	1	0	0	0	0	Sykes (1987[b])
1979-1983	48	2.71[a]	--	--	48	31	105	67	3	2	0	0	0	0	Beissinger (1986)
1986	109	2.59	7	6	31	28	71	65	0	0	0	0	0	0	This study
1987	161	2.53	11	6	55	34	93	58	2	1	0	0	0	0	This study

[a] Beissinger (1986) excluded one-egg clutches as being incomplete.

(1987b); however, they were within the range of variability found by Snyder et al. (in review).

Hatchability was not significantly different between 1986 and 1987 for 2-egg clutches (Mann-Whitney, $P = 0.41$) or for 3-egg clutches (Mann-Whitney, $P = 0.54$) (Table 2). Hatchability differed, however, between 2 and 3-egg clutches during 1986 (Mann-Whitney, $P = 0.04$); differences in hatchability from 2 and 3-egg clutches were nearly significant for 1987 (Mann-Whitney, $P = 0.07$). These results indicate that on a per-egg basis, productivity was greater for 2-egg clutches than for 3-egg clutches.

Although there was a disproportionately higher number of nests that fledged two and three (rather than one) young in 1987 compared with 1986, this difference was not statistically significant ($X^2 = 5.15$, $0.05<P<0.10$, df = 2). Productivity was higher in 1987 than 1986, whether expressed on a per breeding attempt, occupied nest, or successful nest basis (Table 3).

We observed 65 young reach fledging age in 1986, and 172 in 1987. Because it is unlikely that we found all successful nests, these figures should be considered minimum estimates of production. Based on our estimates of the number of nests, their nesting success, and the number of young fledged per successful nest, we estimate that 68-83 young reached fledging age in WCA-3A during 1986, and 178-208 during 1987. These are production values, however, and should not be assumed to represent recruitment estimates since we have no measure of juvenile survival during 1986 or 1987.

Causes of Nest Failure

Predators.-- The most common situation we observed when visiting a failed nest was to find all eggs or young missing, with no indication that the nest structure had been disturbed (Table 4). When this occurred at nests built on a sturdy substrate we suspected that the probable cause of failure was predation. The contents of these empty nests could possibly have been scavenged subsequent to mortality due to other causes; however, the

Table 2. Hatching success from nests with 2 and 3-egg clutches in WCA-3A during 1986 and 1987.

	2-Egg clutches				3-Egg clutches			
Year	No. nests	Total no. young hatched	Percent eggs hatched	X no. young hatched per nest	No. nests	Total no. young hatched	Percent eggs hatched	X no. young hatched per nest
1986	16	30	94	1.88	43	103	80	2.40
1987	37	64	86	1.73	67	155	77	2.31

Table 3. Estimates of Snail Kite productivity in south Florida from 1968 through 1987.

Year	Total no. occupied nests	Total no. active nests	Total no. successful nests	Total no. fledged	No. fledged per occ. nest	No. fledged per act. nest	No. fledged per succ. nest	Source
1968	13	--	11	24	1.85	--	2.18	Sykes (1987b)
1969	13	--	8	13	1.00	--	1.63	Sykes (1987b)
1970	19	--	9	12	0.63	--	1.50	Sykes (1987b)
1971	0[a]	--	--	0	--	--	--	Sykes (1987b)
1972	6	--	3	7	1.17	--	2.33	Sykes (1987b)
1973	34	--	12	29	0.85	--	2.42	Sykes (1987b)
1974	35	--	6	11	0.31	--	1.83	Sykes (1987b)
1975	29	--	14	35	1.21	--	2.50	Sykes (1987b)
1976	34	--	22	30	0.88	--	1.36	Sykes (1987b)
1977	15	--	8	20	1.33	--	2.50	Sykes (1987b)
1978	14	--	11	20	1.43	--	1.82	Sykes (1987b)
1979	131	93	54	108	0.82	1.16	2.00	Beissinger (1986)
1981	12	8	0	0	0.00	0.00	--	Beissinger (1986)
1982	40	19	2	4	0.10	0.13	2.00	Beissinger (1986)
1983	48	32	10	20	0.42	0.63	2.00	Beissinger (1986)
1986	167	148	45	65	0.38	0.44	1.44	This Study
1987	237	227	104	172	0.73	0.76	1.65	This Study

[a] No nesting activity was detected during this year.

Table 4. Condition of unsuccessful Snail Kite nests when found.

Condition of failed nest when found	1986 No.	1986 % of total failures	1987 No.	1987 % of total failures
Empty and intact	58	63	69	64
Structure tilted $>15^{\circ}$ and eggs or young missing	10	11	10	9
Structure tilted $>15^{\circ}$ and broken eggs or dead young present	0	0	4	4
Broken eggs but structure intact	11	12	7	7
Dead young but structure intact	8	9	6	6
Structure intact with eggs or young, but no evidence of adult attendance	5	5	10	9
Predation observed	0	0	1	1

remains (e.g. feathers and bones) of young known to have died from other causes usually were detectable for at least one visit after the death occurred. It was therefore unlikely that widespread mortality with subsequent scavenging went undetected.

In an attempt to assess which predators were responsible for nest losses, we applied a layer of synthetic grease over an approximately 60 cm portion of the trunk of 12 shrubs used to support kite nests. We raked the grease surface with a linoleum comb so that any animal crossing the surface would leave identifiable tracks. Only three such nests failed while this grease was in place: one trunk had positively been climbed by a snake, one had been climbed by what appeared to be a snake, and one showed no apparent signs of having been climbed (although it could have been possible for a snake to have bypassed the grease). Although this evidence certainly is not conclusive as to the cause of these nest failures, we believe that two of the three nests probably were preyed upon by snakes. In addition, two actual observations of attempted snake predation have been reported. Bennetts and Caton (1988) observed a rat snake (Elaphe obsoleta) prey upon a nestling Snail Kite chick; and J. Kern (Toner 1984) photographed a rat snake attempting to swallow a kite egg.

Structural collapse.-- Ten nests (11% of failures) during 1986 and 14 nests (13% of failures) during 1987 experienced some degree (>15% tilted) of structural collapse. Some of these failures, however, may have been caused by other factors.

Abandonment.-- We found a total of 15 cases of apparent abandonment in 1986 and 1987 (see Table 4); however, three of these nests previously had undergone a partial egg or young loss (probably due to predation). In five cases, incubation had extended well beyond the normal incubation period suggesting that the eggs were not viable; in five additional cases the nest had only one egg, suggesting that a partial loss might have occurred prior to our discovery of the nest. In only 2 of 375 nests did we observe what we believed to be abandonment of viable eggs or young in which the nest had not had at least partial predation. Even when eggs were not viable, kites appeared reluctant to abandon their nest.

One pair incubated eggs for at least 84 days (over three times the normal incubation period).

Parasites.-- We frequently found kite chicks with mite infestations, but did not suspect that any failures were attributable directly to these infestations. We found only two nests which had dermestid beetle larvae and, although each had lesions similar to those described by Snyder et al. (1984), both successfully fledged one young.

Human disturbance.-- We observed adult kites that were flushed from nests close to airboat trails (i.e. < 75 m) when airboats passed; however, we did not observe any prolonged disturbance, and the adults usually returned to the nests immediately after the boat had passed.

Our own research effort was another potential cause of disturbance. To assess this impact, we randomly selected 10 nests during incubation in 1986; five nests were not visited until the young were approximately two weeks old and five nests were visited at our regular interval (7-10 days). In each case, two of the five nests failed. Although these sample sizes were too small to draw definitive conclusions, these results suggest that our visitation frequency was not causing increased nest failure.

Influences of Nesting Success

Date of Initiation.-- Nesting success was lowest during late season in both 1986 and 1987 (Fig. 36). Differences were significant for 1987 (standard normal test, $P < 0.05$, Appendix 5), but not for 1986. Overall nesting success was highest during the early period of 1986 and the middle period of 1987.

Nesting substrate.-- Nesting success did not differ significantly among nests built on the four major substrates in either 1986 or 1987 (standard normal test, $P > 0.05$, Appendix 6). The ranking of nesting success in relation to substrate was the same in each year; nests in melaleuca were most successful, followed in decreasing order of success by willow, cypress, and pond apple (Fig. 37).

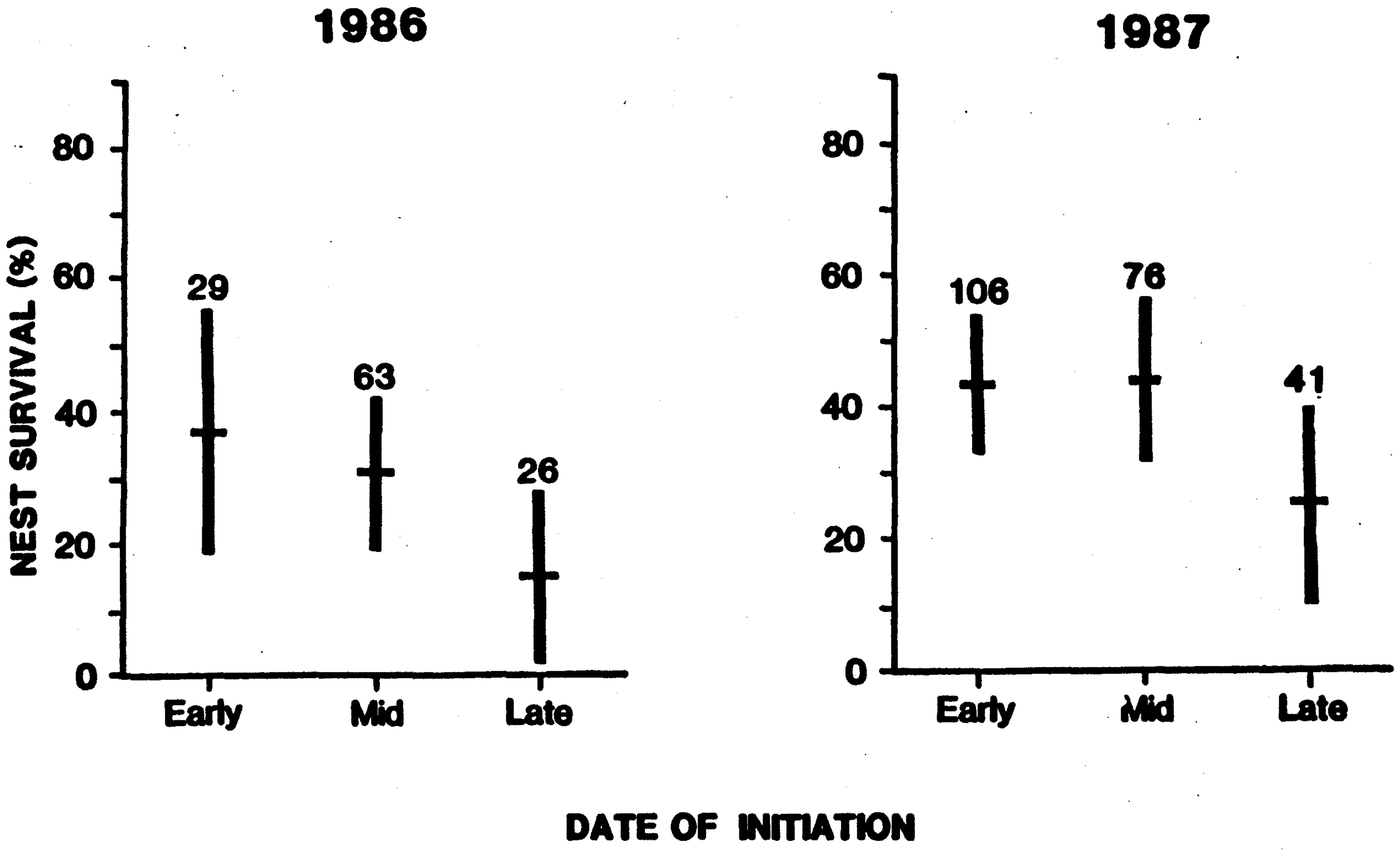


Figure 36. Mayfield estimates of overall nesting success of Snail Kite nests in WCA-3A that were initiated early, middle, and late season (see methods). Ninety-five percent confidence intervals about the estimates and sample sizes are shown.

the estimates and sample sizes are

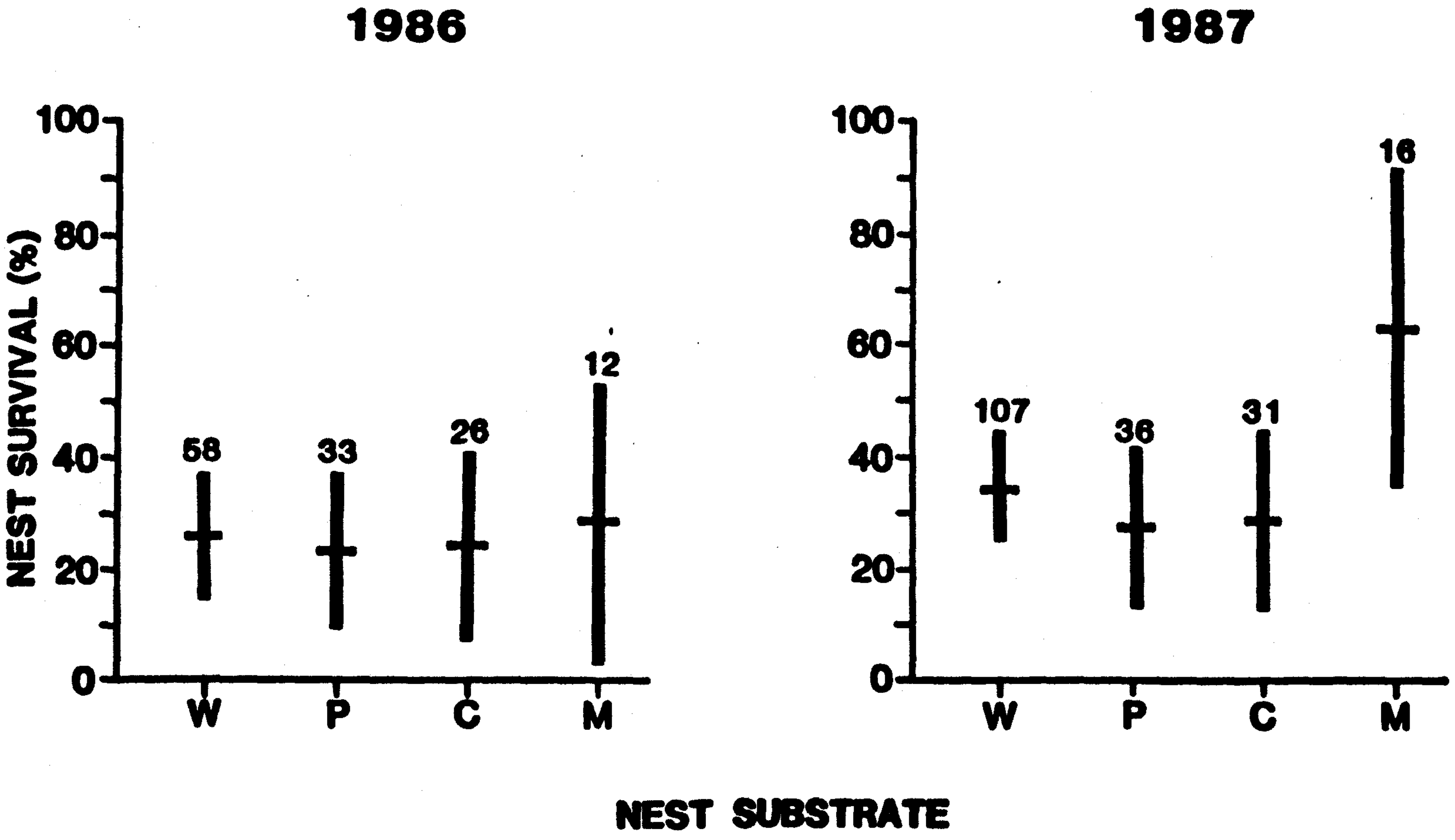


Figure 37. Mayfield estimates of overall nesting success of Snail Kite nests in WCA-3A in nesting substrates willow, pond apple, cypress, and melaleuca. Ninety-five percent confidence intervals about the estimates and sample sizes are shown.

Nest height.-- Nesting success did not differ significantly with respect to nest height during 1986 (standard normal tests, P > 0.05, Appendix 7). Although not statistically significant, nesting success increased with height during 1986 (Fig. 38). During 1987, the highest nests (>3 m) were most successful, but nesting success was lowest for nests of intermediate height (2-3 m).

Distance from land.-- Nesting success during 1986 was significantly higher for nests that were greater than 500 m from uplands compared with nests that were from 100 - 500 m (Z = 3.09, P = 0.002). Nests that were less than 100 m from uplands had the highest success, but did not differ significantly from those of greater distance (standard normal test, P > 0.05, Appendix 8). Nesting success during 1987 tended to increase with increasing distance from upland habitat (Fig. 39), but differences were not significant (standard normal test, P > 0.05).

Water depth.-- As with the other environmental variables (e.g. weather), water depth changes throughout the season at each nest. For this reason, we compared daily nest survival (as opposed to overall nesting success) among nests while they were within a given water depth class (see Methods). Daily nest survival during 1986 or 1987 did not differ significantly among nests that were in shallow (<25 cm), intermediate (25-50 cm), or deep (50-75 cm) water (standard normal test, P > 0.05, Appendix 9) (Fig. 40).

Rainfall.-- Daily nest survivorship was highest when the average daily rainfall was lowest in both 1986 and 1987 (Fig. 41); however, differences were not significant in either year (standard normal test, P > 0.05, Appendix 10). During 1986, daily nest survivorship was lowest when average daily rainfall was highest. In 1987, survivorship was lowest when rainfall was intermediate.

Wind speed.-- We detected no significant differences in daily nest survivorship with varying levels of average daily wind speed (standard normal test, P > 0.05, Appendix 11). In 1986, daily nest survivorship was highest when the average daily wind speed was highest (Fig. 42); however, in 1987 daily survivorship was lowest when wind speed was highest.

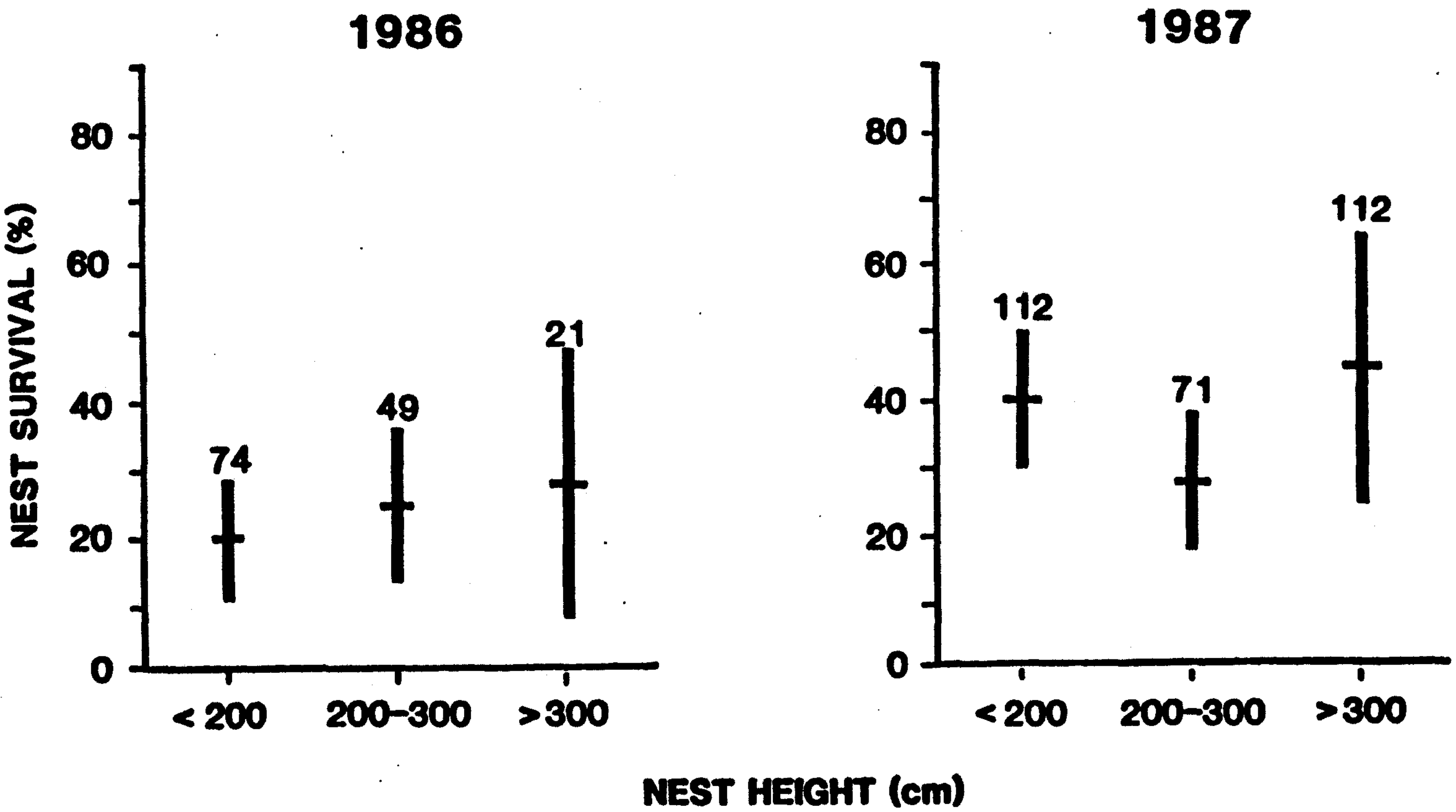


Figure 38. Mayfield estimates of overall nesting success of Snail Kite nests in WCA-3A at nest heights <200 cm, 200-300 cm, and >300 cm. Ninety-five percent confidence intervals about the estimates and sample sizes are shown.

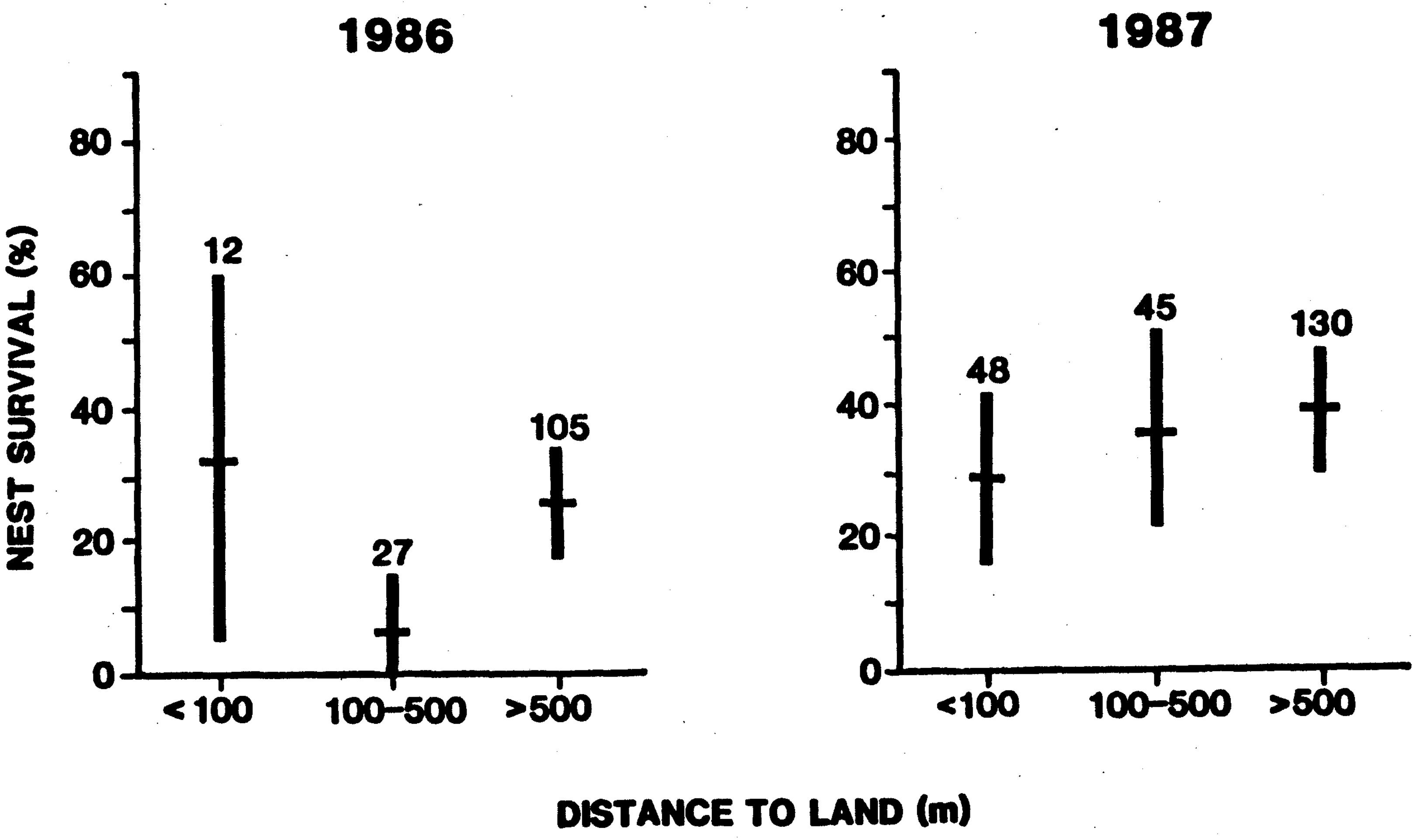


Figure 39. Mayfield estimates of overall nesting success of Snail Kite nests in WCA-3A in which the distance to land was <100 m, 100-500 m, >500 m. Ninety-five percent confidence intervals about the estimates and sample sizes are shown.

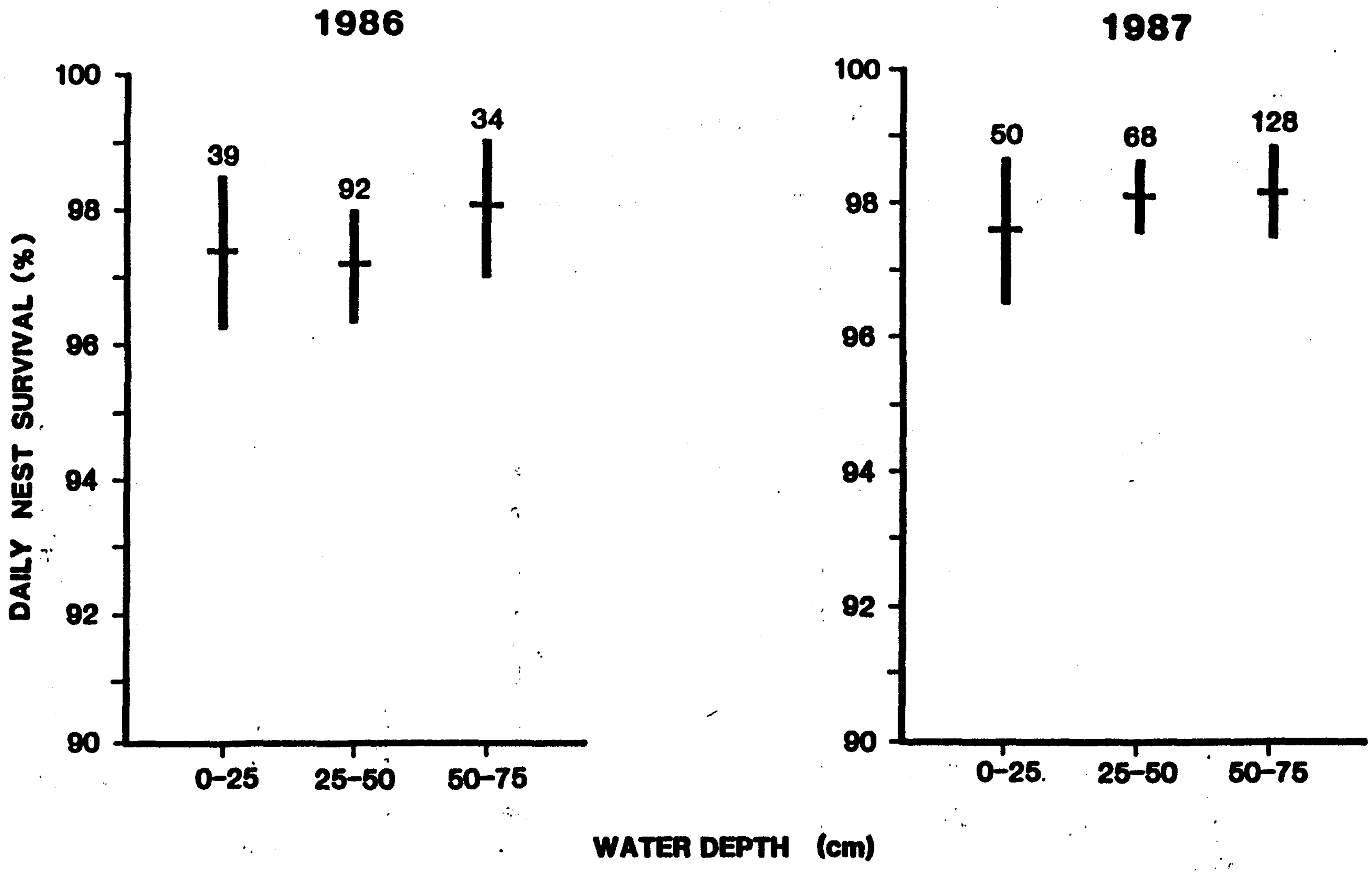


Figure 40. Mayfield estimates of daily nest survival of Snail Kite nests in WCA-3A at water depths 0-25 cm, 25-50 cm, and 50-75 cm. Ninety-five percent confidence intervals about the estimates and sample sizes are shown.

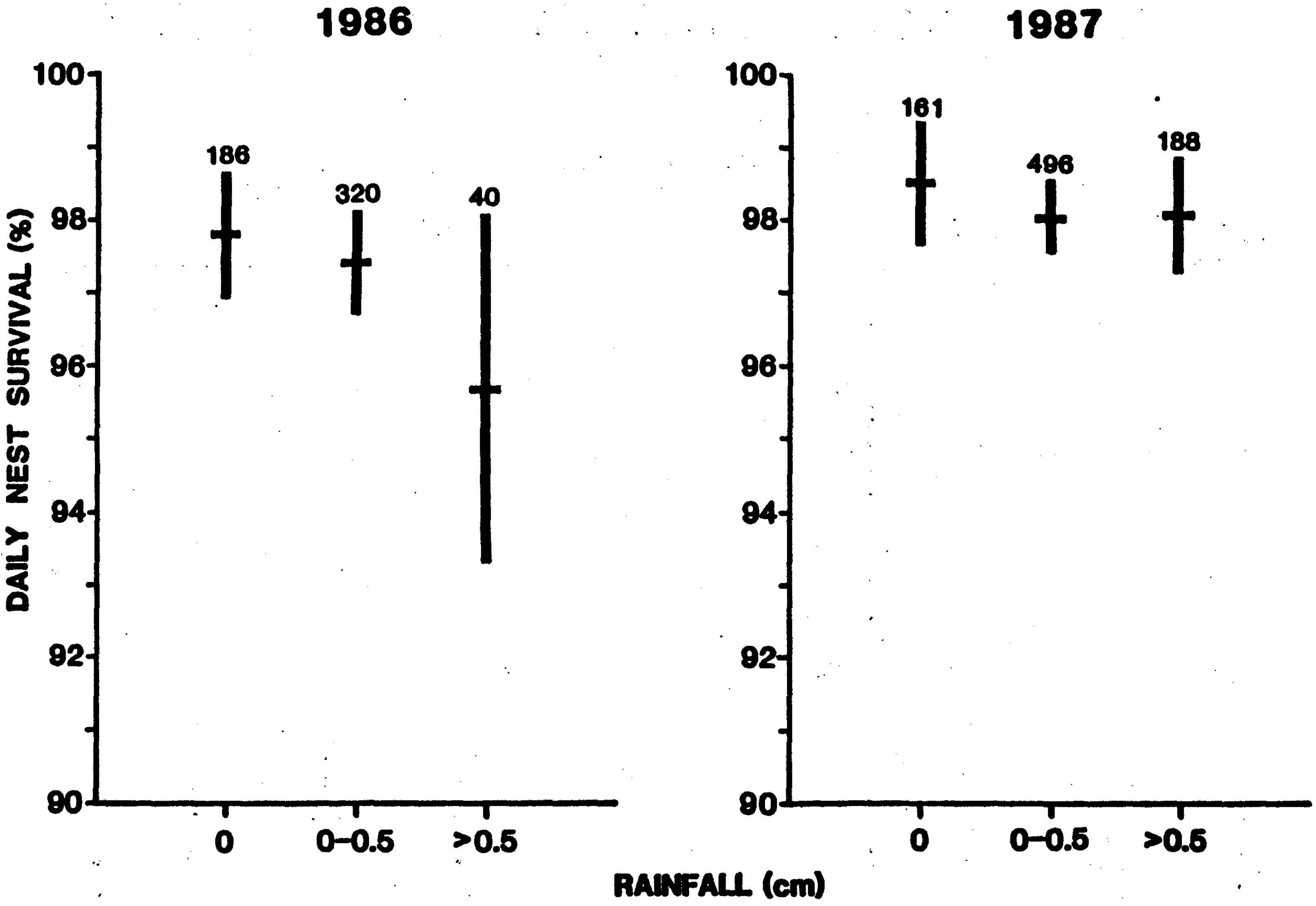


Figure 41. Mayfield estimates of daily nest survival of Snail Kite nests in WCA-3A when average daily rainfall between nest visits was 0 cm, 0-0.5 cm, >0.5 cm. Ninety-five percent confidence intervals about the estimates and sample sizes are shown.

about the estimates and sample sizes are shown.

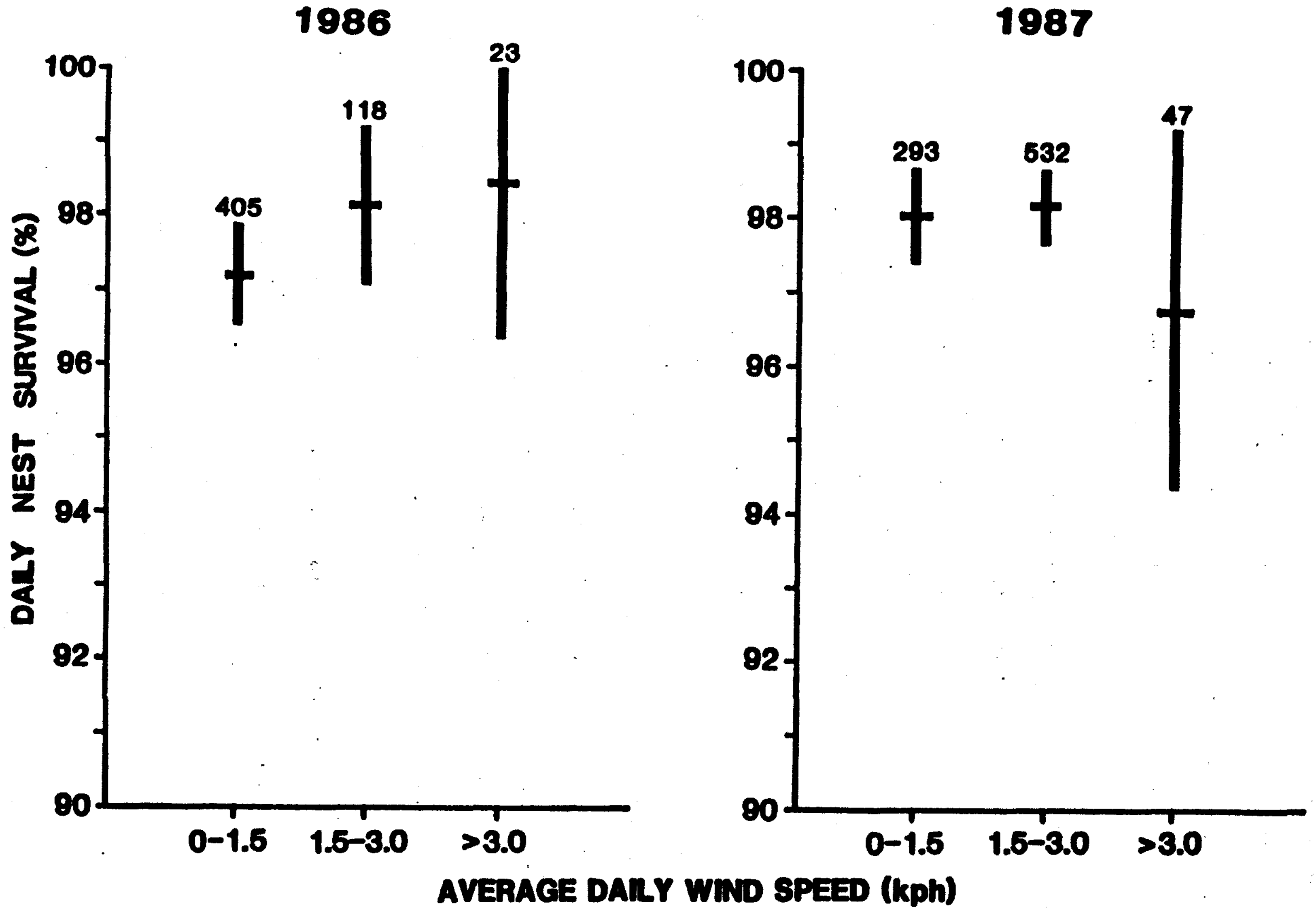


Figure 42. Mayfield estimates of daily nest survival of Snail Kite nests in WCA-3A in which average daily wind speeds were 0-1.5 kph, 1.5-3.0 kph, and >3.0 kph. Ninety-five percent confidence intervals about the estimates and sample sizes are shown.

<u>Temperature</u>.-- Daily nest survivorship differed significantly (standard normal tests, $P < 0.05$, Appendix 12) among nests experiencing low (< 10°C), intermediate (10 - 20°C), and high (>20°C) minimum temperatures during both 1986 and 1987 (Figs. 43 and 44); with the exception that nests experiencing low minimum temperatures did not differ significantly (although nearly so) from those with intermediate minimum temperatures in 1986 ($Z = 1.93$, $P = 0.052$).

In 1986, low sample size ($N = 5$) precluded statistical comparison of daily nest survivorship when maximum temperatures were less than 20°C; however, differences in daily survivorship between nests when maximum temperatures were intermediate (20°C - 30°C) and high (>30°C) were not significant ($Z = 1.80$, $P = 0.08$) (Appendix 13). In 1987, daily survivorship differed between nests when maximum temperatures were low verses high ($Z = 2.04$, $P = 0.04$); nests with intermediate maximum temperatures did not differ significantly from either nests with low maximum ($Z = 1.52$, $P = 0.13$) or high maximum ($Z = 1.48$, $P = 0.14$) temperatures.

<u>Relative importance of factors influencing nesting success</u>.-- Stepwise logistic regression showed that of those influences that we measured, date of nest initiation (i.e. when the first egg was laid) was the single most important determinant of whether a nest succeeded or failed (Table 5). The coefficient for FE-DATE (first egg date) was negative, indicating that nesting success decreased through the season; this is consistent with the results of the Mayfield analyses.

Water level during the observation interval prior to a given nest succeeding or failing (H2O-FIN, see Methods) also had a negative coefficient. This indicates that a lower water depth at this time is associated with higher nesting success. This result is not consistent with our Mayfield analyses which showed that daily nest survival was highest during periods of highest water depth; nor is it consistent with the positive coefficient for H2O-INIT (water level at time of initiation), which indicated that higher water depths at initiation are associated with higher success.

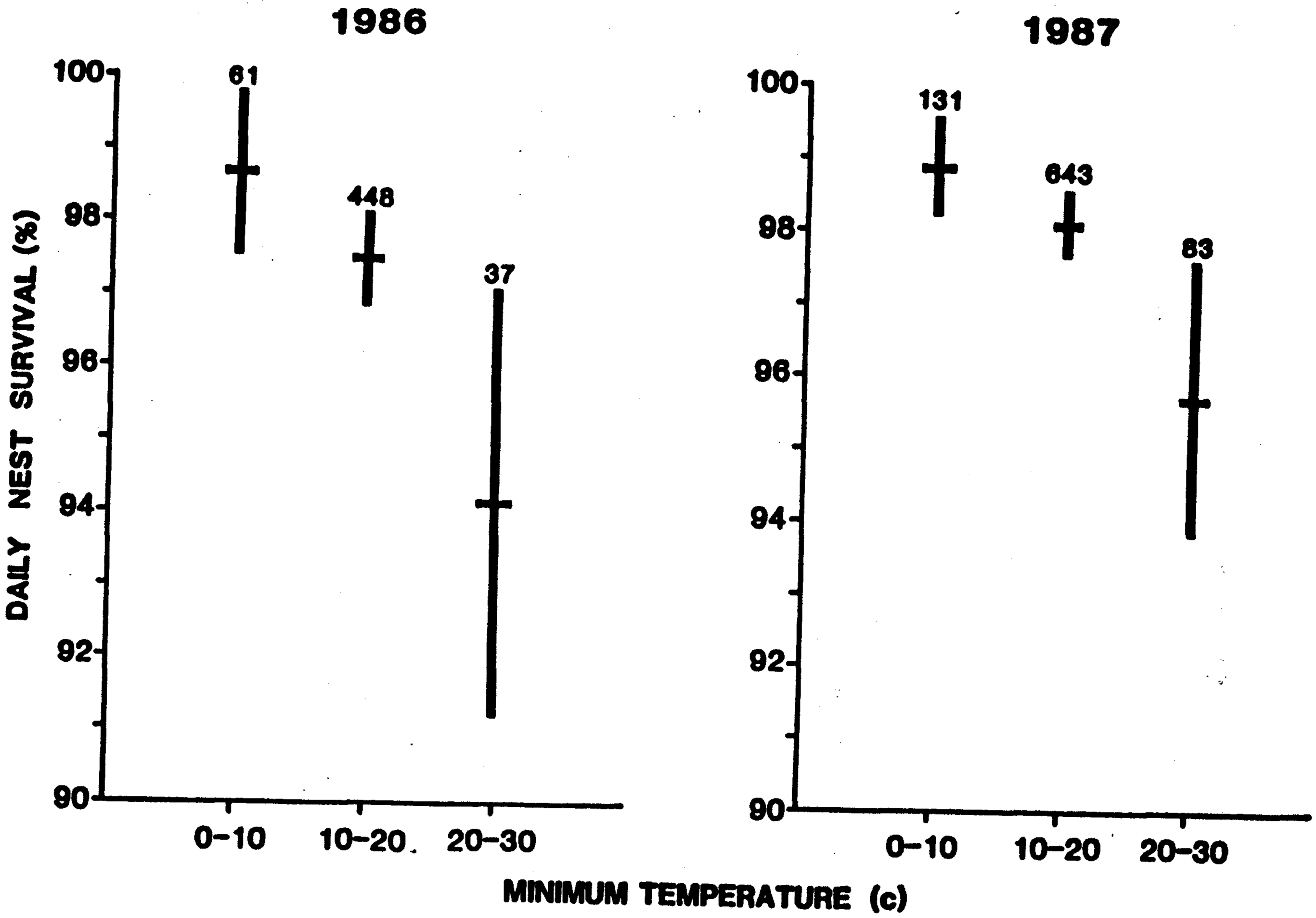


Figure 43. Mayfield estimates of daily nest survival of Snail Kite nests in WCA-3A in which the minimum temperatures were 0-10°C, 10-20°C, 20-30°C. Ninety-five percent confidence intervals about the estimates and sample sizes are shown.

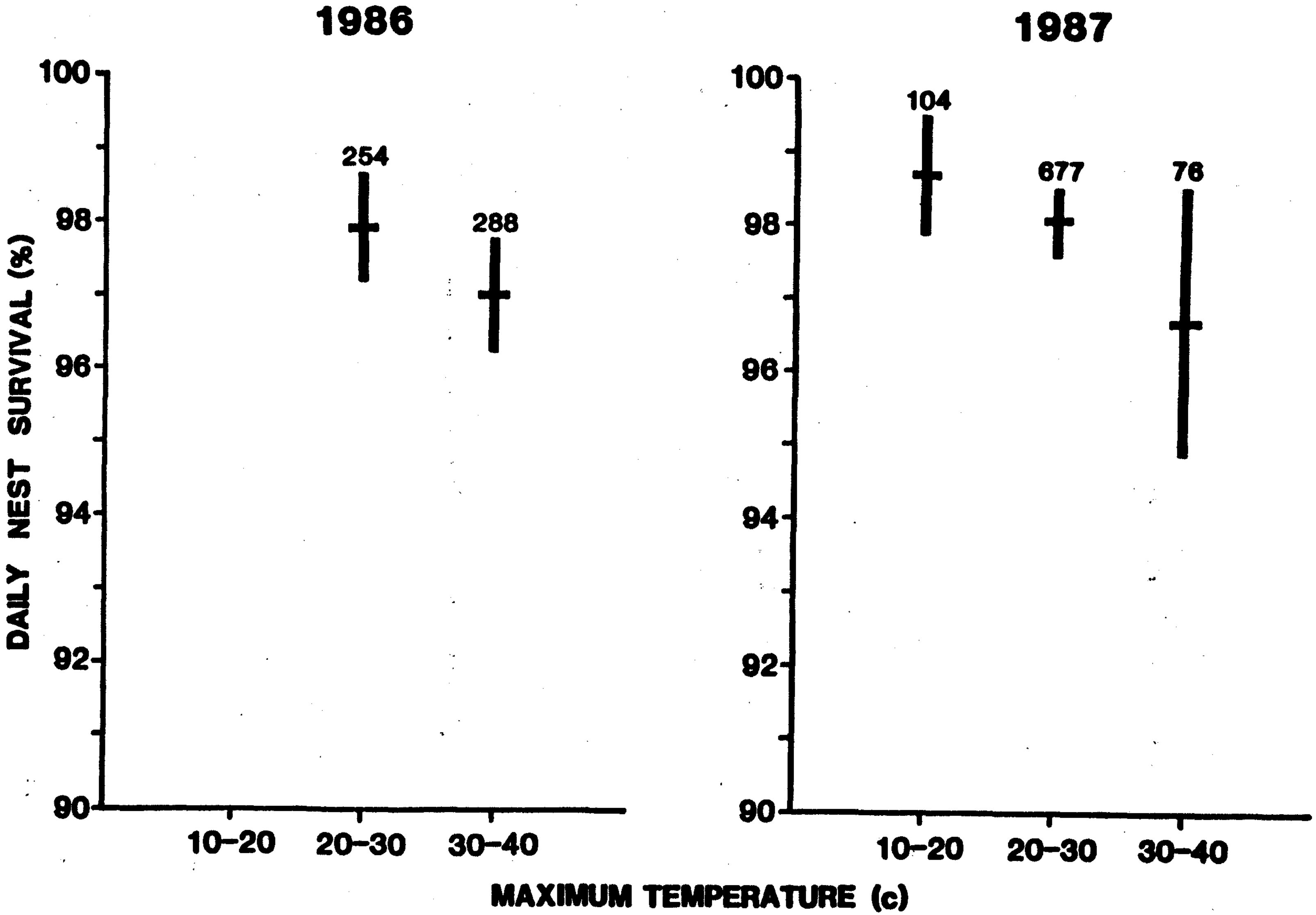


Figure 44. Mayfield estimates of daily nest survival of Snail Kite nests in WCA-3A with maximum temperatures 10-20°C, 20-30°C, 30-40°C. Ninety-five percent confidence intervals about the estimates and sample sizes are shown. Insufficient sample size precluded calculation for nests during 1986 in which the maximum temperature was from 10-20°C.

and sample sizes are shown. Insufficient sample size precluded calculation for nests during 1986 in which the maximum temperature was from 10-20°C.

Table 5. Results from stepwise logistic regression analyses for discriminating between successful and unsuccessful nests with respect to influencing variables. Variables are listed in the order they were entered into the model (by order of the highest initial Chi-square value, see Harrell 1980).

1986 (n = 142)[a]				1987 (n = 212)[b]				1986 and 1987 Combined[c]			
Variable[de]	Coefficient	SE	R	Variable[de]	Coefficient	SE	R	Variable[de]	Coefficient	SE	R
FE-DATE	-0.124	0.02	-0.396	FE-DATE	-0.076	0.01	-0.357	FE-DATE	-0.077	0.01	-0.376
H20-FIN	-0.043	0.02	-0.154	H20-FIN	-0.239	0.04	-0.372	H20-FIN	-0.155	0.02	-0.339
WIND	-1.087	0.31	-0.237	H20-INIT	0.178	0.03	0.293	H20-INIT	0.111	0.02	0.248
MIN-TEMP	0.298	0.11	0.175	NS	1.450	0.46	0.163	N-HGT	0.003	0.00	0.140
SUBS-3	2.247	0.75	0.201	SUBS-4	-1.412	0.5	-0.142	WIND	-0.517	0.12	-0.178
MAX-TEMP	0.349	0.15	0.139					RAIN	0.829	0.31	0.104

[a] Residual $X^2 = 54.13$, $P = 0.05$, df = 13; Model $X^2 = 12.11$, $P < 0.01$, df = 1

[b] Residual $X^2 = 95.48$, $P < 0.01$, df = 13; Model $X^2 = 12.17$, $P < 0.01$, df = 1

[c] Residual $X^2 = 128.47$, $P < 0.01$, df = 13; Model $X^2 = 29.44$, $P < 0.01$, df = 1

[d] Input variables were: FE-DATE (date 1st egg was laid); N-HGT (nest height); MAX-TEMP (maximum temperature during the last observation period prior to fledging or failing); MIN-TEMP (minimum temperature during the last observation period prior to fledging or failing); WIND (average daily wind speed during the last observation period prior to fledging or failing); RAIN (average daily rainfall during the observation period prior to fledging or failing); SUBS-X (nesting substrate). See Appendix 2 for detailed descriptions.

[e] Variables not listed for a given analysis implies that the initial Chi-square value was not significant at $P < 0.05$.

The remaining variables were not consistent between years regarding their relative contribution toward discriminating successful from unsuccessful nests. Distance from land, stand size, and nest substrates (other than pond apple or cypress) did not have significant initial Chi-square values ($P > 0.05$) during either year and were not entered into any of the final models.

DISCUSSION

Habitat Selection

Water depth.-- Most Snail Kites (94% of 281 nests) selected nest sites that had water depths ranging from 20 - 80 cm. Steiglitz and Thompson (1967) and Sykes (1987c) reported nest sites having similar depths, and Schortemeyer (1980) suggested similar depths as being optimum for Snail Kites.

Kites rarely (3% of 281 nests) built nests at a site with less than 20 cm of water. Nesting success during 1986 and 1987 was not significantly lower when water depths were below 25 cm; however, no nesting areas completely dried out during this study (see Influences of Nesting Success). Complete drying of an area would likely cause apple snails to aestivate and/or die (Hanning 1978) and ultimately may reduce snail populations (Kushlan 1975). Drying also may result in increased access by terrestrial predators to kite nests (Beissinger 1984, Sykes 1987c).

Water depth typically decreased through the nesting season in WCA-3A. The minimum water depths usually selected by nesting kites at the time of nest initiation (i.e. 20 cm at nest sites or 30 cm in sloughs) may therefore be the minimum depths which would not likely dry out during the breeding cycle.

Snail Kites also rarely (2% of 281 nests) initiated nests at sites with greater than 80 cm of water. The reasons why kites might not select sites in deeper water are less clear than for avoiding shallow water, and may be related more to foraging than nesting habitat. Hanning (1978) suggested, however, that depths of up to 1 m had suitable light penetration and buffering of extreme air temperatures to maintain apple snail populations. Less woody vegetation and sparser sawgrass also is generally found in deeper water; although this may in part be attributable to a longer hydroperiod. The lack of woody vegetation in deeper sites results in fewer strong nesting sites and a complete lack of emergent vegetation also may reduce apple snail availability to kites because it is when snails are on emergent vegetation that they may be most vulnerable to kites (see Proportion of Open Water). The lack of nests found in water depths greater than 80 cm may, in part, be an artifact of the environmental conditions under which this study was conducted. Under different conditions (e.g. lakes or years) kites commonly may nest in depths greater than 80 cm (Snyder et al. in review). Proximity to suitable foraging areas is probably a major factor in the selection of these deeper sites.

We have expressed habitat suitability with respect to water depth at Snail Kite nest sites (Fig. 45). We base this assessment on the range of water depths selected by nesting Snail Kites during this and previous studies in the Everglades, the probable negative effects of selecting nest sites outside this range, and an expected annual hydrologic pattern of decreasing water level through the spring months. For example, nesting success did not differ between nests while they were in water shallower than 25 cm compared to those in deeper sites; however, because of the drying rates during the breeding season (water levels dropped by 40 cm or more), nests that initially were built in less than 20 cm of water (implies foraging areas <30 cm) would have been at high risk of both the nest site and the foraging areas drying out. We therefore suggest that 20 cm is the minimum water depth for suitable Snail Kite nesting habitat.

The range of water depths that we consider suitable for nesting Snail Kites is intended only for the Everglades habitat (e.g. WCA-3A). Suitable water depths in lake habitats should be evaluated separately because these habitats have different environmental conditions and constraints (e.g. steeper elevational gradients, wave influences, etc.) which may influence their suitability for nesting.

Although areas of deeper water (>110 cm) in the Everglades currently lack nesting populations of kites they may serve as refugia during droughts for both kites and apple snails. When nesting areas dry out during periods of drought, these deeper sites are more likely to remain inundated and may provide enough apple snails to sustain a greater number of kites during the drought period than could otherwise survive. They also may serve as a

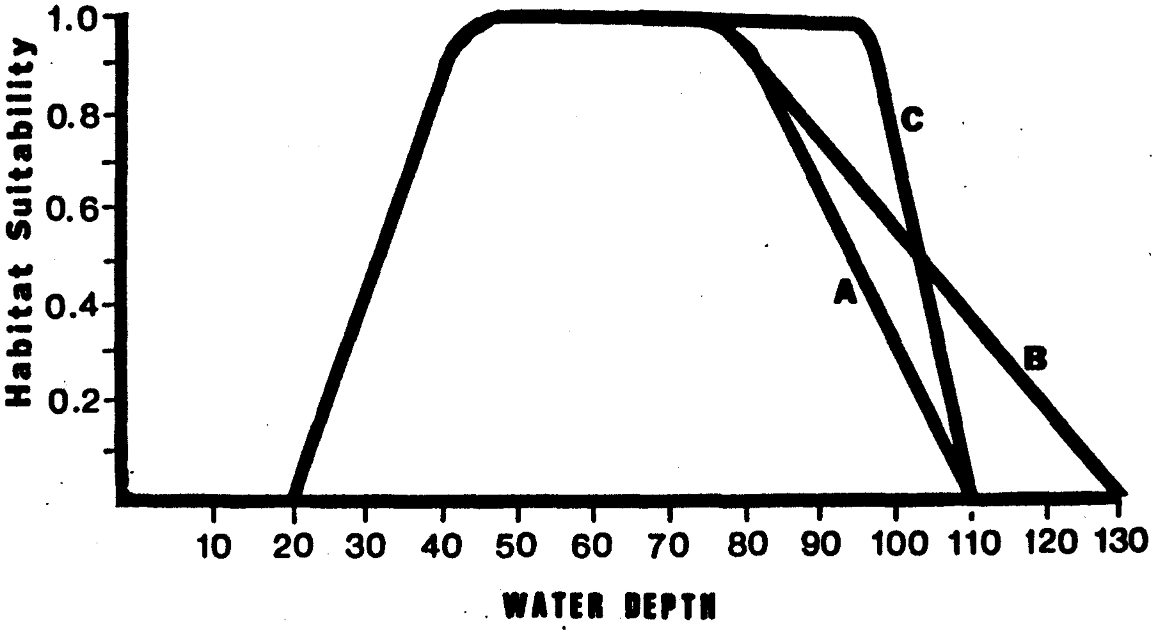


Figure 45. Habitat suitability of Snail Kite nesting habitat in relation to water depth. Suitability of 0 implies that the habitat is not suitable and suitability of 1 implies that the habitat is completely suitable with respect to water depth. Becuase of the uncertainty regarding the nature of the upper limit, we present three possible scenarios: A) a rapid linear decline; B) a slower linear decline (with uncertain intercept); and C) a threshold decline.

reservoir of apple snails to recolonize areas following population declines resulting from drought.

Dry-down interval and hydroperiod.-- There is little doubt that the extent to which areas are inundated has a major influence on the quality of habitat for nesting Snail Kites. In the short term, the desiccation of an area will likely result in Snail Kite nesting failure (Sykes 1979, Beissinger 1986), massive dispersal (Beissinger and Takekawa 1983), and adult mortality (Sykes 1979, Beissinger and Takekawa 1983). In the long term, the extent of inundation will likely influence overall apple snail populations (Kushlan 1975) and the vegetative communities of the habitat (Loveless 1959, U.S. Department of Interior 1972, McPherson 1973, Worth 1983, Olmsted and Loope 1984). What is less clear are the lower and upper limits of inundation frequencies required to maintain suitable nesting habitat for Snail Kites.

The extent to which an area is inundated most often is expressed in terms of hydroperiod. This is the proportion of time or number of days per year that an area is inundated (Olmsted and Loope 1984). While this measure may be useful for many purposes, it can be somewhat misleading with regards to Snail Kite habitat. For example, a hydroperiod of 95% could mean that each year an area is inundated 95% of the time (i.e. it dries for 5% of every year) or it could mean that in most years the area is flooded 100% of the time and dries out for a longer (> 5%) period during an occasional dry year. The difference between these interpretations could be quite significant with respect to Snail Kite habitat. For this reason, we have expressed the frequency of inundation in terms of the interval between dry downs; but have provided an approximate hydroperiod equivalent based on recent hydrologic patterns in WCA-3A.

There is little disagreement among those who have studied Snail Kites that frequent (e.g. annual) desiccation is detrimental to Snail Kite habitat. Apple snail populations increase with prolonged flooding (Kushlan 1975), and the wet prairie and open slough communities used by foraging kites occur under relatively wet conditions (Zaffke 1983).

Based on the distribution of Snail Kites in WCA-3A and in the other Water Conservation Areas and the corresponding dry-down intervals of areas used by nesting kites (Table 6), we suggest that areas that dry down more frequently than every 1.6-1.7 years probably are unsuitable for nesting kites. Drier areas may be used intermittently by foraging kites provided that they do not dry out so frequently that apple snails are absent. We point out, however, that this is a superficial assessment. Additional information is needed on the influences of such factors as the duration and frequency of drying, and the frequency of burning on snail populations and vegetation.

There is less agreement among those who have studied Snail Kites that there exists an upper limit of inundation for suitable nesting habitat. Several authors (e.g. Howell 1932, Bent 1937, Steiglitz 1965, Steiglitz and Thompson 1967, Beissinger 1983a, in press) have reported that Snail Kite nesting habitat is enhanced by continuous flooding because snail populations (Kushlan 1975) and kite reproduction (Sykes 1979, Beissinger 1986) both decline when areas completely dry out. Sykes (1983), however, suggested that some parts of the conservation areas are flooded too deeply and for too long a period.

Although areas that dry down more frequently than once every 1.7 years appear to be unsuitable for nesting kites; an excessively long interval (>4-5 years) between dry downs also may be detrimental to suitable nesting habitat. Continuous flooding inevitably results in the loss of woody vegetation (U.S. Dept. of Interior 1972, McPherson 1973, Worth 1983, Alexander and Crook 1984). Since more than 95% of the Snail Kite nests in WCA-3A were located in woody vegetation, this would result in a significant loss in the number of nest sites. Nesting Snail Kites regularly use cattails as a nest substrate in regions outside of WCA-3A where woody vegetation is lacking; however, cattails are structurally weak and these nests frequently fail unless artificial nest baskets are provided (Sykes and Chandler 1974, Beissinger 1986).

Willow is more tolerant of prolonged flooding than most woody species in the Everglades (Loveless 1959); however, continuous flooding of even water tolerant species

Table 6. **Range of ground elevations for which Snail Kite nests have been reported in the water conservation areas. Dry down intervals were derived for these elevation ranges from the gauging station shown.**

Area	Gauging station	Minimum elevation of nesting	Maximum elevation of nesting	Minimum dry-down interval	Maximum dry-down interval
WCA-1	1-19	13.9	14.4[a]	1.6	2.3
WCA-2A	2-17	10.0	11.2	2.3	5.3[b]
WCA-2B	2-21	7.2	7.5	--	--
SCA-3A[c]	3-28	6.8	8.2	1.9	3.3
WCA-3A[d]	3-3	8.3	8.3	1.9	1.9
WCA-3B[e]	Shark 1	6.5	6.5	2.5[f]	2.5[f]

[a] Additional nesting was reported along L-40 canal up to 17 ft. elevation, but nesting activity was restricted to the zone of canal influence. Areas within the interior of WCA-1 at this elevation are almost continuously dry.

[b] Includes nine years of continuous flooding prior to a population decline.

[c] South of Alligator Alley.

[d] North of Alligator Alley.

[e] Consists of a single nesting area with three nests from 1986.

[f] Based on 6-year period of record.

results in detrimental accumulation of toxic compounds in the root zone (Harms et al. 1974, Patrick 1974). Willow is receding in the wetter areas of WCA-3A (McPherson 1973), and has receded in other Water Conservation Areas that have experienced prolonged flooding (see U.S. Dept. of Interior 1972, Worth 1983).

Compared to earlier conditions of frequent dry downs, WCA-2A and the deepest parts of WCAs 1 and 3A have had a reduction in woody vegetation as a result of prolonged innundation (U.S. Dept. of Interior 1972, McPherson 1973, Worth 1983). Snail Kite use in WCA 1 and 2A has decreased (Fig. 46a and b) following prolonged flooding and subsequent loss of shrubs and trees, even though the general population trend of Snail Kites in Florida has been increasing since 1968 (Fig. 47a). Although the population trend in WCA-3A also has been increasing (Fig. 47b), we observed relatively few Snail Kites in the deepest portions of WCA-3A where tree loss has been most pronounced. Populations also have increased in WCA 2B and 3B (Fig. 48a and b) in areas having a more frequent dry interval than the wetter areas of WCA 1 and 2A where kite populations have declined. Although loss of woody vegetation may have contributed to these declines, other factors (e.g. water quality) probably are also important.

The specific hydrologic regime which results in the loss of woody vegetation is unclear; however, U.S. Department of Interior (1972) suggested that if water level changes persist for longer than five years major vegetative changes would undoubtedly result. In addition, Snail Kites in the water conservation areas do not appear to nest in areas that dry down less frequently than approximately every four years, even though such areas are available in WCA 1, 2A, and 3A.

There is an apparent paradox regarding the upper limit of inundation frequency, in that prolonged flooding probably is beneficial to apple snail populations, but detrimental to woody vegetation (i.e. nesting substrates). This paradox might be partially mediated in lake habitats, where the littoral zone may provide prolonged inundation with suitable water depths for apple snail populations to prosper. Because these conditions occur in the

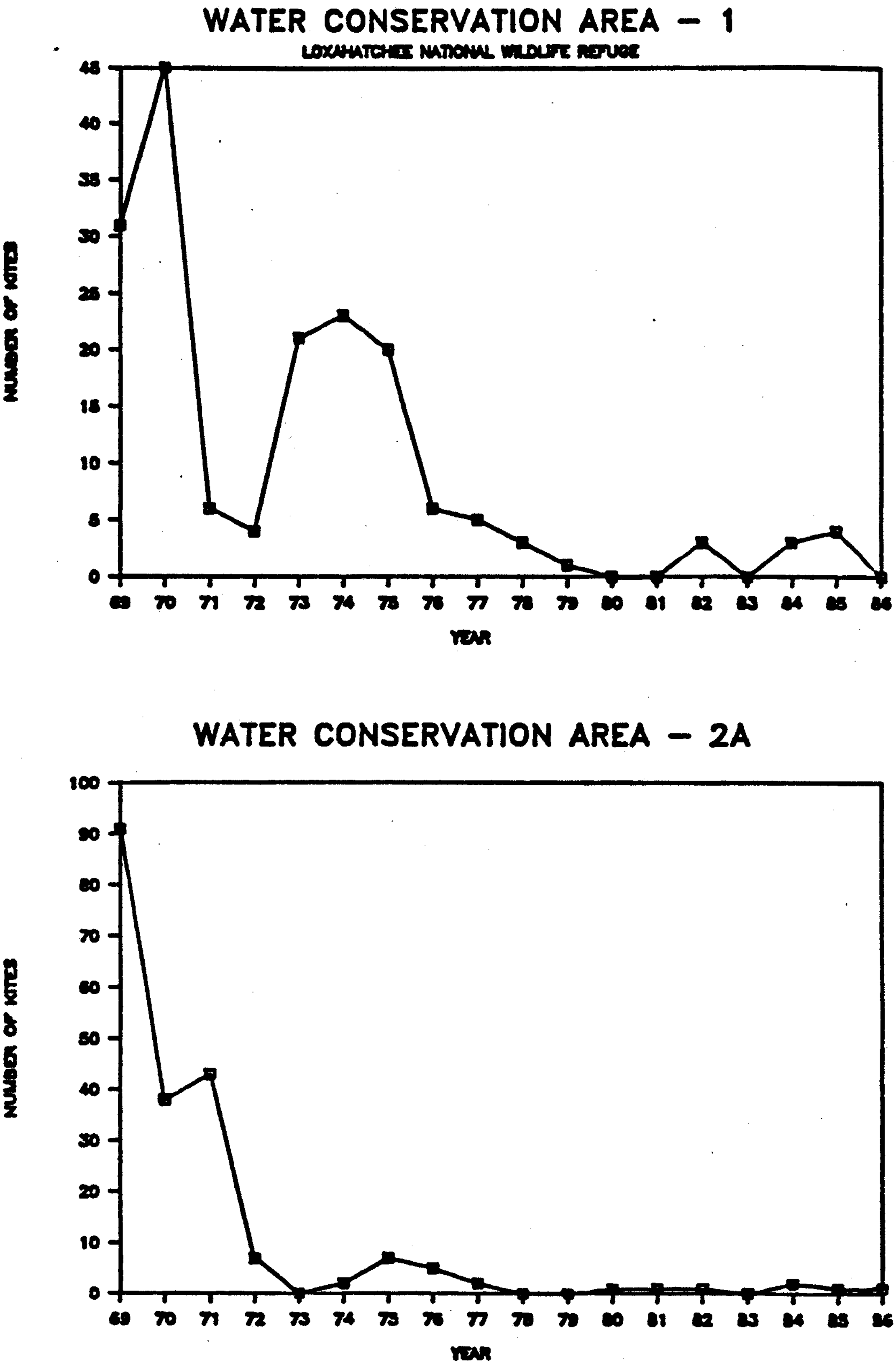


Figure 46. Snail Kite populations in WCA-1 and WCA-2A from 1969 through 1986, as determined from annual Snail Kite Surveys. Surveys from 1968 - 1980 were conducted by the USFWS (Sykes 1983a, 1983b), and surveys from 1981 - 1986 were conducted by FGFWFC (FGFWFC unpubl. data).

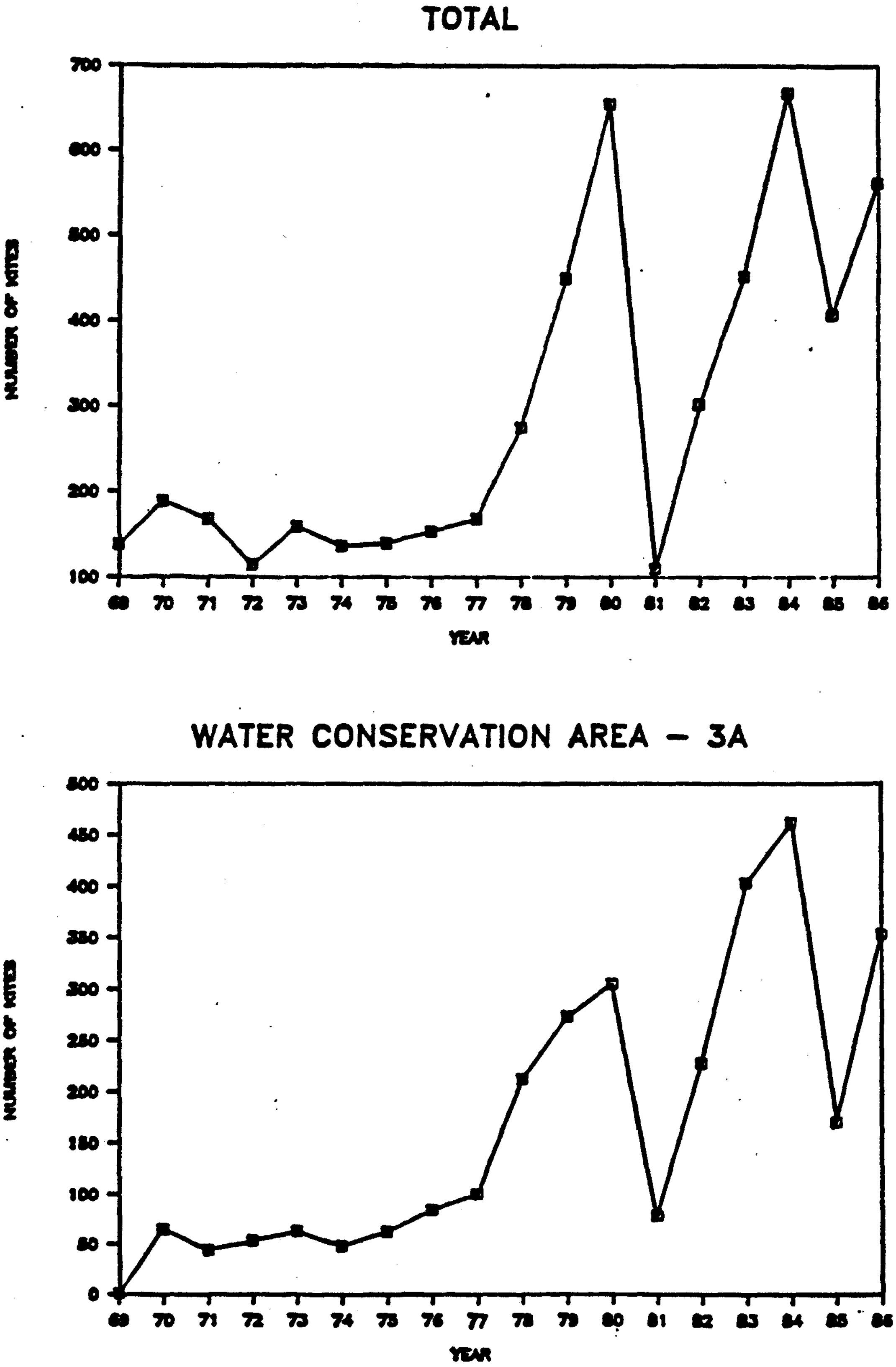
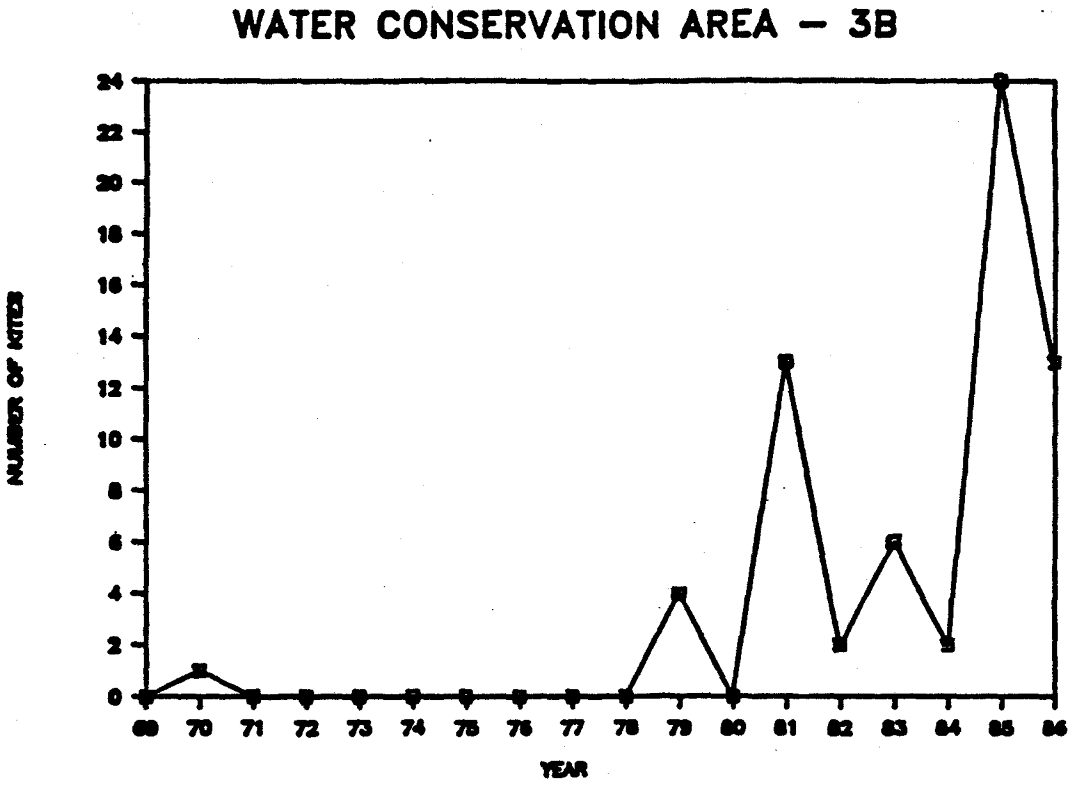


Figure 47. Snail Kite populations for south Florida and WCA-3A from 1969 through 1986, as determined from annual Snail Kite Surveys. Surveys from 1968 - 1980 were conducted by the USFWS (Sykes 1983a, 1983b), and surveys from 1981 - 1986 were conducted by FGFWFC (FGFWFC unpubl. data).



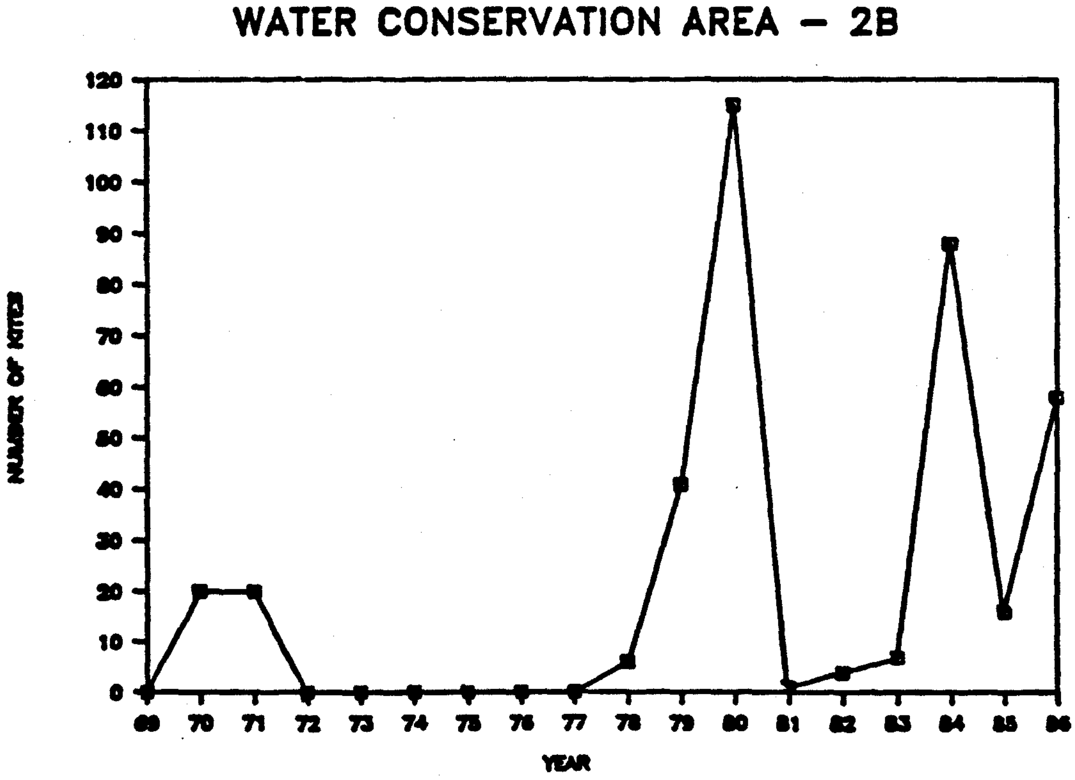


Figure 48. Snail Kite populations in WCA-3B and WCA-2B from 1969 through 1986, as determined from annual Snail Kite Surveys. Surveys from 1968 - 1980 were conducted by the USFWS (Sykes 1983a, 1983b), and surveys from 1981 - 1986 were conducted by FGFWFC (FGFWFC unpubl. data).

littoral zone, woody vegetation often is available along adjacent shores or on islands. This vegetation often is used for nesting during years of high water when these sites are inundated; however, access by predators during years of low water reduces the potential for successful nesting at these sites (Beissinger 1986). During periods of low water, Snail Kites often select sites in structurally weaker cattails rather than nest in the stronger, but more vulnerable woody vegetation (Beissinger 1986). Unlike these lake habitats, the everglades habitats lack a pronounced littoral zone. Consequently, woody vegetation may be several kilometers removed from foraging areas that have lost this vegetation through prolonged flooding.

Confounding the difficulty in assessing the lower and upper limits of inundation frequencies required for suitable nesting habitat are the lag times between hydrologic changes (i.e. prolonged or reduced flooding), vegetative and apple snail responses to the hydrologic changes, and ultimately the response of Snail Kite populations. It required 10 to 15 years for Snail Kite populations to respond (i.e. increase) following the initial impoundment of WCA-3A; although there were several dry years which may have slowed the rate of increase. Lag times also may occur in relation to population declines. For example, Snail Kite populations in WCA-2A declined dramatically after 9 years of continuous flooding.

It also is difficult to distinguish the influence of inundation frequencies from those of water quality. Both Conservation Areas 1 and 2A have received increasing amounts of nutrients in recent years (J. Richardson, pers. comm.). Consequently, Snail Kite population declines in these areas may have resulted from decreased water quality rather than prolonged innundation. The influence of water quality on apple snail populations currently is unknown and future studies are needed.

In spite of the difficulties associated with determining the specific inundation frequencies required for suitable nesting habitat, the current evidence indicates that the lower inundation limit of suitable habitat in the Everglades is a dry down interval of approximately every 1.6 - 1.7 years (roughly an 80% hydroperiod), and the upper limit is approximately 4 to 5 years (roughly a 90% hydroperiod) (Fig. 49).

These ranges of dry down intervals are approximations based on our current knowledge of how the hydrologic regime influences the environment. As more specific data become available, these ranges of hydrologic conditions required to maintain suitable nesting habitat should be refined. In addition, we do not intend these ranges of inundation frequencies to be applicable to habitats outside of the Everglades (e.g. lakes) where environmental conditions may be quite different. For example, kites may find suitable nesting habitat on lakes with considerably longer periods of inundation provided that suitable nest sites are located on islands, along shores, etc.

In summary, the hydrologic conditions that appear most suitable for nesting Snail Kites are a dry down interval long enough (> 1.7 years) to maintain apple snail populations and allow open slough communities, but short enough (< 5 years) to maintain woody vegetation (i.e. willows, etc.) for nest sites.

Proportion of open water.-- Snail Kites select habitat having an interspersion of open water and emergent vegetation (Steiglitz and Thompson 1967, Sykes 1983, 1987a). Open water communities are an important element of suitable Snail Kite habitat because kites are unable to effectively forage in dense vegetation (see Beissinger 1983b, Sykes 1987a) and because slough communities provide important foraging habitat for apple snails (Hanning 1978). These open water areas can be either wet prairie or slough communities (see Loveless 1959 for detailed descriptions of community types) provided that they are sparsely vegetated to allow kites to forage effectively.

Although areas of open water are important, some emergent vegetation also is necessary. Snail Kites capture snails that are usually within the top few centimeters of water (Sykes 1987a, pers. observ.). Consequently, apple snails probably are most vulnerable to kites when they climb emergent vegetation to respirate, feed, or lay eggs.

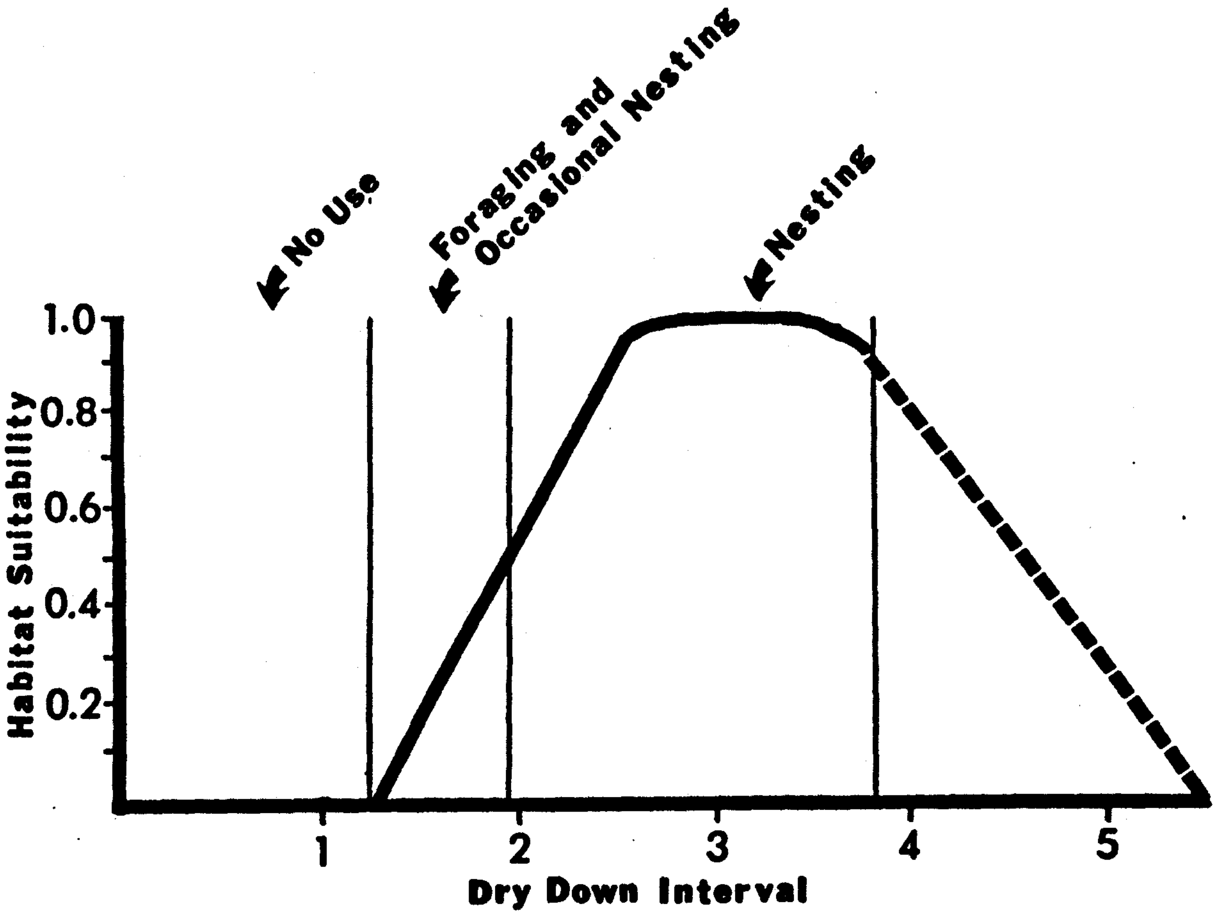


Figure 49. Habitat suitability of Snail Kite nesting habitat in relation to dry down interval. Suitability of 0 implies that the habitat is not suitable and suitability of 1 implies that the habitat is completely suitable with respect to dry-down interval. The effects of a higher dry-down interval (--) are unclear; they may be negative on woody vegetation and positive on apple snail populations.

The proportion of open water to sawgrass in the nesting habitat in WCA-3A averaged 29% in 1986, and 40% in 1987. This is similar to the 41.2% (combined open slough and wet prairie habitat) reported by Sykes (1987c).

Interspersion of open water and sawgrass communities results from the hydrologic conditions described above (see Loveless 1959, McPherson 1973, Zafke 1983, Tanner et al. 1986). Consequently, we have not provided a separate habitat suitability model of this variable; however, suitable nesting habitat in the Everglades probably ranges from a ratio of 20 - 50% open water-to-sawgrass. Areas of shallow water that frequent dry down tend to have relatively more uniform stands of sawgrass (see Tanner et al. 1986); conversely, continuous inundation appears to result in reduced emergent vegetation.

Apple snail abundance.-- Our data were inconclusive regarding the importance of apple snail abundance in nesting habitat selection; however, two of three measures indicated that kites tended to nest in higher densities in areas with higher snail abundance. A minimum abundance of snails obviously is required in order for Snail Kites to survive and breed in an area; however, the relative importance of apple snail abundance above this minimum threshold as a selection criteria of nesting habitat remains unclear.

Current methods of sampling apple snails have been far from adequate (see Sykes 1983, Beissinger and Snyder 1987, Owre and Rich 1987). Consequently, our lack of conclusive evidence regarding the relative importance of snail abundance in locations where kites choose to nest may reflect problems with our sampling rather than any lack of a biological relationship.

Our data on the foraging time required by Snail Kites to capture apple snails was the only index of snail abundance that was not consistent with the hypothesis that kites nested in areas of high apple snail densities. This index, however, suffers from several sources of bias. In addition to snail abundance, the ability for Snail Kites to capture snails may be influenced by the vegetation (Beissinger 1983b, Bourne 1985, Sykes 1987a), time of season (Cary 1985), temperature (Cary 1985), time of day (Bourne 1985, Cary 1985), rainfall

(Cary 1985), wind speed (Cary 1985), and sex of the foraging bird (Sykes 1987a). We attempted to minimize these biases by conducting simultaneous paired observations in high and low density kite nesting areas, however, some of those variables no doubt influenced our results.

An additional problem associated with using capture times as an index of apple snail abundance is that it may vary temporally with kite densities. Unless capture times are assessed during the time of initial habitat selection, areas of high kite nesting density are more likely to have experienced local snail depletion by kites. We noted that foraging distances tended to increase as the nesting season progressed, suggesting that some localized snail depletion may have occurred. Since nest initiation at a given colony often is asynchronous (pers. observ.), we were not able to identify high nesting density areas, and measure capture times, until after several nests had been initiated. By this time the earlier nests usually had persisted for several weeks. Local depletion of apple snails might explain why the areas of high nesting density tended to have longer, rather than shorter, capture times even if snail densities at these areas initially were higher.

Variation in capture time was greatest in area 1, which was the area observed earliest in the season. Although no cold fronts passed through during these observations, temperatures generally were cooler earlier in the season. Lower temperatures result in decreased snail activity (Hanning 1978) and may have been an influence on this early sample (see Cary 1985).

The egg cluster index was consistent with the hypothesis that Snail Kites selected habitat with denser snail populations, however, the relationship between actual snail density and the number of egg clusters is unknown. Female apple snails are capable of laying a clutch every eight days and the frequency of laying changes over time and with environmental conditions (Hanning 1978, Owre and Rich 1987). We believe that by comparing paired samples that were taken during the same time period, we have reduced the seasonal and environmental biases. Comparisons of samples taken at different times, however, would likely yield nebulous results.

Although we only were able to sample one area of high nesting density and one of low density using a slurry pump, the results were consistent with the hypothesis that higher nesting densities of kites were in areas of higher snail abundance. These results also were consistent with the egg cluster indices for these areas, but not with capture times. The suction dredge, although labor intensive, was the most direct measure of snail abundance and we believe warrants further evaluation as a method for assessing apple snail densities.

Nest Site Selection

Snail Kites in WCA-3A appeared to select nest sites that provided strong support, but were relatively safe from predation. Willow and sweet bay, the species that were selected disproportionately less than their availability, were the species that tended to provide relatively less structural support. Although some willows provide good support, most were relatively unstable and nests placed in them were at high risk of damage from wind or structural collapse. Willows that were selected for nest substrates appeared to be the stronger of those available. Although sweet bay in WCA-3A may grow to medium-sized trees (often 5 m or more), most (outside of hammocks) were relatively small (<3 m) and unstable with few horizontal branches that could support a kite nest. In contrast, melaleuca and pond apples, which tended to provide good support for nests, were used more frequently than their relative abundance.

Numerous mature trees that would have been extremely sturdy were located in the hardwood hammocks on the northern portion of many of the large tree islands. These hammocks, however, usually were associated with dry land. Although these hammocks would have provided many stable nest sites, the potential for predators to be present also would have been greater. Most of the potential predators of Snail Kite nests (e.g. rat snakes and raccoons) would more likely be found in association with these hammocks rather than the inundated marsh.

Size of the Breeding Population

Knowing only the number nests in which breeding occurred may not provide a good indication of the size of the breeding or potentially breeding population. To determine the size of the breeding population using the number of nests, we also would have to have reliable estimates for: (1) the number of renesting attempts; (2) the extent of iteroparity; (3) the extent of movements in or out of WCA-3A; and (4) the proportion of the population that did not attempt to breed.

Beissinger (1986) found both renesting attempts after failure (N=2) and iteroparity (N=7); however, the extent to which these occurred in 1986 and 1987 is unknown. Beissinger (1986) also reported that considerable movement between areas may occur during the breeding season.

Snail Kites are capable of breeding at one year of age (Beissinger 1986); however, the extent to which this occurs particularly during a given year varies (Snyder et al., in review). Consequently, the potential breeding population may include all but young-of-the-year birds. We were unable to estimate of the number of non-breeding kites during 1986 or 1987.

The life history attributes of Snail Kites make estimating the size of the breeding population strictly from the number of nests difficult and probably unreliable. To obtain the additional information required to enable these estimates (e.g. the extent of re-nesting and iteroparity) would have required time and resources beyond the scope of this study.

An alternative to using the number of nests to estimate the size of the breeding population involves the annual Snail Kite Survey (SKS) conducted by the Florida Game and Fresh Water Fish Commission (FGFWFC). These surveys are conducted during November and

December of each year and thus estimate the population approximately one to two months before the onset of the primary breeding season. The SKS should be considered an approximation because of the difficulties associated with such a large scale survey in a difficult habitat (J. Rodgers, pers. comm.). It also does not account for movements of kites in and out WCA-3A during the breeding season. At the present time, however, the SKS may provide a more consistent estimate of the size of breeding population because it does not have the problems associated with renesting, iteroparity, and the non-breeding segment of the population. These problems essentially are eliminated by sampling the population during a restricted period of time.

The SKS results in WCA-3A for 1985 and 1986 were 170 and 353 kites, respectively (FGFWFC, unpubl. data). The high number of nests we found relative to the SKS results (the number of breeding individuals exceeded the survey results for both years) suggests that a relatively high proportion of the population, probably attempted to breed in both years, and that considerable renesting and/or iteroparity probably occurred.

Comparison of Nesting Success During 1986 and 1987 to Previous Years

Nesting success traditionally has been reported as the proportion of observed nests that are successful (i.e. fledge at least one young). This traditional approach, however, is inherently biased and tends to overestimate success (Mayfield 1961, 1975, Miller and Johnson 1978, Steenhof and Kochert 1982, Hensler 1985, Steenhof 1987). Widespread use of the Mayfield approach, however, is relatively recent and has not been used in previous studies of kites. We therefore have provided traditional estimates for our study and those from previous reports (Table 7).

Our traditional estimates of nesting success were 21% for 1986 and 40% for 1987. These values are similar to those reported by Beissinger (1986) and Snyder et al. (in review), but low compared to those reported by Sykes (1987b). Because traditional analyses that include nests found late in the nesting season yield inflated estimates (Mayfield 1961, 1975, Miller and Johnson 1978, Steenhof and Kochert 1982) the traditional estimates

Table 7. Traditional estimates of nesting success of Snail Kites in south Florida from 1968 to 1987. Includes nests found before eggs were laid (i.e. all occupied nests).

Year	Number of observed nests	Number of successful nests	Percent successful	Source
1968	13	11	84.6	Sykes (1987b)
1969	13	8	80.0	Sykes (1987b)
1970	19	8	44.4	Sykes (1987b)
1971	0	--	--	Sykes (1987b)
1972	6	3	50.0	Sykes (1987b)
1973	34	12	35.3	Sykes (1987b)
1974	35	6	17.1	Sykes (1987b)
1975	29	14	48.3	Sykes (1987b)
1976	34	22	73.3	Sykes (1987b)
1977	15	8	53.3	Sykes (1987b)
1978	14	11	78.6	Sykes (1987b)
1978	100[a]	40	40.0	Beissinger (1986)
1979	131[a]	54	41.2	Beissinger (1986)
1981	12[a]	0	0.0	Beissinger (1986)
1982	40[a]	2	5.0	Beissinger (1986)
1983	48[a]	10	20.8	Beissinger (1986)
1986	147[a]	31	21.1	This study
1987	211[a]	85	40.3	This study

[a] Includes only nests found before hatching (see text).

from this and Beissinger's (1986) studies include only nests found before hatching (see Steenhof 1987). Sykes (1979, 1987b) included nests found in all stages of the nesting cycle (P. Sykes, pers. comm.), which may in part account for the higher success he reports. 2Snyder et al. (in review) criticized Syke's (1979b) data, claiming that the inclusion of basketed nests and nests found after hatching greatly inflated his estimates of nest success. Snyder et al. (in review) summarized 18 years of study for 666 nests, over half of which had previously been reported on by Sykes (1979, 1987b), and found that only 22.8% of all nests found before hatching (including those found during nest building) successfully fledged young.

Because of the problems associated with traditional estimates and because the data from these previous studies were collected throughout South Florida (not just WCA-3A as in our study), we recommend that comparisons of these data be interpreted cautiously. For example, methodological differences have resulted in radically different estimates of nesting success for the same year; in 1978 Beissinger (1986) and Sykes (1987b) reported success rates of 40% and 78.6%, respectively.

Evaluation of the Mayfield Method for Snail Kites

As expected, our estimates of nesting success using the Mayfield method were lower than those derived by the traditional approach for the same period of the nesting cycle (i.e. excluding nests found before egg laying) (Table 8). Unless all nests are found on the first day of egg laying the traditional approach tends to overestimate success (Mayfield 1961,1975, Miller and Johnson 1978, Steenhof and Kochert 1982, Hensler 1985, Steenhof 1987), because nests found in latter stages of the nesting cycle are more likely to succeed and nests that fail early in the nesting cycle are more likely to be missed during nest searches (Mayfield 1961, 1975, Miller and Johnson 1978). The Mayfield Method minimizes this inherent bias of the traditional approach because daily nest survival is

Table 8. Comparison of nesting success during 1986 and 1987 calculated using traditional and Mayfield methods.

Year	Number of nests	Number of successful nests	Traditional estimate of success (%)	Mayfield estimate of success (%)
1986	144	43	30	23
1987	223	103	46	36

[a] Includes only nests in which we had complete observations to enable Mayfield analyses (e.g. two visits).

calculated only for the period of time that each nest is under observation (Mayfield 1961, 1975, Miller and Johnson 1978, Steenhof and Kochert 1982, Hensler 1985, Steenhof 1987).

Although the Mayfield method reduces the inherent bias of the traditional approach, it is important to recognize that this approach also has limitations. One assumption of the model is that nest failures occur at a constant rate throughout the nesting period (Hensler and Nichols 1981, Hensler 1985) and this assumption is not always valid (Green 1977). Our results showed that success during the incubation period differed from the nestling period for 1986. This violation of the constancy assumption did not cause a problem in this study since our overall estimates of nesting success were derived from separate estimates for each of the two stages (Hensler 1985). Of more serious concern, however, was whether the constancy assumption was violated within each of the nesting stages.

Survivorship curves and comparisons of 6-day intervals of the nestling periods for 1986 and 1987 showed that nest failure was skewed towards the latter part of the incubation period and the earlier portion of the nestling period. During 1987, the extent to which the constancy assumption was violated was similar between the incubation and nestling periods, but skewed in opposite directions. As a result, these violations are probably compensatory and not of major concern.

During 1986, however, the tendency toward late failure of the incubation stage appears stronger than the tendency toward early failure of the nestling period. As a consequence, the estimate of nesting success for 1986 may be slightly inflated. This occurs because more exposure days accumulate and are used in calculating daily survivorship than would occur if nests were failing throughout the period. Even so, the traditional value for 1986 was higher than the Mayfield estimate, suggesting that the Mayfield estimate was closer to the actual nesting success.

An additional consideration of using the Mayfield approach is that it is inappropriate to include failures that occur before eggs are laid. Calculation of the overall success rate during a given period of the nesting cycle (i.e. pre-laying) requires assigning a length of time to the period (e.g. the incubation period for Snail Kites is 27 days) (Mayfield 1961, Hensler 1985, Steenhof 1987). The pre-laying period for Snail Kites is highly variable (pers. observ.) and has been reported ranging from less than 7 to greater than 30 days (Snyder et al. in review). The implications of excluding pre-laying failure are discussed in the following section (see Reproductive Success and Productivity); however, it is important to realize that success estimates (either the Mayfield or traditional method) will be lower when pre-laying failures are included.

For the purposes of this study, we believe that the Mayfield Method is the more appropriate estimator of nesting success for Snail Kites. It is important, however, that survivorship curves be used in conjunction with nesting success estimates to aid in interpreting any bias resulting from violations of the constancy assumption. It also is important to realize that estimates of success using the Mayfield Method probably will be lower than traditional estimates, and that any estimate that excludes failures before eggs are laid will be higher than estimates that include these failures. If the nesting cycle is considered to begin at the onset of courtship (as it well may, for some demographic models), then use of the Mayfield Method may be more tenuous because the method requires each stage of the nesting cycle to be of known duration; this may be a problem with species such as the Snail Kite, where the length of the courtship period may be highly variable and nest building may be suspended frequently. We also emphacize that nesting success is only one measure of reproduction and may have limited meaning without consideration of additional reproductive parameters (e.g. number of young fledged per female and proportion of population breeding).

Reproductive Success and Productivity

Data required for effective studies of raptor reproduction include: (1) the total number of pairs in the area; (2) the total number of pairs that actually breed; (3) the number that are successful; and (4) the total number of young reared (Brown 1974). Several life history attributes of Snail Kites, however, result in these data being both difficult to obtain and easy to mis-interpret, particularly in comparison with other North American raptors.

Failure of breeding-age adults to lay eggs in a given year may be an extremely important indicator of unfavorable environmental conditions (Postupalsky 1974). Underlying the importance of this type of failure is the assumption that this represents a failure to breed for a given year. While this assumption is probably true for many North American raptors, it is probably not true for Snail Kites. Snail Kites frequently may terminate courtship (including nest building) early during the nesting season when cold fronts pass through the region (Beissinger 1984, pers. observ.) and decreased water temperatures result in decreased snail activity (McClary 1964) and foraging success by kites (Cary 1985). Courtship resumes, however, after temperatures increase, but often at a new location (pers. observ.). This behavior may be a regular part of early season nest initiation (see also Sykes 1987c) and should not be assumed to represent failure of the birds to breed for the season.

Excluding drought years, nesting success during 1986 and 1987 was intermediate among those years previously reported (see Beissinger 1986, Sykes 1987b). Sykes (1987b) suggested that a nesting success of 40-50% is sufficient to maintain Snail Kite populations in Florida. It is unclear, however, how he derived this figure since the recruitment of young into the population is dependent upon not only nesting success, but also the extent to which breeding-age adults acquire mates, lay eggs, and ultimately produce fledglings (Newton 1979).

The single most important measure of the reproductive health of a raptor population is the number of young fledged per breeding-age female; however, because of the difficulty in assessing the non-breeding segment of the population the most meaningful measure may in most cases be the number of young produced per pair or per occupied territory (Steenhof 1987). Brown (1974), Postupalsky (1974), and Newton (1979) also emphasized the importance of reporting productivity in relation to the number of occupied nests in an area. This measure presumably expresses annual productivity relative to the size of the potentially breeding population and is thus of major demographic importance (Postupalsky 1974). Unlike most North American raptors, the number of occupied Snail Kite nests may be a poor indicator of the number of breeding-age females; principally because Snail Kites may be highly iteroparous (Snyder et al. in review), frequently renest after failure (often at a new location and with a new mate) (Beissinger 1986), and may be sequentially polygamous within a single breeding season (Beissinger and Snyder 1987). Since each female Snail Kite potentially could succeed in fledging up to four broods per year and may regularly produce two (Beissinger 1986), productivity expressed per occupied nest may grossly underestimate the number of young produced per breeding-age female during favorable years for breeding.

The problem of underestimating Snail Kite productivity by using a per-occupied-nest scale might be lessened by evaluating productivity in relation to a population estimate taken at one point in time (e.g. the annual SKS). If we assume a 50/50 sex ratio, our productivity estimate for WCA-3A in 1986 would have increased from 0.38 (young fledged per occupied nest) to 0.76 (young fledged per female from the 1985 SKS). Relating productivity to the SKS has its own problems (i.e. assuming a 50/50 sex ratio and not accounting for immigration or emigration); however, it is probably a more consistent measure from year to year because it is not influenced by the extent of re-nesting, iteroparity, polygamy, or shifts in the location of nesting within WCA-3A.

Annual productivity of Snail Kites previously has been reported on a per-successful-nest basis (Sykes 1979, 1987b, Beissinger 1984, 1986); however, reporting productivity on this basis may be extremely misleading for Snail Kites. Successful pairs of raptors often produce normal numbers of young even during periods of depressed productivity (Brown 1974, Steenhof 1987). This is exemplified for Snail Kites by the annual productivity estimates of 2.0 from 1979 through 1983 (Beissinger 1986), even though conditions and the productivity per breeding-age-female probably differed among those years. Productivity per successful nest may be a useful measure in combination with other reproductive measures (e.g. nesting success) to estimate productivity per pair (Steenhof 1987), but in itself probably should be avoided for comparisons of productivity between locations or years.

In summary, nesting success during 1986 and 1987 was intermediate among previous reports, excluding drought years in which success was virtually zero. Nesting success appears to increase for at least the first two years following a drought, probably due to increasing snail populations. During years of favorable water, predation appears to be the major cause of nesting failure in WCA-3A. The number of young fledged per successful nest can be a misleading measure of productivity for Snail Kites and should only be used in conjunction with other measures. Because Snail Kites often renest after failure and are iteroparous, they have high reproductive potential and often exhibit rapid population increases following depressed periods of droughts. This boom or bust population pattern may well be an evolutionary consequence of a highly specialized species that exists in a dynamic and highly variable environment. This condition sets the stage for water management to be a major factor in the future of this species in Florida. Water management must now take into account not only the increasing demands for water, but the hydrologic regime (including variability) necessary to maintain the biological integrity of the Everglades system.

Causes of Nest Failure

It is common for researchers studying nesting success to report the causes of nest failure (see Sykes 1987b); however, unless a study is designed specifically to address this issue, it often is difficult to document. It is extremely rare that an actual failure is observed and evidence left at failed nests (e.g. broken egg shells, collapsed structures) can be misleading. For example, a nest may have been abandoned outright or the young may have died and been subsequently scavenged. In the latter case the cause of failure may have falsely appeared to be predation. However, a basic understanding of why nests fail is important in understanding how nest-site characteristics and environmental conditions influence nesting success. Based on evidence accumulated during this and previous studies we have included a discussion of what we believe to be the probable causes of nesting failure of Snail Kites in WCA-3A.

Predation.-- Predation probably was the most frequent cause of nesting failure in WCA-3A during 1986 and 1987 because (1) abandonment of eggs or young appeared to be rare; and (2) failures most frequently occurred when abandonment was unlikely (i.e. immediately after hatching).

Just as it is difficult to determine with certainty that predation was the actual cause of a nest failure it is equally difficult to determine which predator(s) were involved. We discuss below each of the predators that might have preyed upon Snail Kite nests in WCA-3A. Our assessment of their relative impact to nesting success is based on evidence (or lack of evidence) left at nests, their relative abundance in WCA-3A, and if their known foraging behavior would make kite nests a likely target for predation.

We believe snakes were a major predator of Snail Kite nests in WCA-3A. This also was the conclusion of Sykes (1987b) after 10 years of study throughout south Florida, and the conclusion of Frederick and Collopy (1987) for wading bird nest predators in WCA-3A.

The potential for predation by snakes probably varies seasonally. Unlike snake populations in more temperate regions, snakes in south Florida are active throughout most of the year (Dalrymple 1986). They do, however, show a pronounced bi-modal activity pattern (Dalrymple 1986) which could influence their tendency to prey on Snail Kites. A period of relatively low snake activity occurs from December through February or March. Early nesting by kites may coincide with this inactive period of snakes, resulting in reduced potential for predation. Snake activity increases greatly in March and April and generally reaches its first seasonal peak by May or June. Consequently, nests occurring during May or June may be most vulnerable to predation by snakes. A second peak of snake activity usually occurs during October; however, this is not a period of major nesting activity by kites.

The likelihood for snakes to prey on kite nests also varies with species of snake. Of the common snakes in the Everglades, the rat snake and the cottonmouth (Agkistrodon piscivorus) are most likely to be found in the aquatic habitat of the Snail Kite and be important predators of eggs or young. Although it certainly is possible that other species (e.g. water snakes, Nerodia spp.) are common in this habitat, they are not likely to be major predators at kite nests.

The cottonmouth is a common snake throughout WCA-3A (pers. observ.). In Florida, the cottonmouth feeds primarily on fish and frogs (Allen and Swindell 1948), but has been reported to prey upon Snail Kite nests (Beissinger 1986, Sykes 1987b). Although cottonmouths undoubtedly prey upon some kite nests, there are some probable limitations to the extent of their predation. These snakes occasionally will eat eggs (Allen and Swindell 1948), but seldom do eggs comprise a significant portion of their diet (P. Andreatis, D. Franz, pers. comm.). Predation by cottonmouths most likely occurs on young chicks; however, even when cottonmouths were densely aggregated at a Florida wading bird colony (feeding on dropped fish and regurgitants) nestlings and eggs were insignificant food sources (Wharton 1969).

Cottonmouths generally hunt at the water surface, are not avid climbers, and consequently would not be likely to prey upon kites in nests above 1 or 2 m (P. Andreatis, pers. comm.). The majority of nests in WCA-3A probably are too high to experience major predation by cottonmouths; however, in other regions of Florida where Snail Kites often nest in cattails and other low substrates (e.g. Lake Okeechobee and Lake Kissimmee), cottomouths may be a major predator.

Beissinger (1986) and Sykes (1987) have reported that the Everglades rat snake (E. o. rossalleni) was a major predator of Snail Kite nests. The Everglades rat snake and the yellow rat snake (E. o. quadrivittata) both are common in the Everglades (G. Dalrymple, pers. comm.) and numerous intergrades may exist between these two subspecies (Neill 1949).

Unlike the cottonmouth, which primarily hunts at the water surface for fish and frogs, rat snakes are highly arboreal (Jackson 1976) and obtain much food by searching out nests containing eggs or young (Fitch 1963, G. Dalrymple pers. comm.). Although rat snakes in Florida can be highly aquatic (Allen and Neill 1950, D. Franz pers. comm.), they are more likely to be found near hammocks or disturbed uplands (e.g. dikes) than in open wet prairies (Dalrymple 1986). This may result in predation by rat snakes being more pronounced near land.

Fish Crows (Corvus ossifragus) have been reported to prey on kite eggs (Bailey 1884, Sykes 1987b). Both Fish Crows and Common Crows (C. brachyrhynchos) occur along U.S. Highway 41 (Tamiami Trail), but are seldom seen far from the uplands in WCA-3A (Sykes 1987b, pers. observ.). Consequently, they are not likely to be major predators of kite nests in WCA-3A, but may occasionally prey upon nests that are located near U.S. Highway 41.

Boat-tailed Grackles (Quiscalus major) and Red-winged Blackbirds (Agelaius phoeniceus) both are common throughout WCA-3A. Steiglitz and Thompson (1967) and Chandler and Anderson (1974) reported nest losses of Snail Kites resulting from predation by Boat-tailed Grackles. We found 3 nests in which the eggs had been broken by what appeared to be an avian predator, however this loss might not be attributable to grackles since they often carry eggs away from nests (T. Bancroft, pers. comm.). Although we know of no reported cases of Red-winged Blackbirds preying on kite nests, they have been observed preying upon the eggs of White-crowned Pigeons (Columba leucocephala) (Bancroft and Bowman 1987).

Sykes (1987b) suspected that Great-horned Owls (Bubo virginianus) preyed on one kite nest which was within the nesting territory of the owls and in which the young were too large for snakes to have consumed. We monitored one nest which we strongly suspect was preyed upon by Great-horned Owls. In this case, the partially consumed remains of the adult female was found on the nest and the young were missing. An adult Great-horned Owl had twice been seen in the immediate vicinity.

During 1986 and 1987, we are aware of two incidents where Turkey Vultures (*Cathartes aura*) were flushed off Great Blue Heron (*Ardea herodias*) nests containing the fresh remains of chicks (P. Frederick pers. comm; pers. observ.). Although we were unable to determine if the heron chicks had been killed by the vultures or were scavenged subsequent to another cause of death, we cannot rule out the possibility that vultures occasionally may kill young chicks, including kites. Black Vultures (*Coragyps atratus*), although common along U.S. Highway 41, seldom were seen in the interior of WCA-3A.

Although mammalian predation has been reported at Snail Kite nests (Beissinger 1986, Sykes 1987b) and undoubtedly occurs in WCA-3A (particularly in proximity to uplands), we believe that, at least during wet years, it is a relatively minor cause of nest failure in WCA-3A. This belief is based on both a lack of evidence of widespread occurrence of potential mammalian predators in WCA-3A, and a lack of evidence that nests were preyed upon by mammals (e.g. crushed egg shells). Access by mammals to most Snail Kite nests in WCA-3A would have involved swimming several kilometers. This is feasible for otters (*Lutra canadensis*), mink (*Mustela vison*), and rice rats (*Oryzomys palustris*), but probably would have been prohibitive to skunks (*Mephitis mephitis* and *Spilogale putoris*), and discouraging to raccoons (*Procyon lotor*). Frederick and Collopy (1987) placed track detection stations at 24 locations throughout WCA-3A in areas of deep (approximately 50 cm) and shallow (approximately 10-12 cm) water. These stations were platforms elevated a few centimeters above the water surface and baited with sardines. Of 341 total days of record, only five incidents of visitation by potential mammalian predators occurred: these included one otter, one raccoon, and three unidentified mammals of the approximate size of a mink or small raccoon (P. Frederick, pers. comm.).

Raccoons would be the most likely mammalian predator in WCA-3A (see Beissinger 1986 and Sykes 1987b). During 1986 and 1987, we only observed one raccoon in WCA-3A, but saw them frequently in nearby upland habitats. During the course of a two-year study of wading birds, P. Frederick (pers. comm.) also saw only one raccoon in WCA-3A. Both our and P. Frederick's sightings were in proximity (< 0.5 km) to upland habitat. Based on the lack evidence remaining at nests, the low frequency of sightings, and low detection at baited track stations, we believe that raccoons probably prey on some kite nests in proximity to upland habitats, but that raccoon predation is probably of minor importance in the interior portions of WCA-3A during years of inundation.

Mink and otters may opportunistically prey on the nests of Snail Kites, but we have no evidence that it occurs frequently. Rice rats are reported to prey upon the eggs of passerine birds (Kale 1965, Orians 1973, Bancroft 1986), but we know of no reported incidents of them preying upon Snail Kite nests. These rodents probably would not be capable of displacing an adult Snail Kite from its nest and thus would only be likely predators on kite nests when the adults were not present. Since rice rats are primarily nocturnal predators (Bancroft 1986), it is not likely that they would frequently encounter unattended nests. Therefore we do not believe that rice rats are a major predator of Snail Kite nests.

Structural collapse.-- Beissinger (1986) and Snyder et al. (in review) reported that structural collapse of nests was one of the most important causes of nest failure. In contrast, we found considerably fewer incidences of structural collapse (see Table 4). This difference probably reflects the difference between the lake habitats and WCA-3A. In the lake habitats, Snail Kites often nested in cattails (Beissinger 1986, Snyder et al. in review). This study was conducted entirely in WCA-3A, where these structurally weak substrates seldom were used. Snyder et al. (in review) also attributed much of the nesting failures from structural collapse to nests located in cattails. The few cases of structural collapse we observed almost always were found after severe storms.

Abandonment.-- Although termination of nesting initiations (i.e. courtship) commonly may occur before eggs are laid (Snyder et al. in review), we found few incidences of abandonment of eggs or young. It is possible, however, that nest failures in which we found an empty nest actually had been abandoned and subsequently preyed upon or scavenged.

Parasites.-- Two species of parasites have been reported to cause mortality in Snail Kites: mites (Ornithonyssus bursa) (Sykes and Forrester 1983) and dermestid beetle larvae (Dermestes nidum) (Snyder et al. 1984). We found infestations of both mites and dermestid beetles; however, we believe that these parasites were not a major cause of nesting failure in WCA-3A during 1986 or 1987.

Human disturbance.-- The major human activity we observed in WCA-3A was airboating. Airboaters, however, typically stayed on established airboat trails, in the open water sloughs, or in relatively light vegetation. Snail kite nests usually were in denser vegetation than is normally traveled by airboaters, but nests often were in proximity to travel routes (e.g. airboat trails). Although nests could be damaged by airboats, we did not find any evidence of such an occurrence during 1986 or 1987. Sykes (1987b) reported two nest failures resulting from airboating over a 10-year period. He believed that these airboat disturbances were accidental, and most likely occurred at night during frogging activities.

Some Snail Kites in WCA-3A nested immediately adjacent to the L-28 canal (N=10) where fishing boats were common. These nests probably were more prone to failure from human disturbance that were those located in the interior of WCA-3A. As with airboating, it is doubtful that most fishermen intentionally disturb kite nests, but fishing in the immediate vicinity of a nest (i.e. < 75 m) would likely have kept the adults off of their nest. Snail Kite nests on the canal probably were prone to such disturbance, but few failures during 1986 and 1987 could be attributed to this cause.

Influences of Nesting Success

Environmental conditions and nest-site characteristics that most influenced nesting success in WCA-3A during 1986 and 1987 appeared to reflect the potential for nests to be preyed upon. Except when extreme conditions prevailed, hydrologic and climatologic conditions appeared to have a relatively minor influence on nesting success. It cannot be overemphasized, however, that both 1986 and 1987 were years of relatively high water conditions. Previous studies (e.g. Beissinger 1986, Sykes 1979) have shown clearly that drought conditions inevitably result in major, if not complete, nesting failure.

Date of initiation.-- We found a general trend of decreasing nesting success through the 1986 and 1987 seasons. Snyder et al. (in review) found no such trend over an 18-year period; however, they recorded nests over a broader nesting season (November - August). There are two probable explanations why nesting success might be lower late in the season. First, decreasing nesting success coincides with increasing snake activity. Dalrymple (1986) showed that snake activity in the Everglades increases from January, when snakes are relatively inactive, through May (Fig. 50). Snake activity first peaks from May to June, when widespread initiation of kite nesting decreases or stops. If predation by snakes is a major cause of nesting failure (see Beissinger 1986, Sykes 1987b) this increase in snake activity could account for the corresponding decrease in nesting success.

An alternative, but not necessarily mutually exclusive, explanation for the decrease in nesting success throughout the season is that kites may locally deplete food supplies. Kites may be highly nomadic during the nonbreeding season, probably in response to food availability (Sykes 1979); the restricted movement associated with a breeding effort may result in the depletion of snail populations through the breeding season. In support of this explanation is the apparent increase in nesting activity during 1987 in areas that were not used during 1986, and the corresponding decrease in use of many areas that were heavily used during 1986. This result would be expected if kites locally depleted snail populations in areas of concentrated use. We also observed a tendency for foraging distances to increase over time in areas of high kite nesting densities and for turtle shells to appear under nests and feeding perches late during the seasons. Having to travel further distances to obtain food would be an expected result of lower food supplies

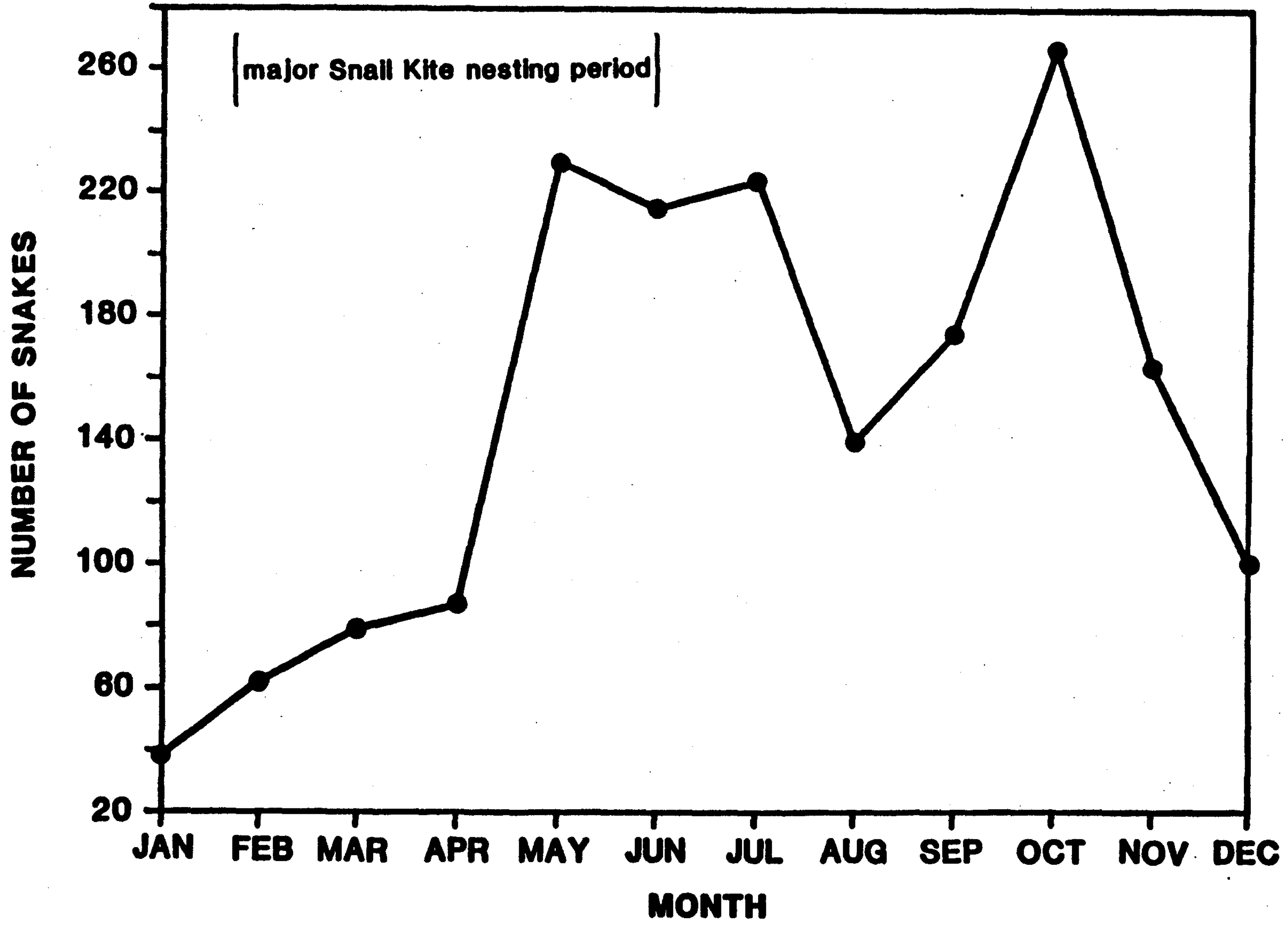


Figure 50. Snake activity in the Everglades, as determined from capture frequency of systematic monthly effort from 1984-1986 (after Dalrymple 1986); shown in conjunction with the primary period of Snail Kite nesting activity.

(Beissinger and Snyder 1987). Beissinger (in press) suggested that the inclusion of turtles in the diet of Snail Kites is associated with low snail abundance.

Nest substrate.-- Nest substrate is associated with several other potential influences of nesting success. Knowing the substrate of a nest in WCA-3A provides a good indication of the nest height, distance to land, nest stability, and perhaps even the time of season that the nest was initiated. Nests located in melaleuca were most successful during both 1986 and 1987. Melaleuca provides a relatively sturdy substrate, nests were usually above 2 m, and most were greater than 500 m from upland habitats. Melaleuca in WCA-3A, however, is an introduced species in the beginning stages of encroachment (see LaHart 1977). Widespread infestation of melaleuca inevitably would result in habitat loss for Snail Kites, as this introduced species replaces the open marsh communities with closed structure melaleuca forests (see Lahart 1977). Nests built in cypress also tended to be greater than 2 m in height and relatively sturdy, however, most were initiated relatively late during the season and were within 500 m of land.

Nesting success was lowest for nests in pond apple. Nests in pond apple were relatively sturdy and tended to occur greater than 500 m from land, but most were relatively low and had high visibility (i.e. they usually were in isolated single shrubs). Consequently, nests in pond apples probably were not prone to weather damage or to predation by the more terrestrial species (e.g. rat snakes and raccoons), but highly susceptible to predation by birds or cottonmouths.

Nest height.-- Probable mechanisms by which nest height would likely have influenced nesting success was through its effects on predator access and structural strength. Nests that were higher than 3 m had the highest success during both years. These nests are probably too high to be preyed upon by cottonmouths (P. Andreatis, pers. comm.) which are common throughout the Everglades. Nests that were less than 2 m had the lowest success in 1986, but not in 1987.

Although overall nesting success was higher in the highest nests, some high nests (e.g. those in willow) tended to be more prone to loss from high winds. In 1987, for example, nests higher than 2 m high that were in willow had lower nesting success (27%) than those in other substrates (35%), even though nests in willow (all heights) had relatively high success (36%).

Distance to land.-- The primary effect of distance to land on the nesting success of Snail Kites is probably through accessability of terrestrial or at least semi-terrestrial predators. Nesting success increased with increasing distance from uplands during 1987, but nests that were within 100 m of land had the highest success during 1986. Success was greater in nests that were greater than 500 m from land during 1986 compared to those that were from 100-500 m, and it is possible that the high success of those nests in proximity to land was attributable to a low sample size (N=12 for nests within 100 m).

Sykes (1987c) reported that 83% of the nest failures at Loxahatchee National Wildlife Refuge (L.N.W.R.) during 1970 were attributable to predation at nests less than 180 m from upland habitats, and concluded that nesting sites within 200 m of upland habitats act as "predator sinks". It should be noted, however, that he did not indicate: (1) that this determination was made from a sample size of six failed nests at L.N.W.R. during 1970 (see Sykes 1979); (2) how many of the 11 nests he observed during 1970 at L.N.W.R. were located greater than 180 m from the uplands; (3) how he determined that predation was the cause of the nest failures; and (4) why he excluded most of the 175 nests he observed from this analysis. Although we do not completely disagree with Sykes' (1987c) conclusion that nests in proximity to land are more prone to predation, we feel that his evidence is weak and that the importance of this influence may be overstated. For example, our data supported his conclusion for 1987, but not for 1986.

Water level.-- The effect of site-specific water levels on nesting success appears to be a threshold response. Nesting success during 1986 and 1987 did not differ among nests in different water depth classes. Sykes (1987c) also did not find significant differences in water levels between successful and unsuccessful nests. It has been shown convincingly in previous studies (e.g. Beissinger 1986, Sykes 1987b), however, that drought conditions inevitably results in increased, if not complete, nesting failure. Nesting failure is an unavoidable consequence when an area completely drys down; Hanning (1978) found that desiccation of an area resulted in adult snail mortality or aestivation, either of which renders them unavailable to kites. In addition to the loss of food, low water levels may result in increased access to kite nests by mammalian predators.

The minimum water depth likely to result in widespread nest failures remains unknown. Although we had eight nests in which water levels at the nest reached zero, the surrounding sloughs never dropped below approximately 10 cm in depth. Based on our results and those from previous studies, we suggest that water levels dropping below 10 cm would likely result in widespread nesting failure of Snail Kites.

Increased water depth above the 80 cm level would not likely cause as an immediate effect on nesting success as that of low water, however, negative effects may occur. Snail availability to kites would likely be lower in deeper water if increased water depth resulted in lower water temperatures. Lower water temperature results in decreased snail activity (McClary 1964, Hanning 1978).

Substantial increases in water level may result in damage to the egg clusters of apple snails (Hanning 1978). Female snails generally lay eggs approximately 6 cm above the water surface. Because the eggs cannot survive when submerged (Hanning 1978), water level increases in excess of a few centimeters may result in destroying egg clusters.

Inter-relationships and relative importance of factors influencing nesting success.-- It is apparent that many of the factors that influence the nesting success of Snail Kites are inter-related. For example, date of initiation, rainfall, and temperature all are a function of time. As the nesting season progresses from January through June (and dates of initiation progress) temperatures generally increase. Although rainfall occurs throughout the spring as storm systems pass through the region, daily thunderstorms begin occurring toward the latter part of the nesting season. Consequently, it becomes difficult to determine whether the nest site characteristics and environmental conditions that we have measured are actually what is influencing nesting success or whether we have measured correlates of the actual influencing factor. In the discussion that follows, we hope to identify at least some of the major inter-relationships among the variables, and to best interpret their relative importance as influences of nesting success.

It cannot be overemphasized that the conditions under which this study was conducted involved two years of favorable water conditions (i.e. the nesting areas did not dry out). It is clear from previous studies and from the life history requirements of Snail Kites, that drought (whether natural or induced by management) is probably the single most important influence of reproduction and adult survival. The results that we discuss should be considered only in the context of being of secondary importance to drought.

The most consistent influence of nesting success during 1986 and 1987 appeared to be the date of initiation. A trend of decreasing nesting success in the latter part of each season was shown using Mayfield analyses, and was the best discriminator of successful and unsuccessful nests during both years using stepwise logistic regression. Snyder et al. (in prep), however, did not find a pattern of decreasing success through the season.

We believe that either the causal influence associated with date of initiation is not weather related, or that only in combination do these weather factors become important influences of nesting success. We have previously discussed that depletion of food sources and increasing snake activity could be causal mechanisms that reduce nesting success through the season. It is likely that these mechanisms are not mutually exclusive. During the latter part of the nesting season: (1) snake activity is at a peak; (2) young-of-the-year snails probably are not yet large enough to be prey at a time when nesting kites have the additional requirements of providing food for their young; and (3) daily thunderstorms typically occur. In combination, these factors may considerably reduce the probability that a nest would be successful.

Nest-site characteristics also are highly inter-related. For example, the species of nest substrate that a kite selects influences nest height and the structural stability of the nest. The area that a kite selects for nesting influences which nest substrates were available.

We believe that the advantages and disadvantages of nest-site characteristics vary with the conditions under which the nest occurs (i.e. when and where). For example, if predation by cottonmouths were the primary reason for lower nesting success in pond apples (i.e. because of their low height), then it might be advantageous for a kite to select this species early during the season when snake activity is low but structural strength might be needed to survive the winds associated with the cold fronts that move through the region during this period.

Height might be a deterrent to some predators, but the species that provide high nest sites have corresponding disadvantages. The taller hardwoods generally are associated with hammocks that support resident predator populations. Cypress in WCA-3A tend to be located near the L-28 levee (i.e. upland habitat). Tall willows tend to be structurally weak and more prone to weather-induced nest loss.

While these inter-relationships appear to mask our understanding the influences of nesting success, they illustrate the biological complexity of the reproductive ecology surrounding Snail Kites. Our multivariate analyses indicated that, with the exception of date of initiation, the variables influencing nesting success in one year may provide little insight toward predicting nesting success in another year with different environmental conditions.

It is clear that drought negatively influences nesting success. Beyond that, management of nesting habitat which maximizes the positive features would likely work in combination to increase reproductive success. For example, management considerations of nesting habitat might include: (1) a dry-down interval which is long enough to maintain high snail populations (i.e. >1.7 years) and open slough communities; (2) a hydrologic regime that maintains woody nesting substrates (i.e. the depth or hydroperiod is not so long so as to convert an area to structurally weak cattails); (3) providing for adequate nesting areas away from upland habitats; and (4) maintaining water quality so as not to jeopardize the prey and vegetative characteristics of the Everglades ecosystem.

Predicted Influence of the Alternative Water Delivery Plans on Nesting Snail Kites and Mitigation Alternatives

The Snail Kite is an obligate wetland species that requires flooded areas to procure its food, the apple snail. WCA-3A has been the stronghold for the vast majority of the Snail Kite population in Florida for the past 15 years and has received federal designation as "critical habitat" for the kite. Before significant nesting occurred in WCA-3A (pre-1972), kite numbers hovered between 50-120 individuals (Sykes 1979). As a result of extended flooding in WCA-3A from 1976 to 1980 and 1982 to 1984, Florida kite populations expanded rapidly, climbing to over 650 birds in 1980 and 1984. Kite populations probably declined in 1981 and 1985 as a result of drought conditions and a dry-down in WCA-3A and throughout the Everglades region (Beissinger and Takekawa 1983, Takekawa and Beissinger in prep. Therefore, any change in the management of water in WCA-3A must be evaluated carefully in light of its potential impact on Snail Kites.

The present study, as well as previous ones (Beissinger and Takekawa 1983, Sykes 1983b, Beissinger 1986, Beissinger and Snyder 1987, Takekawa and Beissinger in prep., Snyder et al. in prep.) has shown that the hydrological regime is a major factor influencing the nesting success and demography of the Snail Kite in Florida. Two characteristics of the hydrological regime in the Everglades critically effect Snail Kites: water depth and dry-down intervals. Complete dry downs may result in little or no nesting success. During this study, shallow (<20 cm) and deep (>110 cm) water areas were rarely used for nest sites. Dry-down intervals may affect not only nest success and recruitment but also adult mortality: (1) nest success is virtually non-existent during drought or dry-downs, which usually occur in the midst of the nesting season (April-June), and frequently nesting success is reduced during the year after low water conditions; (2) adult mortality may be high during low water or drought conditions; (3) kites rarely nest in locations with dry-down intervals of less than two years (hydroperiod of 305 days) or greater than 4 to 5 years; (4) extended periods of prolonged flooding can stress Everglades vegetation, possibly reducing the availability of kite nesting areas.

Conclusions from these studies appear in part contradictory. Kites require at least two years of flooding for snail populations to increase and allow successful nesting and population growth. On the other hand, prolonged flooding may cause declines in the availability of kite nesting substrates. It is probably easier to estimate minimum flooding requirements for this bird (i.e., >20 cm depth, 2 year dry-down interval, and a hydroperiod of at least 305 days) than maximum levels. Although nest sites used by kites in this study were found in areas with inter-drought intervals up to 5 years, it is not clear whether sites with longer intervals would be used if they contained suitable vegetation for nesting.

Based on the General Design Memorandum (GDM) for modified water deliveries to Everglades National Park, the basic rainfall-driven water delivery system (hereafter the Basic Plan) probably would have a small effect on the hydroperiod in WCA-3A (Table 9). While there would be a very slight increase in the hydroperiod in the northern parts of WCA-3A (gauges 3-2, 3-3, 3-4), the current upper elevation where kites nest in WCA-3A is approximately 2.5 m (8.2-8.3 ft), which has a hydroperiod under base conditions of approximately 84% (305 days). The slight increase in hydroperiod in northern WCA-3A is unlikely to be large enough to create significant new nesting areas. In contrast, there would be a small decline in hydroperiod in the southern part of WCA-3A (gauge 3-28). This small decline in hydroperiod could result in slightly more frequent dry-downs in WCA-3A; however, the impacts of this change would not be entirely negative, as lowering the hydroperiods slightly may reduce tree loss in the deeper portions of WCA-3A.

The Basic Plan also should affect Snail Kite use of other Everglades areas. Some new marginal habitat may be created through increased hydroperiods in North East Shark River Slough (NESRS) also known as the East Everglades (Table 9). Predicted flooding regimes from the Basic Plan (Table 9), probably would render all of Everglades National Park too dry for Snail Kite nesting, even the northern end which had been used occasionally by kites (Kushlan and Bass 1983).

In contrast to the Basic Plan, predicted changes in hydroperiod from the alternatives currently being considered for the GDM are considerable (Table 9). The more northern parts of WCA-3A (gauges 3-2, 3-3, 3-4) would have a slight increase in hydroperiod, but this increase is likely to be large enough to create only a limited amount of kite habitat. All of the alternatives, however, would result in a decrease in hydroperiod for the southern part of WCA-3A (gauge 3-28), the areas of intensive use by kites. Of particular concern is the decrease in hydroperiod predicted at gauging station 3-28, located in the heart of the nesting area used by kites throughout the past decade. This decrease in hydroperiod is most severe for the alternatives that include the construction of the S-349 structures along the L-67 levee. Such a decrease in hydroperiod could have several potential effects on the Florida Snail Kite population, depending both on how closely the actual post-construction hydroperiod matches the predictions and on how accurately we have estimated the lower limits of suitable nesting habitat.

We believe that the construction of the S-349 structures will result in the potential for a large part of the southern WCA-3A to move dangerously close to or below the lower limit of the hydroperiod required for suitable nesting habitat for Snail Kites. The current upper elevation where kites nest in WCA-3A is approximately 2.5 m (8.2-8.3 ft), which has a hydroperiod under base conditions of approximately 84% (305 days). The alternatives in the GDM with the S-349 structures would result in lowering the hydroperiod at 3-28 gauge from its present 99% (360 days) to approximately 85-86% (309-314 days).

Table 9. Predicted hydroperiods (days/yr) for the alternative water delivery plans currently being considered under the General Design Memorandum. Base condition is the "no action" alternative.

Gauging station	Base condition	Basic	Average of alternatives with S349	Restricted
<u>WCA-3A</u>				
3-3	305	300	310	318
3-4	305	310	315	310
3-28	360	349	311	334
<u>WCA-3B</u>				
3-29	279	279	290	294
East <u>Everglades</u>				
NE-1	297	326	330	328
NE-2	277	341	335	334
<u>ENP</u>				
NP-201	312	285	299	281
NP-205	300	271	269	271

A decline in hydroperiod of this magnitude also is likely to result in shorter dry-down intervals. More frequent dry-outs of WCA-3A will increase the frequency of kite dispersal, which may result in population declines (Beissinger and Takekawa 1983, Beissinger 1986, Takekawa and Beissinger in prep.), and shorten the time between droughts for the kite population to recover (due to lag year effects on food supplies). This would speed up the oscillations of population cycles of the kite, probably resulting in a downward cycling trend (because of the lack of sufficient recovery time from dry-down induced, mortality events). Presently, kite populations have been oscillating upwards because of a 3 to 4-year recovery period after dry-downs in WCA-3A. We believe that more kite demographic data should be collected (to ascertain the reproductive potential of individuals and better estimates of dry-down survivorship) in order to construct reliable simulation models of the effects of changing the current dry-down interval on kite population trends.

Changes in the hydroperiods of surrounding Everglades areas, as a result of the construction of the S-349 structures, would not likely create much new habitat for the Snail Kite that would not be available under the Basic Plan. Although NESRS should be sufficiently inundated to support kite use, reduced hydroperiods in Everglades National Park would likely make present marginal habitat too dry. Any habitat created by lengthening the hydroperiod in WCA-3B (gauge 3-29) would likely affect only the very southern portion of this marsh, where the water pools, and therefore be a very small area.

We also offer the following suggestions that could help to minimize negative impacts on the Florida Snail Kite population resulting from the implementation of the previously discussed water management options:

1) Our current knowledge of the specific points at which a reduced or extended hydroperiod becomes detrimental or beneficial to the Snail Kite needs considerable refining. For this reason, we would strongly recommend that any changes in water management operations include monitoring of the Snail Kite population and nesting

success. Should the Snail Kite population decline in WCA-3A for more than two years, the hydroperiod should be increased.

2) There would likely be a time lag, possibly 10 or more years, before major Snail Kite population increases would be expected in habitats such as NESRS that would be experiencing increased hydroperiods as a result of the Basic Plan or delivery alternatives. This lag time results from the time it takes for apple snail populations to respond to the increased hydroperiod and for kites to colonize the area. Consequently, we recommend a gradual phasing in of any management alternative that affects water levels in WCA-3A. This could include both the construction and implementation phases of the selected alternative. For instance, construction of the S-355 structures and/or degradation of the L-29 levee prior to construction of the S-349 structures would allow the hydroperiod to increase in NESRS before water would be diverted from WCA-3A. Additional phasing in might be accomplished by maintaining outflows from the S-349 structures below the desired level until Snail Kite populations begin increasing in NESRS.

3) Despite the benefits of periodic drying to the maintenance of woody vegetation, extreme drying out of Snail Kite habitat will result in increased mortality of snails and considerable dispersal and mortality. Historially, this apparent paradox probably was resolved by kites seeking refugia in the deeper water areas such as the center of Shark River Slough, which probably rarely dried out, and smaller lakes, ponds, and wetlands along Florida's east coast and Lake Okeechobee-Kissimmee River system. Unfortunately, these same areas have had water levels dropped or the wetlands are disappearing due rapid development (Takekawa and Beissinger in prep.). For this reason, we recommend that consideration be given to a management scheme that allows smaller wetland units to remain inundated during periods of drought (whether natural or management-induced). These wetlands would allow Snail Kites and other species

similarly affected by drought to survive dry-downs when current demands for water limit their potential refugia. During years of higher water, these wetlands could be drawn down to maintain vegetation.

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APPENDICES

Appendix 1. Formulae and definitions for calculating nesting success using the Mayfield Method. Derivations for formulae are in Hensler and Nichols (1981) and Hensler (1985).

K = number of nests observed

Y = a random variable taking the value of 1 if the Kth nest is successful

T = a random variable denoting the number of days the Kth nest was observed until it succeeded or failed

E = the total number of exposure days (ΣT)

p = the daily survival rate

j = the number of days in a given nesting period (e.g., incubation)

Daily survival rate (p):

$$p = 1 - ((K - Y) / E)$$

Variance of (p) (v):

$$v = p(1 - p) / E$$

Survival for period: (pj):

$$pj = (p)^j$$

Variance of pj (vj):

$$vj = (p(1-p)/E)(jp^{j-1})^2$$

Overall nesting success for two periods (P);

$$P = (p_1)^{j1} (p_2)^{j2}$$

Overall variance of P (V):

$$V = (pj_1)^2(vj_2)^2+(pj_2)^2(vj_1)+(vj_1)(vj_2)$$

Z statistic used to test differences between nesting success estimates:

$$Z = (P1 - P2) / \sqrt{V1 + V2}$$

95% Confidence interval about the Mayfield estimate:

$$(p - z_{a/2}\, v,\ p + z_{a/2}\, v)$$

Appendix 2. Variables that were input into stepwise logistic regression analyses.

FE-DATE	Date first egg was laid (Julian date).	
FE-DATE2	Date first egg was laid . (Julian date).	Dates that were estimated using a formula are assigned missing value.
H20-INIT	Water depth (cm) at time the first egg laid.	
H20-FIN	Water depth (cm) on last viable nest visit.	
N-HGT	Nest height above ground level in centimeters.	
LAND	Distance to nearest upland.	1 = > 500 m 2 = 100 - 500 m 3 = < 100 m
NS	Nest structure	1 = Strong structure (estimated to sway < 5° in 25 kph wind) 2 = Unsteady structure
MAX-TEMP	Maximum temperature	Maximum temperature within the visit interval prior to failing or succeeding.
MIN-TEMP	Minimum temperature	Minimum temperature (°C) within the visit interval prior to failing or succeeding.
WIND	Average wind speed	Maximum average daily wind speed (kph) from the interval before failing or succeeding.
RAIN	Average rainfall	Average daily rainfall (cm) from the interval before failing or succeeding.
SUB-X	Nest substrate	Values of X: 1 = Willow 2 = Melaleuca 3 = Cypress 4 = Pond apple 5 = Other

Appendix 3, Table 1. Summary statistics for the Mayfield estimate of nesting success for nests in WCA-3A during 1986

	Nesting Period		
	Incubation	Nestling	Overall
Number of nests; K	128	97	144
Number of successful nests; ΣY	81	43	43
Estimated number of days in period; J	27	24	51
Total nest days of observation; ΣT	2424	1377	3801
Estimate of daily survival; p	0.981	0.961	---
Standard deviation of p	0.003	0.005	---
Estimate of survival through period; p_j	0.589	0.383	0.226
Standard deviation of p_j	0.045	0.050	0.034

Appendix 3, Table 2. Summary statistics for the Mayfield estimate of nesting success for nests in WCA-3A during 1987.

	Nesting Period		
	Incubation	Nestling	Overall
Number of nests; K	201	148	223
Number of successful nests; ΣY	126	103	103
Estimated number of days in period; J	27	24	51
Total nest days of observation; ΣT	3385	2667	6052
Estimate of daily survival; p	0.978	0.983	---
Standard deviation of p	0.003	0.002	---
Estimate of survival through period; p_j	0.546	0.665	0.363
Standard deviation of p_j	0.038	0.040	0.034

Appendix 4, Table 1. Summary statistics for the Mayfield estimate of daily nesting success for nests in WCA-3A during 1986 for four consecutive six-day intervals after hatching.

	6-DAY INTERVAL AFTER HATCHING			
	1st	2nd	3rd	4th
Number of nests; K	92	72	59	48
Number of successful nests; ΣY	69	58	47	44
Total nest days of observation; ΣT	413	369	317	257
Estimate of daily survival; p	0.944	0.962	0.962	0.984
Standard deviation of p	0.011	0.010	0.011	0.008

Appendix 4, Table 2. Summary statistics for the Mayfield estimate of daily nesting success for nests in WCA-3A during 1987 for four consecutive six-day intervals after hatching.

	6-DAY INTERVAL AFTER HATCHING			
	1st	2nd	3rd	4th
Number of nests; K	141	121	111	107
Number of successful nests; ΣY	119	109	106	100
Total nest days of observation; ΣT	737	670	649	614
Estimate of daily survival; p	0.970	0.982	0.992	0.989
Standard deviation of p	0.006	0.005	0.003	0.004

Appendix 5, Table 1. Summary statistics for the Mayfield estimate of nesting success for nests in WCA-3A during 1986 in which the first egg was laid on or before 6 March.

	Nesting Period		
	Incubation	Nestling	Overall
Number of nests; K	22	25	29
Number of successful nests; ΣY	18	14	14
Estimated number of days in period; J	27	24	51
Total nest days of observation; ΣT	377	390	767
Estimate of daily survival; p	0.989	0.972	---
Standard deviation of p	0.005	0.008	---
Estimate of survival through period; p^j	0.750	0.503	0.377
Standard deviation of p^j	0.108	0.104	0.096

Appendix 5, Table 2. Summary statistics for the Mayfield estimate of nesting success for nests in WCA-3A during 1986 in which the first egg was laid after 6 March, but before 12 April.

	Nesting Period		
	Incubation	Nestling	Overall
Number of nests; K	58	53	63
Number of successful nests; ΣY	48	23	23
Estimated number of days in period; J	27	24	51
Total nest days of observation; ΣT	1179	773	1952
Estimate of daily survival; p	0.992	0.961	---
Standard deviation of p	0.003	0.007	---
Estimate of survival through period; p_j	0.795	0.387	0.307
Standard deviation of p_j	0.058	0.067	0.058

Appendix 5, Table 3. Summary statistics for the Mayfield estimate of nesting success for nests in WCA-3A during 1986 in which the first egg was laid after 11 April.

	Nesting Period		
	Incubation	Nestling	Overall
Number of nests; K	22	18	26
Number of successful nests; ΣY	14	6	6
Estimated number of days in period; J	27	24	51
Total nest days of observation; ΣT	422	214	636
Estimate of daily survival; p	0.981	0.944	---
Standard deviation of p	0.007	0.016	---
Estimate of survival through period; pj	0.596	0.250	0.149
Standard deviation of pj	0.109	0.100	0.067

Appendix 5, Table 4. Summary statistics for the Mayfield estimate of nesting success for nests in WCA-3A during 1987 in which the first egg was laid on or before 6 March.

	Nesting Period		
	Incubation	Nestling	Overall
Number of nests; K	87	78	106
Number of successful nests; ΣY	61	56	56
Estimated number of days in period; J	27	24	51
Total nest days of observation; ΣT	1543	1422	2965
Estimate of daily survival; p	0.983	0.985	---
Standard deviation of p	0.003	0.003	---
Estimate of survival through period; p^j	0.632	0.688	0.435
Standard deviation of p^j	0.057	0.055	0.052

Appendix 5, Table 5. Summary statistics for the Mayfield estimate of nesting success for nests in WCA-3A during 1987 in which the first egg was laid after 6 March, but before 12 April.

	Nesting Period		
	Incubation	Nestling	Overall
Number of nests; K	66	52	76
Number of successful nests; ΣY	48	36	36
Estimated number of days in period; J	27	24	51
Total nest days of observation; ΣT	1260	951	2211
Estimate of daily survival; p	0.986	0.983	---
Standard deviation of p	0.003	0.004	---
Estimate of survival through period; p_j	0.678	0.665	0.451
Standard deviation of p_j	0.062	0.068	0.062

Appendix 5, Table 6. Summary statistics for the Mayfield estimate of nesting success for nests in WCA-3A during 1987 in which the first egg was laid after 11 April.

	Nesting Period		
	Incubation	Nestling	Overall
Number of nests; K	33	18	41
Number of successful nests; ΣY	16	11	11
Estimated number of days in period; J	27	24	51
Total nest days of observation; ΣT	582	294	876
Estimate of daily survival; p	0.971	0.976	---
Standard deviation of p	0.007	0.009	---
Estimate of survival through period; p^j	0.449	0.561	0.252
Standard deviation of p^j	0.087	0.123	0.074

Appendix 6, Table 1. Summary statistics for the Mayfield estimate of nesting success for nests in WCA-3A during 1986 in which the substrate was willow.

	Nesting Period		
	Incubation	Nestling	Overall
Number of nests; K	52	42	58
Number of successful nests; Σ Y	36	19	19
Estimated number of days in period; J	27	24	51
Total nest days of observation; Σ T	996	617	1613
Estimate of daily survival; p	0.984	0.963	---
Standard deviation of p	0.004	0.008	---
Estimate of survival through period; pj	0.646	0.402	0.259
Standard deviation of pj	0.071	0.076	0.057

Appendix 6, Table 2. Summary statistics for the Mayfield estimate of nesting success for nests in WCA-3A during 1986 in which the substrate was pond apple.

	Nesting Period		
	Incubation	Nestling	Overall
Number of nests; K	30	23	33
Number of successful nests; ΣY	20	10	10
Estimated number of days in period; J	27	24	51
Total nest days of observation; ΣT	596	323	919
Estimate of daily survival; p	0.983	0.960	---
Standard deviation of p	0.005	0.011	---
Estimate of survival through period; pj	0.633	0.373	0.236
Standard deviation of pj	0.091	0.102	0.074

Appendix 6, Table 3. Summary statistics for the Mayfield estimate of nesting success for nests in WCA-3A during 1986 in which the substrate was cypress.

	Nesting Period		
	Incubation	Nestling	Overall
Number of nests; K	20	14	26
Number of successful nests; ΣY	8	9	9
Estimated number of days in period; J	27	24	51
Total nest days of observation; ΣT	374	224	598
Estimate of daily survival; p	0.968	0.978	---
Standard deviation of p	0.009	0.010	---
Estimate of survival through period; pj	0.415	0.582	0.241
Standard deviation of pj	0.105	0.141	0.086

Appendix 6, Table 4. Summary statistics for the Mayfield estimate of nesting success for nests in WCA-3A during 1986 in which the substrate was maleleuca.

	Nesting Period		
	Incubation	Nestling	Overall
Number of nests; K	12	8	12
Number of successful nests; Σ Y	8	4	4
Estimated number of days in period; J	27	24	51
Total nest days of observation; Σ T	195	136	331
Estimate of daily survival; p	0.979	0.971	---
Standard deviation of p	0.010	0.014	---
Estimate of survival through period; pj	0.571	0.488	0.279
Standard deviation of pj	0.160	0.175	0.130

Appendix 6, Table 5. Summary statistics for the Mayfield estimate of nesting success for nests in WCA-3A during 1987 in which the substrate was willow.

	Nesting Period		
	Incubation	Nestling	Overall
Number of nests; K	97	72	107
Number of successful nests; ΣY	61	50	50
Estimated number of days in period; J	27	24	51
Total nest days of observation; ΣT	1569	1338	2907
Estimate of daily survival; p	0.977	0.984	---
Standard deviation of p	0.004	0.003	---
Estimate of survival through period; pj	0.534	0.672	0.359
Standard deviation of p j	0.056	0.057	0.048

Appendix 6, Table 6. Summary statistics for the Mayfield estimate of nesting success for nests in WCA-3A during 1987 in which the substrate was pond apple.

	Nesting Period		
	Incubation	Nestling	Overall
Number of nests; K	34	24	36
Number of successful nests; ΣY	22	12	12
Estimated number of days in period; J	27	24	51
Total nest days of observation; ΣT	607	379	986
Estimate of daily survival; p	0.980	0.968	---
Standard deviation of p	0.006	0.009	---
Estimate of survival through period; p_j	0.583	0.462	0.269
Standard deviation of p_j	0.091	0.103	0.074

Appendix 6, Table 7. Summary statistics for the Mayfield estimate of nesting success for nests in WCA-3A during 1987 in which the substrate was cypress.

	Nesting Period		
	Incubation	Nestling	Overall
Number of nests; K	30	17	31
Number of successful nests; ΣY	16	11	11
Estimated number of days in period; J	27	24	51
Total nest days of observation; ΣT	526	285	811
Estimate of daily survival; p	0.973	0.979	---
Standard deviation of p	0.007	0.009	---
Estimate of survival through period; pj	0.483	0.600	0.290
Standard deviation of pj	0.094	0.125	0.083

Appendix 6, Table 8. Summary statistics for the Mayfield estimate of nesting success for nests in WCA-3A during 1987 in which the substrate was maleleuca.

	Nesting Period		
	Incubation	Nestling	Overall
Number of nests; K	11	14	16
Number of successful nests; ΣY	10	11	11
Estimated number of days in period; J	27	24	51
Total nest days of observation; ΣT	220	227	447
Estimate of daily survival; p	0.995	0.987	---
Standard deviation of p	0.005	0.008	---
Estimate of survival through period; p^j	0.884	0.727	0.643
Standard deviation of p^j	0.109	0.134	0.143

Appendix 7, Table 1. Summary statistics for the Mayfield estimate of nesting success for nests in WCA-3A during 1986 in which the nest height was less than or equal to 2 m.

	Nesting Period		
	Incubation	Nestling	Overall
Number of nests; K	66	52	74
Number of successful nests; ΣY	44	20	20
Estimated number of days in period; J	27	24	51
Total nest days of observation; ΣT	1252	685	1937
Estimate of daily survival; p	0.982	0.953	---
Standard deviation of p	0.004	0.008	---
Estimate of survival through period; p_j	0.620	0.317	0.197
Standard deviation of p_j	0.063	0.064	0.045

Appendix 7, Table 2. Summary statistics for the Mayfield estimate of nesting success for nests in WCA-3A during 1986 in which the nest height was greater than 2 m, but less tha or equal to 3m.

	Nesting Period		
	Incubation	Nestling	Overall
Number of nests; K	47	32	49
Number of successful nests; ΣY	30	15	15
Estimated number of days in period; J	27	24	51
Total nest days of observation; ΣT	847	491	1338
Estimate of daily survival; p	0.980	0.965	---
Standard deviation of p	0.005	0.008	---
Estimate of survival through period; pj	0.578	0.429	0.248
Standard deviation of pj	0.077	0.088	0.061

Appendix 7, Table 3. Summary statistics for the Mayfield estimate of nesting success for nests in WCA-3A during 1986 in which the nest height was greater than 3 m.

	Nesting Period		
	Incubation	Nestling	Overall
Number of nests; K	15	13	21
Number of successful nests; ΣY	7	8	8
Estimated number of days in period; J	27	24	51
Total nest days of observation; ΣT	325	201	526
Estimate of daily survival; p	0.975	0.975	---
Standard deviation of p	0.009	0.011	---
Estimate of survival through period; p^j	0.510	0.546	0.279
Standard deviation of p^j	0.121	0.148	0.102

Appendix 7, Table 4. Summary statistics for the Mayfield estimate of nesting success for nests in WCA-3A during 1987 in which the nest height was less than or equal to 2 m.

	Nesting Period		
	Incubation	Nestling	Overall
Number of nests; K	102	77	112
Number of successful nests; ΣY	66	56	56
Estimated number of days in period; J	27	24	51
Total nest days of observation; ΣT	1784	1469	3253
Estimate of daily survival; p	0.980	0.986	---
Standard deviation of p	0.003	0.003	---
Estimate of survival through period; pj	0.577	0.708	0.408
Standard deviation of pj	0.053	0.053	0.049

Appendix 7, Table 5. Summary statistics for the Mayfield estimate of nesting success for nests in WCA-3A during 1987 in which the nest height was greater than 2 m, but less tha or equal to 3m.

	Nesting Period		
	Incubation	Nestling	Overall
Number of nests; K	64	47	71
Number of successful nests; ΣY	40	26	26
Estimated number of days in period; J	27	24	51
Total nest days of observation; ΣT	1098	745	1843
Estimate of daily survival; p	0.978	0.972	---
Standard deviation of p	0.004	0.006	---
Estimate of survival through period; pj	0.551	0.503	0.277
Standard deviation of pj	0.067	0.075	0.054

Appendix 7, Table 6. Summary statistics for the Mayfield estimate of nesting success for nests in WCA-3A during 1987 in which the nest height was greater than 3 m.

	Nesting Period		
	Incubation	Nestling	Overall
Number of nests; K	29	23	34
Number of successful nests; ΣY	19	20	20
Estimated number of days in period; J	27	24	51
Total nest days of observation; ΣT	424	429	853
Estimate of daily survival; p	0.976	0.993	---
Standard deviation of p	0.007	0.004	---
Estimate of survival through period; pj	0.525	0.845	0.444
Standard deviation of pj	0.107	0.082	0.101

Appendix 8, Table 1. Summary statistics for the Mayfield estimate of nesting success for nests in WCA-3A during 1986 in which the nest was located less than 100 m from land.

	Nesting Period		
	Incubation	Nestling	Overall
Number of nests; K	9	6	12
Number of successful nests; ΣY	3	5	5
Estimated number of days in period; J	27	24	51
Total nest days of observation; ΣT	182	105	287
Estimate of daily survival; p	0.967	0.990	---
Standard deviation of p	0.013	0.009	---
Estimate of survival through period; p_j	0.404	0.795	0.321
Standard deviation of p_j	0.149	0.183	0.143

Appendix 8, Table 2. Summary statistics for the Mayfield estimate of nesting success for nests in WCA-3A during 1986 in which the nest was located greater than 100 m from land, but less than 500 m.

	Nesting Period		
	Incubation	Nestling	Overall
Number of nests; K	24	15	27
Number of successful nests; ΣY	12	4	4
Estimated number of days in period; J	27	24	51
Total nest days of observation; ΣT	514	134	648
Estimate of daily survival; p	0.977	0.918	---
Standard deviation of p	0.007	0.024	---
Estimate of survival through period; pj	0.528	0.128	0.068
Standard deviation of p_j	0.097	0.079	0.044

Appendix 8, Table 3. Summary statistics for the Mayfield estimate of nesting success for nests in WCA-3A during 1986 in which the nest was located greater than 500 m from land.

	Nesting Period		
	Incubation	Nestling	Overall
Number of nests; K	95	76	105
Number of successful nests; ΣY	66	34	34
Estimated number of days in period; J	27	24	51
Total nest days of observation; ΣT	1728	1138	2866
Estimate of daily survival; p	0.983	0.963	---
Standard deviation of p	0.003	0.006	---
Estimate of survival through period; pj	0.633	0.406	0.257
Standard deviation of pj	0.054	0.056	0.042

Appendix 8, Table 4. Summary statistics for the Mayfield estimate of nesting success for nests in WCA-3A during 1987 in which the nest was located less than 100 m from land.

	Nesting Period		
	Incubation	Nestling	Overall
Number of nests; K	45	28	48
Number of successful nests; ΣY	25	18	18
Estimated number of days in period; J	27	24	51
Total nest days of observation; ΣT	745	488	1233
Estimate of daily survival; p	0.973	0.980	---
Standard deviation of p	0.006	0.006	---
Estimate of survival through period; p_j	0.480	0.608	0.292
Standard deviation of pj	0.079	0.096	0.067

Appendix 8, Table 5. Summary statistics for the Mayfield estimate of nesting success for nests in WCA-3A during 1987 in which the nest was located greater than 100 m from land, but less than 500 m.

	Nesting Period		
	Incubation	Nestling	Overall
Number of nests; K	40	27	45
Number of successful nests; Σ Y	23	20	20
Estimated number of days in period; J	27	24	51
Total nest days of observation; Σ T	693	502	1195
Estimate of daily survival; p	0.975	0.986	---
Standard deviation of p	0.006	0.005	---
Estimate of survival through period; pj	0.511	0.714	0.365
Standard deviation of pj	0.083	0.091	0.076

Appendix 8, Table 6. Summary statistics for the Mayfield estimate of nesting success for nests in WCA-3A during 1987 in which the nest was located greater than 500 m from land.

	Nesting Period		
	Incubation	Nestling	Overall
Number of nests; K	116	93	130
Number of successful nests; Σ Y	78	65	65
Estimated number of days in period; J	27	24	51
Total nest days of observation; Σ T	1947	1677	3624
Estimate of daily survival; p	0.980	0.983	---
Standard deviation of p	0.003	0.003	---
Estimate of survival through period; pj	0.587	0.668	0.392
Standard deviation of pj	0.051	0.051	0.045

Appendix 9, Table 1. Summary statistics for the Mayfield estimate of daily nesting success for nests in WCA-3A during 1986 while they were within different water depth (cm) classes.

	WATER DEPTH		
	0 - 25	25 - 50	50 - 75
Number of nests; K	39	92	34
Number of successful nests; ΣY	19	49	22
Total nest days of observation; ΣT	775	1556	635
Estimate of daily survival; p	0.974	0.972	0.981
Standard deviation of p	0.006	0.004	0.005

Appendix 9, Table 2. Summary statistics for the Mayfield estimate of daily nesting success for nests in WCA-3A during 1987 while they were within different water depth (cm) classes.

	WATER DEPTH		
	0 - 25	25 - 50	50 - 75
Number of nests; K	39	92	34
Number of successful nests; ΣY	19	49	22
Total nest days of observation; ΣT	775	1556	635
Estimate of daily survival; p	0.974	0.972	0.981
Standard deviation of p	0.006	0.004	0.005

Appendix 10, Table 1. Summary statistics for the Mayfield estimate of daily nest survival for nests in WCA-3A during 1986 in which the average daily rainfall (cm) for the observation interval varied.

	RAINFALL		
	0	>0 - 0.5	> 0.5
Number of nests; K	186	320	40
Number of successful nests; ΣY	158	261	28
Total nest days of observation; ΣT	1271	2284	279
Estimate of daily survival; p	0.978	0.974	0.957
Standard deviation of p	0.004	0.003	0.012

Appendix 10, Table 2. Summary statistics for the Mayfield estimate of daily nest survival for nests in WCA-3A during 1987 in which the average daily rainfall (cm) for the observation interval varied.

	RAINFALL		
	0	>0 - 0.5	> 0.5
Number of nests; K	161	496	188
Number of successful nests; ΣY	148	422	163
Total nest days of observation; ΣT	875	3809	1296
Estimate of daily survival; p	0.985	0.981	0.981
Standard deviation of p	0.004	0.002	0.004

Appendix 11, Table 1. Summary statistics for the Mayfield estimate of daily nest survival for nests in WCA-3A during 1986 in which the average daily wind speed (kph) for the observation interval varied.

	WIND SPEED		
	0 - 1.5	1.5 - 3.0	> 3.0
Number of nests; K	405	118	23
Number of successful nests; ΣY	322	104	21
Total nest days of observation; ΣT	2964	741	129
Estimate of daily survival; p	0.972	0.981	0.984
Standard deviation of p	0.003	0.005	0.011

Appendix 11, Table 2. Summary statistics for the Mayfield estimate of daily nest survival for nests in WCA-3A during 1987 in which the average daily wind speed (kph) for the observation interval varied.

	WIND SPEED		
	0 - 1.5	1.5 - 3.0	> 3.0
Number of nests; K	293	532	47
Number of successful nests; ΣY	249	464	40
Total nest days of observation; ΣT	2233	3705	216
Estimate of daily survival; p	0.980	0.982	0.968
Standard deviation of p	0.003	0.002	0.012

Appendix 12, Table 1. Summary statistics for the Mayfield estimate of daily nest survival for nests in WCA-3A during 1986 in which the average daily minimum temperature (c) for the observation interval varied.

	MINIMUM TEMPERATURE		
	0 -10	10 - 20	20 - 30
Number of nests; K	61	448	37
Number of successful nests; Σ Y	55	370	22
Total nest days of observation; Σ T	450	3128	256
Estimate of daily survival; p	0.987	0.975	0.941
Standard deviation of p	0.005	0.003	0.015

Appendix 12, Table 2. Summary statistics for the Mayfield estimate of daily nest survival for nests in WCA-3A during 1987 in which the average daily minimum temperature (c) for the observation interval varied.

	MINIMUM TEMPERATURE		
	0 -10	10 - 20	20 - 30
Number of nests; K	131	643	83
Number of successful nests; ΣY	119	556	63
Total nest days of observation; ΣT	1068	4585	467
Estimate of daily survival; p	0.989	0.981	0.957
Standard deviation of p	0.003	0.002	0.009

Appendix 13, Table 1. Summary statistics for the Mayfield estimate of daily nesting success for nests in WCA-3A during 1986 in which the maximum temperature (C) during the observation interval varied.

	MAXIMUM TEMPERATURE		
	10 - 20[a]	20 - 30	30 - 40
Number of nests; K	---	254	288
Number of successful nests; ΣY	---	219	224
Total nest days of observation; ΣT	---	1683	2147
Estimate of daily survival; p	---	0.979	0.970
Standard deviation of p	---	0.003	0.004

[a] insufficient sample size precluded calculation.

Appendix 13, Table 2. Summary statistics for the Mayfield estimate of daily nesting success for nests in WCA-3A during 1987 in which the maximum temperature (C) during the observation interval varied.

	MAXIMUM TEMPERATURE		
	10 - 20	20 - 30	30 - 40
Number of nests; K	104	677	76
Number of successful nests; ΣY	92	583	63
Total nest days of observation; ΣT	907	4820	393
Estimate of daily survival; p	0.987	0.980	0.967
Standard deviation of p	0.004	0.002	0.009