Responses of Marsh Fishes and Breeding Wading Birds to Low Temperatures: A Possible Behavioral Link Between Predator and Prey

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ABSTRACT: In the Everglades of southern Florida, several species of spring- and winter-nesting wading birds (Ciconiiformes) often abandon their nests in response to periods of cold or wet and windy weather. Using stepwise logistic regression of a variety of hydrologic and meteorologic variables on the probability of great egret nest failure, we found that cold temperatures and high wind speeds were most closely associated with nest failure in the Everglades. Water level fluctuation was not a significant correlate of failure. Quantitative visual surveys in the field showed that even moderate cooling events (15°C minimum daily temperature) dramatically altered the observed densities of marsh fishes. In controlled conditions in the laboratory, we observed centrarchid, poeciliid, and cyprinodontid fishes during normal high (19–23°C) and simulated cold snap (8–11°C) temperatures. At low temperatures, the fishes exhibited reduced activity, sought refuge by hiding in vegetation and/or substrate, and fled our approach to the tank at much greater distances. Threshold temperatures for these behaviors varied considerably between the laboratory (9–11°C) and field (15–20°C), and may be explained by differences in the previous thermal experience of the two groups of fishes. We hypothesize that the temperature-induced scarcity of fishes during spring cold snaps is an important cause of disruption of nesting for several species of wading birds in the Everglades.

Introduction

In the freshwater and estuarine marshes of the subtropical Florida Everglades, Kahl (1964), Kushlan et al. (1975) and Frederick and Collopy (1989) have noted that piscivorous, long-legged wading birds often synchronously abandon nesting during episodes of cold and sometimes wet weather during late winter and early spring. These studies have focussed on the possible role of fluctuating water levels on the availability of prey, and the influence of temperature was not considered directly. While water level fluctuation does affect prey availability (Kushlan 1974; Kushlan et al. 1975; Powell 1987), reproductive failures have been noted during periods of cold, dry weather, which produce little change in water level (Frederick and Collopy 1989). Cold temperatures therefore seemed to be implicated in some of the reproductive failures, though the mechanism was unknown.

Most marsh-dwelling fishes in the North American temperate and subtropical regions seem to be quite resistant to the effects of cold weather, especially when compared with larger salt water or estuarine species (Gunter 1947; Reid 1954; Simpson and Gunter 1956; Springer and Woodburn 1960; Umminger 1971). A number of physiological adaptations (Umminger 1969a, b, 1970, 1971; Stauffer 1980) and behavioral strategies have been noted. The fishes may move into depressions and holes (Reid 1954; Kahl 1964; Kaill 1967) or into offshore waters where temperatures are moderated (Gunter 1947; Gunter and Hildebrand 1951; Springer and Woodburn 1960; Smith 1971; Fritz and Lotrich 1975), or they may simply burrow into the substrate (Chidester 1916, 1920; Greenwood 1975). We hypothesized that behavioral responses of marsh fishes to cold temperatures make them unavailable to birds in the Everglades for periods

long enough to interrupt nesting attempts, a time when energy and food requirements of the birds are extremely high (Kahl 1964; Kushlan 1977). The pertinent questions are whether such behavioral modifications are actually used by Everglades marsh fishes, whether this makes them difficult to find, and if so, at what temperature range.

In this paper, we explore the statistical effect of cold temperature on nesting success of spring-nesting, piscivorous great egrets (*Casmerodius albus*) in the Everglades, quantify the relative abundances of fishes in Everglades marshes before, during, and after the passage of cold weather, and document the behavioral responses of seven species of Everglades fishes to cooling regimes imposed in the laboratory. Although our observations do not allow us to directly link the availability of fishes with the nesting responses of birds, the results lead us to hypothesize that the two responses are causally related.

Methods

Environmental Conditions Associated With Wading Bird Nesting Failures

We analyzed the environmental conditions associated with both success (production of at least one young to an age of 21 d or more) and failure of 198 individual great egret nests monitored during the nesting seasons of 1986 and 1987 at locations throughout the Everglades (see Frederick and Collopy 1989 for details of data collection). Using stepwise logistic regression in the SAS software package (Lachenbruch 1975; Harrell 1980), we assessed the relative ability of several local environmental variables to predict success or failure of the nests. The independent variables used were the total amount of rainfall, mean depth, and recession rate of water in marshes within 0.25 km of the colony during the 30 d prior to the success or failure of nests. The mean minimum daily air temperature and mean maximum daily wind speed recorded during the 14 d prior to success or failure were also used as variables.

Variables could enter or leave our analysis based on a tolerance level of p = 0.05. This data set was originally reported and analyzed similarly by Frederick and Collopy (1989), except temperature and wind were not included as variables in that analysis. The original results were inconclusive, and reanalysis seemed justified in light of the results of our observations on the effect of temperature on the prey of great egrets.

To determine frequency of specific low temperature events, we analyzed long-term air temperature data for the available period of record (February 1 through April 30, 1949–1989) at Tamiami Trail Ranger Station, situated in the middle of the southern Everglades.

Field Observations of Fish Abundance

During January and February 1991, we conducted visual counts of marsh fishes in marked plots to compare numbers before, during, and after the onset of short periods of cold weather. Four observation sites were located in open oligohaline marshes (1–2‰) east of the main Everglades National Park Road, opposite Paurotis Pond. The corners of each 4-m² plot were marked by 5-cm strips of surveyor's flagging tied to rush stems. The study plots were located in sparsely vegetated marshes dominated by spikerushes (*Eleocharis* spp.), with nearby, denser stands of sawgrass (*Cladium jamaicense*), isolated clumps of red mangrove (*Rhizophora mangle*), and a substrate of peat overlain by a light-colored algal mat. Water depths ranged between 10 cm and 25 cm during our observations. The clear water, sparse vegetation, and light-colored substrate made accurate visual counts of fishes possible. These plots typified the feeding habitat used by many species of wading birds, including great egrets (Frederick and Collopy 1988; Bancroft et al. 1990).

The observer (WFL) identified and counted numbers of individual fishes within the plots using 8 × 30 power binoculars and called out counts of each species to the recorder. The observer stood 3–4 m from the edge of the sampling plot, usually hidden by vegetation, and the recorder sat hidden from view of the sampling plot. Plots were sampled once daily between 0830 and 1000 EST. Fishes within each plot were counted ten times, each count taking 1.5 min, with a one min break between successive counts. Water temperature was recorded at the water-substrate interface at the end of each sampling period at each site. We compared fish abundances on warm mornings (January 17 and 25) with counts in the same plots on mornings following the passage of cold fronts (January 23 and February 12).

Laboratory Studies

Collection and Housing of Animals

On February 15, 1990, we netted between five and 50 individuals of bluegill (*Lepomis macrochirus*), warmouth (*Lepomis gulosus*), mosquitofish (*Gambusia holbrooki*), sailfin molly (*Poecilia latipinna*), flagfish (*Jordanella floridae*), bluefin killifish (*Lucania goodei*), and marsh killifish (*Fundulus confluentus*) from a ditch draining freshwater marshes on Florida S.R. 94 approximately 3.2 km west of its junction with Tamiami Trail (U.S. 41), and netted 40 sheepshead minnows (*Cyprinodon variegatus*) from

TABLE 1. Discrimination of successful (n = 74) and failed (n = 124) great egret nesting attempts using stepwise logistic regression analysis, with failure as the dependent variable. Nest records from 1986 and 1987 were pooled.

Variable	Coefficient	SE	r	P
Temperature	−0.459	0.0993	−0.277	<0.0000
Wind	0.804	0.3025	0.142	0.0079
Rainfall	1.311	0.4791	0.148	0.0062
Nesting date	0.031	0.0134	0.116	0.0205

TABLE 2. Mean fish densities observed on warm and cool mornings in the southern Everglades in early 1991, including 40 observations of fish densities at four sites on each date.

Date	Mean Fish m^{-2}	Standard Deviation	Mean Water Temperature (°C)
January 17	24.6	19.09	27.3
January 23	0.1	0.35	16.9
January 25	52.4	44.26	26.0
February 12	0.1	0.22	16.9

a shallow, marine (30‰) embayment of Florida Bay on northern Plantation Key. These species are common prey of great egrets (Bancroft et al. 1990, unpublished data) and are among the most abundant fishes in the Everglades (Loftus and Kushlan 1987). Fishes were immediately transported with supplemental aeration to the National Fisheries Research Laboratory in Gainesville, Florida, where they were housed in species-specific, 114-l glass aquaria on a L:D 14:10 photoperiod, at between 20°C and 23°C. Fishes were provided *ad lib* flaked aquarium fish food (35% protein, Mardel Laboratories), at 1000 and 1600 each day.

Following 19 d of habituation to captivity, fishes were moved to artificial cooling tanks. These 20-l aerated aquaria contained 10 cm of substrate from the collection sites and 15 cm of water (similar to conditions at the collection sites), with 3–5 sprigs of fanwort (*Cabomba caroliniana*) in one corner for cover. Individual tanks were placed inside circulating Living Stream (LS) cooling baths (2.1 × 0.6 × 0.6 m), and were visible through the glass side of the LS. The three small aquaria in each LS were visually isolated from each other by baffles. To mimic the delayed cooling of substrate that occurs in the field during cold weather, we insulated the outside bottom and sides of the small aquaria, to

the level of the surface of the substrate, with 1.3 cm thick, closed-cell white styrofoam.

Because of their larger size and usage of deeper habitats, centrarchids were artificially cooled in a single, undivided LS tank with 35 cm of water containing approximately 10 l fanwort and rock refugia in the corners.

Fishes were observed in the cooling tanks at ambient temperature (17–23°C) for 3 d, and then cooled at a rate of 1°C h^{-1}. They reached a low of between 4°C and 6°C by the following morning of March 13, began a return to ambient temperatures 12 h later, and thereafter fluctuated between 17°C and 23°C for 24 h. Activity and tendency to use refugia were monitored throughout the period. We cooled one tank of centrarchids (11 bluegill and 2 warmouth) and sheepshead minnows (5 individuals), and two each of mosquitofish (15 individuals), flagfish (10 individuals), and sailfin mollies and bluefin killifish together (8 and 3 individuals, respectively).

Observation Protocol

One observer (PCF) sat quietly 0.5 m from the edge of the tank, and waited for 3 min before beginning to record behavior. At ambient temperatures, fishes did not appear to change behavior when the observer moved about the room or sat in front of the tank. Observation bouts were performed once at each tank during three periods of each day (0800–1000, 1200–1400, 1600–1800). During each bout, we recorded the activity of each individual in the tank once, and recorded ten scan samples of the locations of all individuals. Fishes were considered to be in refugia if within 2 cm of vegetation or burrowed in the substrate.

A 2-cm square grid was drawn directly onto the outside viewing glass of all the LS, and the number of 2-cm vertical and horizontal grid cells crossed during a period of 2 min (all centrarchids) or 1 min (all other species) was used as an index of activity. The activity of sheepshead minnows proved difficult to record at all but the lowest activity levels because the colloidal substrate produced extremely cloudy water when disturbed.

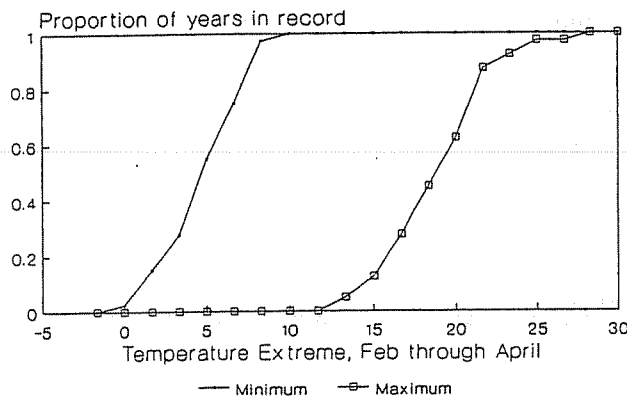We compared activity and use of refugia in high (19–23°C) and low (8–11°C) temperature catego-

Fig. 1. Relative frequencies of cold temperatures during the period February 1 through April 30, from 1949 to 1989, at 40-Mile Bend (Tamiami Ranger Station, Everglades National Park). Frequencies are expressed as proportion of days in record with daily maximum or daily minimum temperatures less than indicated, or as the proportion of years in which at least one day during the period was less than the indicated temperature.

TABLE 3. Activity (number of 2-cm grid lines crossed min^{-1}) of four species of marsh fishes in relation to high ambient (19–23°C) and low (8–11°C) temperatures. Sample size in all cases is the number of fish in each replicate, not the number of observations.

Species		Tank 1				Tank 2			
		Low	High	t	P	Low	High	t	P
Gambusia affinis	x̄	0.8	50.3	−2.19	0.047	1.2	52.9	−2.21	0.024
	SD	6.35	87.14			5.99	90.53		
	n	15	15			15	15		
Jordanella florida	x̄	1.5	63.6	−2.33	0.046	0.3	40.0	−1.96	0.885
	SD	6.26	84.15			2.84	63.99		
	n	10	10			10	10		
Poecilia lattipinna	x̄	2.5	66.6	−1.70	0.14	1.9	43.9	−1.95	0.094
	SD	13.45	105.78			11.29	59.75		
	n	8	8			8	8		
Lepomis sp.	x̄	3.4	78.7	−2.08	0.052	No replicate			
	SD	16.26	119.06						
	n	11	11						

ries. When analyzing our data, we estimated standard deviations quite liberally, by using the number of individuals in a tank as the sample size, rather than the number of observations. This resulted in extremely conservative tests of significance, which justify an alpha level of 0.10.

Results

CORRELATES OF GREAT EGRET NESTING SUCCESSES

The stepwise logistic regression analysis of the 74 successful and 124 unsuccessful great egret nests showed that no variables were highly correlated with one another (Pearson correlation coefficient <0.69 for all dyadic combinations, see Table 1), and the overall model was significant (model χ^2 = 98.13, 4 df, p < 0.0000), with no significant residual (χ^2 = 4.16, 3 df, p = 0.245). Temperature, wind, rainfall, and initiation date were all picked as significant variables (in that order) in the model, while water depth and water recession rate were not significant correlates of nest failure.

The coldest single daily minimum air temperatures experienced over the 14-d period prior to failures of individual great egret nests averaged 13.5°C (SD = 3.07, range = 7.5–22°C); the coldest single daily maximum air temperatures experienced prior to failures averaged 21.9°C (SD = 4.30, range = 15.5–30.5°C). During the 40-yr record (1949–1989) of daily temperatures at the Tamiami Trail Ranger Station, daily maximum temperatures during February–April never fell below 9°C; daily maxima of 10°, 15°, and 25° or less were encountered at least once per year in 3%, 33%, and 98% of years, respectively (Fig. 1).

FIELD OBSERVATIONS OF FISH ABUNDANCE

On the two cold mornings, mean water temperatures were at least 9.1°C lower than on the two warm mornings (Fig. 2). Very few fish were observed in the marked plots (0.05–0.08 m^{-2}, see Table 2). Although there was considerable variation in total abundance (Table 2) and species composition of fish (Fig. 2) on the warm mornings (3–7 m^{-2}, total counts), in all cases warm-morning counts were at least one order of magnitude greater than on cold mornings, and the ranges of densities did not overlap. On warm mornings, all species fed, courted, and schooled in apparently undisturbed fashion while being observed. On cold mornings, we found aggregations of fishes only within dense sawgrass stands or around the prop roots of red mangroves. We collected numerous sheepshead minnows, flagfish, least killifish (Heterandria formosa), and marsh killifish that were buried in the mud in open prairies on the cold mornings. As the water warmed to 20–21°C, buried fish would dart out of the mud at our approach. Following the observations on the cold morning of February 12, we observed fishes emerging from the mud as water temperatures exceeded 20°C.

LABORATORY OBSERVATIONS OF FISH BEHAVIOR

All species used the entire water column at ambient temperatures (19–25°C). In contrast, all species confined their activity to the surface of the substrate when the water temperature declined to 14°C. All species also exhibited more rapid fanning of pectoral fins at about 14°C. We observed significant differences in mean activity levels between high and low temperature categories for mosquitofish, flagfish, mollies, and bluegills (those species for which sample size was large enough for analysis; Table 3). Below 10°C no individuals of any species could be induced to feed, and below about 5°C, they rarely moved. Four of the 30 mosquitofish had trouble maintaining an upright resting posi-

TABLE 4. Numbers of individuals of four species of fish found burrowed in substrate, or within 1 cm of vegetative refugia in relation to high ambient (19–23°C) and low (8–11°C) temperatures. Sample size in all cases is the number of fish in each replicate, not the number of observations.

Species		Tank 1				Tank 2			
		Low	High	t	p	Low	High	t	p
Gambusia affinis	x̄	13.8	3.2	2.35	0.037	6.8	4.3	1.92	0.078
	SD	17.18	3.02			3.39	3.91		
	n	15	15			15	15		
Jordanella floridae	x̄	6.7	0.4	5.24	0.002	5.2	1.6	3.96	0.004
	SD	3.66	0.99			2.56	1.23		
	n	10	10			10	10		
Poecilia lattipinna	x̄	0.0	0.8	−1.69	0.130	4.1	2.5	1.62	0.150
	SD	0.0	1.32			2.29	1.63		
	n	8	8			8	8		
Lepomis sp.	x̄	3.5	2.6	1.22	0.026	No replicate			
—	SD	1.41	2.04						
	n	11	11						

tion below 5°C but recovered full equilibrium after warming to 19–23°C. Warmouth, bluefin killifish, and marsh killifish did not show marked changes in activity with decreasing temperature, and tended to move little at both extremes of temperature. Although cryptically colored warmouth and marsh killifish are rather sedentary in the wild, bluefin killifish are not. The low activity of the latter may therefore have been an artifact of laboratory conditions.

Warmouth and marsh killifish were found in refugia in over 90% of observations at warm and cold temperatures (Table 4). Bluegills, mosquitofish, and flagfish were found in refugia significantly more often during cold temperatures than during ambient warm temperatures, and sailfin mollies showed nearly significant tendencies in the same direction.

Between 9°C and 7°C, all of the sheepshead minnows were found buried horizontally in the substrate, some with orbits above the substrate, and others up to 1 cm below the surface of the substrate. Flocculent mud settling on the exposed parts of partially burrowed fishes camouflaged them very effectively. Even in the well-lit confines of the 20-l aquaria, we had to count burrowed sheepshead minnows by shining a flashlight beam onto the reflective surface of their eyes. Burrowing by sheepshead minnows may have been a response to the mud being warmer than the water (1.5–2°C difference) during the initial cooling phase, but the cooled fish did not come out of the substrate when the water became 1.5°C warmer than the mud. Rather, the fish gradually emerged as the water warmed, between about 7°C and 9°C, or about the same range at which they buried.

Flagfish did not bury when the substrate was cooler than the water, even when at 6°C. However,

when the substrate was slightly warmer than the tank water (1°C), four of the 10 flagfish buried at 8°C. After five h at 6–7°C, all of the flagfish had re-emerged. The four marsh killifish burrowed in sediments occasionally during warm temperatures, but all of them remained burrowed continuously below 6°C.

The six bluefin killifish sought refuge in both the substrate and vegetation below 9°C (Table 3). Below 8°C, this species was usually buried in the substrate, when the substrate was both warmer and colder than the water.

Most species responded differently to our movements at warm and cold temperatures. During warm temperatures, all species except the marsh killifish swam actively at the surface of the water when we approached (probably a conditioned response to being fed). At temperatures below 9°C, the same stimulus resulted in all species swimming rapidly at the bottom of the tank, and clustering in the vegetation (mosquitofish, sailfin mollies, bluefin killifish) or burying (sheepshead minnows, flagfish, marsh killifish). Centrarchids hid at our approach at both warm and cool temperatures, though much less rapidly at cool temperatures.

The observer approach distance that elicited this behavior increased dramatically at lower temperatures, so that by about 8°C, fishes buried or hid at an approach distance of 6 m.

Discussion

Our analysis suggests that great egrets nests do not fail in relation to changes in local water depths or surface water recession rate. This implies that, unlike the cases for wood storks (Mycteria americana) or white ibises (Eudocimus albus) in the Everglades (Kushlan et al. 1975; Frederick and Collopy 1989), the concentration of prey brought about

by surface water recession in marshes is not a key determinant of nesting success in great egrets, or at least not by comparison with the effect of cold weather events.

Instead, we found that nesting failures were strongly associated with (in order of strength of association) low daily minimum temperatures, high peak daily wind speeds, high rainfall, and early nesting. Early nesting is probably correlated with failure simply because early nests are likely to encounter more cold and rainy weather events, as well as those of greater severity (Chen and Waylen 1987). The fact that temperature, wind, and rainfall were picked as significant variables suggests that either physiological stress on incubating birds, or reduced hunting success, or a combination of both, causes abandonment of nests. Great egrets nesting in more northerly latitudes regularly incubate successfully during periods of much colder temperatures than those experienced in the Everglades (Simmons 1959; Palmer 1962). Thus we doubt that the (usually well above freezing) temperatures experienced during cold snaps in extreme southern Florida exceed physiological stress limits for incubating great egrets or their chicks. We feel it is more likely that the cessation of nesting results in large part from a reduced ability to forage, a process in which the cold-temperature behavior of piscine prey may well play a role.

The responses of fishes to cooling under natural and laboratory conditions suggests that fishes may be much more difficult to hunt during periods of even moderate cold. In the field, the observed abundances and activity of several species dropped virtually to zero under moderate cooling events, and burrowing, use of vegetative refugia, and increased approach distances were documented. In the laboratory, these tendencies were also observed unambiguously, in a situation in which the effect of water temperature could be isolated.

Hiding in vegetation or sediments by killifishes has been explained as a mechanism to escape from predators, as a response to disturbance (Foster 1967), and as a means for coping with unsuitable environments (Minckley and Klaassen 1969). Because sheepshead minnows and bluefin killifish buried (or remained buried) when the substrate was both warmer and cooler than the tank water, it is unlikely that they were seeking thermal refuge, and may have buried to escape predation.

While burying and hiding were seen in both laboratory and field conditions, these behaviors occurred at a much higher threshold in the field (15–20°C) than in laboratory conditions (9–11°C). This difference may be explained by the rather limited choice of refugia presented to fishes in the laboratory, coupled with the fact that the laboratory
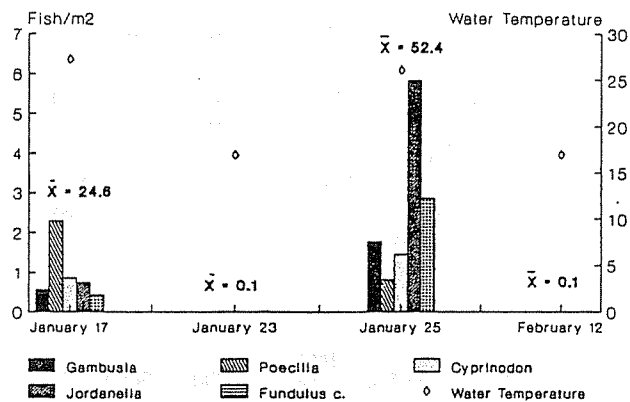

Fig. 2. Densities of marsh fishes observed in marked plots in the southern Everglades on warm (January 17 and 25, 1991) and cool (January 23, February 12, 1991) mornings. Mean water temperatures at observation plots on each date are shown as diamonds.

fishes may have been disturbed more often by the observer during cooling than were those in the field. Both conditions might make fishes more active and less willing to pick a refuge. Because of that, the laboratory thresholds should probably be considered less reliable in threshold prediction than the field observations.

The different temperature thresholds may also be explained by differing acclimation of laboratory and field populations of fishes to cold weather. The laboratory animals collected in January 1990 had experienced several strong cooling events, including a severe freeze during late December 1989, whereas the field animals observed in January 1991 had previously not experienced daily minima below 19°C. Thermal history and acclimation temperatures are related directly to preferred temperatures for a variety of fishes, as well as to their susceptibility to low temperatures (reviewed in Stauffer 1980). If acclimation to cold determines temperature thresholds for inactivity or refuge-seeking, the availability of fishes to predators in any given cold snap may depend as much upon the previous history of cold events during a winter, as upon the severity of any particular cold event. This hypothesis provides a framework for future research.

It should be noted, however, that both temperature ranges occur in the Everglades with enough regularity to be a strong selective force on the evolution of both fish behavior and wading bird nesting responses (Fig. 2).

Proposed Hypothesis

Our results confirm that, during cold weather, wading bird nests fail and fishes are likely to become unavailable to birds, but we are unable at

present to demonstrate that the two phenomena are causally linked. We propose that they are, because food stress on great egrets appears to be the best explanation for the failures, and because wading birds typically abandon nesting during other conditions which make food unavailable for short periods (Kahl 1964; Frederick and Collopy 1989; Ramo and Busto 1992).

ACKNOWLEDGMENTS

LITERATURE CITED

BANCROFT, G. T., S. D. JEWELL, AND A. M. STRONG. 1990. Foraging and nesting ecology of herons in the lower Everglades relative to water conditions. South Florida Water Management District, West Palm Beach, Florida.

CHEN, E. AND P. R. WAYLEN. 1987. Handbook of minimum temperatures: the Florida winter. Meteorological Engineering, Gainesville, Florida.

CHIDESTER, F. E. 1916. A biological study of the more important of the fish enemies of the salt marsh mosquitos. *New Jersey Agricultural Experiment Station Bulletin* 300:1–16.

CHIDESTER, F. E. 1920. The behavior of *Fundulus heteroclitus* on the salt marshes of New Jersey. *American Naturalist* 54:551–557.

FOSTER, N. R. 1967. Comparative studies on the biology of killifishes (Pisces: Cyprinodontidae). Ph.D. Dissertation, Cornell University, Ithaca, New York. 369 p.

FREDERICK, P. C. AND M. W. COLLOPY. 1988. Reproductive ecology of wading birds in relation to water conditions in the Florida Everglades. Florida Cooperative Fish and Wildlife Research Unit, School of Forest Resources and Conservation, University of Florida, Gainesville, Florida. Technical Report # 30. 259 p.

FREDERICK, P. C. AND M. W. COLLOPY. 1989. Nesting success of five ciconiiform species in relation to water conditions in the Florida Everglades. *Auk* 106:625–634.

FRITZ, E. S. AND V. A. LOTRICH. 1975. Fall and winter movements and activity level of the mummichog, *Fundulus heteroclitus*, in a tidal creek. *Chesapeake Science* 16:211–215.

GREENWOOD, P. H. 1975. A History of Fishes. Third edition. Ernest Bean Ltd., London, England. 467 p.

GUNTER, G. 1947. Differential rate of death for large and small fishes caused by hard cold waves. *Science* 106:472.

GUNTER, G. AND H. H. HILDEBRAND. 1951. Destruction of fishes and other organisms on the south Texas coast by the cold wave of January 28–February 3, 1951. *Ecology* 32:731–736.

HARRELL, F. E. 1980. The LOGIST procedure, p. 269–274. *In* P.S. Reinhardt (ed.), SAS Supplement User's Guide. SAS Institute Inc., Cary, North Carolina.

KAHL, M. P. 1964. Food ecology of the wood stork (*Mycteria americana*). *Ecological Monographs* 34:97–117.

KAILL, W. M. 1967. Ecology and behavior of the cyprinodontid fishes *Jordanella floridae* Goode and Bean, *Floridichthys carpio* Gunther, and *Cyprinodon variegatus* Lacépède. Ph.D. Dissertation, Cornell University, Ithaca, New York.

KUSHLAN, J. A. 1974. The ecology of the white ibis in southern Florida, a regional study. Ph.D. Dissertation, University of Miami, Coral Gables, Florida. 129 p.

KUSHLAN, J. A. 1977. Population energetics of the American White Ibis. *Auk* 94:114–122.

KUSHLAN, J. A., J. C. OGDEN, AND J. L. TILMANT. 1975. Relation of water level and fish availability to wood stork reproduction in the southern Everglades, Florida. United States Geological Survey, Open File Report 75–434.

LACHENBRUCH, B. A. 1975. Discriminant Analysis. Hafner Press, New York.

LOFTUS, W. F. AND J. A. KUSHLAN. 1987. Freshwater fishes of southern Florida. *Bulletin of the Florida State Museum, Biological Sciences* 31:137–344.

MINCKLEY, C. O. AND H. E. KLAASSEN. 1969. Burying behavior of the plains killifish, *Fundulus kansae. Copeia* 1969:200–201.

PALMER, R. S. 1962. Handbook of North American Birds, Vol. 1. Yale University Press, New Haven, Connecticut. 567 p.

POWELL, G. V. N. 1987. Habitat use by wading birds in a subtropical estuary: Implications of hydrography. *Auk* 104:740–749.

RAMO, C. AND B. BUSTO. 1992. Nesting failure of the wood stork in a neotropical wetland. *Condor* 94:777–781.

REID, G. K., JR. 1954. An ecological study of the Gulf of Mexico fishes in the vicinity of Cedar Key, Florida. *Bulletin of Marine Science of the Gulf and Carribbean* 4:1–94.

SIMMONS, E. M. 1959. Observations on effects of cold weather on nesting common egrets. *Auk* 76:239–241.

SIMPSON, D. G. AND G. GUNTER. 1956. Notes on habitats, systematic characters and life histories of Texas salt water cyprinodontes. *Tulane Studies in Zoology* 3:115–134.

SMITH, B. A. 1971. The fishes of four low salinity tidal tributaries of the Delaware River Estuary. *Ichthyological Associates Bulletin* #5.

SPRINGER, V. G. AND K. D. WOODBURN. 1960. An ecological study of the fishes of the Tampa Bay area. Florida State Board of Conservation Marine Laboratory Professional Paper Series #1. St. Petersburg, Florida. 104 p.

STAUFFER, J. R. 1980. Influence of temperature on fish behavior, Chapter V, p. 103–141. *In* C. H. Hocutt, J. R. Stauffer, Jr., J. E. Edinger, L. W. Hall, Jr., and R. P. Morgan II (eds.), Power Plants: Effects on Fish and Shellfish Behavior. Academic Press, New York.

UMMINGER, B. L. 1969a. Physiological studies on supercooled killifish (*Fundulus heteroclitus*). I. Serum inorganic constituents in relation to osmotic and ionic regulation at subzero temperatures. *Journal of Experimental Zoology* 172:283–302.

UMMINGER, B. L. 1969b. Physiological studies on supercooled killifish (*Fundulus heteroclitus*). II. Serum organic constituents and the problem of supercooling. *Journal of Experimental Zoology* 172:409–424.

UMMINGER, B. L. 1970. Physiological studies on supercooled killifish (*Fundulus heteroclitus*). III. Carbohydrate metabolism and survival at subzero temperatures. *Journal of Experimental Zoology* 173:159–174.

UMMINGER, B. L. 1971. Osmoregulatory role of serum glucose in freshwater-adapted killifish (*Fundulus heteroclitus*) at temperatures near freezing. *Comparative Biochemistry and Physiology* 38:141–145.