

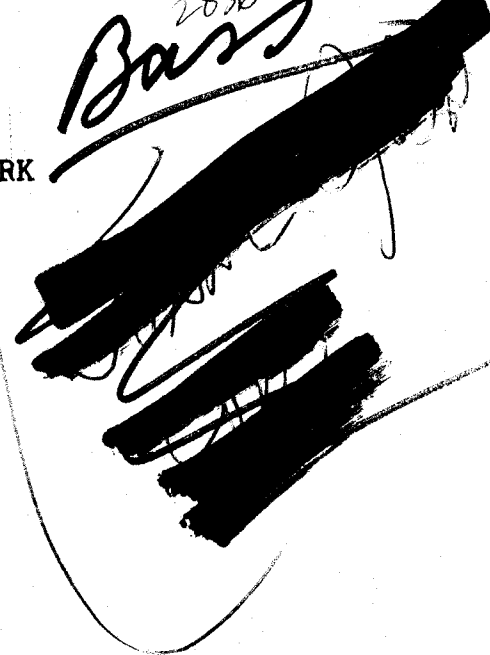
HERONS IN EVERGLADES NATIONAL PARK

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SUMMARY

The Everglades is a seasonally fluctuating wetland, typically experiencing a 4-6 month dry season in Spring. Ciconiiform wading birds are characteristic species of the Everglades, and one of them, the Wood Stork, has decreased over the past three decades owing to repeated nesting failure. A study in 1974 showed a positive correlation between the rate the marsh dried and time of nesting (and therefore nesting success). The White Ibis, too has been shown to depend on water level fluctuation. Based in these findings, the current study explored the hypothesis that hydrological conditions correlate with the nesting success of four other wading birds (Great Egret, Snowy Egret, Tricolored Heron and Little Blue Heron).

Foraging sites changed seasonally and from year to year, depending on the pattern of water level fluctuation. Only moderate levels of food were required at these sites to support feeding outside of nesting. During nesting, the amount of food available correlated with nesting success, successful nesting requiring higher concentrations of food biomass. In all cases herons could feed only in shallow depths. Thus they require shallow depth, high food density, brought about by falling water levels in the drying season.

A goal of the study was to find a method of assessing nesting success. Residual analysis of growth rates proved to be an economical, useful, and statistically analyzable, and is appropriate for use in a monitoring mode. It is based on creation of a model that accounts for intrinsic growth factors, leaving environmental variables to account for variation from the model prediction. A primary set of environmental variables can explain over 60% of the residual variation and can be used to classify nesting episodes into success categories with high accuracy.

Very importantly residual growth rates correlated with four sets of independent environmental variables measuring water depth, water level recession rates, food availability, and food consumption. For all heron species, the shallower the water depths and faster the Everglades dried in the dry season, the better nesting success. Also critical was the amount of food available, and additional variables for the various species. This result is consistent with those for Wood Storks, suggesting that a management plan could be devised to accommodate all six species of wading birds. Although the series of analytical steps was complex, management implications are elegantly simple. Barring heavy spring rainfall, successful wading bird nesting requires maintenance of a succession of feeding areas of 15 cm depth through uninterrupted high recession rates from February through the beginning of the rainy season, about May 24. An example of this pattern of drying may be seen in 1981 in Conservation Area 3, where it supported the best nesting episode during the study period. Effectiveness of management action to enhance drying rates can be predicted or evaluated by statistically testing residual growth rates.

Several species of wading birds, including herons, are thought to have decreased in population in southern Florida over the several decades since the dedication of Everglades National Park in 1947 (Robertson and Kushlan 1974). Although definitive historical data are limited or lacking, all available evidence suggests that substantial decreases have occurred, at least in the past two decades following the institution of management of the surface water flowing into Everglades National Park. Such a decline has been documented best in the Wood Stork (Mycteria americana) (Kushlan and Frohring 1986, Ogden et al. 1987). The collapse of the southern Florida Wood Stork population is clearly related to the effects of drainage and water management (Kushlan et al. 1975, Ogden et al. 1978, Kushlan and Frohring 1986, Ogden et al. 1987).

The changing population status of other wading birds is less well documentable, but it seems likely that other species nesting in the normal spring dry season might also be affected by changes in the hydrological regime that determines habitat availability and foraging effectiveness. The focus of the current study was to determine patterns of habitat use, prey consumption, and nesting success of four species of herons and to seek relationships between nesting success and environmental conditions.

Heron species studied were the Great Egret (Casmerodius alba), Snowy Egret (Egretta thula), Tricolored Heron (Egretta tricolor), and the Little Blue Heron (Egretta caerulea). All are long legged aquatic birds that nest colonially (see Hancock and

Kushlan 1984 for an account of their general ecology). In the southern Florida, they often nest together and feed in the interior and coastal wetlands, including the Everglades marsh. Our study was conducted in southern Florida in 1977-1981. The study concentrated on birds that nested in the spring drying and fed in the interior Everglades of Everglades National Park. For comparisons we also studied colony sites in the Everglades of Conservation Area 3, the Big Cypress Swamp, and Florida Bay in some years.

The study was conducted in southern Florida, in and near Everglades National Park. From 1977 to 1981, eight colony sites were studied, the locations of which are shown in Figure 1. Not all sites were active or were studied in each year. In most cases, nesting occurred from March to early May. However some nesting episodes are distinguished by occurring during and after the onset of the rainy season, in April or May (Table 1). Overall, we studied twenty-one nesting episodes, which are identified by a code that includes a two-letter colony site abbreviation, year, and in some cases a letter, the latter distinguishing between drying season (A) and post-drying season (B) nesting. These are shown in Table 1.

Hydrological conditions varied seasonally, from year to year and among the various feeding sites chosen by the herons. These differences constituted natural experiments on the impact of hydrological parameters on heron nesting. To evaluate hydrological conditions during the study, we examined data from three monitoring stations. P-36 in Shark Slough in Everglades National Park reflected water conditions affecting habitat use and food availability near Lane River and Rodgers River colony sites. OT, in the west coast headwaters in Everglades National Park near Indian Camp Creek, reflected hydrological conditions in the feeding areas used by birds from the Rodgers River colony site. G 33, in the northern Everglades in Conservation Area 3, reflected hydrological conditions in the feeding areas used by birds from the Andytown colony site.

The annual patterns of water level fluctuation are shown in Figure 2. In 1978, in the southern Everglades drying began early. By February water depths were relatively low. In the northern Everglades, water levels remained high throughout the spring because drying was interrupted in both February and April with rising water levels. The general drying trend continued, however, into in May. Water levels rose in June, during a small renesting attempt.

In 1979, water levels fell smoothly in the southern Everglades and relatively rapidly. On April 24 nesting was abruptly interrupted by heavy rains that elevated water levels. In Shark Slough colonies, two nesting episodes were recognized, before and after the rains. In the Northern Everglades, water levels decreased after March.

In 1980, water levels were higher in February than in the previous two years. The recession was intermittently interrupted by water level rises throughout the usual drying season. Nesting began in April and as late as May. Water levels remained relatively high throughout the spring, and rose even higher in June. In the northern Everglades, water levels also started high in February decreasing slowly to April, when they increased again.

In 1981, water levels began high in February and increased further in mid month. This event was followed by an uninterrupted drying, but because the recession began from such high levels, water was still relatively deep in May. As a result no nesting took place in the southern Everglades. Water depths in the northern Everglades began in February at relatively low levels in

February and an uninterrupted recession continued through the end of May. As will be shown beyond, the pattern of hydrological fluctuations at G33 in 1981 supported the most successful nesting of the study period, and represent a model seasonal fluctuation.

Table 1. Nesting episodes studied.

Colony Site	Year	Abbrev.	Nesting timing	Species	1
Lane River	1978	LA78	Spring	GE, SE, TH, LB	
Rodgers River	1978	RO78A	Spring	GE, SE, TH, LB	
Rodgers River	1978	RO78B	> April	SE, TH	
Frank Key	1978	FR78A	Spring	GE, SE,	
Frank Key	1978	FR78B	> May	GE, SE	
Sandy Key	1978	SA78	Spring		TH
Oil Well	1978	OW78	Spring		LB
Lane River	1979	LA79A	Spring	GE, SE, TH	
Lane River	1979	LA79B	> 24 April	SE, TH	
Rodgers River	1979	RO79A	Spring	GE, SE, TH	
Rodgers River	1979	RO79B	> 24 April	TH	
Andytown	1979	AN79A	Spring	GE, SE, TH	
Andytown	1979	AN79B	> 24 April	GE, TH	
Frank Key	1979	FR79	Spring	SE, TH, LB	
Heron Hammock	1979	HH79	Spring	TH, LB	
Reed Pond	1979	RP79	Spring	TH, LB	
Lane River	1980	LA80	Spring	GE, SE, TH	
Rodgers River	1980	RO80	Spring	GE, SE, TH	
Andytown	1980	AN80	Spring	TH	
Heron Hammock	1980	HH80	Spring	TH, LB	
Andytown	1981	AN81	Spring	GE, SE TH, LB	

1

Abbreviations are: GE = Great Egret, SE = Snowy Egret, TH = Tricolored Heron, LB = Little Blue Heron.

Figure 1. Locations of colony sites studied. HH = Heron Hammock; LA = Lane River; RO = Rodgers River; FR = Frank Key; SA = Sandy Key; OW = Oil Well; AN = Andytown; RP = Reed Pond.

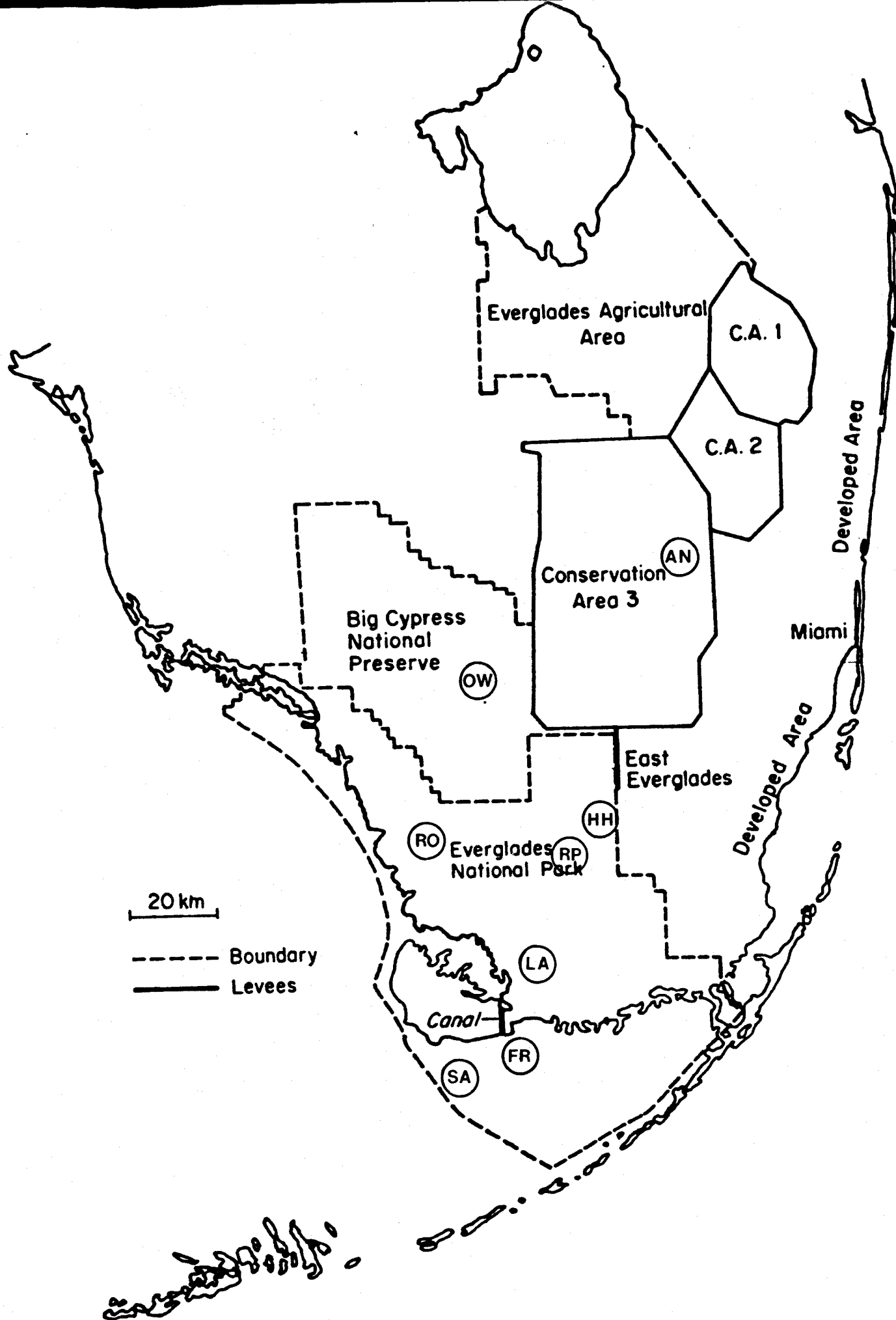
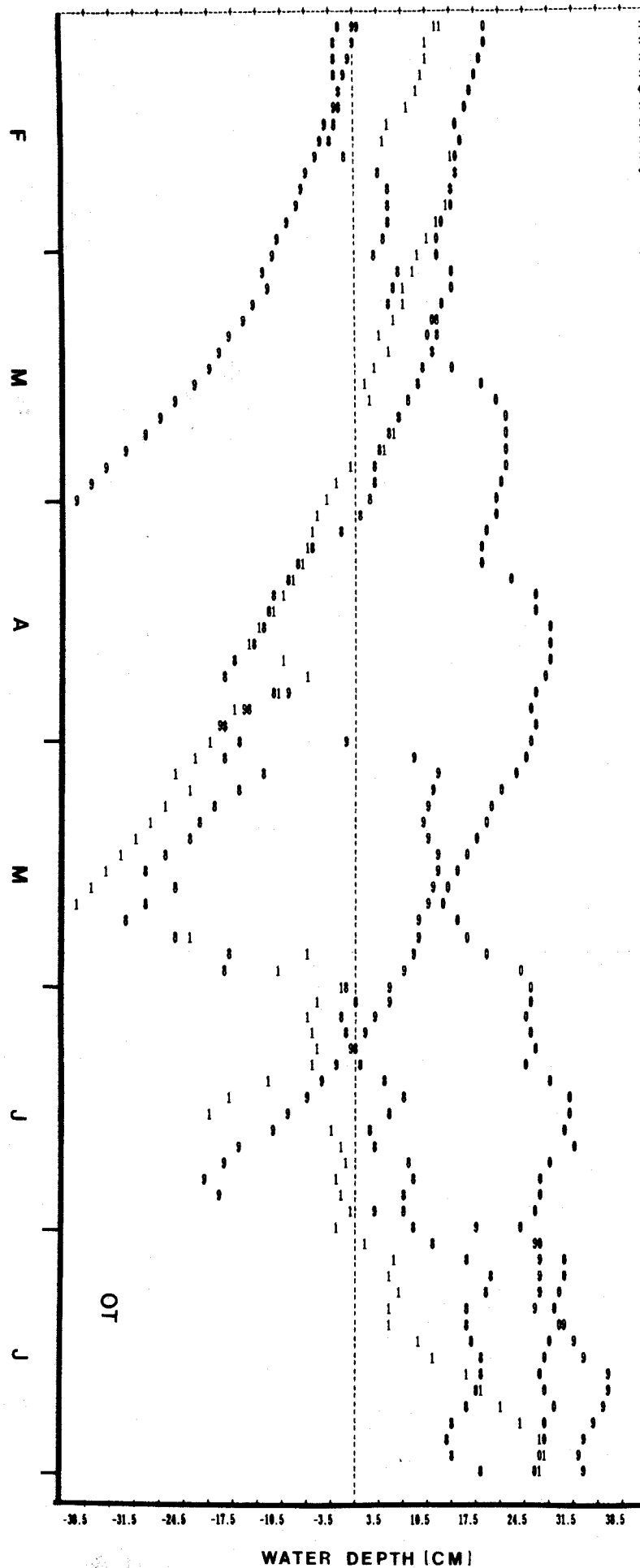


Figure 2. Water depth fluctuations in February-July in the four years of the study, 1978 (=8) - 1981 (=1). Page 1: P-36 = Shark Slough; Page 2: OT = western headwaters; Page 3: G33 = Conservation Area 3.

1979 = (9)
1980 = (10)



tidal fluctuations, in addition to seasonal fluctuations.

In January 1981, we undertook a more extensive census over Everglades National Park, the Big Cypress Swamp, and the Conservation Areas. Although the coverage was not complete, it was exhaustive. Data are evaluated only in comparative sense. Counts of nesting birds were also made on the ground at the major nesting colonies in the Park (Fig. 1).

FEEDING DISPERSAL FROM NESTING SITES

The feeding sites selected by foraging birds were determined for herons nesting at the two major colony sites near the southern Everglades (Shark Slough), the Lane River Site and the Rogers River Site (Fig. 1). Flight lines and individual birds flying from the colony were followed using fixed-wing aircraft. Altitudes of 500 ft were maintained so as not to disturb the flying birds. When the birds landed the location was noted on suitable maps. How many?

STANDING CROP SAMPLES OF PREY ORGANISMS

Access to feeding sites was gained by helicopter. Feeding sites were found by following birds from their colony to feeding sites and by revisiting sites found on fixed-wing surveys both during and outside of the nesting season. In each case the most heavily used site was selected for sampling.

Sampling the heavy feed-out

The availability of food organisms was determined by enclosure sampling. In marshes and shallow pools sampling was accomplished using a 1-M 2 throw trap following the protocols of Kushlan (1981a), the efficacy of which has been demonstrated by Jacobsen and Kushlan (1987). Sampling in streams and deeper pools was accomplished by blocknetting. The sample area enclosed by a block net was poisoned by rotenone, and fish collected over a period of several hours (Thayer et al. 1987). Water depth was recorded at each trap site. Fish and invertebrates were preserved in the field. In laboratory the specimens were identified, measured, and weighed. The mass of specimens not weighed directly was determined by the meristic equations provided in Kushlan et al. (1986). Availability was expressed as number, live weight mass, and mean prey length and evaluated in a comparative rather than absolute sense. As it is impossible to obtain availability samples prior to the bird's choosing a foraging site, in each case food availability samples were affected to a greater or lesser degree by previous consumption of prey. As a result they can provide only an indication of food available at the time of sampling, not necessarily that available when the birds first chose the site. For multivariate analyses the average number of each species of food item per m², biomass per m³ and length data were log transformed (Gauch 1982). Data on percentage composition were arcsine transformed. The patterns of prey availability at sites were determined by cluster analyses using Euclidian distance and the relationships among prey abundance and habitat variables were determined by factor analyses (SPSS, Inc. 1983).

FOOD SAMPLES COLLECTED IN COLONIES

When handled by investigators, herons often regurgitate their recent meals. These regurgitants were collected as available, preserved in the field, and the dispensing bird species was recorded. The propensity to regurgitate differed among species, colonies, and bird age and condition. As a result the sample are not consistent across colonies or species and are evaluated with respect to relative composition of prey items, of each heron species on one day in a colony. In lab, the prey species were identified, and whole items were weighed and measured. The length of digested items was estimated and mass determined following Kushlan et al. (1986). For multivariate analyses, length and weight data were log transformed. Percentage data were evaluated as both raw scores and after arcsine transformation.

WEIGHTS AND MEASUREMENTS OF PRE-FLEDGING YOUNG

Nests were marked when found and contents were recorded. Young were banded and marked with indelible ink. The culmen was measured in cm using calipers. Birds were weighing with a Pesola scale. Surviving birds were remeasured and weighed during subsequent visits, approximately five days apart. Growth was expressed as change in mass per day (gm/d) over the measurement interval. Absolute age was available for only a few birds, as it is not possible to estimate age of a bird accurately without knowing hatching date. Consequently we evaluated growth of birds in various colonies and times by constructing a multivariate regression model of daily weight change vs independent variables

(all log transformed), and distance of feeding sites from colonies in km. Prey consumed data included the percent of total weight for a daily sample and the percent of total daily count (both arcsine transformed) of the four prey most frequently consumed by each heron species (see eg., Table 10), mean daily prey length, and mean daily prey mass (both log transformed). Variables entered in each discriminant analysis were selected on the basis of relatively high correlations in bivariate correlations ($R^2 > 0.40$), and were entered stepwise.

ECOLOGICAL RELATIONSHIPS

The relationships of environmental conditions to growth rates were determined using multiple regression and discriminate function analyses (SPSS, Inc. 1983). Independent environmental variables measured hydrology, food availability, and food consumed. Hydrological variables evaluated were water depth at the nearby food availability sampling site and several types of data from the gauging station nearest the colony site (Lane River site = P36, Rodgers River Site = OT, Andytown site = G33), which in each case reflected water conditions in nearby feeding areas. Because of tidal influence in its feeding areas, the Frank Key colony was not included in this analysis. Gauging station variables included water depth at the station on the day that growth data were collected in the colony, mean water depths in February, March, April (through 24 April when rains began in 1978), and May, the mean recession rate in February through March, the mean recession rates in March, April, May, and the mean recession rates over the seven days prior to collection of data at a colony. In order to obtain a equivalent water depth for different stations, depth and recession rates were corrected to account for the difference between above and below ground recession rates. When water levels were below the ground surface, they were multiplied by 0.27, the porosity of Everglades soils (Parker et al. 1955). Water depth data were Z transformed by standardizing against the mean water depth in February through July. Both transformed and untransformed variables were examined.

Food availability data included mean number of prey items per m², mean biomass per M³, mean prey length and mean prey mass

indicative of bird size, past conditions, and the competitive situation in the nest. To do this we followed the methodology of Ricklefs et al. (1984). Variables evaluated included culmen length at the time of the first measurement (OCUL), original culmen length squared (OCULSQ), weight at first measurement (OWT), and order of hatching (HTCHSEQ). Values having standardized residuals of greater than + or - 2.5 were considered outliers. The distance and direction of the residuals, of the growth rates of birds from various colonies and times, from the overall model for the species were used as an indication of the relative success of the nesting episode.

NESTING SUCCESS AND MORTALITY

Nesting success was also evaluated by determining mortality of individual birds marked as hatchlings through approximately the third week of life. Variables evaluated included change in number of young per nest, final number of young per nest, and mortality (percent of marked chicks that were observed dead, experienced negative weight change and then disappeared, or disappeared within approximately the first five days of life). The success of various colonies at various times was categorized into three groups based on cluster analysis of mortality rates supplemented by chi-square contingency tests (SPSS, Inc. 1983).

RESULTS

CENSUS DATA ON HERONS

Censuses of foraging herons were flown over Everglades National Park and adjacent Big Cypress in 1979 and 1980. The regional monthly census data are provided in Table 2. The movement of herons along the west coast and Shark Slough during the course of the drying season can be visualized by the changes in numbers of Great Egrets and Snowy Egrets observed in 1979 (Fig. 3, 4). Nesting census data we collected for colonies in Everglades National Park provided in Table 3. Nesting numbers were below numbers observed in the foraging areas, indicating the presence of nonnesting birds, probably both wintering and nonnesting residents.

* Jan 81 census det = where

Dramatic seasonal shifts occur in the numbers and proportions of birds using various parts of the southern Florida wetlands during the course of the year. The 1979 monthly census showed the general overall pattern of feeding movements. In 1980, higher water levels caused birds to shift more to coastal feeding areas, and in 1981 a postponed drying brought birds into Shark Slough, though much later in the season, and too late for nesting. In January, Great Egrets occurred along the entire stairsteps feeding in sparse marshes and in open mangrove pools. Cape Sable mudflats were also used in large numbers as were the interior marshes. Snowy Egrets were more concentrated, being found almost entirely in aggregations. In January, this species was concentrated in the mud flats and mangrove ponds on Cape Sable and in similar habitats near Alligator Bay and Rodgers River Bay. Smaller aggregations

Need more info.
on Fig 3 & 4

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Table 2. Numbers of herons in eight regions by month in 1979, 1980, and 1981.

Month	Year	Region							
		Headwaters: Roberts to Indian Camp Creek				Stairsteps: Rodgers to North of Turner River			
		Species ¹				Species			
		GR	LB	TH	SE	GR	LB	TH	SE
January	1979	328	36	9	40	1240	182	174	207
	1980	114	82	84	0	963	20	192	75
	1981	162	47	80	86	912	144	106	667
February	1979	294	352	114	221	779	264	55	269
	1980	206	57	57	4	469	257	129	247
	1981	302	40	100	12	1882	225	156	1070
March	1979	205	72	64	35	401	192	31	533
	1980	59	30	34	0	191	135	63	114
	1981	47	0	0	0	231	110	54	0
April	1979	138	43	24	35	193	177	82	280
	1980	26	15	5	0	162	124	16	230
	1981	125	6	67	47	122	0	150	329
May	1979	44	0	0	4	77	0	6	99
	1980	26	18	3	1	109	57	49	37
	1981	78	10	79	0	20	0	55	215
June	1979	32	2	8	0	20	25	13	0
	1980	52	6	2	1	61	16	0	6
	1981	16	0	0	6	3	0	0	0
		Coastal Interior: Lopez to Harney River				Cape Sable (Snake Bight separated in 1980 & 1981)			
		GR	LB	TH	SE	GR	LB	TH	SE
		GR	LB	TH	SE	GR	LB	TH	SE
January	1979	148	14	68	353	505	94	52	507
	1980	526	0	152	339	814	47	171	878
	1981	121	0	60	68	(18)			(244)
February	1979	43	0	45	30	437	371	168	320
	1980	44	37	6	103	559	121	492	1087
	1981	144	0	85	78	(56)	(205)	(19)	(203)
March	1979	0	0	0	0	92	10	129	300
	1980	26	0	32	20	(28)	(199)	(91)	(0)
	1981	73	0	15	42	(not surveyed)			
April	1979	143	3	3	120	52			
	1980	166	0	38	480	(73)	(40)	(110)	(55)
	1981	9	0	0	17	324	0	263	346
May	1979	57	0	210	241	(24)	(142)	(59)	(155)
	1980	38	2	25	40	(not surveyed)			
	1981	120	10	55	215	40	0	79	155
June	1979	56	0	0	0	(279)	(85)	(72)	(55)
	1980	78	0	35	300	137	0	85	416
	1981	68	0	0	95	(not surveyed)			
						142	0	115	435
						30	52	12	11
						(not surveyed)			
						54	105	5	45
						(163)	(40)	(0)	(46)
						5	0	333	221
						(52)	(158)	(0)	(83)

Table 2 cont. Numbers of herons in eight regions by month in 1979, 1980 and 1981.

Month	Year	Region							
		Shark Slough north of Panther Mound				Shark Slough south of Panther Mound			
		Species				Species			
		GE	LB	TH	SE	GE	LB	TH	SE
January	1979	230	48	0	0	428	16	3	0
	1980	28	0	0	0	86	20	4	0
	1981	43	0	0	0	46	0	0	0
February	1979	197	36	1	0	201	4	4	0
	1980	53	0	0	0	132	2	2	0
	1981	33	0	0	0	256	0	0	45
March	1979	151	24	2	55	140	55	27	0
	1980	10	0	0	0	28	0	0	0
	1981	46	0	0	0	35	0	0	0
April	1979	108	37	33	2	258	3	102	461
	1980	0	0	0	0	14	2	0	0
	1981	62	0	11	0	232	21	102	110
May	1979	51	2	8	0	38	0	0	0
	1980	0	0	0	0	17	0	0	0
	1981	4176	57	413	1095	565	63	629	335
June	1979	30	10	0	9	32	10	0	0
	1980	3	0	0	0	18	0	3	0
	1981	15	0	0	0	0	0	0	0

		Big Cypress South of Loop Road to Park Boundary				NE Florida Bay: US 1 to Seven Palm Lake			
		GE	LB	TH	SE	GE	LB	TH	SE
January	1979	213	4	0	0	(not surveyed)			
	1980	53	0	0	0	185	100	82	123
	1981	195	30	6	0	150	5	80	15
February	1979	359	42	8	0	(not surveyed)			
	1980	35	0	0	0	254	38	64	200
	1981	116	0	0	0	32	9	2	0
March	1979	137	8	0	0	(not surveyed)			
	1980	8	0	0	0	53	0	111	0
	1981	15	0	0	0	29	45	13	0
April	1979	0	0	0	0	(not surveyed)			
	1980	15	0	0	0	46	0	0	35
	1981	44	0	0	0	(not surveyed)			
May	1979	0	0	0	0	(not surveyed)			
	1980	6	0	0	0	(not surveyed)			
	1981	0	0	0	0	(not surveyed)			
June	1979	0	0	0	0	(not surveyed)			
	1980	34	0	0	0	0	0	0	0

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See Table 1 for species abbreviations.

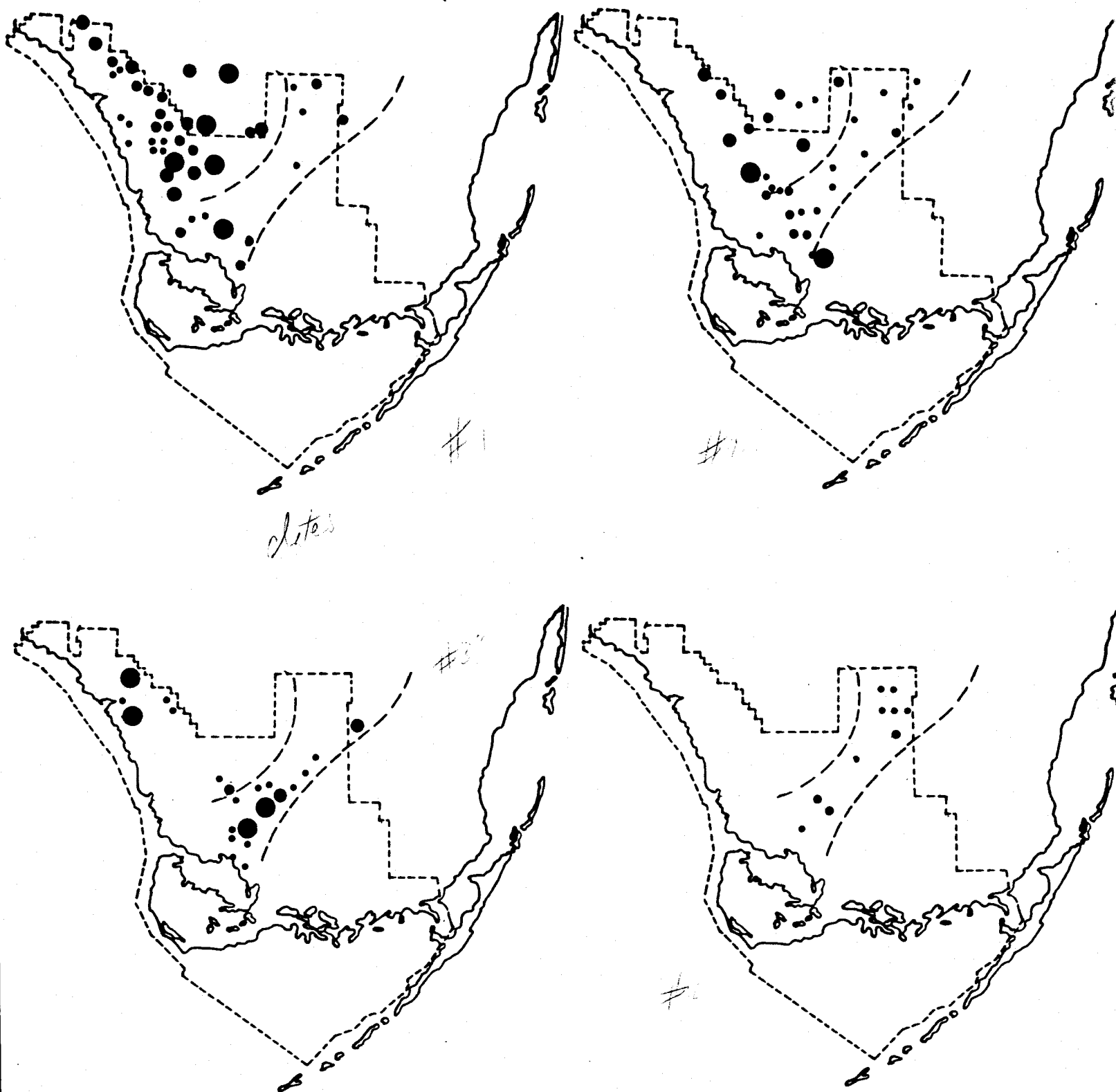


Figure 3. Feeding dispersion of Great Egrets in 1979. Size of the dot indicates the numbers counted: > 60, 30 - 60, 20 - 30, 10 - 20.

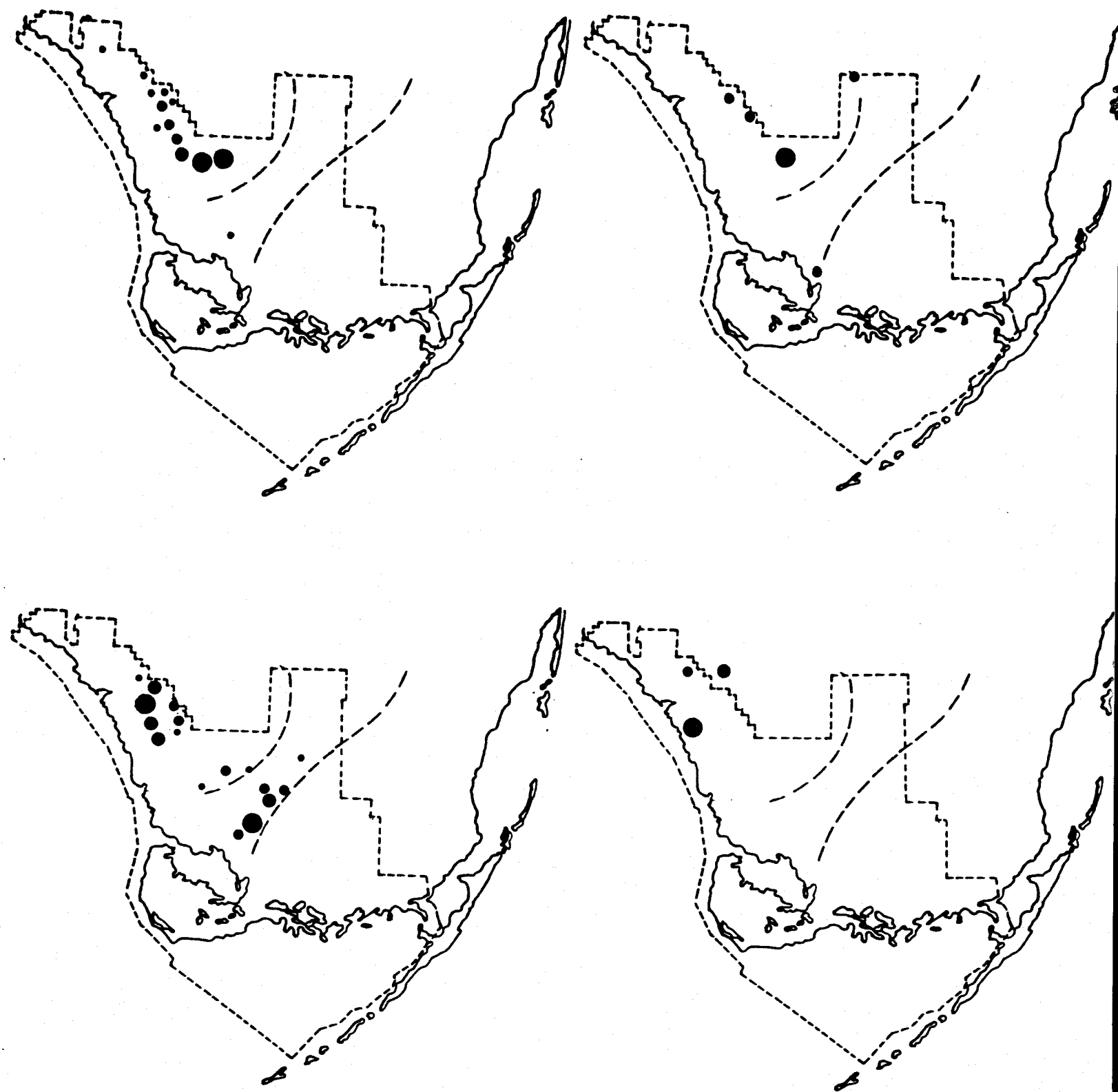


Figure 4. Feeding dispersion of Snowy Egrets in 1979. Size of the dot indicates the numbers counted: > 60, 30 - 60, 20 - 30, 10 - 20.

Table 3. Censuses of nesting pairs of herons in Everglades National Park.

Year	Lane River				Rodgers River			
	GE	SE	TH	LB	GE	SE	TH	LB
1977	150	109	150	0	155	720	431	0
1978	140	150	125	0	250	550	125	0
1979	350	450	500	0	750	2500	500	0
1980	100	200	500	11	260	650	265	0

Year	East River				Frank Key			
	GE	SE	TH	LB	GE	SE	TH	LB
1978	85	0	0	0	175	175	50	0
1979	250	10	0	0	225	300	0	0
1980	0	0	0	0	150	200	0	0

Year	Madeira				Total			
	GE	SE	TH	LB	GE	SE	TH	LB
1978	125	0	0	0	775	1605	300	0
1979	200	125	0	0	1775	3450	1000	0
1980	85	0	0	0	595	1050	765	11

1981
 occurred in the mangroves in northeastern Florida Bay, the
 Lostmans's headwaters and the northern stairstep. Tricolored
 Herons fed both individually and in aggregations, only the latter
 birds being counted in our censuses. In January aggregations
 including Tricolored Herons were primarily on Cape Sable, north of
 Joe Bay, and southwest of Alligator Bay. Smaller clusters of
 birds were found in the sparse marshes in the Broad River Basin.
 Little Blue Herons were found in only small concentrations north
 of Joe Bay, in Taylor Slough, and on Cape Sable.

As the drying season progresses beyond January, it is a
 general trend observed in all species that numbers decrease, a
 pattern especially noticable along the coasts. The overall
 decline reflects the return to the north of wintering birds,
 whereas the precipitous coastal decrease also reflects the
 movement inland with the drying season in the interior marshes.

By February, Great Egrets appeared to disperse into numerous
 aggregations covering a broader area, especially along the western
 stairstep boundary of Everglades National Park. Cape Sable
 continued to support the largest numbers of this species outside
 the interior marshes. Numbers in the interior marshes of the
 Everglades increased, responding to drying conditions there.
 Snowy Egrets shifted from the coastal marshes to the mangrove
 creeks of the western and southern headwaters. Tricolored Herons
 remained in the same areas as the previous month, although numbers
 counted decreased. The largest numbers of Little Blue Herons were
 in the headwaters marshes from Lostmans to Cabbage Bay.

In March, the numbers of all species had substantially

declined. The remaining Great Egrets were widely scattered along the mangrove/marsh interface in the stairsteps and in Shark Slough and the mangrove swamps north of Florida Bay and Cape Sable. Snowy Egrets were concentrated in the mangrove creeks of the Lostman's headwaters, on Cape Sable in the mangrove ponds west of the Cattail Lakes and at Snake Bight where they fed on sea grass flats. Tricolored Herons occurred in small concentrations on the mangrove swamps north of Joe Bay, on Cape Sable, near Rock Creek in the stairsteps, on Gopher Key, and at Snake Bight. Little Blue Herons were found in only a few sites, including Snake Bight, Cape Sable, and in the mangrove/marsh interface at Loastman's River.

By April, the Great Egrets used the interior Everglades during drying and then moved coastwise after these dried. Shifts from the stairsteps toward mangrove pools near Alligator Bay were due to the interior marsh drying. Other concentrations included Snake Bight, Taylor River, and Cattail Lake. Snowy Egrets and Tricolored Herons were distributed with Great Egrets. Little Blue Herons were found only in Snake Bight and in the northern stairsteps.

By May and June, although Great Egrets continue to be scattered throughout the interior, most species, such as the Snowy Egret, choose coastal foraging sites, especially near Alligator Bay, Gopher Key, Cape Sable, and Snake Bight, all tidal habitats. This shift demonstrated the importance of coastal habitats when the interior marshes become extremely dry or flood with the onset of the rainy season.

The more extensive census of January 1981, revealed the larger patterns of late winter dispersion of wading birds (Table 2) through the southern Florida wetlands. White Ibis accounted for 71% of the total number of wading birds counted, with the Great Egret being the most counted heron. Overall, 69% of the birds were in or adjacent to Everglades National Park with 31% in the three Conservation Areas. Only 5% were found in the Big Cypress Swamp, which had nearly dried by the time of the census.

data
map
An extensive late May *survey* provided documentation that although herons appeared to have moved out of the Park entirely during the nesting season, quite a few had returned by May. The survey, on 24 May, found 4641 Great Egrets, 2492 Wood Storks, 1042 Tricolored Herons, 120 Little Blue Herons, 1430 Snowy Egrets, and 6250 White Ibis in the area of north and south Shark Slough. For all species, over 70% of the numbers were in the northern section. These data indicate that the regional heron population remains capable of using the southern Everglades marsh when appropriate conditions are provided.

FEEDING DISPERSAL FROM NESTING SITES

The dispersal of birds from the colony site to feeding sites was studied at the colonies most likely to use the southern Everglades, Rodgers River and Lane River, in 1977, 1978, 1979, and 1980.

Birds nesting in the Lane River colony site were found to forage from 1 to 33 km from the colony site, averaging 17.6 km (Table 4). In general, foraging is well dispersed in March, but by the height of the dry season in April, most foraging centered on Shark Slough (Fig. 5). By May and into the summer, feeding dispersed, especially toward Cape Sable. This succession of foraging sites used correspond to the typical drying pattern as shown by Ogden et al. (1978) In 1978 and 1980 water levels rose in April and May, and the birds moved to Cape Sable. Drier conditions prevailed in 1977 and 1979, and by March most birds were feeding in headwaters creeks at the drying interface between march and mangroves. This pattern continued in April, with birds moving into the interior Everglades. P. 26

Birds nesting in the Rodgers River colony foraged closer to the colony site, ranging from 5 to 23 km and averaging 10.5 km (Table 4). Birds from this colony site fed mostly along the edges of the Everglades and along the coast, rather than in the interior Everglades. In general the pattern of use begins in the northern stairsteps. As the marshes dry toward the western mangroves and toward the southeast, birds feed in interior streams. If the interior floods, birds retreat to the coastal mangroves. They used the northern edges of Shark River Slough only in March of Map
let

1980, April of 1979 and in the summer of 1978 (Fig. 6). In the dry years, water levels dropped along the airstep by February permitting feeding there. By April the birds had moved to mangrove swamps, which provided tidal foraging sites. In the wetter years such as 1980, birds fed only along the airsteps or coast.

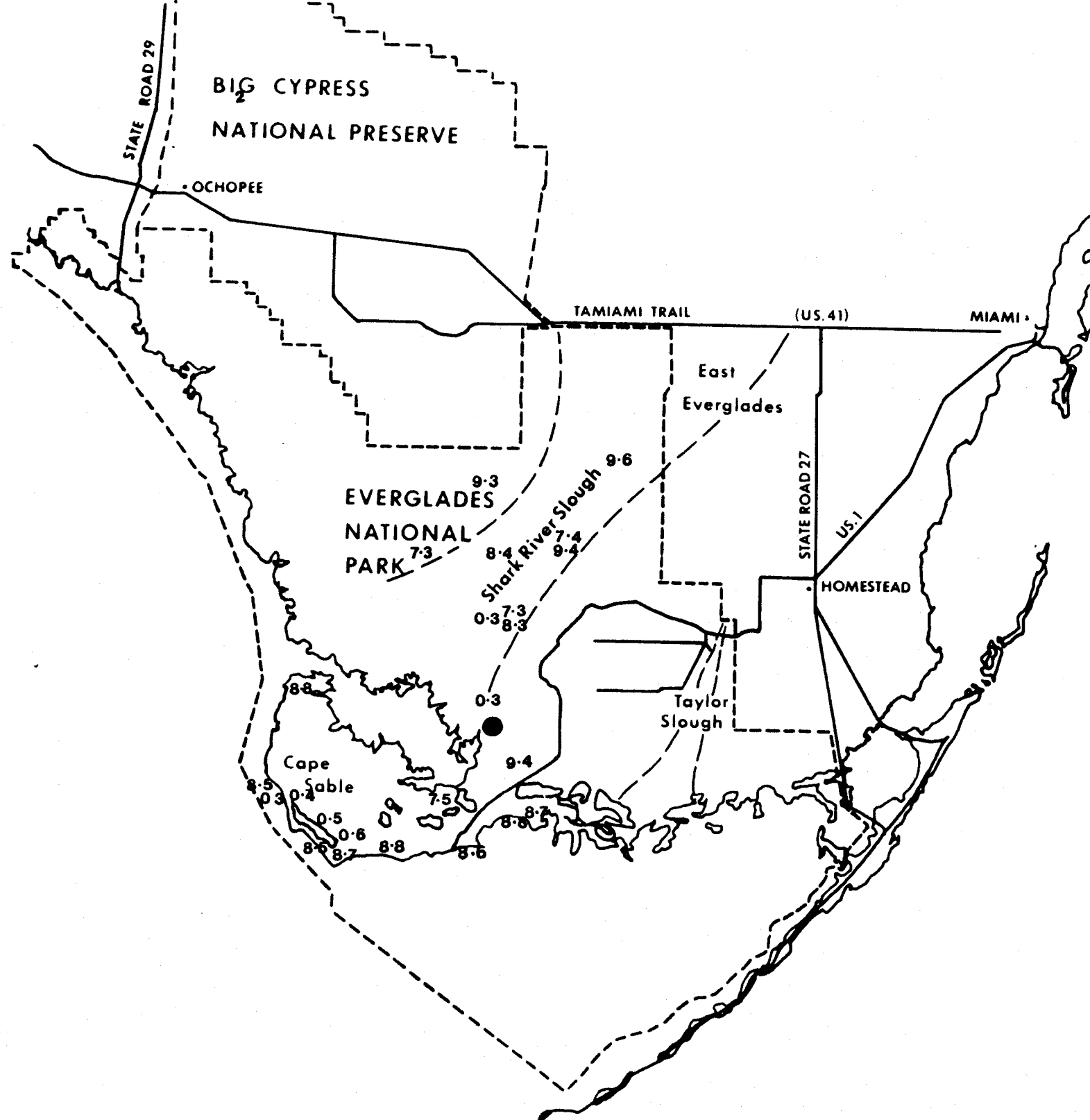
*J = m.p. size
separate by species
separate by years*

Table 4. Distance from colony sites to feeding sites.

Colony Site	Year	Distance (km)				
		Feb	Mar	Apr	May	Jun
Lane River	1977		25.9	22.7	15.0	
	1978		5.7	10.0	25.9	
	1979		33.2	18.5	8.9	31.1
	1980		1.1	21.2	22.7	
			3.9			
Rodgers River	1977		10.5	8.1	17.0	
				22.7	11.8	
	1978		6.5	7.8	8.6	8.1
	1979	9.1	13.8	16.5	19.4	15.6
	1980		7.0	13.5	14.5	
			4.9			

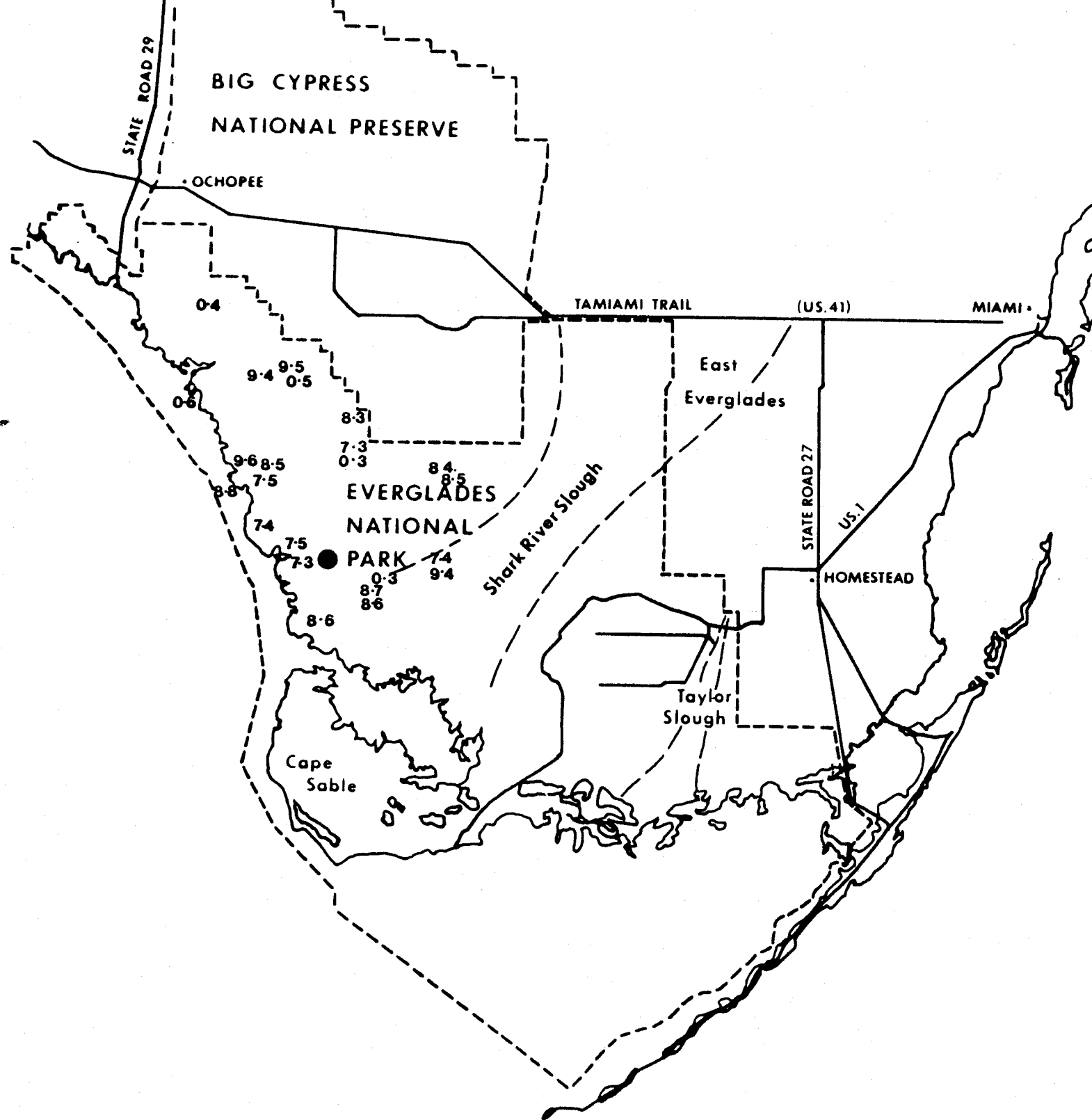
sample size 111

Figure 5. Locations of foraging birds from Lane River colony site (large dot). Locations are shown by the year and month, eg 9-3 = March 1979 and 0-3 = March 1980.



sample 11300

Figure 6. Locations of foraging birds from Rodgers River colony site (large dot). Locations are shown by the year and month, eg 9-3 = March 1979 and 0-3 = March 1980.



OVERALL FOOD CONSUMPTION.-- The overall food consumption of four species of herons is shown in Table 5. The data on mass, length, and number of prey items for each collection is presented Table 6.

The diets of all four species depend upon a few species of fish and macroinvertebrates. Three herons eat fish primarily, and the Great Egret can eat larger fishes than can the smaller Snowy Egret and Tricolored Heron. The diet of the Little Blue Heron is very different, concentrating on invertebrates and amphibians in the southern Everglades, but also including small fishes when available and along the coast.

Fifty percent of the biomass consumed by the Great Egret consisted of spotted sunfish (Lepomis punctatus), averaging 5.5 cm long, and sailfin mollies (Poecilia latipinna), averaging 2.9 cm long. Warmouth sunfish (Lepomis gulosus), dollar sunfish (L. marginatus), silver perch (Bardiella chrysoura), bullhead catfish (Ictalurus sp. including I. natalis), and marsh killifish (Fundulus confluentus) comprised another 25% of the diet by weight. Nonfish prey figuring in the diet of Great Egrets included tadpoles (Rana utricularia) and prawns (Palaemonetes paludosus). The most important prey by frequency were sailfin mollies, mosquitofish (Gambusia affinis), prawns, spotted sunfish, flagfish (Jordanella floridae), and marsh killifish, which together comprised 80% of the items consumed.

Table 5. Food consumed by herons nesting in the Everglades, expressed as percent of total weight (W), percent of total number (N), and mean prey length in mm (L)

Prey Species		Great Egret			Snowy Egret			Tricolored Heron			Little Blue Heron		
Code	Name	N	W	L	N	W	L	N	W	L	N	W	L
1	<i>Gambusia affinis</i>	18.4	1.4	20.81	28.4	8.9	18.79	29.0	8.2	19.53	17.5	1.2	16.00
2	<i>Poecilia latipinna</i>	31.1	11.3	29.32	17.2	26.9	27.47	20.7	27.1	27.77	0.8	0.6	28.23
3	<i>Cyprinodon variegatus</i>	2.6	0.8	25.05	10.9	9.7	20.54	10.4	12.8	24.40	0.1	t	15.25
4	<i>Fundulus confluentus</i>	4.6	2.8	39.26	5.2	6.7	25.80	7.7	14.1	34.71	0.6	0.4	34.45
5	<i>Jordanella floridae</i>	5.5	1.4	24.68	3.0	3.3	22.83	7.5	8.9	25.34	0.2	0.1	23.67
6	<i>Meterandria formosa</i>	0.4	t	12.70	5.4	0.5	12.51	5.2	0.3	14.13	24.1	0.9	12.52
7	<i>Lucania goodei</i>	1.6	0.2	23.17	4.4	1.5	19.68	4.3	1.3	20.04	5.6	0.3	14.01
8	<i>Fundulus chrysotus</i>	2.4	1.2	35.63	3.8	5.9	30.09	5.2	8.1	32.00	4.2	1.7	24.89
11	<i>Ictalurus natalis</i>	0.5	3.2	73.25	---	---	---	---	---	---	---	---	---
12	<i>Menidia beryllina</i>	0.1	t	44.63	---	---	---	1.2	0.5	25.60	---	---	---
15	<i>Adinia xenica</i>	0.4	t	22.45	0.3	0.3	24.03	0.3	0.2	23.50	---	---	---
17	<i>Lepisosteus platyrhinchus</i>	0.1	0.9	166.17	---	---	---	t	t	11.80	0.2	0.5	85.50
19	<i>Lepomis</i> sp.	0.1	0.8	76.67	---	---	---	0.1	0.2	27.00	---	---	---
20	<i>Micropterus salmoides</i>	0.2	1.4	99.30	t	1.3	99.00	0.2	0.3	35.64	---	---	---
21	<i>Procambarus alleni</i>	0.8	1.6	41.34	0.3	1.4	29.21	0.1	0.5	33.33	10.1	38.0	38.20
22	<i>Palaemonetes paludosus</i>	10.1	3.5	21.79	17.0	19.9	19.16	1.8	2.5	21.47	17.8	7.0	18.76
26	Odonata (naiad)	0.2	0.4	23.42	0.3	1.0	16.58	0.2	0.9	21.20	2.1	4.2	15.61
29	<i>Pomacea paludosus</i>	t	t	11.50	---	---	---	---	---	---	---	---	---
32	<i>Notropis maculatus</i>	---	---	---	---	---	---	0.1	0.1	32.25	---	---	---
33	<i>Kribia succetta</i>	0.1	1.0	109.00	t	0.4	54.75	0.1	0.6	52.33	---	---	---
34	<i>Fundulus seminolis</i>	0.2	0.7	87.70	---	---	---	---	---	---	---	---	---
35	<i>Eucinostomus gula</i>	0.1	0.4	81.75	---	---	---	t	0.1	41.50	---	---	---
38	<i>Lepomis gulosus</i>	1.1	7.9	71.97	0.1	0.9	48.13	0.1	0.4	47.00	---	---	---
39	<i>Lepomis macrochirus</i>	0.1	1.2	86.17	---	---	---	---	---	---	---	---	---
40	<i>Lepomis microlophus</i>	0.1	0.5	57.00	t	0.1	46.00	---	---	---	---	---	---
41	<i>Lepomis punctatus</i>	10.4	38.7	55.28	0.7	3.5	41.05	0.4	0.6	36.72	1.7	0.9	41.83
42	<i>Lepomis marginatus</i>	3.0	2.5	35.20	0.2	1.1	36.68	0.8	2.7	37.44	0.2	0.2	34.33
46	<i>Kribia evergladei</i>	---	---	---	---	---	---	t	t	18.50	0.7	0.1	14.54
47	<i>Kribia gloriosus</i>	---	---	---	0.1	0.2	27.44	t	t	18.00	0.2	0.1	20.13
48	<i>Ictalurus nebulosus</i>	t	0.1	64.50	---	---	---	---	---	---	---	---	---
52	<i>Ciclasoma bimaculatum</i>	0.1	0.9	82.00	t	0.1	27.50	t	0.6	55.00	---	---	---
54	<i>Anguilla rostrata</i>	t	t	159.50	---	---	---	---	---	---	---	---	---
58	<i>Lucania parva</i>	t	t	26.00	t	t	14.50	0.5	1.7	21.53	---	---	---
59	<i>Floridaichthys carpio</i>	t	t	31.50	0.2	0.5	31.33	0.4	2.8	38.57	---	---	---
68	<i>Mugil</i> spp.	---	---	---	t	0.4	57.75	---	---	---	---	---	---
75	<i>Fundulus grandis</i>	t	0.1	64.00	0.3	0.4	32.43	1.0	3.4	35.28	---	---	---
76	<i>Bagre marinus</i>	t	0.1	67.50	---	---	---	---	---	---	---	---	---
79	<i>Rivulus marmoratus</i>	---	---	---	0.1	0.1	31.17	0.1	0.1	31.00	---	---	---
82	<i>Opsanus beta</i>	---	---	---	t	1.6	117.00	---	---	---	---	---	---
83	<i>Strongylura notata</i>	---	---	---	---	---	---	t	t	54.00	---	---	---
100	<i>Rana grylio</i> (tadpole)	t	t	35.00	t	0.1	54.50	0.1	0.3	40.00	0.2	0.2	47.20
101	<i>Rana utricularia</i> (tadpole)	3.5	3.6	56.06	0.5	2.1	53.63	---	---	---	8.0	12.6	49.76
102	unid frog/tadpole remains	---	---	---	t	0.1	52.00	---	---	---	0.2	0.3	52.00
105	<i>Belostoma flumineae</i>	0.1	t	10.25	0.2	0.1	16.75	0.3	0.1	16.56	0.6	0.1	15.64
107	Diptera larva	---	---	---	0.1	t	22.25	0.1	t	26.67	0.2	t	22.67
108	<i>Mugil curema</i>	0.1	0.5	90.75	---	---	---	---	---	---	---	---	---

Table 5 cont. Food consumed by herons nesting in the Everglades, expressed as percent of total weight (W), percent of total number (N), and mean prey length in mm (L)¹

Code	Prey Species Name	Great Egret			Snowy Egret			Tricolored Heron			Little Blue Heron		
		N	W	L	N	W	L	N	W	L	N	W	L
109	<i>Hops saurus</i>	0.2	1.1	88.80	---	---	---	---	---	---	---	---	---
110	Isopoda	t	t	9.50	0.1	t	14.17	0.1	t	14.00	---	---	---
111	<i>Anchoa hepsetus</i>	0.1	0.1	50.67	---	---	---	---	---	---	---	---	---
112	<i>Bardiella chrysoura</i>	0.5	6.2	48.81	---	---	---	---	---	---	---	---	---
113	Orthoptera	---	---	---	---	---	---	t	t	28.00	0.1	t	28.00
114	<i>Rana utricularia</i> (adult)	0.1	0.3	30.75	t	0.3	28.75	---	---	---	2.1	t	45.54
115	Hylidae	---	---	---	---	---	---	---	---	---	0.1	0.1	16.00
116	<i>Dormator maculatus</i>	---	---	---	---	---	---	---	---	---	0.1	t	33.50
117	<i>Synodus foetens</i>	---	---	---	0.1	0.3	40.29	---	---	---	---	---	---
118	Odonota (adult)	0.4	t	36.72	t	t	20.50	0.8	0.4	27.53	0.1	t	37.00
119	Araneae	---	---	---	0.1	t	10.08	0.2	t	11.44	0.3	t	14.40
120	Hydrophilidae	---	---	---	0.1	0.1	11.14	0.2	0.1	8.70	---	---	---
121	<i>Pelocoris</i> sp.	---	---	---	t	t	7.75	0.1	t	6.25	0.2	t	8.17
122	Gobiidae	---	---	---	---	---	---	---	---	---	0.1	t	30.00
123	Apidae	t	t	22.50	---	---	---	---	---	---	---	---	---
124	<i>Acris gryllus</i>	t	t	15.00	---	---	---	---	---	---	0.1	0.1	22.00
125	<i>Ictalurus</i> sp.	0.2	2.0	78.20	---	---	---	---	---	---	---	---	---
126	Coleoptera (larva)	---	---	---	0.1	t	17.25	t	t	16.00	0.1	t	28.50
127	Ephemeroptera (adult)	---	---	---	t	t	14.00	---	---	---	---	---	---
128	Dytiscidae (adult)	---	---	---	0.1	0.1	11.90	0.1	t	14.00	---	---	---
129	<i>Bufo quercicus</i>	---	---	---	---	---	---	---	---	---	0.2	t	9.63
130	<i>Rana grylio</i> (adult)	0.1	0.6	63.00	---	---	---	---	---	---	0.6	9.3	59.30
131	<i>Benacus</i> sp.	---	---	---	---	---	---	---	---	---	0.3	0.2	35.30
132	<i>Liodytes alleni</i>	0.1	t	424.75	---	---	---	---	---	---	---	---	---
133	Coleoptera (adult)	---	---	---	---	---	---	t	t	17.20	0.1	t	17.20
135	Diptera (adult)	---	---	---	---	---	---	0.1	t	10.25	---	---	---
146	unid tadpole	---	---	---	---	---	---	---	---	---	0.5	0.8	52.00
170	Aeshnidae (adult)	---	---	---	---	---	---	---	---	---	0.1	t	17.00
172	<i>Dytiscus</i> spp. (adult)	---	---	---	---	---	---	---	---	---	0.1	t	10.50
317	unid cyprinodontid	0.1	0.1	35.67	t	t	18.50	---	---	---	0.1	t	18.50
TOTAL		2807	674.88g		4768	223.88g		2865	163.24g		1771	219.76g	

¹

t = trace, less than 0.1%.

The diet of the Snowy Egret is very restricted, being dominated by two species, sailfin mollies and prawns, which together constitute 47% of the diet by weight. These plus sheepshead minnow (Cyprinodon variegatus), mosquitofish, marsh killifish, and golden topminnows (Fundulus chrysotus) encompassed 78 % of the diet. The two most important species averaged only 2.7 cm and 1.9 cm respectively. By frequency of occurrence, mosquitofish, sailfin mollies, prawns, and sheepshead minnows accounted for 63% of the items consumed.

Tricolored Herons also consumed sailfin mollies, which alone accounted for 27% of the diet by weight. Other important prey items were marsh killifish, sheepshead minnows, golden topminnows, and mosquitofish, the five top prey accounting for 79% of the biomass consumed. On a frequency basis, these same species represented 73% of the items taken.

Little Blue Herons, concentrated on invertebrates and tadpoles. By weight crayfish (Procambarus alleni) accounted for 38% of the diet, and tadpoles and frogs accounted for 23%. An additional 4% was composed of prawns. The most frequently taken prey items were least killifish (Heterandria formosa), mosquitofish, prawns, and crayfish. The first three items relatively small, averaging 1.3 cm, 1.6 cm, and 1.8 cm long, respectively.

These results indicate that only a few species accounted for a large proportion of the diet of each heron species. On average, only six species constituted 5 % of either numbers and weight of prey consumed during a nesting episode. Table 6 shows the

Table 6. Prey consumed by herons at various colony sites and time periods, expressed as percent of total weight (H), percent of total number (N), and mean prey length (L). Prey accounting for greater than 5% of diet.

1 Nesting Episodes	Great Egret				Snowy Egret				Tricolored Heron				Little Blue Heron			
	Prey Code	N	H	L	Prey Code	N	H	L	Prey Code	N	H	L	Prey Code	N	H	L
LA78	1	22.6	7.1	26.14	1	27.0	10.5	19.01	1	24.6	4.0	16.30	21	53.4	54.5	33.89
	2	33.9	21.0	28.38	2	14.6	16.2	23.50	2	24.6	23.1	25.59	22	8.0	1.9	21.14
	3	8.1	2.7	21.80	3	41.0	41.5	19.30	3	10.1	7.8	22.74	101	22.7	14.9	47.73
	4	22.6	24.8	37.89	22	7.4	15.1	20.96	4	20.2	26.6	30.08	114	3.4	7.9	34.13
	22	1.6	14.1	49.00					42	0.8	5.3	45.50	130	2.3	19.2	65.50
	38	3.2	27.7	63.50					59	4.0	17.3	41.15				
TOTAL		62.0	7.34g			515.0	19.92g			248.0	15.47g			88.0	25.54g	
R078A	1	32.5	2.9	21.21	1	48.8	14.1	18.69	1	39.8	10.8	19.27	21	19.2	39.7	44.10
	2	36.7	17.5	30.91	2	30.4	49.1	28.85	2	21.5	27.2	26.37	101	68.5	46.5	54.67
	38	0.9	10.5	83.50	3	10.0	8.4	21.67	3	24.7	49.4	28.93	114	4.6	12.1	40.50
	101	15.6	17.1	56.06	101	2.3	9.2	55.67	4	10.8	11.5	29.85				
	109	0.8	5.2	88.80												
	112	2.1	30.0	48.81												
TOTAL		633.0	140.80g			923.0	48.84g			93.0	5.38g			130.0	42.38g	
FR78A	1	5.8	1.2	17.67	1	44.9	23.9	18.23								
	2	11.3	7.6	22.76	2	26.1	34.3	20.29								
	3	49.2	30.6	19.59	3	5.4	3.8	16.21								
	21	0.6	10.0	49.50	4	16.5	17.0	20.20								
	22	26.9	36.4	21.15	81	1.1	5.8	31.25								
	72	2.9	6.7	43.44												
TOTAL		309.0	15.73g			352.0	8.62g									
AN79B	1	15.4	0.2	23.33	1	19.3	8.4	23.77	1	12.0	3.8	24.20				
	2	23.1	2.0	35.33	2	17.5	25.5	32.35	4	9.6	19.2	42.75				
	4	7.7	0.3	32.50	5	45.6	31.2	23.13	5	42.4	36.5	26.55				
	8	7.7	0.3	33.50	22	1.8	5.2	23.13	6	7.2	0.6	15.39				
	39	7.7	20.8	112.00	42	5.3	25.1	45.00	8	11.2	12.4	32.07				
	40	7.7	9.9	91.80	126	5.3	0.0	17.33	42	4.0	6.8	37.32				
	41	30.8	66.5	92.62					52	0.8	8.1	55.00				
TOTAL		13.0	24.80g			57.0	4.10g			125.0	11.06g					
LA79A	1	10.4	0.6	19.58	1	26.9	9.8	19.11	1	21.7	4.5	21.20				
	2	46.8	14.5	28.96	2	16.6	27.6	27.34	2	39.1	30.8	27.17				
	4	6.4	2.6	36.42	4	7.1	23.9	40.08	4	17.4	26.9	37.50				
	5	5.3	1.2	23.90	5	4.9	9.7	25.40	5	8.7	4.7	23.25				
	8	5.9	2.8	35.50	6	19.4	1.9	12.38	8	4.3	14.5	50.50				
	38	0.8	6.1	38.83	22	15.5	15.6	17.67	42	8.7	18.6	37.25				
	41	10.2	56.8	68.20												
TOTAL		393.0	100.66g			535.0	21.91g			23.0	1.98g					

Table 6, continued.

1 Nesting Episodes	Great Egret				Snowy Egret				Tricolored Heron				Little Blue Heron			
	Prey Code	N	H	L	Prey Code	N	H	L	Prey Code	N	H	L	Prey Code	N	H	L
R079A	1	8.0	0.9	21.58	1	10.8	2.7	17.38	1	35.1	10.7	18.09				
	2	39.3	15.8	28.05	2	16.6	20.3	25.64	2	48.6	68.3	27.03				
	3	5.1	2.5	26.17	4	3.2	5.3	31.88	4	6.4	12.0	33.95				
	5	12.6	3.9	24.31	6	6.2	0.5	11.73	5	3.9	5.1	23.82				
	22	14.0	8.0	23.35	7	6.6	2.3	19.46								
	41	9.0	39.7	56.03	8	6.9	7.2	26.28								
	125	0.7	11.6	87.30	22	42.2	43.9	18.53								
					41	1.5	11.8	42.15								
TOTAL		565.0	106.89			870.0	39.32g			362.0	16.72g					
AN79A	1	17.2	1.2	21.73					1	25.7	7.5	19.03				
	2	19.4	6.2	30.17					2	8.1	14.1	29.25				
	5	9.7	1.4	22.56					4	2.7	13.8	47.00				
	11	1.6	27.8	119.17					5	24.3	22.2	22.50				
	38	2.2	11.1	70.88					6	20.3	2.8	14.50				
	41	9.1	25.3	51.32					8	13.5	35.8	36.45				
	42	29.6	23.9	36.48												
TOTAL		186.0	54.36g							74.0	3.51g					
LA80	2	75.0	10.6	35.75	1	11.2	2.1	18.39	1	39.4	14.4	20.65				
	19	12.5	19.1	74.00	2	18.9	32.4	31.66	2	28.2	40.0	27.10				
	38	12.5	70.3	113.50	3	31.1	23.2	22.48	4	9.9	21.5	35.59				
					4	11.7	16.6	34.35	8	5.0	9.1	32.34				
					5	10.2	5.5	21.05								
					22	11.7	9.2	19.87								
TOTAL		8.0	7.75g			196.0	14.14g			383.0	13.5 g					
R080	1	22.8	2.3	19.81	1	26.5	8.2	18.46	1	56.2	16.6	19.41				
	2	24.2	11.2	28.02	2	16.7	24.2	26.82	2	6.7	9.0	28.43				
	4	6.4	5.7	38.54	3	6.5	6.4	21.41	3	21.0	24.0	24.76				
	5	6.2	3.0	26.37	4	16.8	7.4	17.39	22	6.2	6.3	20.58				
	21	2.3	8.2	43.69	20	0.3	8.8	99.00								
	22	22.3	10.9	21.67	22	25.7	29.8	19.00								
	41	2.3	26.2	69.12												
	52	0.4	6.7	82.00												
TOTAL		565.0	89.72g			756.0	33.86g			20.0	12.36g					
AN81	1	14.2	0.6	19.83	1	36.9	14.8	19.33	1	40.5	18.4	19.86	1	23.3	7.4	16.00
	7	6.0	0.3	20.02	2	5.6	8.7	25.72	2	8.2	23.5	29.66	6	32.6	5.4	12.51
	22	14.8	1.9	19.61	6	10.2	1.3	13.09	6	13.1	2.3	14.02	7	7.6	1.8	14.01
	38	2.4	10.9	69.80	7	17.6	7.9	20.05	7	17.2	7.2	19.31	8	4.8	6.9	23.17
	41	47.6	96.5	49.68	8	13.8	31.1	32.03	8	13.7	29.2	30.68	22	22.6	38.1	18.47
	22	11.4	25.4	21.45	22	3.0	7.3	22.18	26	2.5	23.9	15.54				
													41	2.3	5.3	41.83
TOTAL		332.0	126.98g			737.0	27.69g			571.0	19.90g			1304.0	35.62g	

Table 6, continued.

1 Nesting Episodes	Great Egret			Snowy Egret			Tricolored Heron			Little Blue Heron		
	Prey Code	N	H	L	Prey Code	N	H	L	Prey Code	N	H	L
FR78B	3	64.4	5.9	19.26	1	7.2	7.6	18.10				
	81	6.1	9.8	54.00	2	4.3	11.4	21.79				
	82	14.7	49.2	71.50	21	0.7	5.6	22.50				
	136	6.8	31.7	49.56	26	0.7	7.4	14.75				
					107	35.5	7.4	16.26				
					110	6.8	6.2	15.92				
					119	7.2	1.2	7.70				
					126	29.4	0.8	16.95				
					136	0.4	41.7	53.00				
TOTAL		278.0	79.64g			279.0	3.23g					
FR79					2	6.6	5.4	19.94	1	31.6	7.6	19.25
					3	53.9	30.2	18.14	2	5.3	0.9	16.50
					21	0.4	8.0	50.00	3	10.5	6.0	22.75
					22	1.5	5.7	24.12	58	15.8	34.5	19.50
					58	3.7	10.8	17.10	59	36.8	50.9	29.29
					59	12.9	16.0	23.13				
					101	1.5	8.3	53.75				
					113	14.0	13.0	12.24				
TOTAL						271.0	10.08g		19.0	1.35g		
										39.0	59.23g	
R078B					1	25.9	4.0	17.7	1	6.6	1.4	20.50
					2	14.8	35.1	37.17	2	23.1	23.2	29.07
					3	17.3	17.4	27.04	3	29.7	28.4	26.57
					4	16.0	20.4	34.73	4	25.3	36.0	37.52
					5	12.3	7.8	23.35	5	8.8	5.8	24.56
					68	2.5	12.7	57.75				
TOTAL						81.0	6.45g		91.0	7.51g		
LA79B					3	96.5	88.1	19.44	1	14.6	2.3	20.43
					75	1.2	9.1	45.00	2	25.0	8.8	22.75
									3	8.3	7.1	26.87
									4	12.5	18.0	38.17
									22	6.3	6.6	24.00
									58	8.3	14.4	20.13
									59	20.8	40.9	36.00
TOTAL						85.0	2.70g		48.0	4.65g		

Table 6, continued.

1 Nesting Episodes	Great Egret			Snowy Egret			Tricolored Heron			Little Blue Heron		
	Prey Code	N	H	L	Prey Code	N	H	L	Prey Code	N	H	L
RP79									1	16.7	3.1	19.25
									2	29.2	40.8	32.14
									5	33.3	36.1	26.75
									7	8.3	2.2	22.75
									8	8.3	14.0	37.75
TOTAL									24.0	2.05g		96.0 52.01g
NH80									1	6.6	1.7	24.25
									2	25.3	22.6	31.91
									4	22.0	23.5	36.90
									5	20.9	15.7	26.61
									8	7.7	10.8	39.50
									41	3.3	5.1	37.17
									42	6.6	14.6	40.83
												21 12.0 0.6 16.08
												2 14.0 10.9 33.79
												4 12.0 5.5 32.92
												8 22.0 13.8 34.82
												21 2.0 7.7 47.00
												22 14.0 6.2 22.14
												42 4.0 5.5 40.25
												114 4.0 15.0 48.50
												130 6.0 33.6 45.50
TOTAL									91.0	10.57g		50.0 8.64g
RO79B									1	7.5	1.6	21.36
									2	37.6	38.0	30.51
									3	18.3	27.2	30.18
									4	15.1	13.6	34.32
									5	11.8	8.1	25.91
TOTAL									93.0	8.84g		
AN80									1	16.3	4.0	19.43
									2	13.3	26.0	32.41
									4	7.2	15.4	39.37
									5	33.1	36.2	25.73
									6	12.0	1.3	14.05
									8	6.0	5.5	28.60
TOTAL									166.0	10.63g		
SA78									1	26.8	7.0	17.44
									2	10.3	13.4	26.18
									3	36.3	43.2	22.37
									5	4.2	5.4	24.50
									12	5.9	2.3	24.50
									58	1.3	6.4	21.86
									59	3.9	6.8	27.33
									75	4.1	6.7	27.50
TOTAL									542.0	23.86g		

Table 6, continued.

		Great Egret			Snowy Egret			Tricolored Heron				Little Blue Heron							
1																			
Nesting Episodes	Prey Code	N	H	L	Prey Code	N	H	L	Prey Code	N	H	L	Prey Code	N	H	L			
													21	44.4	47.4	41.54			
													22	7.4	2.1	27.00			
													101	7.4	2.4	52.50			
													114	29.6	46.7	34.69			
TOTAL																	27.0	15.44g	

1

See Table 1 for nesting episode listings.

frequency that specific prey organisms made up more than 5 % of 39 the diet among nesting episodes. These data can be used to examine variability and consistancy of prey consumption within and among heron species and nesting episodes.

VARIABILITY WITHIN NESTING EPISODES AMONG SPECIES.-- Diet differed among species within a single nesting episode. Spring nesting in the main Park colonies shows clearly the typical differences among heron species noted above. For example, during LA78, the dominant prey species are those of the core diet, with Great Egrets concentrating on relatively large fish, Snowy Egrets and Tricolored Herons consuming smaller fishes, especially mosquitofish, sailfin, sheepshead minnow, and marsh killifish. Such a diet indicates feeding in both freshwater marshes and in the estuary. Snowy Egrets also ate prawns, whereas Tricolored Herons also ate sunfish. The Little Blue Heron, on the other hand, specialized in crayfish, prawns, and amphibians. Thus the diets differed markedly among the herons species. These are the typical diets for spring nesting in the major southern Everglades colonies, and were similar at these colony sites during other spring nesting episodes.

At Andytown colony site, eg AN81, sunfish dominated the Great Egret diet, whereas Snowy Egrets and Tricolored Herons pursisted in their small fish and prawn diet. Little Blue Herons, however, ate fish including sunfish in addition to prawns and insect larvae.

Comparisons at a coastal colony sites, such as Frank Key

(FR78B, FR79), show marine and coastal influences on diet. The three smaller herons concentrated on marine and estuarine species. However, the Great Egrets continued their predominantly fresh water diet during spring nesting (eg FK78A), demonstrating that they were able to fly inland to forage, a pattern we confirmed by following birds from the colony site.

VARIABILITY WITHIN SPECIES AMONG NESTING EPISODES.-- For the Great Egret, mosquitofish, sailfin mollies, sheepshead minnows, marsh killifish, flagfish, golden topminnow, crayfish, prawns, warmouth, and spotted sunfish constituted over 5% of the diet in more than half the nesting episodes (Table 7). The several species of sunfish (*Lepomis* spp) taken together were also regularly consumed in high proportions. Similarly, mosquitofish, sailfin, sheepshead minnows, marsh killifish, flagfish, least killifish, prawns, and crayfish were important in over half the episodes for Snowy Egrets; mosquitofish, sailfins, marsh killifish, and flagfish were important over half the times for Tricolored Herons. In the Little Blue Heron, a different array constituted the dietary core: prawns, crayfish, and tadpoles. In each case these arrays of species could be considered the core of the diets.

Differences in the dominant prey items in the diet among nesting episodes were also evident. For the Great Egret, the diet of herons during the spring nesting episodes at Rodgers River and Lane River and both spring and summer nesting at Andytown colony sites were dominated by the core array of fishes noted above. Great Egrets nesting in spring at Frank Key also took the the

Table 7. Frequency of occurrence of species in the top 5% of the diet during nesting episodes. Species with percentages given are those present in over 50% of the nesting episodes.

Species	GE	SE	TH	LB
1	82	85	100	P
2	82	92	94	P
3	55	62	P	P
4	55	46	71	P
5	55	31	59	
6		62	P	P
7	P	P	P	P
8	36	P	P	P
10				
11	P			
12			P	
19	P			
20				
21	P	23		86
22	45	64	P	57
26				P
38	P			
39	P			
40	P			
41	63	P	P	P
42	P	P	P	P
52	P		P	
58		P	P	P
59		P	P	P
61		P		
68		P		
72	P			
75		P	P	
81	P	P		
82	P			
101	P	P		71
107		P		
109	P			
112	P			
113		P		
114				P
119		P		
125	P			
126		P		
130				P
136	P	P		P
Number of episodes	11	13	17	7

typical fresh-water species indicating inland feeding sites were used. However, the diet for summer nesting at Frank Key (FR78B) was dominated by sheepshead minnows, toadfish (Opsanus beta) and pinfish (Lagodon rhomboides) and pink shrimp (Penaeus duorum) indicating that those birds fed in Florida Bay and nearby Cape Sable.

For the Snowy Egret, the typical core diet was taken in most nesting episodes. Birds nesting in summer at Frank Key also ate marine fishes.

For Tricolored Herons, mosquitofish and sailfin dominated the diet in nearly all nesting episodes, with marsh killifish and flagfish being less consistently dominant in the diet. Nesting at Lane River (LA79B) after the water levels had risen in the interior featured rainwater killifish (Lucania parva) and the goldspotted killifish (Floridichthys carpio), which are taken from estuarine mangrove swamps, reflecting a switch of feeding sites after the rains began. Birds nesting at Sandy Key had a similar diet, which also included Gulf killifish (Fundulus grandis), indicative of feeding in the mangroves on Cape Sable or in tidal grass flats. Tidal feeding also occurred during spring nesting episodes at Lane River, as indicated by goldspotted killifish Floridichthys as a dominant in the diet.

Little Blue Herons showed considerable variability in the dominant prey items taken during different nesting episodes. During spring nesting at Lane and Rodgers River colony sites, they depended on crustaceans and amphibians. However in more interior colonies, such as Heron Hammock and Andytown, they added several

species of fish, although the crustaceans continued to dominate the diet in biomass. Birds nesting at Frank Key apparently did not have access to these fresh water forms, and brackish-water fish predominated in their diet.

CONSUMPTION OF MAJOR PREY ITEMS.-- As indicated by Table 7, only 11 species are frequently consumed in over trace amounts. The bulk of the diets of Everglades herons can be understood through the following prey: mosquitofish, sailfin molly, spotted sunfish, prawns, sheepshead minnow, marsh killifish, flagfish, least killifish, golden topminnow, and crayfish, and for Little Blue Herons, frogs and tadpoles. Of these the first four species make up the bulk of the diet. The consumption of these prey species is shown in Table 8 broken down by date and nesting episode.

Table 8. Consumption of four most commonly eaten prey items for each heron species during various nesting episodes.

Species	Nesting Episode	Month	Day	Prey Species											
				Gambusia affinis			Poecilla latipinna			Lepomis punctatus			Palacnorneles paludosus		
				N	M	L	N	M	L	N	M	L	N	M	L
Great Egret	LA78	5	8	26.09	9.27	27.29	32.61	21.13	28.47	---	---	---	---	---	---
		5	13	12.50	1.28	19.25	37.50	20.77	28.17	---	---	---	6.25	51.58	49.00
	R078A	4	29	---	---	---	---	---	---	---	---	---	---	---	---
		5	3	---	---	---	---	---	---	---	---	---	---	---	---
		5	10	2.13	0.10	18.00	27.66	15.93	33.12	---	---	---	---	---	---
		5	14	25.00	2.87	22.30	11.67	6.50	28.64	---	---	---	---	---	---
		5	21	44.29	8.56	21.34	42.56	41.36	30.41	---	---	---	1.73	2.13	24.60
		R078B	6	3	23.46	3.09	20.74	46.60	25.50	31.47	---	---	0.52	0.19	22.00
			7	8	---	---	---	---	---	---	---	---	---	---	---
	FR78A	5	4	---	---	---	9.41	6.41	21.62	---	---	---	---	---	---
		5	9	3.47	1.02	19.40	7.64	7.02	24.45	---	---	---	52.08	78.89	21.45
		5	16	16.25	2.27	17.00	20.00	9.12	22.16	---	---	---	10.00	7.44	18.31
	FR78B	6	1	---	---	---	---	---	---	---	---	---	---	---	---
		6	28	---	---	---	4.23	2.72	19.31	---	---	---	---	---	---
		7	14	---	---	---	10.00	1.73	33.20	---	---	---	2.00	0.09	17.00
		7	20	---	---	---	---	---	---	---	---	---	---	---	---
	LA79A	3	15	8.57	0.86	23.83	35.71	10.36	28.54	8.57	63.45	78.00	2.86	0.63	20.50
		3	26	46.55	11.73	17.48	18.97	26.66	26.23	1.72	0.85	44.10	12.07	11.69	18.14
		4	2	3.30	0.20	27.17	42.86	16.20	31.92	12.09	64.63	69.01	7.69	1.14	18.28
		4	9	1.99	0.28	24.00	72.19	28.15	28.28	6.62	40.80	63.95	1.32	0.62	23.00
		4	23	8.70	0.27	26.25	---	---	---	52.17	66.74	68.12	---	---	---

Table 8. cont. Consumption of four most commonly eaten prey items for each heron species during various nesting episodes.

Species	Nesting Episode	Month	Day	Prey Species											
				Gambusia affinis			Poecilla latipinna			Lepomis punctatus			Palacmones paludosus		
				N	M	L	N	M	L	N	M	L	N	M	L
	LA79B	5	4	---	---	---	32.00	15.90	36.81	16.00	67.15	63.76	2.00	0.81	26.00
	R079A	3	5	1.41	0.08	20.00	1.41	0.58	33.00	---	---	---	9.86	5.90	27.00
		3	13	5.52	1.43	19.90	66.85	74.92	27.00	---	---	---	8.29	9.57	21.57
		3	27	7.69	0.42	22.00	7.69	1.70	30.00	30.77	60.57	53.75	---	---	---
		4	3	14.47	1.59	20.98	40.13	17.28	28.45	9.21	37.56	58.18	19.74	11.75	22.47
		4	10	7.14	0.65	23.44	23.21	8.99	30.96	23.21	55.48	52.25	24.11	10.53	24.37
		4	17	15.79	1.48	27.00	31.58	4.26	25.92	21.05	83.86	73.00	---	---	---
		4	24	---	---	---	35.29	9.73	33.67	17.65	78.79	68.50	---	---	---
	AN79A	4	6	---	---	---	---	---	---	20.00	4.29	40.00	---	---	---
		4	11	17.04	2.56	22.78	19.26	13.14	31.36	8.89	32.16	45.21	2.96	1.67	22.75
		4	18	---	---	---	10.00	0.24	20.00	20.00	43.97	75.00	---	---	---
		4	26	25.00	0.61	19.06	25.00	3.24	27.83	5.56	15.12	70.00	---	---	---
	AN79B	5	3	25.00	2.02	23.00	37.50	22.33	35.33	12.50	69.02	75.00	---	---	---
	LA80	4	28	---	---	---	100.00	100.00	35.75	---	---	---	---	---	---
	R080	4	15	---	---	---	22.22	18.43	29.25	---	---	---	---	---	---
		4	24	21.37	3.00	18.34	49.62	33.47	26.32	0.76	1.21	34.50	15.27	9.04	19.72
		4	29	7.07	0.81	20.21	9.60	5.84	32.03	1.52	15.22	73.67	43.43	20.48	21.97
		5	6	35.48	5.23	18.59	30.65	21.17	27.29	4.84	24.28	42.83	6.45	16.29	30.75
		5	16	20.69	4.49	19.17	62.07	76.99	28.17	---	---	---	17.24	18.52	20.20
		5	18	56.00	8.38	21.06	3.00	4.83	32.83	2.00	32.26	77.75	10.00	4.85	20.30
		5	23	---	---	---	75.00	77.78	31.00	---	---	---	---	---	---
		5	29	27.27	0.24	18.83	---	---	---	27.27	66.62	95.50	9.09	0.31	20.00

Table 8. cont. Consumption of four most commonly eaten prey items for each heron species during various nesting episodes.

Species	Nesting Episode	Month	Day	Prey Species											
				<i>Gambusia affinis</i>			<i>Poecilia latipinna</i>			<i>Lepomis punctatus</i>			<i>Palacmones paludosus</i>		
				N	H	L	N	H	L	N	H	L	N	H	L
	AN81	4	7	1.15	0.06	25.50	1.15	0.26	36.00	85.06	87.39	48.98	---	---	---
		4	13	---	---	---	---	---	---	83.33	96.10	71.50	---	---	---
		4	17	11.76	0.66	19.38	35.29	7.38	26.38	35.29	89.25	56.00	8.82	1.73	20.20
		4	27	---	---	---	---	---	---	62.50	71.59	46.90	---	---	---
		5	1	---	---	---	---	---	---	91.67	70.53	57.10	---	---	---
		5	6	---	---	---	---	---	---	87.50	73.07	56.98	4.17	0.21	20.00
		5	11	26.25	6.25	19.74	1.25	1.98	29.50	18.75	28.33	37.88	28.13	21.15	19.58
Snowy Egrets	LA78	5	8	57.45	25.57	16.52	19.15	26.62	21.00	4.26	16.74	22.50	17.02	27.62	20.69
		5	13	45.29	22.92	19.40	24.22	26.22	22.41	16.14	40.15	20.88	10.31	4.27	15.17
		5	18	26.32	8.47	22.20	23.68	37.35	32.17	---	---	---	21.05	12.61	22.44
		5	19	0.48	0.05	14.00	1.45	1.72	74.67	---	---	---	83.09	79.14	19.65
	RA78A	5	14	51.35	15.48	20.32	35.14	56.25	29.94	0.90	1.62	24.00	4.50	4.31	24.20
		5	21	48.76	15.99	19.26	28.01	48.54	28.29	3.13	7.49	74.21	14.00	12.77	21.63
	RO78B	6	3	47.55	9.17	16.00	35.29	48.55	29.57	---	---	---	0.98	0.27	17.00
	FR78A	5	4	12.50	1.61	16.00	37.50	31.60	24.50	---	---	---	---	---	---
		5	7	---	---	---	100.00	100.00	30.20	---	---	---	---	---	---
		5	9	30.00	15.41	17.83	30.00	26.79	19.17	---	---	---	30.00	38.96	20.50
		5	16	46.81	26.76	18.25	24.62	31.23	19.57	0.30	4.29	34.50	4.86	3.29	15.41
	FR78B	6	1	---	---	---	---	---	---	---	---	---	0.41	0.29	14.00
		7	28	54.05	30.25	18.10	32.43	45.58	22.50	---	---	---	---	---	---

Table 8. cont. Consumption of four most commonly eaten prey items for each heron species during various nesting episodes.

Species	Nesting Episode	Month	Day	Prey Species											
				Gambusia affinis			Poecilia latipinna			Lepomis punctatus			Palacmoneles paludosus		
				N	H	L	N	H	L	N	H	L	N	H	L
LA79A		4	2	33.00	10.23	20.26	27.39	33.47	27.28	10.23	8.52	36.00	1.98	1.94	21.92
		4	9	---	---	---	6.67	5.52	22.00	13.33	16.74	18.00	46.67	27.77	18.78
		4	23	20.28	9.40	16.49	2.30	8.67	29.30	23.04	41.28	17.20	---	---	---
LA79B		5	7	---	---	---	2.35	2.77	23.75	---	---	---	96.47	88.08	19.44
R079A		3	27	25.71	5.59	17.83	28.57	14.54	21.51	27.86	14.80	16.10	---	---	---
		4	3	2.33	0.22	10.50	6.98	6.67	19.50	2.33	10.64	24.00	---	---	---
		4	10	8.46	1.87	16.54	9.92	12.80	25.44	53.01	63.55	18.78	---	---	---
		4	17	16.67	3.10	21.00	33.33	44.77	34.00	---	---	---	---	---	---
		4	24	6.06	2.67	25.00	57.58	66.68	30.34	1.52	3.23	28.00	---	---	---
R079B		5	2	32.26	6.66	16.82	4.84	4.25	24.00	---	---	---	11.29	16.35	25.28
		5	8	5.26	2.02	34.50	47.37	57.77	41.56	---	---	---	36.84	18.17	28.78
AN79A		4	18	---	---	---	52.63	41.02	32.35	5.26	8.44	30.50	---	---	---
		4	26	4.17	1.24	70.00	---	---	---	---	---	---	---	---	---
AN79B		5	3	100.00	100.00	21.12	---	---	---	---	---	---	---	---	---
		5	25	33.33	78.44	36.25	---	---	---	---	---	---	---	---	---
FR79		6	28	2.44	0.32	15.25	4.88	2.66	20.50	1.22	0.14	10.00	1.22	0.60	19.50
		7	14	5.82	2.45	19.09	7.41	7.15	19.78	1.59	9.16	28.83	76.72	48.76	18.13
LA80		4	22	---	---	---	100.00	100.00	29.69	---	---	---	---	---	---
		4	28	---	---	---	---	---	---	9.09	13.61	20.00	18.18	32.47	24.75
		5	5	5.19	1.50	22.38	27.27	34.86	32.02	5.19	4.21	21.00	42.86	35.96	24.15
		5	13	7.32	1.27	20.17	2.44	32.70	73.50	7.32	5.87	22.00	63.41	22.43	20.19
		5	17	25.00	4.15	20.17	25.00	27.63	33.17	16.67	7.75	19.00	---	---	---
		5	23	25.53	6.09	16.17	8.51	7.19	22.12	27.66	39.42	19.15	---	---	---

Table 8. cont. Consumption of four most commonly eaten prey items for each heron species during various nesting episodes.

Species	Nesting Episode	Month	Day	Prey Species											
				Gambusia affinis			Poecilla latipinna			Lepomis punctatus			Palacnorneles paludosus		
				N	M	L	N	M	L	N	M	L	N	M	L
	R080	5	6	28.60	9.64	17.72	14.01	22.31	25.95	36.47	52.28	18.86	0.77	1.44	24.50
		5	13	6.92	1.46	14.39	24.62	42.74	26.72	0.77	1.31	21.00	23.08	13.84	17.92
		5	18	60.29	26.69	22.00	27.94	50.30	29.45	4.41	14.00	27.33	---	---	---
		5	23	---	---	---	---	---	---	---	---	---	65.22	69.65	27.57
		5	26	11.11	3.46	20.00	11.11	7.04	22.00	---	---	---	---	---	---
	AN81	4	22	23.48	9.05	20.34	25.76	33.12	25.29	12.12	22.88	21.44	---	---	---
		4	27	39.39	21.82	20.27	2.36	5.60	27.78	5.39	7.90	18.72	---	---	---
		5	1	12.82	3.18	13.00	---	---	---	33.33	75.35	19.00	---	---	---
		5	6	56.48	26.17	18.37	---	---	---	12.04	23.02	19.85	---	---	---
		5	11	35.11	6.87	18.27	---	---	---	18.32	44.58	25.17	---	---	---
Tri-colored Egrets	LA78	5	8	24.74	2.71	13.27	22.68	11.54	20.16	8.25	8.96	22.25	---	---	---
		5	13	10.34	1.80	20.83	37.93	37.78	31.23	24.14	8.45	21.00	3.45	2.08	25.50
		5	18	51.11	8.91	16.11	8.89	18.82	31.50	4.44	7.12	27.25	4.44	6.03	26.00
		5	19	16.67	5.86	22.50	24.07	21.08	25.73	12.96	8.56	23.00	3.70	3.83	26.50
		6	2	8.70	1.45	20.25	47.83	36.84	28.50	4.35	4.03	28.00	---	---	---
	R078A	5	21	39.78	10.80	24.24	21.51	27.20	26.38	24.73	49.39	28.93	---	---	---
	R078B	6	3	4.82	0.91	19.25	20.48	16.22	27.35	32.53	31.42	26.57	9.64	6.48	24.56
		7	8	25.00	6.02	23.00	50.00	88.29	36.38	---	---	---	---	---	---
	FR78A	5	16	61.11	19.79	16.44	1.11	1.23	22.75	21.67	26.88	21.17	---	---	---

Table 8. cont. Consumption of four most commonly eaten prey items for each heron species during various nesting episodes.

Species	Nesting Episode	Month	Day	Prey Species											
				Gambusia affinis			Poecilla latipinna			Lepomis punctatus			Palacmonetes paludosus		
				N	H	L	N	H	L	N	H	L	N	H	L
FR78B		6	1	18.97	4.12	17.18	24.14	29.64	26.64	6.90	4.14	19.00	15.52	18.01	24.22
		6	2	34.15	13.81	21.00	36.59	44.84	26.13	---	---	---	21.95	30.70	25.06
SA78		5	17	2.80	2.51	22.62	11.19	26.11	26.44	53.85	42.67	17.86	---	---	---
		5	29	5.00	1.69	24.50	7.50	5.07	25.83	64.17	69.60	27.66	4.17	2.48	24.00
LA79A		4	9	27.27	5.54	20.00	45.45	46.11	29.00	---	---	---	18.18	11.85	23.25
		4	16	16.67	3.88	23.00	33.33	20.73	27.12	---	---	---	---	---	---
		5	4	12.50	2.34	20.88	37.50	14.49	22.75	---	---	---	---	---	---
		5	7	18.75	2.34	19.83	---	---	---	25.00	17.98	26.88	---	---	---
R079A		4	3	86.79	45.57	15.82	7.55	53.50	32.12	---	---	---	---	---	---
		4	10	12.90	7.09	25.16	64.98	68.75	26.83	0.92	0.45	20.75	6.45	6.62	23.82
		4	17	61.73	19.80	16.02	29.63	72.10	27.42	---	---	---	---	---	---
		4	24	27.27	10.89	21.33	63.64	65.46	26.71	---	---	---	---	---	---
R079B		5	2	10.00	1.86	19.20	28.00	33.23	29.54	12.00	12.64	25.50	16.00	15.15	26.50
		5	8	4.65	1.44	26.75	48.84	41.43	31.17	25.58	37.68	32.73	6.98	3.05	24.33
AN79		4	18	---	---	---	---	---	---	---	---	---	85.71	84.88	22.67
		4	26	30.16	10.75	19.03	9.52	20.25	29.25	---	---	---	17.46	19.09	22.54
		5	3	12.20	3.51	21.30	---	---	---	---	---	---	60.98	63.62	25.56
		5	16	12.50	4.01	24.83	4.17	1.35	21.50	---	---	---	38.89	36.05	27.43
		5	25	8.33	3.36	33.00	25.00	21.45	34.83	---	---	---	---	---	---
FR79		6	28	31.58	7.63	19.25	5.26	0.87	16.50	10.53	6.03	22.75	---	---	---
RP79		6	1	---	---	---	80.00	71.59	34.62	---	---	---	---	---	---
		6	11	25.00	9.58	19.25	18.75	33.63	28.83	---	---	---	31.25	31.83	22.10

Table 8. cont. Consumption of four most commonly eaten prey items for each heron species during various nesting episodes.

Species	Nesting Episode	Month	Day	Prey Species											
				<i>Gambusia affinis</i>			<i>Poecilia latipinna</i>			<i>Lepomis punctatus</i>			<i>Palacmonetes paludosus</i>		
				N	M	L	N	M	L	N	M	L	N	M	L
	AN81	4	22	41.01	20.04	19.86	10.67	24.69	27.95	---	---	---	---	---	---
		4	27	24.32	3.59	19.89	8.11	37.04	52.50	---	---	---	---	---	---
		5	1	73.04	61.70	21.04	7.83	18.77	25.72	---	---	---	---	---	---
		5	6	28.83	19.48	19.11	1.80	1.70	19.25	---	---	---	---	---	---
		5	11	30.95	8.33	17.69	14.29	30.45	30.83	---	---	---	---	---	---
		5	20	11.11	2.11	17.17	---	---	---	---	---	---	---	---	---
Little Blue Heron	LA78	5	8	---	---	---	---	---	---	---	---	---	80.00	98.72	45.75
		5	19	---	---	---	---	1.58	17.50	7.41	---	---	25.93	37.11	32.14
		6	2	---	---	---	---	7.91	28.00	16.67	---	---	16.67	46.49	53.00
	RO78A	5	21	---	---	---	---	---	---	---	---	---	12.50	27.81	64.27
	RO78B	7	8	---	---	---	---	---	---	---	---	---	23.17	49.78	43.00
	LA79B	5	4	---	---	---	---	---	---	---	---	---	89.19	93.59	31.97
	FR79	6	21	---	---	---	---	---	---	---	---	---	---	---	---
		6	25	---	---	---	56.00	---	---	---	36.81	11.93	---	---	---
		6	28	---	---	---	3.70	---	---	---	0.34	15.67	---	---	---
		7	14	---	---	---	---	0.61	32.50	0.52	---	---	5.24	20.35	49.65
	HH79	6	11	6.67	0.14	16.00	---	5.24	27.00	13.33	---	---	33.33	53.96	41.00
		6	26	---	---	---	---	---	---	---	---	---	87.50	94.73	41.86
	RP79	5	29	---	---	---	---	---	---	---	---	---	61.82	33.93	35.20
		6	1	---	---	---	---	---	---	---	---	---	73.68	97.11	36.82
		6	6	---	---	---	---	---	---	---	---	---	55.56	45.77	43.40
		6	11	---	---	---	---	---	---	---	---	---	46.15	52.42	42.50

Table 8. cont. Consumption of four most commonly eaten prey items for each heron species during various nesting episodes.

Species	Nesting Episode	Month	Day	Prey Species											
				Gambusia affinis			Poecilla latipinna			Lepomis punctatus			Palacmonetes paludosus		
				N	H	L	N	H	L	N	H	L	N	H	L
	LA80	5	13	---	---	---	---	4.28	21.25	44.44	---	---	---	---	---
	NH80	5	21	---	---	---	12.00	6.17	40.25	14.00	0.56	16.08	2.00	7.75	47.00
	AN81	5	6	3.15	0.27	12.88	11.02	64.02	19.79	56.69	1.57	15.18	---	---	---
		5	11	23.90	3.90	12.08	38.38	37.78	18.58	20.61	13.84	16.49	---	---	---
		5	15	36.45	6.22	12.88	17.29	33.08	17.67	25.70	4.22	14.76	---	---	---
		5	20	53.24	13.88	12.43	13.99	16.00	17.53	6.48	8.97	16.41	---	---	---

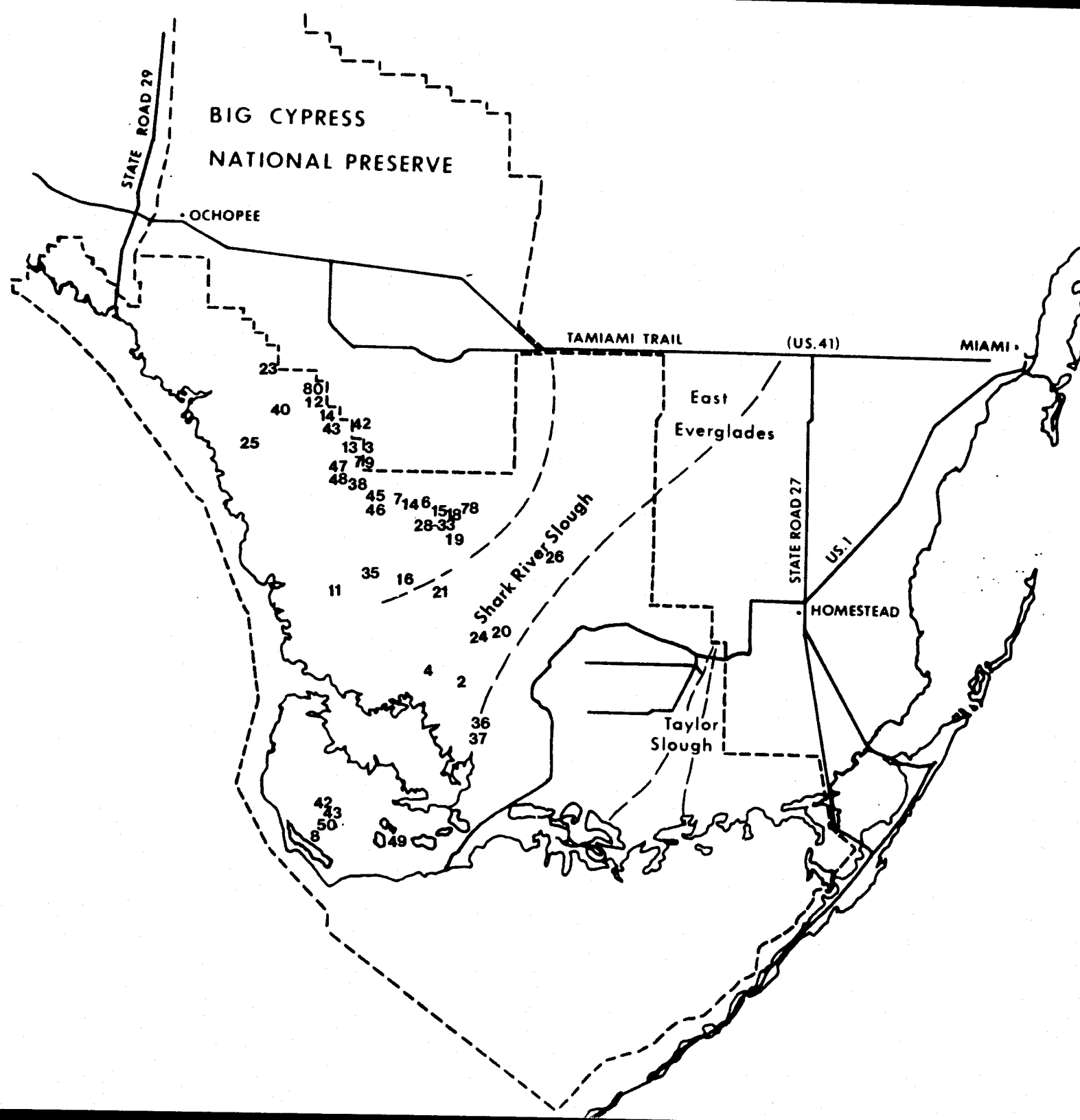
HERON FEEDING SITES.-- Food availability was determined at 53 feeding sites used by herons in the coastal and inland habitats of southern Florida (Figures 7 and 8). These sites were those most heavily used by birds during the sampling period. Herons take a wide variety of prey, perhaps on occasion everything that is available in the Everglades, thus food available consists of all edible items, including fish, amphibians, and invertebrates. It is also useful to evaluate availability in terms of those prey frequently taken. Both approaches will be used.

As noted above, much of the diet of herons can be understood through the several prey items that comprise most of their diet. Table 9 shows 12 of the most commonly taken prey items. Nearly 60% of the food items available are composed of three species and nearly 61 of the biomass available is composed of 6 species. Eight of these 12 species account for the four most important species in the diets of the four species of herons. The availability of these species at each feeding site is shown in Table 10. An important point to note is that the standing crop samples were completely dominated by the mosquitofish, which made it difficult to discern patterns.

Aspects of food availability we studied included biomass per m³, number of food items per m², and the mean length of food items (Tables 11, 12). We explored the relationship among these variables using factor analyses. Two factors accounted for 74% of the variability among feeding sites (Table 13). Factor 1 accounted for 46% of the variability, and was comprised principally

of biomass, with high co-correlated loadings by both numbers and length, and a negative correlation with water depth (see also beyond). The second factor accounted for an additional 28%. Thus it appears that biomass is a primary predictor of food availability, and is probably the most critical aspect of food and feeding site use. Food available differed among locations, ranging from 2.9 to 2600, g/m³ (Table 12). The relationships among food availability, hydrology, and heron nesting success are explored in subsequent sections.

Figure 7. Feeding sites in the southern Everglades where food availability samples were collected.



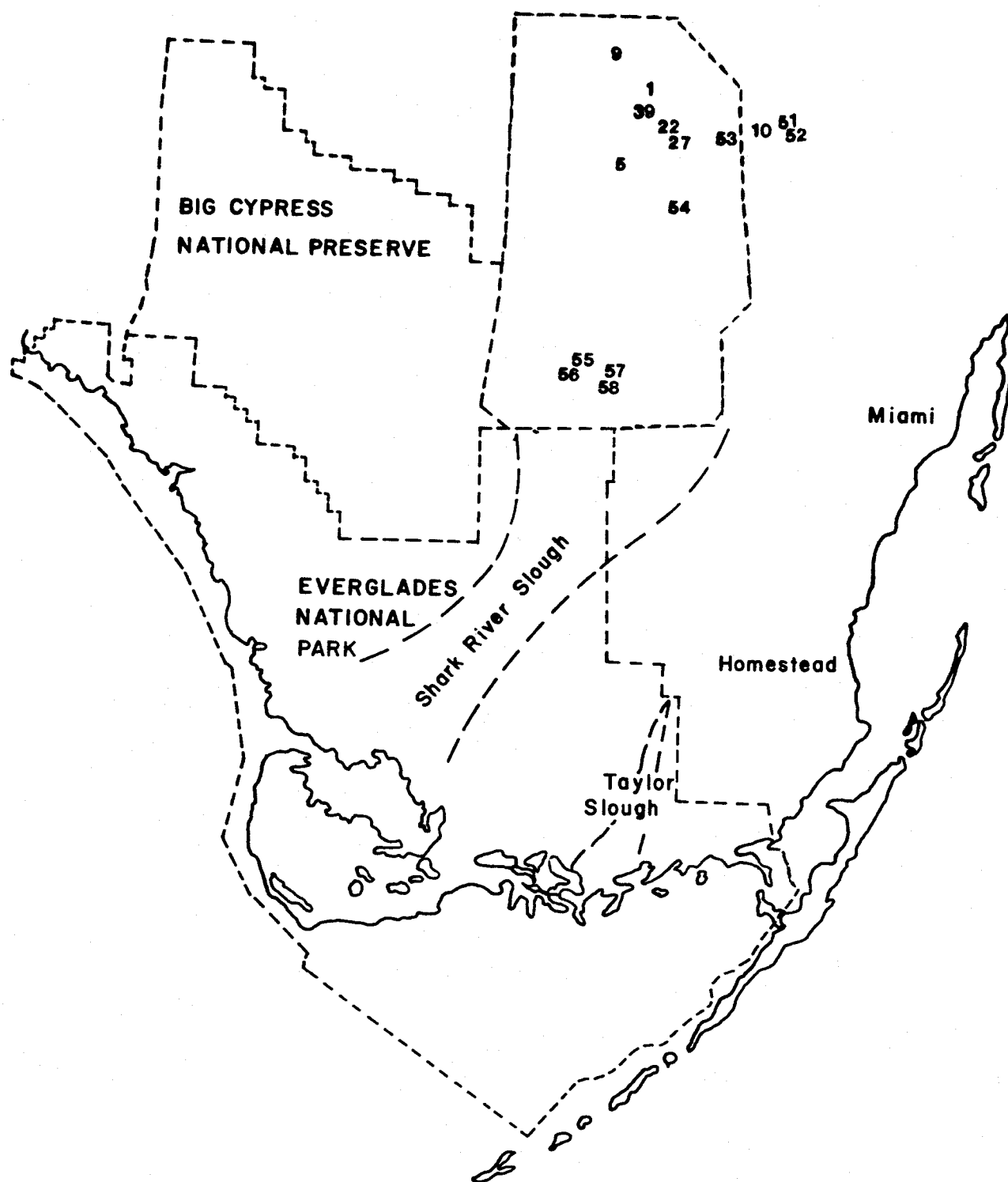


Figure 8. Feeding sites in the northern Everglades where food availability samples were collected.

Table 9. List of prey species available among standing crop sites expressed as percent (at least 1% of total number (N), percent total weight (W) and mean prey length in mm (L). Importance (+) marks those species which are in the group of four highest percent total number for each heron.

Code	Prey Species	N	W	L	GE	SE	TH	LB
1	<i>Gambusia affinis</i>	29.00	8.01	16.79	+	+	+	+
22	<i>Palaemonetes paludosus</i>	17.00	2.27	18.19	+	+		+
6	<i>Heterandria formosa</i>	13.00	1.57	12.70				+
3	<i>Cyprinodon variegatus</i>	9.00	6.22	16.35		+	+	
5	<i>Jordanella floridae</i>	9.00	8.92	20.98			+	
2	<i>Poecilia latipinna</i>	6.00	9.07	24.93	+	+	+	
4	<i>Fundulus confluentus</i>	6.00	12.85	32.36				
7	<i>Lucania goodei</i>	4.00	1.47	18.80				
8	<i>Fundulus chrysotus</i>	3.00	3.43	24.82				
21	<i>Procambarus alleni</i>	1.00	8.32	33.61			+	
41	<i>Lepomis punctatus</i>	1.00	12.73	43.69	+			
47	<i>Brevoortia patronus</i>	1.00	2.58	31.27				
TOTAL		24998	9407.447g.					

Sampling time for each location - duplicate

Tables 10. Relative percent number (N) and mass (M) of the total array prey species representing all of the herons four most commonly eaten prey items for each location.

Location ¹	Prey Species															
	1		2		3		5		6		21		22		41	
	N	M	N	M	N	M	N	M	N	M	N	M	N	M	N	M
1	15.20	10.10	0.00	0.00	0.00	0.00	2.40	4.17	54.40	15.95	20.00	60.39	1.60	0.51	4.80	6.53
2	40.00	14.48	4.44	17.57	33.33	39.34	4.44	17.05	0.00	0.00	0.00	0.00	15.56	10.87	0.00	0.00
3	41.46	18.70	4.88	0.00	0.00	0.00	7.32	15.74	9.76	2.72	9.76	38.77	17.07	7.11	0.00	0.00
4	61.64	35.47	0.00	0.00	13.70	32.64	9.59	13.55	4.11	0.90	0.00	0.00	4.11	2.57	0.00	0.00
5	47.01	36.08	9.60	37.32	0.00	0.00	6.96	14.34	34.59	9.07	0.00	0.00	0.56	0.41	0.00	0.00
6	15.05	3.97	14.13	18.52	29.17	33.59	19.63	13.27	0.55	0.06	2.75	5.08	0.00	0.00	0.00	0.00
7	41.18	9.45	7.62	5.33	3.07	4.73	7.22	9.08	1.87	0.31	0.13	0.26	0.07	0.01	0.00	0.00
8	0.00	0.00	0.00	0.00	99.62	99.87	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
9	48.21	31.35	9.17	4.80	0.00	0.00	7.69	26.35	21.22	6.29	0.00	0.00	0.35	0.24	0.09	0.06
10	30.56	7.33	9.17	0.00	0.00	0.00	19.44	2.14	8.33	0.72	13.89	57.44	8.33	3.61	0.00	0.00
11	54.42	6.55	0.68	0.15	14.97	16.54	8.16	0.69	0.00	0.00	4.76	15.52	4.76	1.63	0.00	0.00
12	32.88	6.73	12.33	25.71	13.70	6.97	10.96	12.83	6.85	0.64	2.74	7.65	4.11	1.20	0.00	0.00
13	17.99	4.38	0.00	0.00	0.00	0.00	2.12	1.80	8.99	1.33	13.23	55.30	50.26	22.02	0.00	0.00
14	11.30	3.94	11.86	32.55	0.56	2.36	9.04	17.44	16.95	2.57	2.26	8.73	42.94	17.37	0.00	0.00
15	14.37	2.84	6.87	11.89	1.25	6.16	14.37	31.24	8.75	0.74	10.00	29.56	33.75	11.91	0.00	0.00
16	13.48	4.70	21.35	30.00	2.25	2.57	5.62	7.71	7.87	1.56	3.93	7.51	24.72	3.91	0.00	0.00
17	17.39	2.00	0.00	0.00	0.00	0.00	60.87	53.36	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
18	26.83	9.55	10.37	23.81	2.21	3.54	9.13	17.22	9.47	2.09	0.62	1.77	23.72	3.20	0.07	0.19
19	18.64	6.00	15.78	52.04	0.13	0.51	9.71	15.32	11.15	1.92	0.00	0.00	35.14	3.26	0.78	2.04
20	22.40	10.93	5.35	23.11	0.00	0.00	8.56	21.73	10.07	2.97	0.06	1.79	38.33	8.17	0.69	4.55
21	41.76	30.24	5.87	22.62	0.00	0.00	2.23	11.98	4.33	1.25	0.28	8.01	37.85	11.94	0.14	1.43

Tables 10. cont. Relative percent number (N) and mass (H) of the total array prey species representing all of the herons four most commonly eaten prey items for each location.

Location	Prey Species															
	1		2		3		5		6		21		22		41	
	N	H	N	H	N	H	N	H	N	H	N	H	N	H	N	H
22	1.80	0.10	1.80	1.71	0.00	0.00	8.98	2.77	23.95	0.83	1.20	2.27	0.00	0.00	0.00	0.00
23	26.56	8.98	12.50	18.05	0.00	0.00	24.22	9.21	7.81	2.54	5.47	38.01	7.81	3.62	0.00	0.00
24	12.57	6.37	2.99	4.49	0.00	0.00	2.99	6.35	14.37	2.70	3.59	56.99	47.31	10.11	0.00	0.00
25	0.11	0.08	1.21	1.06	98.24	98.65	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
26	35.66	9.10	14.34	7.27	0.00	0.00	1.64	3.13	16.80	7.87	0.41	33.67	21.31	15.03	0.00	0.00
27	49.81	20.73	6.95	6.29	0.00	0.00	6.18	15.07	10.42	4.88	1.16	35.81	16.60	8.09	0.39	3.43
28	13.58	0.44	18.52	8.03	0.00	0.00	6.17	1.66	4.94	0.13	30.86	84.81	1.23	0.08	0.00	0.00
29	16.09	0.53	8.05	2.77	0.00	0.00	14.94	4.63	3.45	0.07	34.48	89.66	0.00	0.00	0.00	0.00
30	34.62	2.53	0.00	0.00	0.00	0.00	15.38	3.06	0.00	0.00	32.69	91.23	5.77	0.63	0.00	0.00
31	29.41	2.52	0.00	0.00	0.00	0.00	5.88	0.77	8.82	0.20	32.35	87.83	0.00	0.00	2.94	0.42
32	48.89	6.79	2.22	0.50	0.00	0.00	2.22	0.65	6.67	0.35	22.22	76.35	0.00	0.00	0.00	0.00
33	67.74	40.17	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	29.03	15.10	0.00	0.00
35	27.47	6.87	11.93	13.73	42.54	42.70	0.94	0.86	1.10	0.10	0.00	0.00	0.31	0.04	0.00	0.00
36	35.19	7.79	0.93	0.54	20.37	34.97	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
37	48.96	23.09	1.96	2.23	1.64	1.75	3.27	5.24	13.52	2.04	0.22	2.53	19.52	4.03	4.14	18.51
38	17.27	6.84	2.22	1.70	16.01	18.77	2.38	2.81	5.55	0.73	0.00	0.00	31.22	10.50	0.00	0.00
39	29.55	6.00	6.44	4.65	0.00	0.00	14.39	21.64	17.42	3.49	5.30	50.90	24.24	10.25	0.00	0.00
40	22.12	4.96	1.92	1.79	6.73	8.83	16.35	13.33	0.96	0.04	0.00	0.00	1.92	0.27	0.00	0.00
41	54.65	30.98	2.47	8.02	1.91	4.90	7.40	15.98	15.12	5.50	0.00	0.00	9.31	2.06	0.00	0.00
42	10.92	3.04	2.87	2.17	51.15	18.81	16.67	34.57	1.72	0.38	0.00	0.00	0.57	0.03	0.00	0.00
43	7.96	2.13	1.77	2.29	1.18	2.29	24.48	21.40	19.17	4.09	0.00	0.00	0.00	0.00	0.00	0.00

Tables 10. cont. Relative percent number (N) and mass (M) of the total array prey species representing all of the herons four most commonly eaten prey items for each location.

Location ¹	Prey Species															
	1		2		3		5		6		21		22		41	
	N	M	N	M	N	M	N	M	N	M	N	M	N	M	N	M
45	15.00	12.21	2.50	6.90	0.00	0.00	20.00	41.93	3.75	0.80	0.00	0.00	55.00	25.92	0.00	0.00
46	10.85	2.07	1.55	0.63	10.85	20.19	34.88	27.80	3.88	0.38	0.00	0.00	10.08	1.51	0.78	4.39
47	2.03	0.55	0.58	3.21	2.91	0.65	47.67	41.40	12.21	2.21	0.00	0.00	0.58	0.06	0.00	0.00
48	6.11	2.06	4.63	4.98	1.87	0.79	51.43	51.75	8.57	1.35	0.00	0.00	0.49	0.06	0.00	0.00
49	0.00	0.00	0.00	0.00	98.59	61.81	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
50	0.00	0.00	1.14	7.65	97.73	75.06	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
51	12.59	1.03	0.00	0.00	0.00	0.00	0.00	0.00	0.68	0.01	0.00	0.00	1.02	0.01	26.19	42.60
52	28.57	6.38	0.00	0.00	0.00	0.00	0.00	0.00	19.05	6.47	0.00	0.00	0.00	0.00	0.00	0.00
53	13.64	0.03	0.00	0.00	0.00	0.00	0.00	0.00	1.52	0.01	0.00	0.00	1.52	0.01	6.06	45.41
54	37.25	1.94	0.22	0.15	0.00	0.00	0.00	0.00	8.20	0.24	0.22	0.41	44.57	1.53	1.33	15.51
55	50.43	36.12	5.34	18.59	0.00	0.00	0.00	0.00	7.26	2.12	0.00	0.00	20.94	4.27	0.00	0.00
56	40.33	3.39	0.00	0.00	0.00	0.00	0.00	0.00	14.73	0.64	0.00	0.00	15.27	0.62	2.97	47.70
57	17.85	23.44	0.00	0.00	0.00	0.00	0.00	0.00	32.65	21.98	0.00	0.00	40.80	25.85	0.00	0.00
58	17.66	26.21	0.00	0.00	0.00	0.00	0.00	0.00	12.28	10.88	0.00	0.00	58.38	23.01	0.00	0.00
78	15.79	1.99	2.63	7.48	0.00	0.00	2.63	6.28	30.26	2.88	19.74	53.07	14.47	4.08	1.32	1.03
79	19.40	4.78	4.48	13.69	1.49	2.16	17.91	1.86	17.91	1.86	8.96	38.57	23.88	10.78	0.00	0.00
80	9.80	8.92	6.92	39.22	1.15	7.87	2.02	9.39	6.92	2.99	0.00	0.00	65.42	14.22	0.00	0.00

1

See Figure 8 for locations.

Table 11. Mean mass (M) and mean length (L) of each day sample over total number (N) of prey items collected by herons.

Heron Species	Nesting Episode	Month	Day	M	L	N
Great Egret	LA78A	5	8	.12	30.84	46
		5	13	.13	30.94	16
	R078A	5	2	.17	49.25	8
		5	10	.22	47.76	47
		5	14	.21	41.85	60
		5	21	.10	28.80	289
	FR78A	5	4	.04	21.92	85
		5	9	.05	19.89	144
		5	16	.07	23.99	80
	FR78B	6	1	.93	54.97	16
		6	13	.03	19.60	189
		7	14	.70	58.55	50
		7	20	1.20	65.24	23
	LA79A	3	15	.26	34.03	70
		4	2	.29	35.55	91
		4	9	.19	33.52	151
		4	23	1.13	61.35	23
	LA79B	5	7	.31	36.51	50
	R079A	4	3	.18	30.99	152
		4	10	.27	36.86	112
		4	17	.40	39.61	19
		4	24	.47	37.65	17
	AN79A	4	11	.15	31.67	135
		4	18	.89	50.25	10
		4	26	.54	34.04	36
	AN79B	5	3	.28	36.63	8
	LA80	4	28	.14	35.75	6
	R080	4	24	.09	26.15	131
		4	29	.17	28.38	198
		5	6	.09	32.98	62
		5	18	.12	24.01	100
	AN81	5	23	.09	65.92	12
		4	13	1.75	77.92	6
		4	17	.29	35.34	34
		4	27	.36	42.69	8
		5	1	.98	69.47	12
		5	6	1.06	59.19	24
		5	11	.07	24.15	160
Snowy Egret	LA78	5	8	.02	18.52	47
		5	13	.03	19.86	223
		5	18	.07	25.34	38
		5	19	.05	21.03	207
	FR78A	5	4	.06	27.88	8
		5	7	.08	30.20	5
		5	9	.02	19.50	10
		5	16	.02	18.85	329
	FR78B	6	1	.01	16.48	242
		7	28	.02	18.93	37

Table 11 cont. Mean mass (M) and mean length (L) of each day sample over total number (N) of prey items collected by herons.

Heron Species	Nesting Episode	Month	Day	M	L	N
Snowy Egret	LA79A	4	2	.06	24.33	303
		4	9	.04	22.37	15
		4	23	.02	16.52	217
		5	7	.03	19.89	85
	R079A	3	27	.06	21.48	140
		4	3	.02	18.24	43
		4	10	.04	19.79	615
		4	17	.09	31.58	6
	R079B	4	24	.08	28.57	66
		5	2	.04	22.56	62
		5	8	.20	38.18	19
	AN79A	4	18	.13	31.87	19
		4	26	.05	23.44	24
	AN79B	5	3	.02	21.13	8
		5	25	.04	24.08	6
	FR79	6	28	.05	18.70	82
		7	14	.03	18.94	189
	LA80	4	22	.08	29.69	8
		4	28	.04	20.23	11
		5	5	.08	27.82	77
		5	13	.10	24.46	41
		5	17	.10	30.54	12
	R080	5	23	.04	20.63	47
		5	6	.03	19.50	521
		5	13	.04	18.97	130
		5	18	.05	24.54	68
		5	23	.08	27.13	23
	AN81	5	26	.05	22.11	9
		4	22	.04	23.09	132
		4	27	.03	21.79	297
		5	1	.02	14.45	39
		5	6	.03	20.35	108
		5	11	.06	23.05	131
		5	20	.03	20.93	30
		5	8	.05	21.48	97
Tricolored Heron	LA78A	5	13	.10	29.28	29
		5	18	.05	22.72	45
		5	19	.07	26.77	54
		6	2	.19	29.85	23
	R078A	5	21	.06	24.24	93
	R078B	6	3	.08	29.63	83
		7	12	.09	30.56	8
	FR78B	5	16	.03	19.72	180
		6	1	.05	22.74	58
		6	2	.04	24.52	41
	SA78	5	17	.03	20.83	143
		5	29	.09	26.75	120

Table 11 cont. Mean mass (M) and mean length (L) of each day sample over total number (N) of prey items collected by herons.

Heron Species	Nesting Episode	Month	Day	M	L	N
Tricolored Heron	LA79A	4	9	.07	27.45	11
		4	16	.10	31.58	12
	LA79B	5	4	.09	28.77	32
		5	7	.11	24.88	16
	R079A	4	3	.01	16.76	53
		4	10	.06	26.71	217
		4	17	.03	19.64	81
		4	24	.07	27.00	11
	R079B	5	2	.07	28.46	50
		5	8	.12	30.24	43
	AN79A	4	18	.05	23.00	7
		4	26	.04	22.21	63
	AN79B	5	3	.07	26.10	41
		5	16	.09	28.60	72
		5	25	.06	40.63	12
	FR79	6	28	.07	23.21	19
	RP79	6	1	.17	37.30	5
		6	11	.04	23.09	16
	LA80	4	28	.04	21.35	26
		5	5	.04	22.99	46
		5	6	.02	19.94	9
		5	13	.05	25.89	194
		5	17	.05	24.86	49
		5	22	.05	24.14	59
	R080	4	29	.07	25.17	18
		5	6	.04	25.50	44
		5	18	.02	18.56	90
		5	29	.09	21.96	14
	AN80	5	7	.04	21.38	29
		5	14	.05	21.96	45
		5	19	.08	28.56	44
		5	24	.08	28.10	48
	HH80	5	21	.13	31.78	29
		5	23	.13	35.35	17
		5	27	.13	35.16	25
		6	2	.08	27.97	20
	AN81	4	17	.02	18.58	17
		4	22	.03	20.55	178
		4	27	.10	27.00	37
		5	1	.02	21.28	115
		5	6	.02	20.15	111
		5	11	.05	22.68	84
Little Blue Heron	LA78A	5	20	.05	27.77	27
		5	8	.61	42.60	5
		5	19	.16	36.89	27
		6	2	.34	39.00	6
		5	21	.41	54.17	48
		7	8	.28	47.44	82

Table 11 cont. Mean mass (M) and mean length (L) of each day sample over total number (N) of prey items collected by herons.

Heron Species	Nesting Episode	Month	Day	M	L	N
Little Blue Heron	R078A	5	4	.22	30.38	37
	FR79	6	21	.10	19.23	77
		6	25	.01	13.86	50
		6	28	.10	21.77	81
		7	14	.23	27.28	191
	NH79	6	11	.41	32.97	15
		6	18	1.26	44.38	4
		6	26	.52	43.13	8
	RP79	5	29	.61	40.02	55
		6	1	.27	31.47	19
		6	6	.71	40.50	9
		6	11	.55	55.15	13
	LA80	5	5	.45	34.60	4
		5	13	.69	44.06	9
	NH80	5	21	.17	30.54	50
	AN81	5	6	.05	20.71	127
		5	11	.02	17.09	456
		5	15	.03	15.42	428
		5	20	.02	16.13	293

Table 12. Mean depth, mass/m 3, number of prey/m 2 for each location sampled during nesting at Lane River, Rodgers River and Andytown colonies.

	Local	Year	Month	Depth	Prey mass	Prey count
Rodgers River	36	78	10	29.25	1347.20	540.50
Lane River	2	78	3	18.57	2.88	3.21
	4	78	4	19.00	6.13	6.08
	8	78	5	9.67	56.03	21.67
	20	79	4	15.00	192.95	144.45
	24	79	5	26.80	16.66	16.70
	26	79	6	36.50	6.69	30.50
	36	80	3	7.00	271.92	2.70
	37	80	3	10.00	219.14	57.31
	41	80	4	12.00	104.54	78.56
	42	80	5	15.00	32.32	10.88
	49	81	3	12.00	15.09	5.32
	50	81	3	10.00	8.76	29.33
Rodgers River	3	78	3	22.75	5.81	5.13
	6	78	4	13.75	201.50	45.42
	7	78	5	8.38	1347.20	187.00
	11	78	6	17.91	27.10	13.36
	17	79	2	14.50	30.49	11.50
	21	79	4	16.17	108.35	119.33
	23	79	5	18.00	21.89	12.80
	25	79	6	9.00	42.31	90.80
	35	80	3	8.00	243.78	39.81
	38	80	3	8.00	192.02	39.44
	40	80	4	8.00	37.77	3.25
	43	80	5	3.00	295.26	21.19
	45	81	2	24.00	10.58	2.00
	46	81	2	16.00	97.99	3.22
	47	81	2	12.00	185.20	8.60
	48	81	2	12.00	502.27	25.38
Andytown	1	78	3	27.65	9.14	7.35
	5	78	4	16.00	322.95	354.17
	9	78	5	11.00	279.66	190.83
	10	78	6	31.30	3.07	3.60
	22	79	5	15.25	194.45	20.88
	27	79	6	17.90	19.86	25.90
	39	80	4	21.71	79.07	37.71
	51	81	4	17.80	1011.99	58.80
	52	81	4	11.00	16.92	14.67
	53	81	4	13.50	576.97	11.17
	54	81	5	13.50	2613.42	225.50
	55	81	5	0.00	0.00	234.00
	56	81	5	17.00	1664.72	303.33
	57	81	5	17.50	114.35	540.50
	58	81	5	17.20	35.68	104.20
	78	78	10	39.00	18.71	19.00
	79	78	11	29.25	13.59	16.75
	15	79	1	17.88	32.46	20.00
	16	79	1	15.88	35.54	22.25
Lane and Rodgers Rivers	18	79	3	9.38	406.49	180.75
	19	79	3	13.50	329.74	153.40
	33	80	3	23.25	9.87	8.25
	34	80	3	5.33	0.00	1.00

52 sites

only 5 samples
of same period
the breeding
season.

Table 13. Factor analysis of parameters of food availability

Variable	Loadings	
	Factor 1	Factor 2
mean mass/ m ³	0.921	
mean prey length	0.700	0.618
mean number of prey	0.593	-0.530
mean water depth	-0.374	0.668
cum % explained	45.7	74.0

characteristically feed by wading through shallow water (Kushlan 1978), and foraging opportunities for various species can be limited and determined by water depth (Kushlan 1976a, 1981b, Kushlan et al. 1985). Herons can to some extent compensate for deep water behaviorally, by using feeding behaviors such as diving or plunging, or by perching on top of floating vegetation, such as water lilies or floating bladderwort. Aerial foraging is inefficient, and is used only under particular conditions of high availability of food on top of the water. Lilies are not sufficiently abundant to be used often by large number of birds, although bladderwort is abundant and can to some extent support the weight of the smaller herons. When a heron stands on bladderwort and its attached periphyton, the mass sinks but not necessarily to the bottom, allowing foraging in some water depths that would not otherwise be available. Such foraging is not particularly effective, as most of the prey remain below the periphyton mat and are unavailable to and unseen by the heron. Therefore in most instances it is reasonable to expect depth limits to prevail during the normal wading-foraging of herons.

Some aspects of the limits to foraging depth can be appreciated by evaluating the leg-lengths of the species. The unfeathered portion of the legs of herons from southern Florida are 23 cm long in the Great Egret (23.3, sd=2.07, n=13), 15 cm long in the Snowy Egret (15.3, sd=2.19, n=7), and 16 cm long in the Tricolored Heron and for the Little Blue Heron (15.9, sd=2.32, n=8, and 15.6, sd=1.02, n=9). Herons can forage deeper if willing to get their feathers wet. Although the actual morphological limits are difficult to determine, because of the difficulty of

measuring the belly height of standing birds, maximum wading depths would be about $1/3$ again deeper than the length of the unfeathered legs, or about 30 cm for the Great Egret and about 20 cm for the smaller herons. There is no anatomical restriction on minimum foraging depth as each species can feed on dry land, if food were available (Kushlan 1978a).

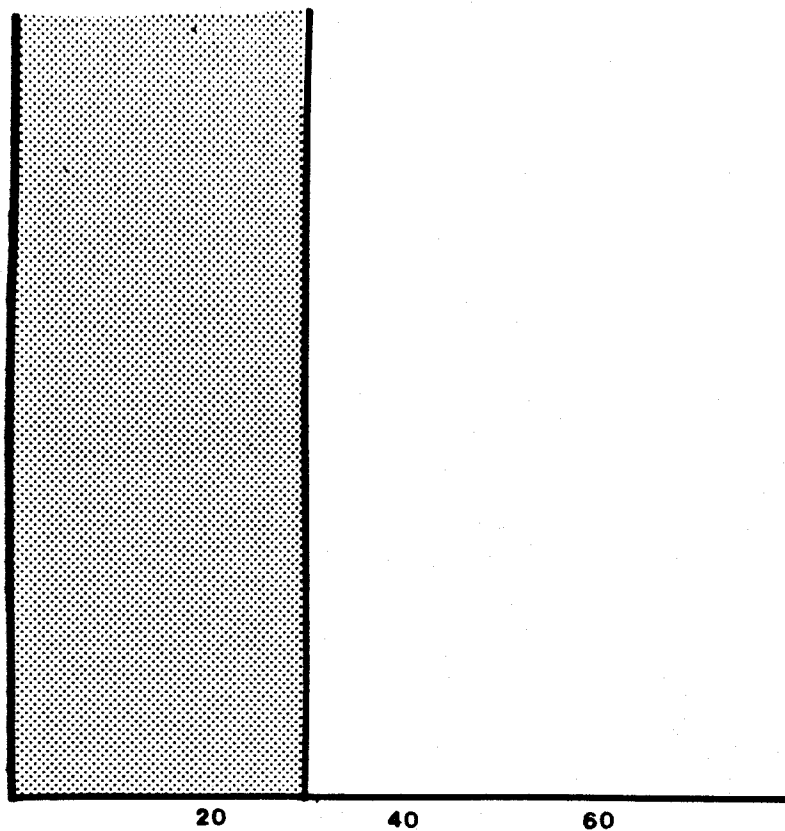
Water depths at sites chosen by aggregations of herons outside of the nesting season averaged about 23 cm deep (22.9, $sd=4.28$, $n=13$), about the same as the unfeathered leg length of Great Egrets. Maximum depths used can be greater. The average depth of sites used by individual herons feeding in the flooded Everglades marsh, also outside the nesting season, was 4-6 cm deeper. Great Egrets fed at depths of nearly 30 cm (29.5, $sd=7.63$, $n=74$), whereas Tricolored and Little Blue herons fed in about 27 cm (27.5, $sd=19.97$, $n=46$, and 26.9, $sd=7.46$, $n=34$). These foraging depths necessarily exceeded the unfeathered leg length. Such foraging is not uncommon for Tricolored and Little Blue herons. The deepest sites were used by taking advantage of the support offered by the bladderwort-periphyton mat.

From these data we can infer that the preferred and maximum foraging depths used by Great Egrets are about 23 cm and 30 cm, whereas the preferred and maximum depths used by the smaller species are 16 cm and 27 cm. For purposes of generalization, we can set the acceptable foraging depth for all species at below 30 cm, given that deeper depths can be used, albeit inefficiently, through behavioral choices or by perching on floating vegetation. This can be modeled as in Figure 9 A, the shaded area indicating the zone available for heron foraging.

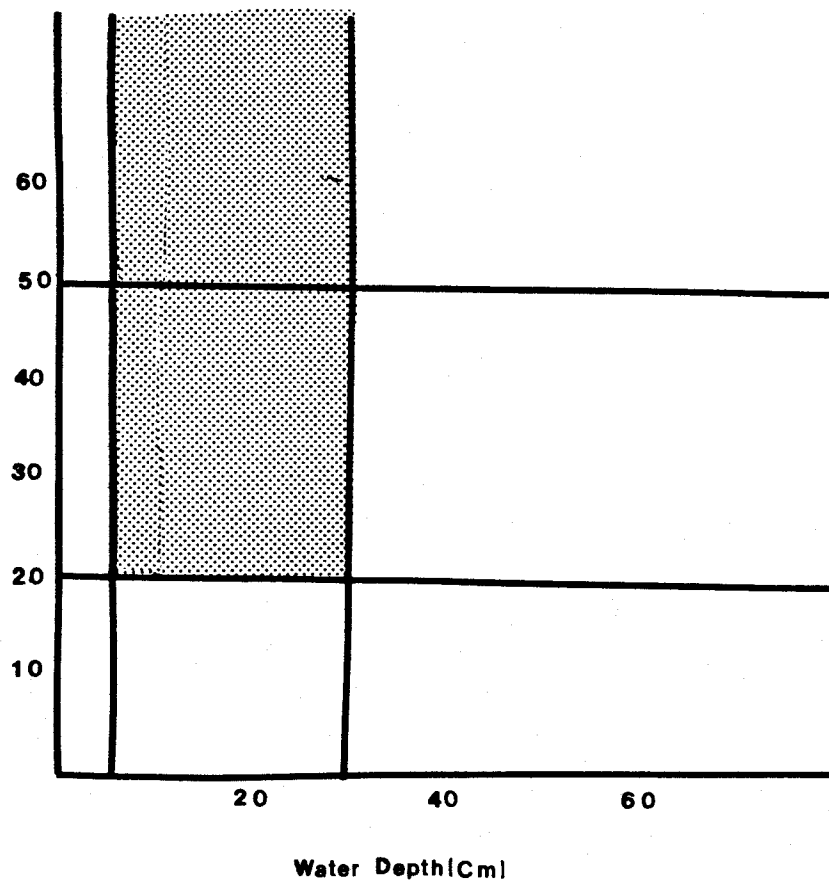
data
??

Figure 9. Water depth preferences of foraging herons.
Top-A. Herons can feed by wading only at water depths less than 30 cm. Bottom-B. Heron foraging depth is also limited by prey availability below 5 cm water depth and at less than 20 g/m³ of prey available. Maintenance levels of prey availability (20-50 g) are shown.

Prey Density



Prey Density



An important aspect of heron use of the Everglades is the seasonality of its use. Information on water depth limits suggests one reason why this is so. The water depths in the Everglades marsh during the wet (nonbreeding, October-February) season exceed that preferred by herons. Data are available from three sites, on each in the lower (Rookery Branch), middle (Panther Mound) and upper (Cottonmouth) parts of the Shark Slough. At the site near the mangroves (where herons do feed in the dry season) nonbreeding season water depths averaged 35 cm (34.8, $sd=9.10$, $n=24$, 1977-1982); in the site near the midpoint of the slough, also used by herons in the dry season, the average nonseason water depth was 43 cm (43.3, $sd=9.41$, $n=24$, 1977-1982); in the upper slough water depths far exceeded potential foraging depth being nearly 50 cm deep (49.0, $sd=83$, $n=24$, 1977-1982). Birds were seldom observed feeding at this site in any numbers throughout the study period. These higher depths, which were in part caused by the input of discharge of surface water into the upper slough immediately to the north. Thus it is clear that, irrespective of food abundance, wet season water levels in the Everglades marsh exceeded those preferred and used by most heron aggregations, and the existence of such water depths precludes the use of the core Everglades marsh as foraging habitat outside the dry season.

FOOD LIMITS.-- It is reasonable to expect that food abundance could also limit foraging site selection. The best estimate of the levels of food required to support extensive feeding is that found at sites where mixed species aggregations occurred outside the nesting season. We found that the prey density at such sites (October through February) was about 35 g/m³ (35.3, sd=23.88, range 18.7 - 107.1, n=13). The choice of such sites indicates the level of food sufficient to support nonnesting maintenance of the herons. Only one of these sites exceeded 100 g /m³, the next highest being 50 g/m³. The use of such a site reflects the fact that herons do not overlook relatively higher densities, should they come available in the nonnesting season. In general, prey abundances on the order of 20 - 50 g/m³ are used during the nonnesting maintenance period of the year.

We also found that prey availabilities at potential feeding sites in the Everglades marsh itself are below maintenance levels during high water periods (9.8 g/m³, sd=9.65, n=24 for the mid slough, and 10.4 g/m³ for the upper slough). Such patterns of food abundance suggest further why herons do not feed in the Everglades in large numbers in the wet season. Interestingly prey densities in the lower slough are not as far below maintenance levels (17.0 g/m³, sd =12.02, n=24), suggesting water depth is the principal inhibitor of foraging in this area in the wet season. In fact herons do feed along the edges of the Everglades in otherwise high water periods, especially along the Stairsteps on the Gulf Coast and in similar locations along the south and southeastern coasts.

Thus the interaction of water depth and food availability

appears to determine foraging sites used by herons. This can be⁷¹
seen by examining, overall, the sites actually chosen by herons
outside of and during nesting (Table 14). Outside the nesting
season, sites used by herons along the coast were shallower and
had higher levels of food available than in the inland marshes
that were available (these near the Stairstep area). Herons
appear to be able to forage sufficiently to maintain themselves at
prey densities of 20 - 50 g/m³ at water depths of less than 30
cm, and preferably near 15 cm deep.

Table 14. Food availability at feeding sites used by herons outside of and during the nesting season.

Time and location	g/ m 3	water depth (cm)	N
Outside nesting season			
Inland	35.3	23.5	13
Coastal	199.0	16.0	4
During nesting season			
Inland	355.2	11.3	27
Coastal	99.1	16.93	16

why?

60 sites
but only have
54 listed
means some
were sample
twice

FOOD AVAILABILITY IN THE NESTING SEASON.-- As can be noted in Table 14, food availability at foraging sites used prior to the nesting season along the coast and during nesting inland ^{or day out} appear to exceed the levels required for maintenance, suggesting that higher food levels are used and probably required for successful nesting.

So why is coastal food so high "outside" nesting season?

Patterns of prey available at foraging sites chosen during various nesting episodes are shown in Table 15 and Figure 10. Food available ranged on average from about 10 to about 860 g/m³, clearly indicating that differences occurred among nesting episodes. These differences are demonstrated in the cluster analysis of Figure 10. Food available during five nesting episodes did not exceed that required for maintenance alone, and two did not even approach maintenance levels. A second cluster of availabilities exceed 220 g/ m³, whereas a third cluster is intermediate, having food availabilities of 100-200 g/ m³. It is hypothesized that these divergent food availabilities might be related to differing nesting success, as is discussed below in the section on Mortality.

Table 15. Food available at foraging sites used by herons during several nesting episodes, and the mortality class for each species of herons.

Episode	Food density			GE	Mortality ¹			LB
	(g/ m ³) x	sd			SE	TH		
LA79B	11.7	7.05	2	-	3	3	-	
LA81	11.9	4.48	2	-	-	-	-	
RO78B	22.1	-	1	-	2	1	1	
RO79B	32.1	14.44	2	-	-	1	-	
LA78	21.7	29.79	3	3	2	1	2	
AN80	79.1	79.07	1	-	-	3	-	
LA80	157.0	108.57	4	3	3	3	-	
AN78	153.7	171.37	4	-	-	-	-	
RO80	129.8	129.57	6	2	3	3	-	
AN79B	107.2	123.45	2	3	1	2	-	
LA79A	192.9	-	1	1	1	2	-	
RO79A	281.5	154.81	3	1	1	2	-	
RO78A	518.2	724.60	3	1	1	1	2	
AN81	862.0	980.76	7	1	1	1	1	

¹ See Mortality section for explanation, - = no nesting attempted.

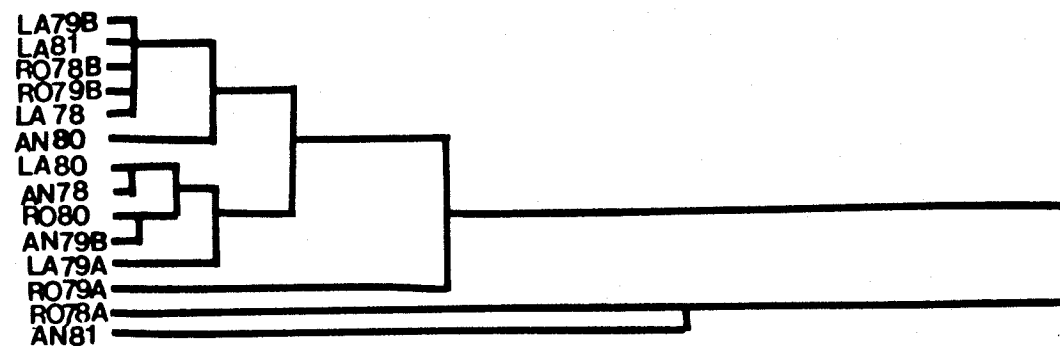


Figure 10. Cluster analysis of the nesting episodes on the basis of food availability.

FOOD AVAILABILITY AND HYDROLOGY.-- Table 14 suggests that the differences in food availability shown in Figure 10 may be related to differences in hydrology, particularly water depths. During the nonnesting period, there seems to be no statistical relationship between prey availability and water depth ($R = -0.17$, $P = 0.28$). Thus prey densities appropriate for maintenance appear to occur at various water depths. The situation becomes very different as feeding sites begin to dry and food become concentrated. Figure 2 shows how water levels fluctuated during the nesting season at representative stations in the Southern Everglades in four years of the study. The general pattern is for a decline in water levels to occur during the Spring, February-May, during which time nesting occurs. During such drying periods, food availability is inversely related to water depth. Higher food densities occur at lower water depths, and lower food densities occur at higher water depths. These general patterns are shown by the trend lines in Figure 11. Moreover, this figure shows that the higher densities within a trend tend to occur in the water depths that are preferred by herons, 10-20 cm.

This general pattern is proven by considering the relationship between water depth and food availability. Overall, there is a significant negative correlation between food availability (g/m^3) and water depth ($R = -0.229$, $P = 0.04$, $N = 59$). This result suggests a causal relationship: as water depths decrease, food density increases.

Despite the significant linear relationship, it appears that the actual model is more complicated, as can be seen in the scatter plot of all trappings taken at heron feeding sites (Figure

12). The inverse relationship between water depth and food is clearly shown in that all trappings having very high food density occur at depths of less than 20 cm. Although traps having low fish densities occur at all water levels, clearly more high density trappings occur at low water depths. The relationship of very high food densities to drying conditions can also be seen in this figure, which shows that the highest densities occur in the spring, rising from March, through April, to May, following the normal drying trend. Figure 12 also suggests that a decrease in food abundance may occur at very shallow depths, eg <5 cm, which may be due to mortality that occurs when oxygen becomes depleted (Kushlan 1979, Kushlan and Hunt 1970).

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M. J. May
The interaction of water depth and prey availability suggest further restriction on suitable foraging sites. This is shown in Figure 9B, where foraging range is limited not only by high but also by low water depths. This figure also shows the restrictions of foraging placed by prey density, showing below maintenance, maintenance, and above maintenance levels of food availability.

We can model the pattern of rise and fall of maximum food density as a skewed bell-shaped curve (Fig. 13) This model, supported by the underlying data, suggests that food densities are low at low water depths and rise to a maximum at about 15 cm and decrease, especially after 25 cm. Because of vagaries of production, dry season concentration, and mortality, any prey densities can occur within the curve of maximums so described. Thus it would be predicted that low availabilities would occur at various water depths, but very high densities can occur only at a specific range of water depths. Comparing Figure 13 and Figure

9B, we can see that the zone of high availability coincides with heron foraging range. Thus it is within this narrow range of water depths that foraging herons can feed, choose to feed, and encounter food densities above maintenance levels. Water depths in the interior achieve these levels only during seasonal drying conditions, when water levels fall from their wet season heights.

The shallow water depths where food concentrates are made available by the falling of water levels. Thus a second hydrological variable that could affect food availability is recession rate. Water depth at feeding sites and the recession rate over the previous 14 days are not significantly correlated ($R = 0.133$, $P = 0.28$, $N = 20$). However, the relationship between prey availability and recession appears to follow the same pattern as does prey availability and water depth (Figure 14). Maximum food availability occurs at rates of -1.2 to -0.7 cm/d, being lower at both higher and lower drying rates. This result suggests a statistically independent role of recession rate in providing food availability and further suggests the optimality of intermediate recession rates.

R-Red

Significant

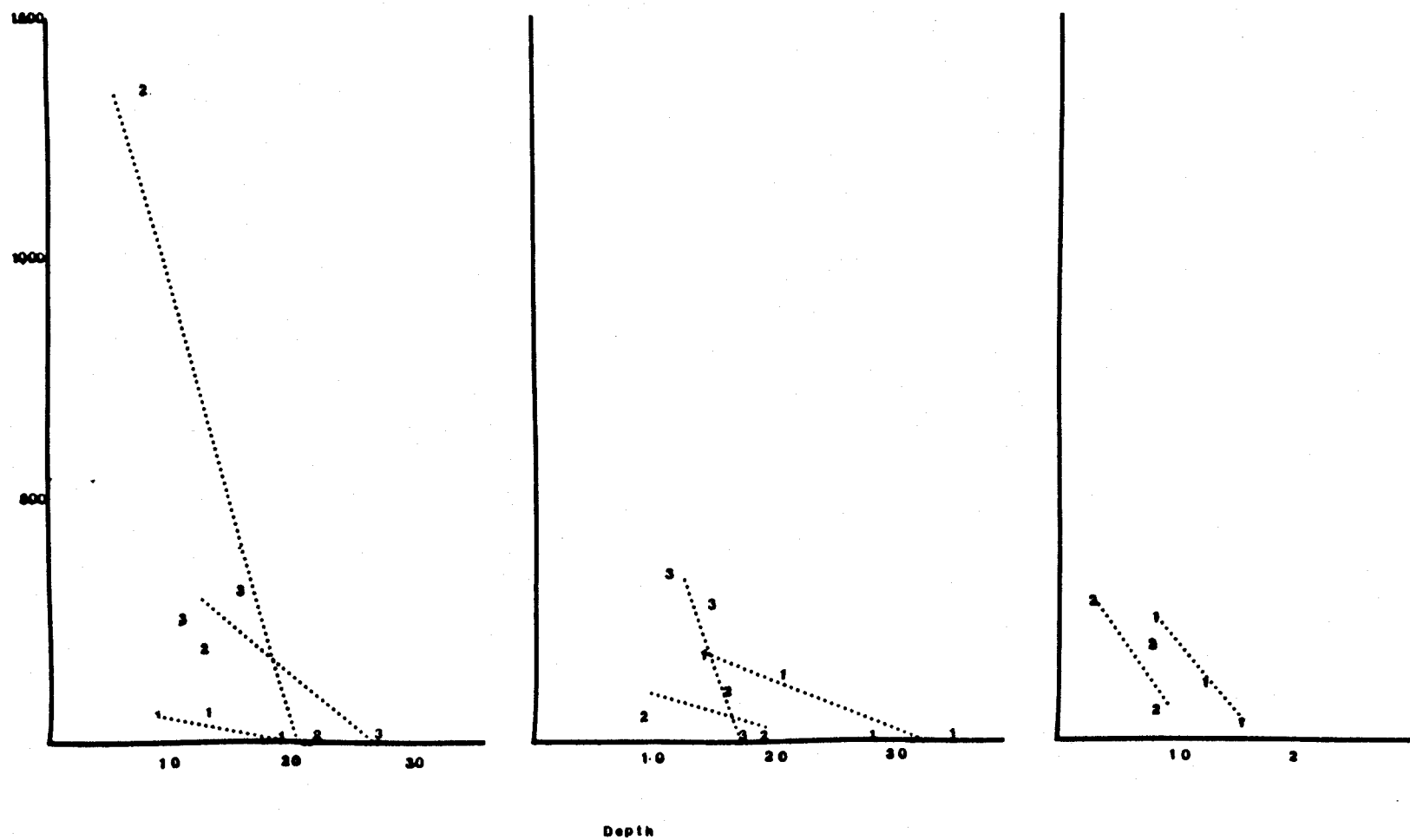


Figure 11. The relationship between water depth and food availability (g/m²) during three years. Lane River = 1, Rodgers River = 2, Andytown = 3.

Does not matter to Table 12.

I assume there is
a point for sampling and
not a point for sampling

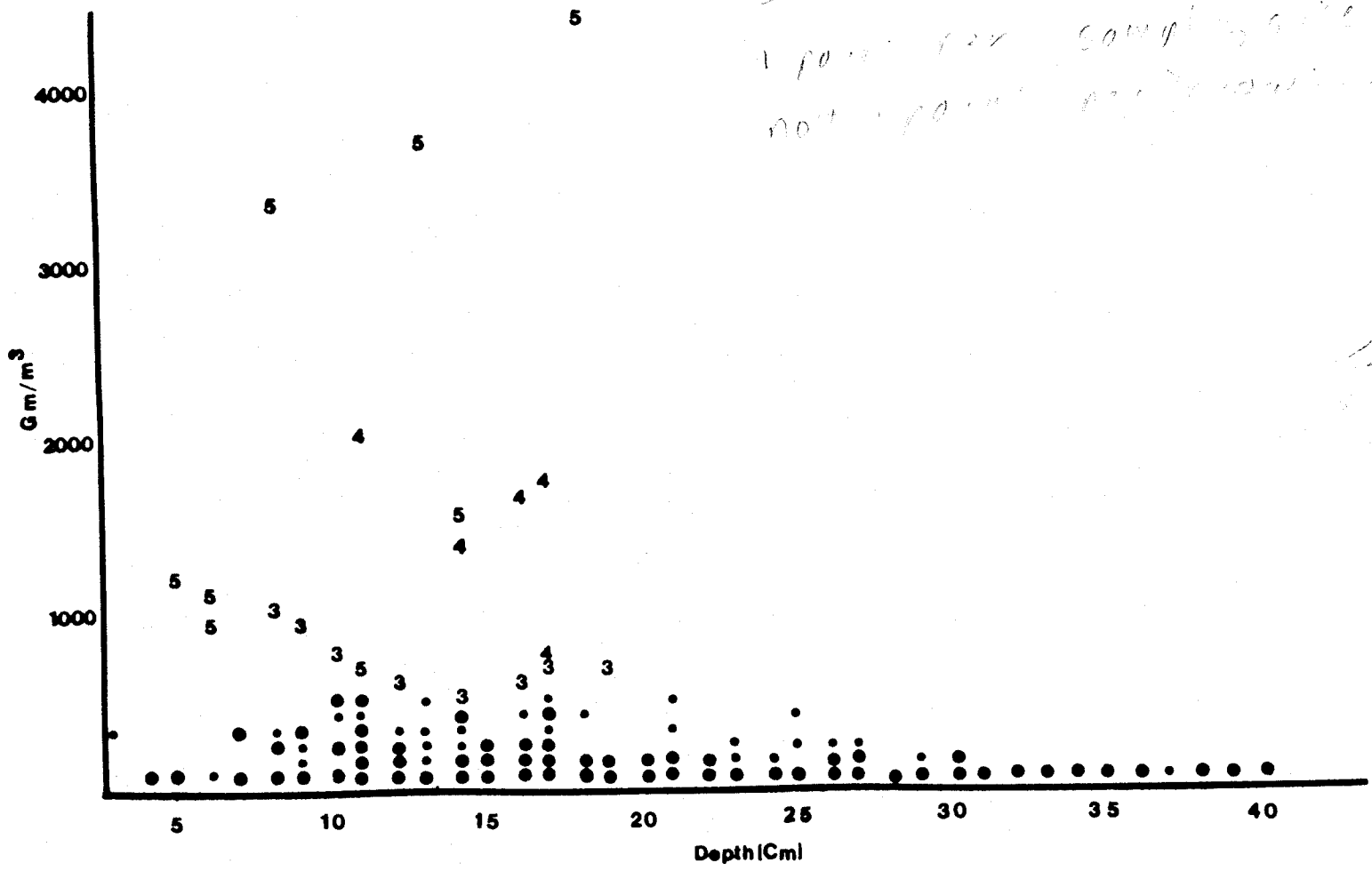


Figure 12. Scatter plot of food availability (g/m³) at various water depths. Data are for individual samples; large dots = multiple observations. Larger observations for March (3), April (4), and May (5) are shown.

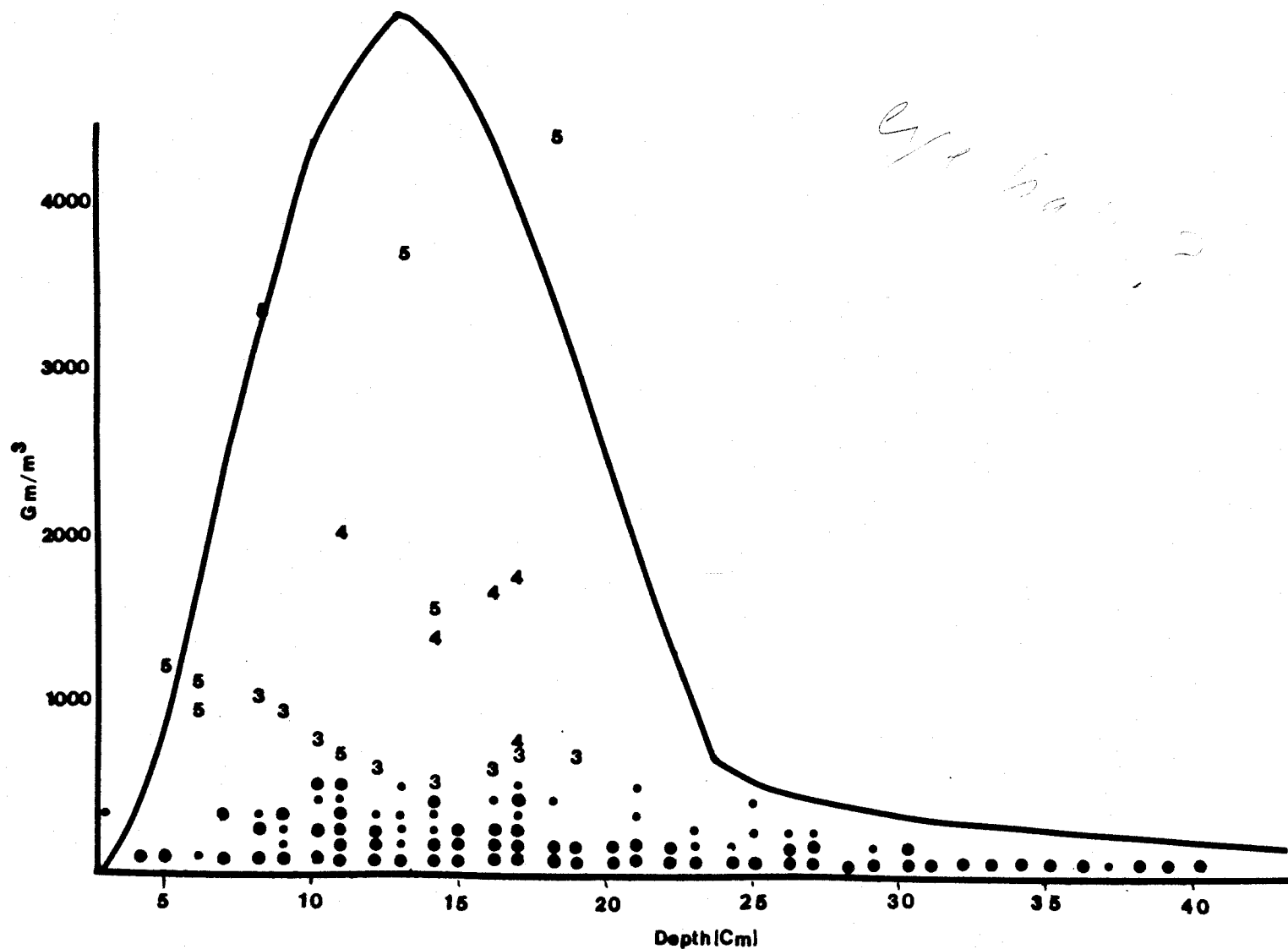
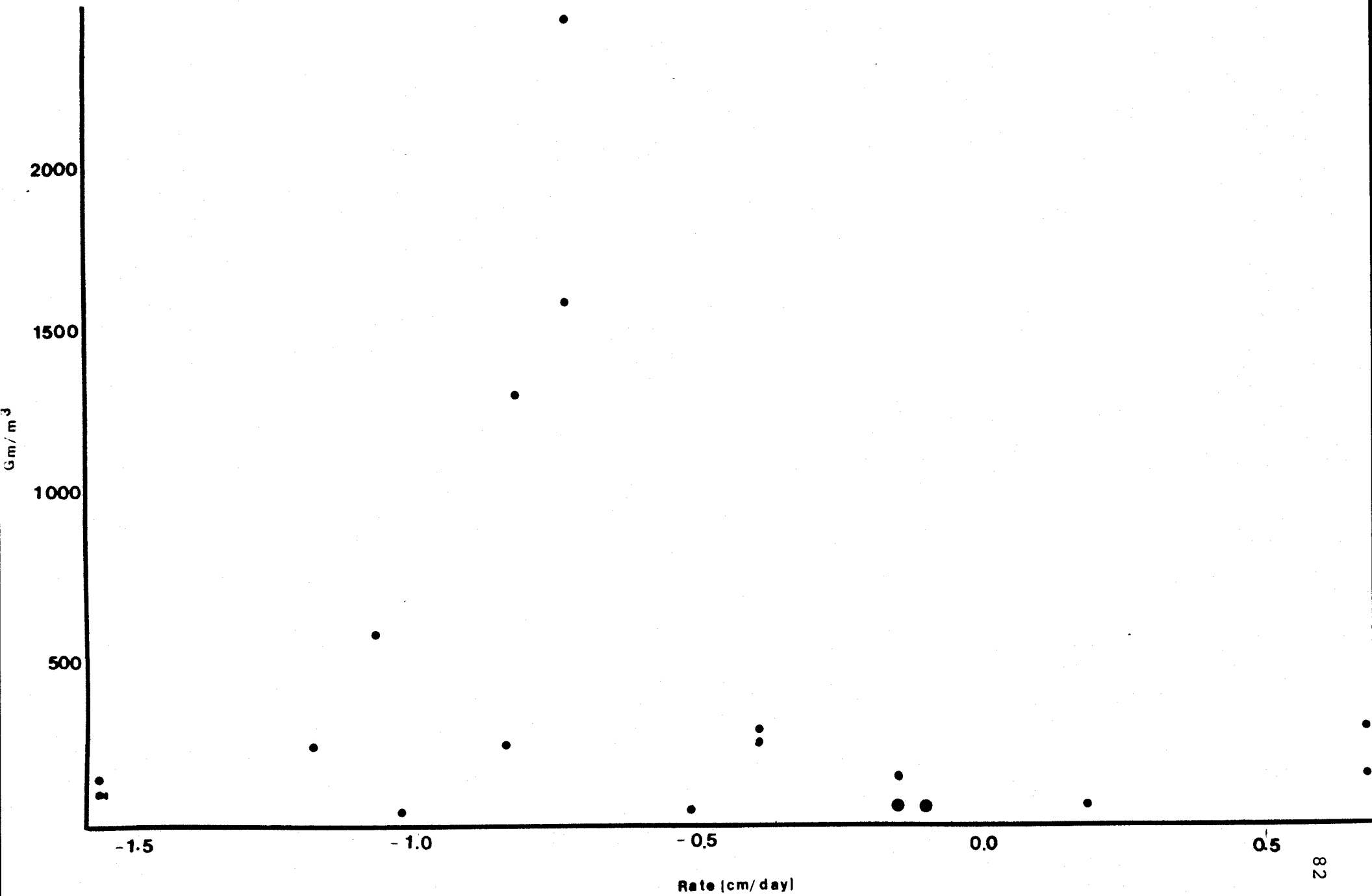


Figure 13. Model of the relationships of food maximum availability and water depth superimposed on a scatter plot of observational data (see Figure 12).

Figure 14. Relation of food availability to recession rate.



Mass and linear measurements of hatching herons increase with age unless low food availability stunts growth. Generally the increase in mass and body parts follow an increasing trajectory leading to an asymptote reflecting fledging size and can be modeled using several appropriate asymptotic curves (Ricklefs 1967, see Kahl 1962 and Kushlan 1977 a, b for an analyses of the growth of the White Ibis and Wood Stork in southern Florida). Such analyses presume knowledge of bird age, and curve fitting disguises significant variation. Although we were able to obtain growth data on an exceptional number of birds for such a study, standard growth analyses are too crude to provide comparisons among nesting episodes.

The mass and culmen growth curves for the four herons are shown in Figures 15 - 22. they demonstrate one important result. In each case the scatter of points is tighter for culmen than for mass, which suggests first that culmen is a better indication of approximate stage of development and second that the variability in mass growth is likely a reflection of differing environmental conditions in the various nesting episodes.

There is in fact significant relationships between culmen and mass for all species. The slopes of all were significantly different from zero ($P < 0.05$ - GE: $T = -5.802$, $n = 1123$; SE: $T = -.274$, $n = 1045$; TH: $T = -16.203$, $n = 1224$; LB: $T = -9.587$, $n = 354$.) An inspection also indicates that substantial deviations of individual points from any model would occur. These deviations were investigated to see if they reflected differential growth and nesting success among nesting episodes.

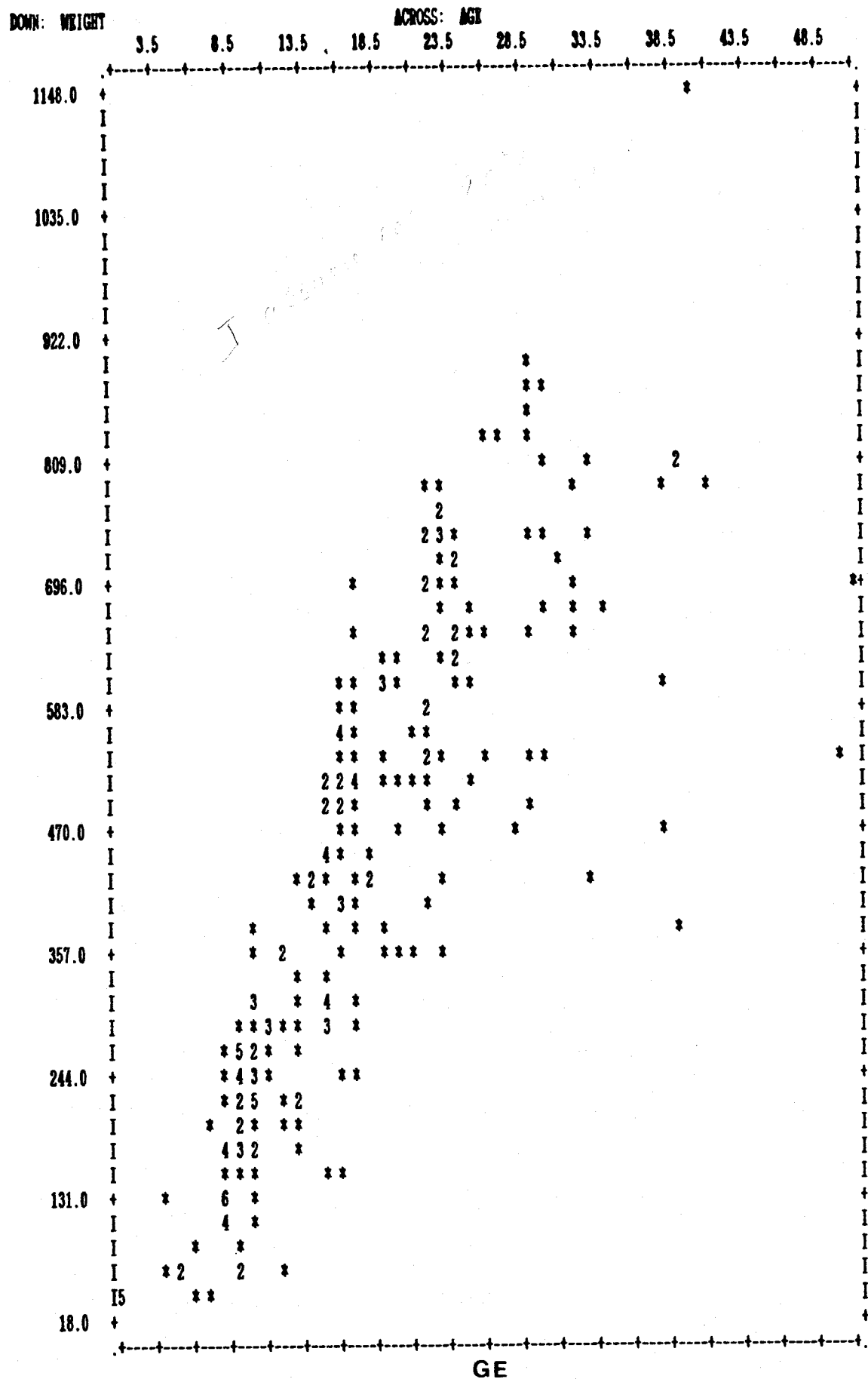


Figure 15. Scatterplot of biomass growth of Great Egrets

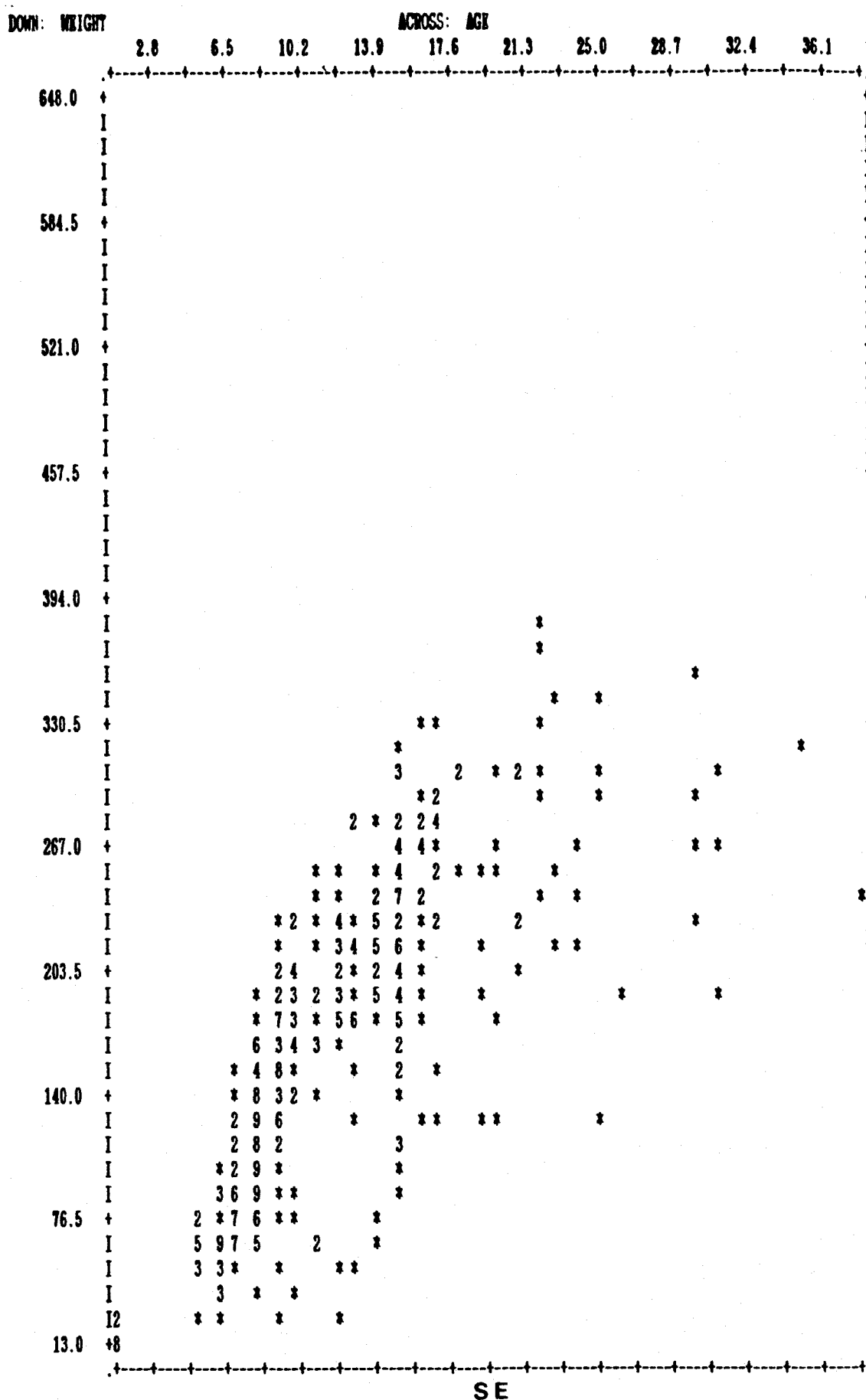


Figure 16. Scatterplot of biomass growth of Snowy Egrets

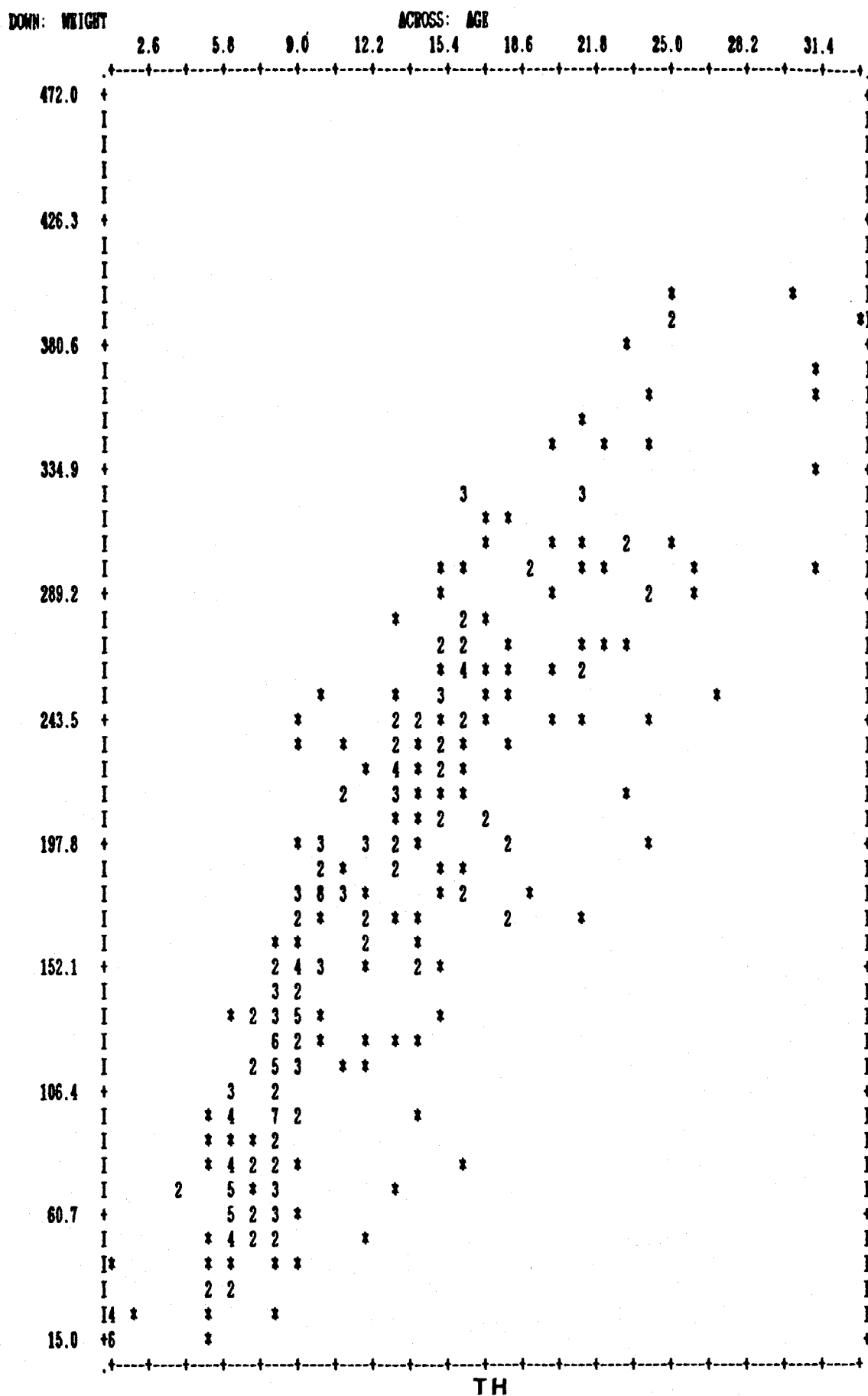


Figure 17. Scatterplot of biomass growth of Tricolored Herons.

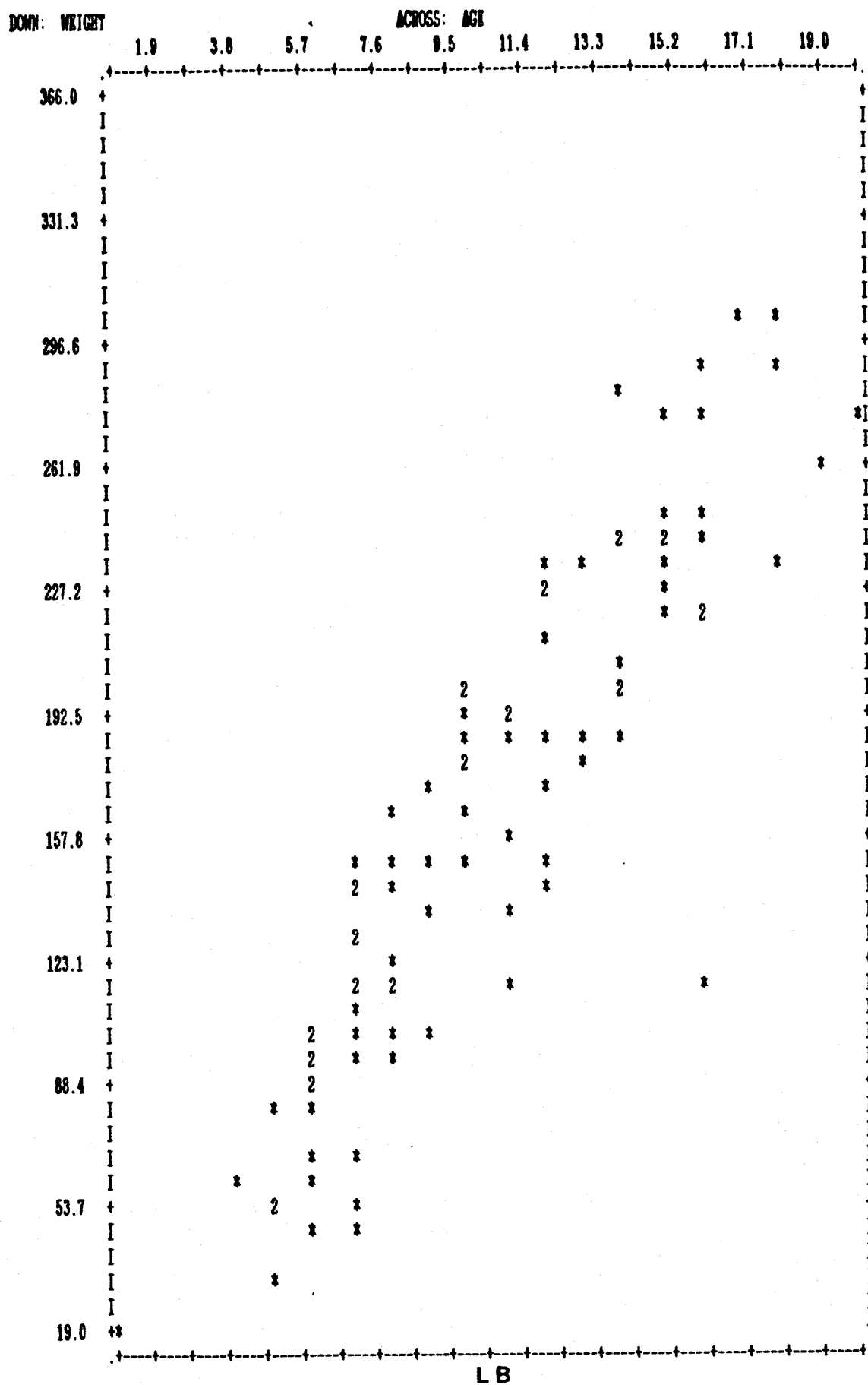


Figure 18. Scatterplot of biomass growth of Little Blue Herons.

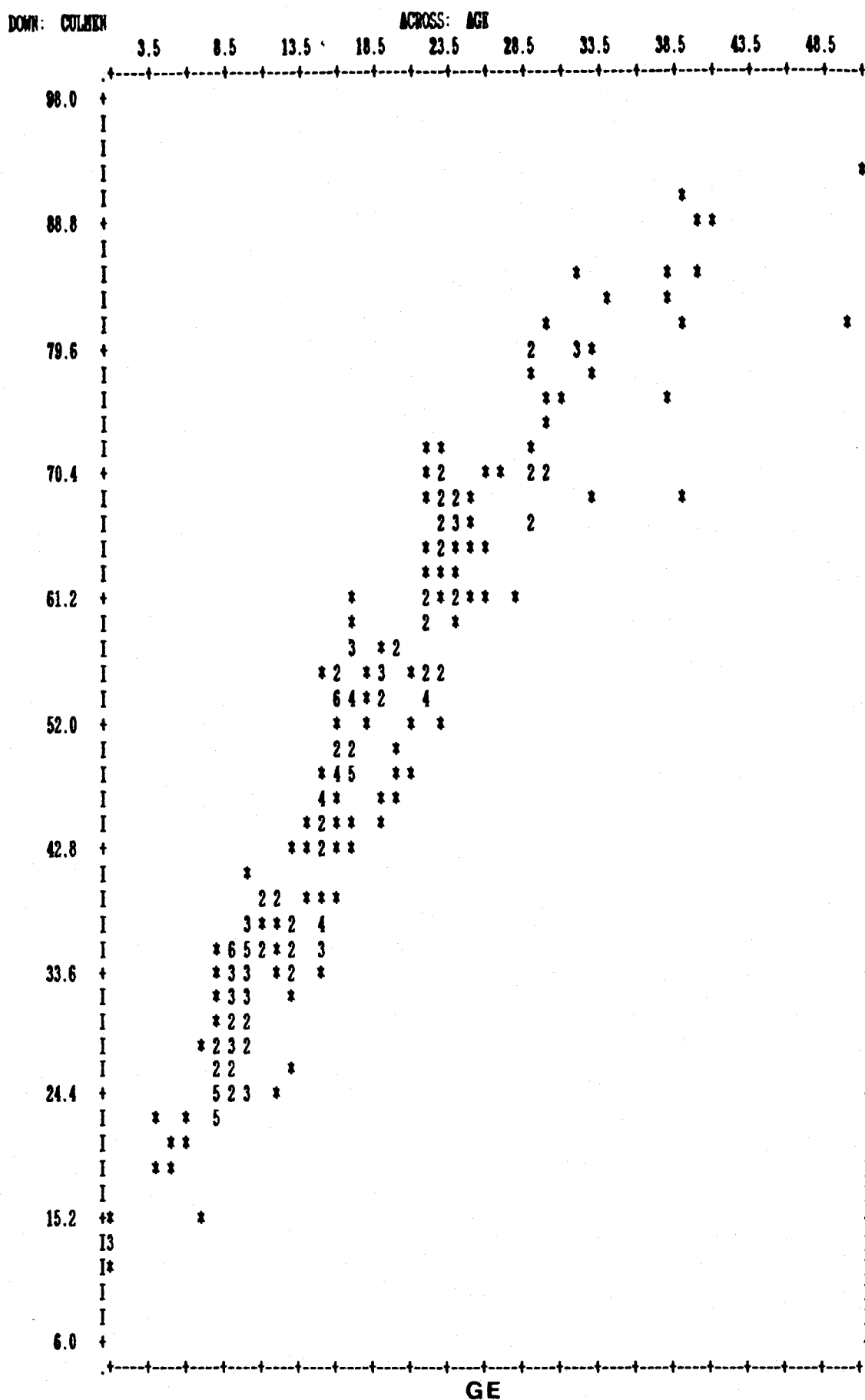


Figure 19. Scatterplot of culmen growth of Great Egrets.

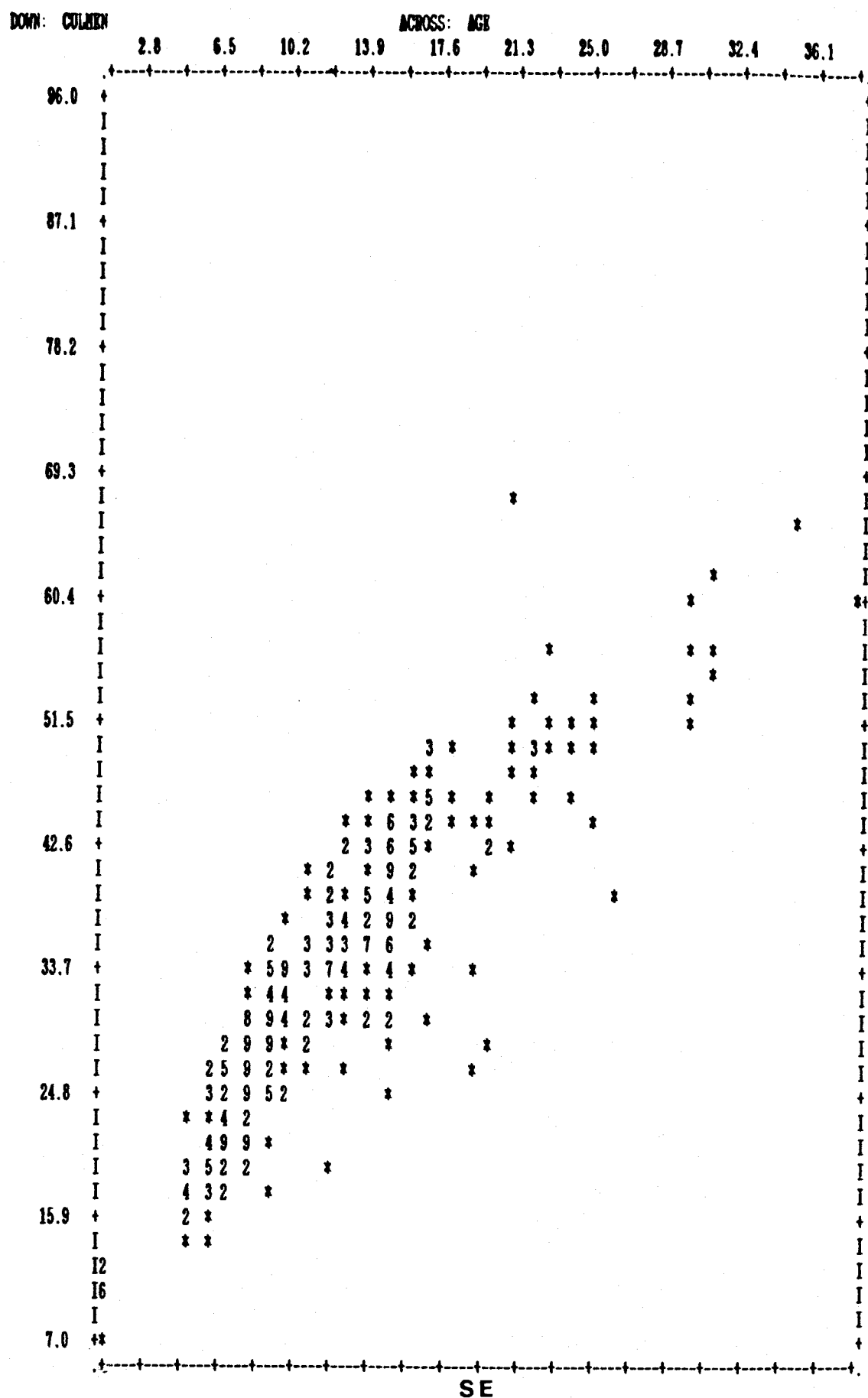


Figure 20. Scatterplot of culmen growth of Snowy Egrets.

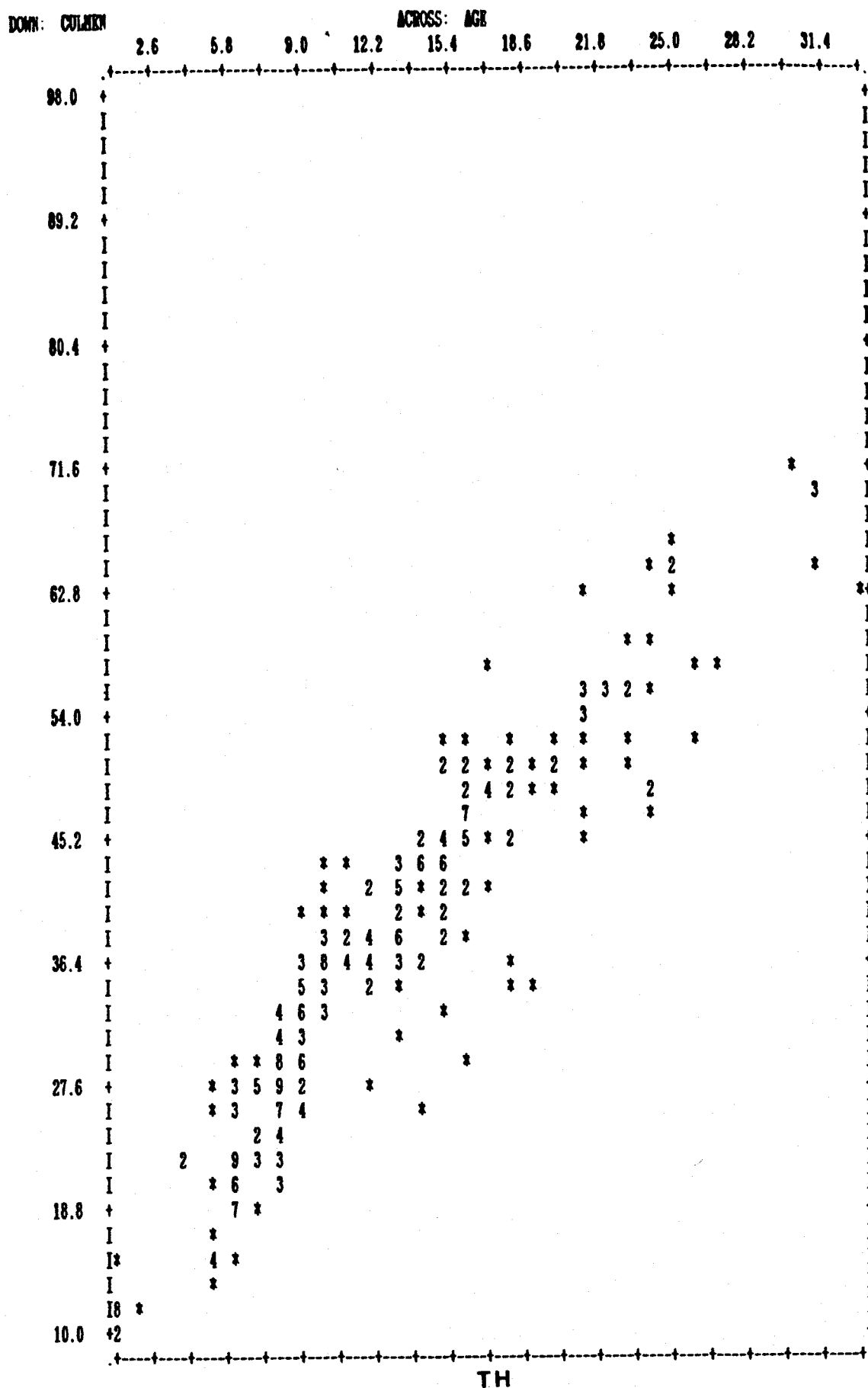


Figure 21. Scatterplot of culmen growth of Tricolored Herons.

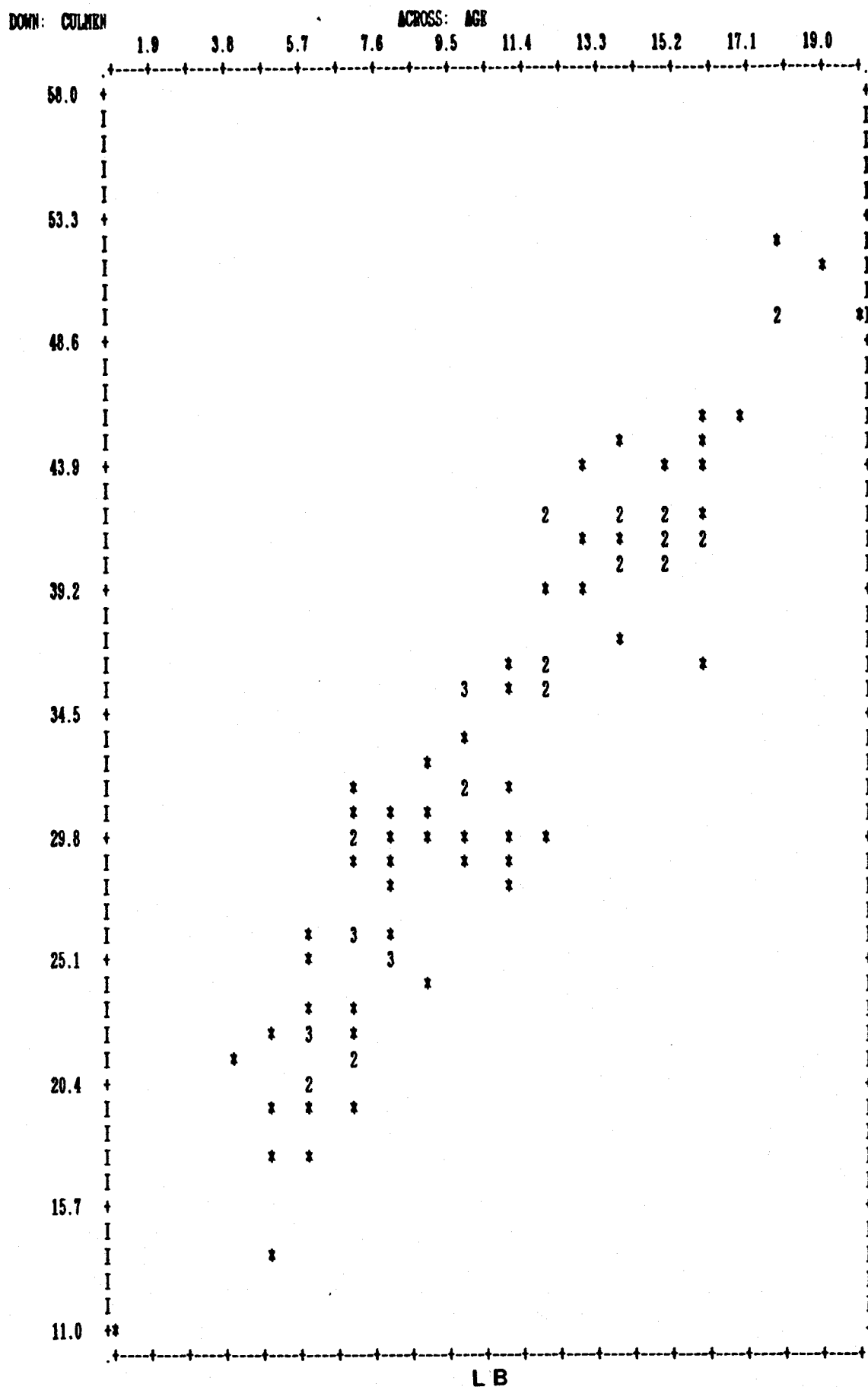


Figure 22. Scatterplot of culmen growth of Little Blue Heron.

NESTING SUCCESS

MORTALITY.-- Nesting mortality is the death of young birds in the nest. In that mortality is seldom actually witnessed, we used several criteria to estimate it. A marked nestling was considered to have died if it was found dead, if it experienced a loss of weight (which was invariably followed by its disappearance), or disappeared from the nest during the first five days of life, that is before it was capable of leaving the nest on its own. Measured in these ways, mortality is a highly conservative measure of nesting success. It does not include the loss of eggs, which if added would increase over all mortality for a nesting episode. The fate of eggs was not considered because in nearly all cases it is impossible to know how many eggs were layed originally and because such loss can be caused by factors other than environmental conditions on the foraging grounds. Secondly, it does not include as dead those chicks that disappeared after being able to leave the nest. Most mortality data are for chicks under three weeks of age, when in fact most mortality occurs (Pratt 1970, Gladstone 1979). Thirdly, it does not include chicks who died in the first days before they could be marked. Thus the overall loss of young is greater than was documentable as mortality. Furthermore the mortality data are biased by the frequency of colony visits, which was limited for some remote out of season sites such as Reed Pond and Oil Well sites. The data from some of these sites is somewhat tenuous.

The mortality rates for the several species in various nesting episodes are given in Table 16. Mortality rates differed among species in the same nesting episodes. Mortality rates also

where 1970-1971

Table. 16. Mortality rates (percent loss of chicks) for each nesting episode.

Nesting episode	GE	SE	TH	LB
	1	2	3	1
LA78	44.7	15.2	3.8	34.6
	3	3	2	3
RO78A	11.5	6.2	13.8	1.8
	2	2		
FR78A	21.6	18.6		
	1	3	2	
AN79B	50.0	9.8	12.1	
	3	3	2	
LA79A	9.1	8.3	7.3	
	3	3	2	
RO79A	6.6	5.7	12.3	
	2		2	
AN79A	24.8		9.5	
	1	1	1	
LA80	80.8	48.4	42.7	
	2	1	1	
RO80	26.2	35.0	28.6	
	3	3	3	3
AN81	8.3	2.7	1.1	6.9
	2	1		
FR78B	26.0	61.9		
		3	2	3
FR79		6.1	5.8	6.1
		2	3	
RO78B		20.8	0.0	
		1	1	
LA79B		63.3	60.4	
			1	1
RP79			0.0	31.3
			2	1
NH80			14.6	45.7
			3	
RO79B			3.8	
			1	
AN80			27.8	
			2	
SA78			6.9	
			3	3
NH79			0.0	8.3
				3
OW78				3.8

1

See Table 1 for colony sites and time of nesting episodes. Episodes sharing superscripts belong to similar clusters in Figure 26.

differed significantly within species among nesting episodes (Tables 17 - 20).

Among-species, fairly high mortality occurred at Lane 1978 for Great Egrets and Little Blue Herons but not for Snowy Egrets and Tricolored Herons. Similarly in the poor nesting episode at Lane 1980, Great Egrets suffered twice as much documented mortality as did Snowy Egrets and Tricolored Herons. In sum, these results reflect the differing responses of the heron species to the same environmental conditions.

For all species in general, the nesting episodes associated with least mortality were those occurring under drying conditions, such as those at Lane River, Rodgers River, and Frank Key sites in 1979, prior to the rainy season (LA79A, RO79A, FR79), and at Andytown (AN81). The best available standard for relatively successful nesting in southern Florida during our study was at the Andytown colony site (AN81), where water levels were to low and recession rates high (see Figure 2).

Hérons suffered more nesting mortality after the beginning of the rainy season. Great Egrets had heavy mortality after the rainy season in 1979 at Andytown (AN79B) and did not even continue nesting after the beginning of the rainy season in other episodes (eg., RO78B, LA79B, or RO79B). Snowy Egrets nesting after the rains in interior colonies did poorly in 1979 (LA79B) and suffered intermediate mortality in 1978 (LA78B). The correlation of relatively low mortality with drying conditions is proven conclusively by the mortality patterns in the high water year of 1980, when nesting mortality was uniformly high at Lane and

Table 17. Chi-square values for comparisons of mortality among nesting for Great Egrets.¹

	LA78	RO78A	AN81	AN79A	LA79A	RO79A	LA80	RO80	FR78A
LA78	---	50.84	81.73	7.06	63.74	112.73	39.52	8.30	12.63
RO78A	34.70	---	1.07*	9.87	0.24*	3.26*	241.19	8.67	5.70
AN81	51.36	0.95*	---	17.54	0.26*	0.53*	324.96	15.85	11.54
AN79A	14.25	28.88	55.79	---	39.94	83.69	215.46	0.08*	1.31*
LA79A	49.48	0.25*	0.34*	15.55	---	1.92*	327.26	13.88	9.67
RO79A	83.16	3.45	0.61*	30.60	1.83*	---	494.97	27.97	21.24
LA80	27.37	245.16	358.81	74.46	292.79	471.95	---	80.08	98.63
RO80	9.05	13.71	29.22	0.05*	19.25	41.31	125.12	---	0.39*
FR78A	33.78	22.18	48.72	1.82*	32.94	77.04	378.73	1.01*	---

¹
* = not significant ($P < 0.05$). See Table 1 for full names and times of nesting episodes.

Λ²

you could expect 5%
significant change in 5%
just out of chance.
Not a good test.

Table 18. Chi-square values for comparisons of mortality among nesting episodes for Snowy Egrets.

	LA78	RO78A	AN81	AN79B	LA79A	RO79A	LA80	RO80	FR78A	FR79	RO78B	LA79B	FR78B
LA78	-----	9.09	38.95	2.13*	4.07	10.97	29.21	11.43	0.52*	9.44	1.28*	65.86	61.16
RO78A	16.21	-----	12.04	3.78	1.49	0.12*	183.96	94.05	26.20	0.01*	33.38	362.07	339.38
AN81	8.97	1.56*	-----	4.22	3.05	1.24*	61.87	33.93	12.35	1.49*	14.71	116.97	109.96
AN79B	1.89*	1.78*	15.54	-----	0.23	2.51*	49.03	22.96	4.24	1.91*	6.07	101.20	94.54
LA79A	3.95	0.85*	13.05	0.26*	-----	1.39*	69.42	33.76	7.52	0.94*	10.20	140.46	131.40
RO79A	9.77	0.06*	4.84	2.64*	1.23	-----	102.14	52.78	15.35	0.04*	19.34	199.84	187.40
LA80	81.34	291.20	755.91	160.30*	200.92	322.57	-----	7.52	55.80	297.06	44.00	9.05	7.32
RO80	48.66	228.20	635.40	114.95	149.86	255.55	11.50	-----	28.42	233.30	19.58	55.16	49.09
FR78A	0.77*	22.75	82.81	7.54	12.00	26.64	30.57	10.16	-----	23.48	0.25*	73.95	68.35
FR79	5.27	0.01*	3.60*	1.27*	0.52	0.02*	58.76	30.11	8.47	-----	10.76	115.50	108.27
RO78B	1.77*	26.51	90.12	9.91	14.86	30.68	21.91	6.35	0.24*	27.29	-----	55.89	51.49
LA79B	53.92	168.39	419.82	97.26	119.38	185.39	2.68*	10.57	39.65	171.56	32.95	-----	0.03*
FR78B	35.54	112.05	280.19	64.50	79.28	123.42	1.53*	6.68	26.01	114.17	21.54	0.02*	-----

1

* = not significant ($P < 0.05$, $df=1$). See Table 1 for full names and times of nesting episodes.

Table 19. Chi-square values for comparisons of mortality among nesting episodes for Tricolored Herons.

		LA78	R078A	AN81	AN79A	LA79A	R079A	LA80	R080	PR79	R078B	SA78	LA79B	R079B
LA78	1	---	10.83	9.01	4.83	2.29*	8.61	80.21	39.01	0.91*	182.62	1.89*	173.83	6.01*
R078A	2	31.69	---	171.79	2.48*	7.23	0.24*	39.62	12.45	13.57	2177.19	8.58	105.35	31.69
AN81	16	1.74*	12.02	---	7.26	5.02	10.31	62.88	32.90	3.56*	9.33	4.62	130.74	1.74*
AN79A	11	5.65	0.97*	41.09	---	0.46*	0.45*	28.34	11.23	1.60*	560.05	0.67*	68.18	5.65
LA79A	9	1.81*	1.97*	19.26	0.32*	---	1.29*	28.21	12.25	0.22*	283.25	0.01*	64.90	1.81*
R079A	10	25.74	0.24*	150.10	1.19*	4.82	---	49.08	16.90	10.08	1939.30	5.92	125.71	25.74
LA80	12	339.13	57.51	1303.33	105.02	151.71	70.17	---	7.96	204.17	14883.99	163.44	10.76	334.13
R080	3	164.50	17.98	679.83	41.46	65.53	24.05	8.00*	---	93.01	7952.04	71.65	41.51	164.50
PR79	7	0.75*	3.71*	13.99	1.10*	0.23*	2.71*	38.41	17.57	---	224.18	0.13*	86.01	0.75
R078B	17	0.32*	1.28*	0.09*	0.84*	0.63*	1.12*	5.96	3.20*	0.49*	---	0.59*	12.20	0.31*
SA78	3	1.71	4.01	31.56	0.78*	0.02*	2.70*	52.81	23.22	0.28*	471.72	---	120.73	2.71*
LA79B	4	420.89	87.69	1552.41	144.74	200.13	103.02	6.16	23.79	262.07	17480.35	214.00	---	420.89
R079B	5	0.00*	2.17*	1.80*	0.97*	0.46*	1.72*	16.04	7.80	0.18*	36.52	0.38*	34.77	---
HH77	8	0.71*	2.88*	0.20*	1.89*	1.42*	2.52*	13.41	7.21	1.11*	0.02*	1.33*	27.45	0.71
AN79B	6	18.75	0.24*	110.54	0.79*	3.40*	0.01*	37.83	13.17	7.24	1432.08	4.20	96.47	18.75
AN80	14	141.55	14.78	588.78	34.97	55.77	20.00	8.19	0.03*	79.57	5901.43	61.07	40.04	141.55
HH80	15	15.27	0.03*	80.21	1.44*	3.76*	0.23*	15.51	4.62	6.78	1007.89	4.41	42.13	15.27
RP79	18	0.51*	2.08*	0.15*	1.37*	1.02*	1.82*	9.69	5.21	0.80*	0.01*	0.96*	19.83	0.51*

¹
* = not significant ($P < 0.05$, $df=1$). See Table 1 for full names and timing of nesting episodes.

Table 19 cont. Chi-square values for comparisons of mortality among nesting episodes for Tricolored Herons.

		HH77	AN79B	AN80	HH80	RP79
LA78	1	182.62	8.33	37.16	12.06	182.62
RO78A	2	2177.19	0.31	11.34	0.07*	2177.19
AN81	16	9.33	10.08	31.55	12.96	9.33
AN79A	11	560.05	0.39*	10.48	1.30*	560.05
LA79A	9	283.25	1.21*	11.55	2.37*	283.25
RO79A	10	1939.30	0.01*	15.55	0.55*	1939.30
LA80	12	14883.99	72.11	4.05	51.87	14883.99
RO80	13	7952.04	25.00	0.03*	15.34	7952.04
RP79	7	224.18	2.58*	16.64	4.29	224.18
RO78B	17	0.01*	1.10*	3.08*	1.37*	0.01*
SA78	3	471.72	2.54	21.91	4.77	471.72
LA79B	4	17480.36	105.36	25.44	80.81	17480.35
RO79B	5	36.52	1.67*	7.43	2.41	36.52
HH77	8	0.02*	2.48*	6.93	3.08*	0.02*
AN79B	6	1432.08	---	12.13	0.49*	1432.08
AN80	14	6901.43	20.80	---	12.54	6901.43
HH80	15	1007.89	0.28*	4.18	---	1007.89
RP79	18	0.01*	1.79*	5.04	2.22*	0.01*

1
 * = not significant ($P < 0.05$, $df = 1$). See Table 1 for full names and timing of nesting episodes.

Table 20. Chi-square values for comparisons of mortality among nesting episodes¹
for Little Blue Herons.

	LA78	RO78A	AN81	FR79	NH80	RP79	OW78	NH79
LA78	---	316.79	62.18	73.82	2.57*	0.27*	135.08	47.31
RO78A	26.65	---	2.28*	1.82*	43.52	22.65	42.95	3.12*
AN81	24.34	10.78	---	0.09*	43.58	19.82	1.95	0.17*
FR79	35.12	10.36	0.09*	---	61.86	28.83	1.45*	0.61*
NH80	1.91*	381.85	82.08	95.89	---	3.40*	168.20	64.37
RP79	0.16*	157.01	29.54	35.34	2.69*	---	65.96	22.15
OW78	10.87	0.62*	0.38*	0.23*	18.35	9.10	---	0.68*
NH79	11.00	8.69	0.12*	0.31*	20.26	8.81	2.02*	---

¹

* = not significant. See Table 1 for full names and timing of nesting episodes.

intermediate at Rodgers for all species. Thus it appears that nesting success of all three species is enhanced by drying conditions. Such conditions appear to be essential for Great Egrets and Snowy Egrets to nest with relatively low mortality.

Great Egrets and Snowy Egrets nesting along the coast on Frank and Sandy Keys were of intermediate success. After the rains in 1978, Great Egrets were able to maintain a moderate nesting success, whereas Snowy Egrets were not.

Tricolored Herons differed substantially from the other species. They were also most successful in the drying seasons of interior colonies, and did poorly in several post rainy season nesting episodes and during the 1980 high water year (LA80, R080, LA79B). This species can feed effectively in tidal mangrove sites, and so was able to continue nesting at the Rodgers River site after rains began. Mortality rates at some other sites are ambiguous, and probably anomalous, representing few individuals or few visits. For purposes of analyses, all data will be included, but with some caution.

Little Blue Herons, having such a different diet from the other herons, are not so dependent on drying conditions inland. They therefore nest both in the drying season and the rainy season in various interior colony sites. Nesting mortality was overall lowest at Frank Key and at two small colony sites in the southern Everglades (HH79). It nonetheless was poor at similar locations in other episodes (RP79, HH80), and in the Lane colony site in 1978.

MORTALITY AND NESTING SUCCESS.-- The significantly differing pattern of mortality among species and its dependence in part on water conditions for at least three of the heron species suggest that this parameter might be used to discriminate among the overall success of a nesting episode. To investigate this possibility we performed cluster analyses (Fig. 23). Three distinct clustering of nesting success as determined by mortality, occurred with Great Egrets, and Snowy Egrets. These may be considered to discriminate among low mortality (0-20%), intermediate mortality (20-30%), and high mortality (>30%) nesting episodes. For Little Blue Herons, only the high and low categories were found (see also Table 16.) The clustering for the Tricolored Heron also breaks into three groups, but differs from the other species in that groups 2 and 3 both represent low documented mortality, and within the mortality range of group 3 of the other species. These clustering patterns also reflected significant differences among nesting episodes as determined by the Chi-square analyses (at $P < 0.05$) (Tables 17-20).

Recognition of distinctive clusters of mortality within species provides the opportunity to search for correlative factors associated with, and possibly causing the patterns observed. Patterns of food availability reflect closely with the mortality classes for three of the species (Table 21). All species with one exception suffered lower mortality in episodes having higher food density. The single exception, for Snowy Egrets, appears to be an anomaly of data collection at only two feeding sites. Also of interest are the levels associated with high mortality, approximately 80 - 120 g/m³. These are levels associated with or slightly greater than maintenance, and indicate the food

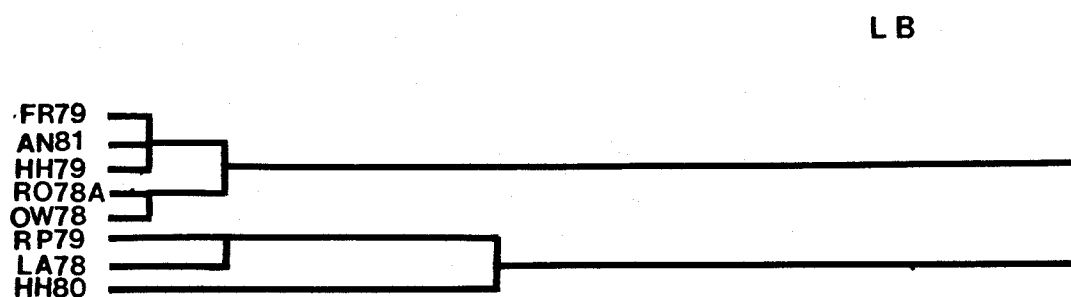
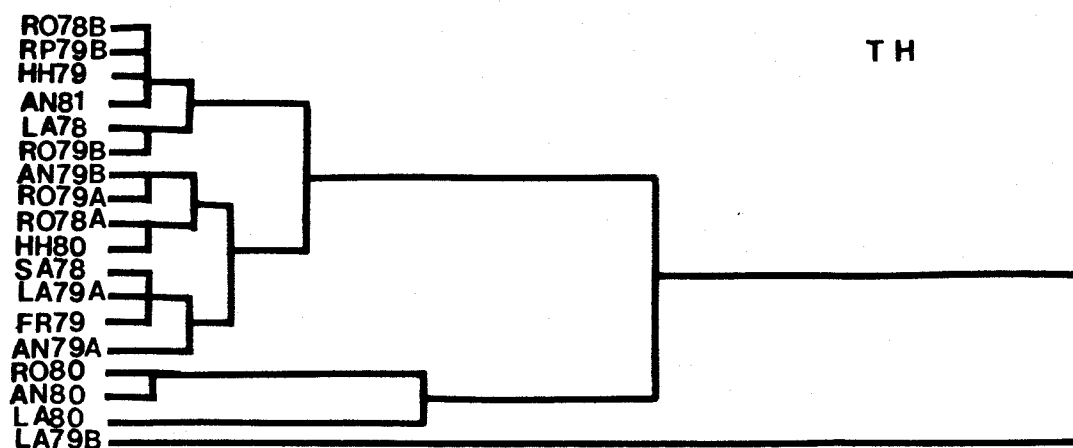
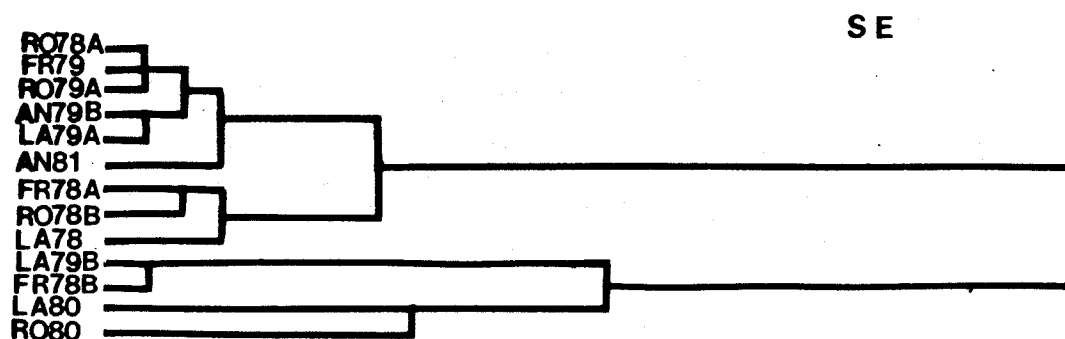
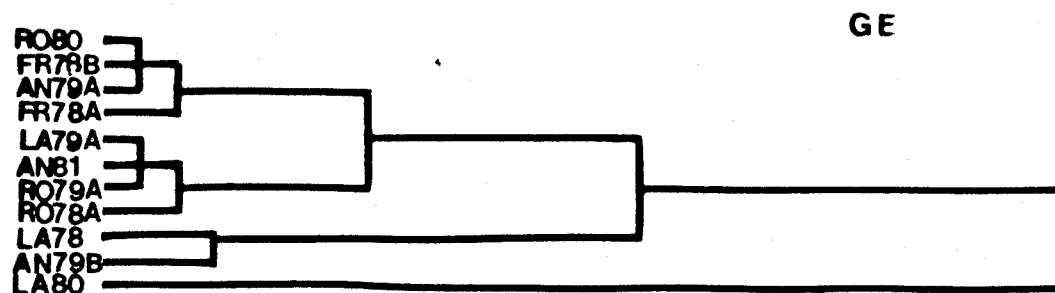


Figure 23. Cluster analysis of nesting episodes by mortality.

Table 21. Mean food availability at feeding sites used by herons during nesting, compared among nesting episodes having differing mortalities.

Species	Mortality								
	Low			Intermediate			High		
	g/m 3	sd	n	g/m 3	sd	n	g/m 3	sd	n
GE	370.3	450.69	7	129.8	129.57	6	79.6	100.27	9
SE	552.5	744.09	16	23.0	24.48	4	119.2	116.33	12
TH	476.2	818.09	13	311.8	409.52	4	116.1	111.9	13
LB	757.6	954.80	8				21.7	29.79	3

↑
 n should be # of
 nesting episodes with
 1 food value per episode

availability in these nesting episodes was insufficient for successful nesting. Among-species comparisons are also noteworthy. Thus the Great Egret appears to require lower food density than do the smaller herons. The Tricolored Heron requires relatively high food abundance, both low and intermediate categories, but these both actually represent low mortality.

Mortality expressed as a percentage of loss does not suggest in itself the level of production attained during a nesting episode. This, however, can be seen in the number of chicks produced per nest (Table 22). These values are underestimates as they include survival to about the third week of life, and additional mortality is likely between that age and fledging. First year mortality has been reported to be at least 70% for all species.

↑
reference

Table 22. Mean, standard deviation (s.d.) and sample size (N) of final brood size (number of chicks) by nesting episode.

Nesting Episode	Heron Species											
	GE			SE			TH			LB		
	Mean	s.d.	N	Mean	s.d.	N	Mean	s.d.	N	Mean	s.d.	N
LA78	1.1	0.96	18	2.4	0.78	18	2.5	0.63	42	1.5	1.38	6
RO78A	2.2	0.85	26	3.1	0.86	63	2.4	0.70	10	2.7	0.84	18
FR78A	1.6	0.67	38	2.2	0.75	25						
AN79B	1.8	0.67	32	2.2	0.81	21	2.3	0.75	29			
LA79A	2.4	0.60	33	2.9	0.64	22	2.6	0.65	13			
RO79A	2.5	0.71	40	3.1	0.82	35	2.8	0.75	27			
AN79A	2.1	0.65	30				2.9	0.93	9			
LA80	0.6	0.65	13	1.6	0.78	29	1.7	0.61	25			
RO80	1.5	0.71	25	1.8	0.91	46	1.9	0.79	31			
AN81	2.5	0.57	29	3.3	0.78	22	3.0	0.64	28	3.2	0.77	21
FR78B	1.5	0.62	18	1.5	0.58	4						
FR79				2.3	0.65	30	1.9	0.79	31	2.7	0.80	29
RO78B				1.8	1.19	12	1.8	0.90	25			
LA79B				1.1	0.67	12	1.2	0.85	20			
RP79							2.2	0.44	5	1.9	0.79	12
HH80							1.9	0.92	15	1.2	0.92	10
RO79B							2.2	0.88	17			
AN80							2.1	0.72	28			
SA78							2.1	0.60	28			
HH79							2.1	0.64	8	2.6	0.51	12
OW78										2.1	0.50	9

WST on weight gain

scatterdiagrams of daily growth rate against culmen length (Fig. 24 - 27) demonstrate a significant linear relationship, suggest that a curvilinear model may be more appropriate, and expose substantial variation in growth among individuals that should be analyzable in terms of environmental causality. Such curvilinearity is reasonable in that one should not expect growth rates to be consistent over the entire developmental period, a implication of the usual sigmoid modeling of mass increase by age. An appropriate model would require a quadratic term in addition to culmen length. Ricklefs et al. (1984) used original culmen (OCUL), original culmen-squared (OCULSQ), and original weight (OWT), each as taken at the beginning of the growth interval being calculated. OWT was included to account for an historical component to current growth. They found no significant effect of clutch size. For Everglades herons, we evaluated multivariable regression models based on OCUL, OCULSQ, OWT, current brood size (CLUTCH), and hatching order (ie, first, second or third hatched - TCHSEQ). The latter two variables provide information on the current competitive situation in the nest. The array of variables was chosen to attempt to account for variability not associated with extrinsic environmental conditions.

Table 23 shows the results of stepwise regression models for each species. Daily growth increases were best modeled using culmen variable (an indication of developmental state) for all species. In addition variables loading included hatching order for the smaller herons, and also original weight for Tricolored and Little Blue Herons. These results suggest that only developmental stage and current conditions, not previous

Figure 24. Scatterplot showing relationship between culmen length (OCUL, cm X 10) and daily growth rate (DWTINC1, g/d X 10) for Great Egrets.

DOWN: DWTINC1

ACROSS: OCUL

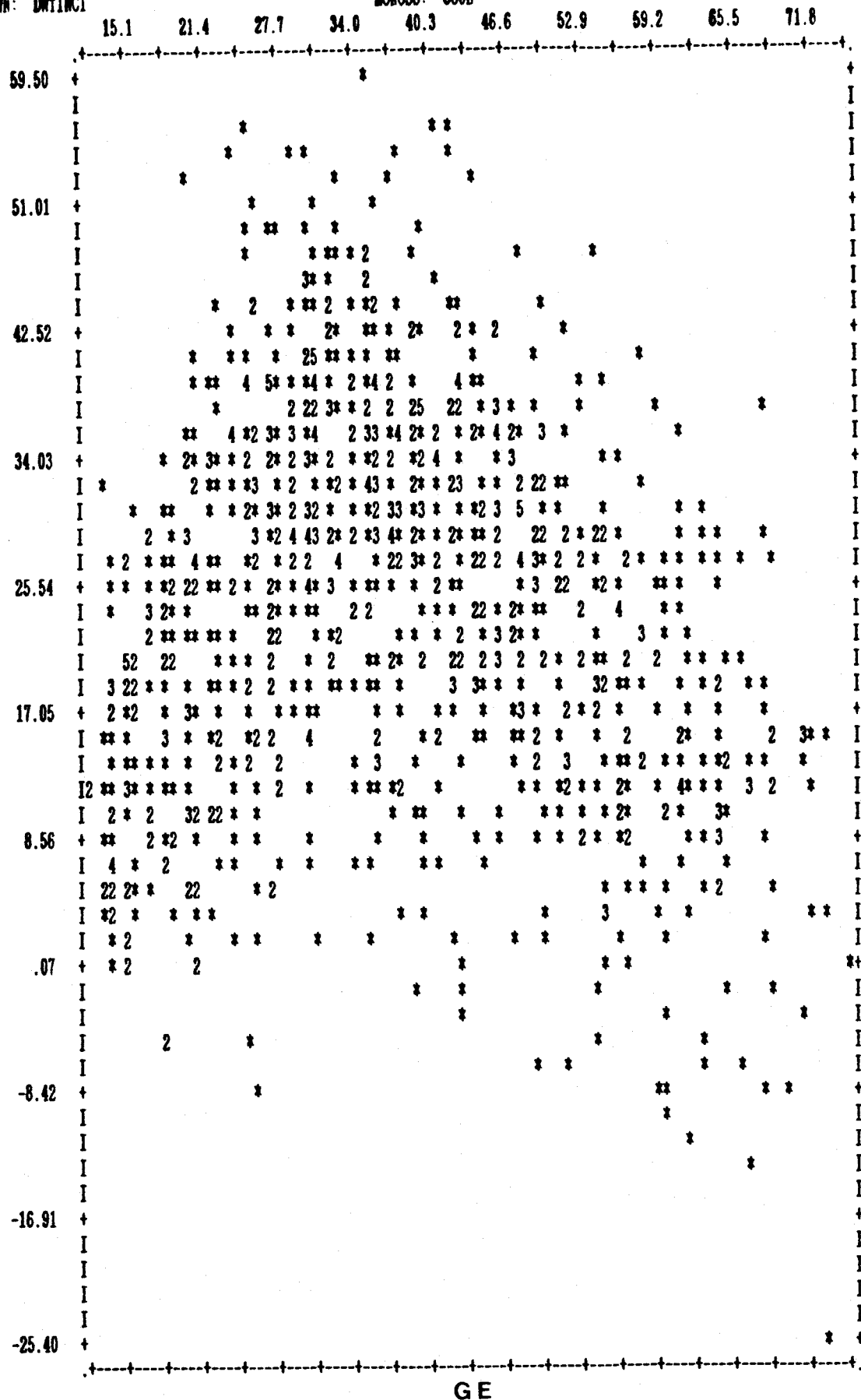


Figure 25. Scatterplot showing relationship between culmen length (OCUL, cm X 10) and daily growth rate (DWTINC1, g/d X 10) for Snowy Egrets.

DOWN: DWTINC1

ACROSS: OCUL

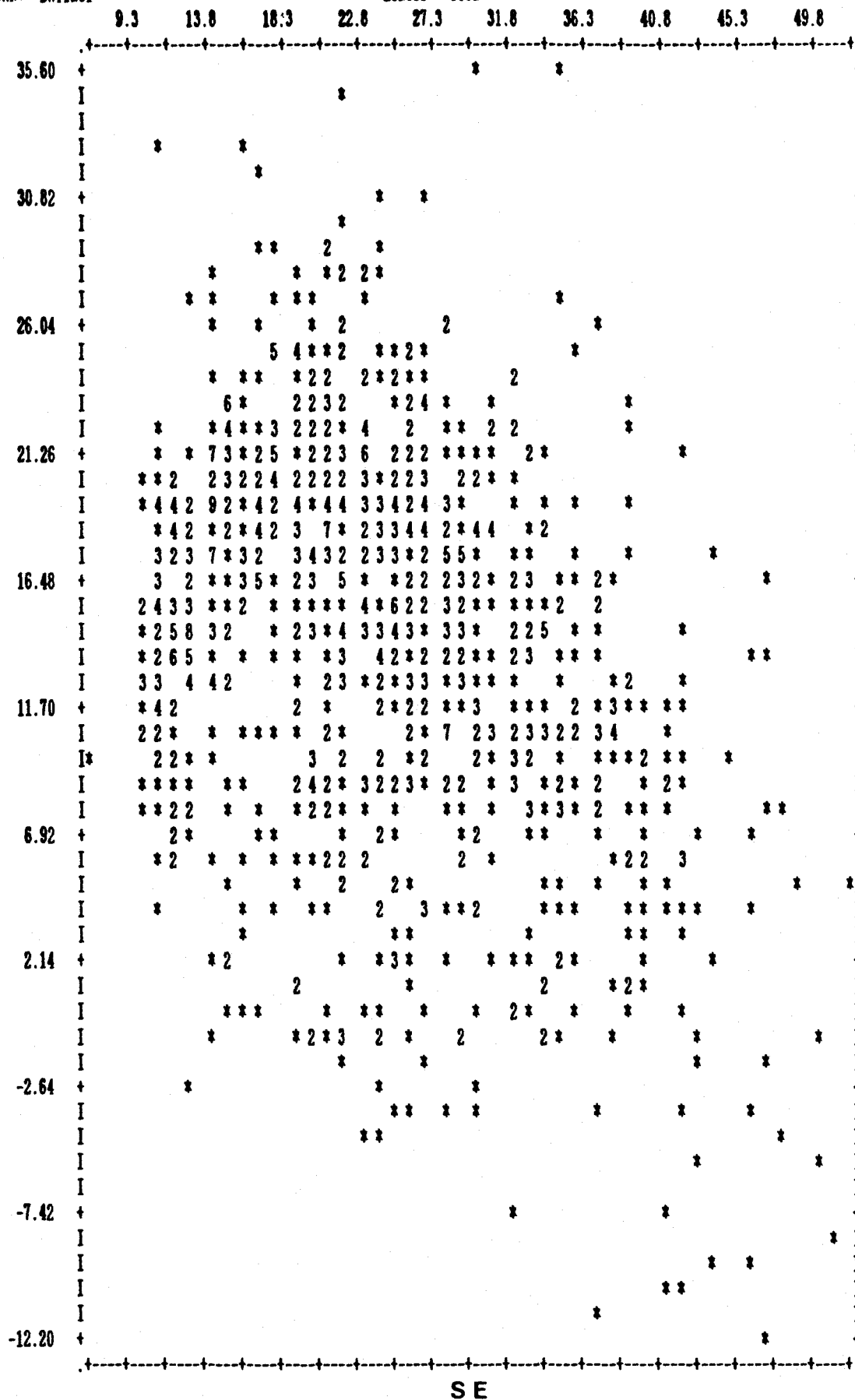


Figure 26. Scatterplot showing relationship between culmen length (OCUL, cm X 10) and daily growth rate (DWTINC1, g/d X 10) for Tricolored Herons.

DOWN: DWTINC1

ACROSS: OCUL

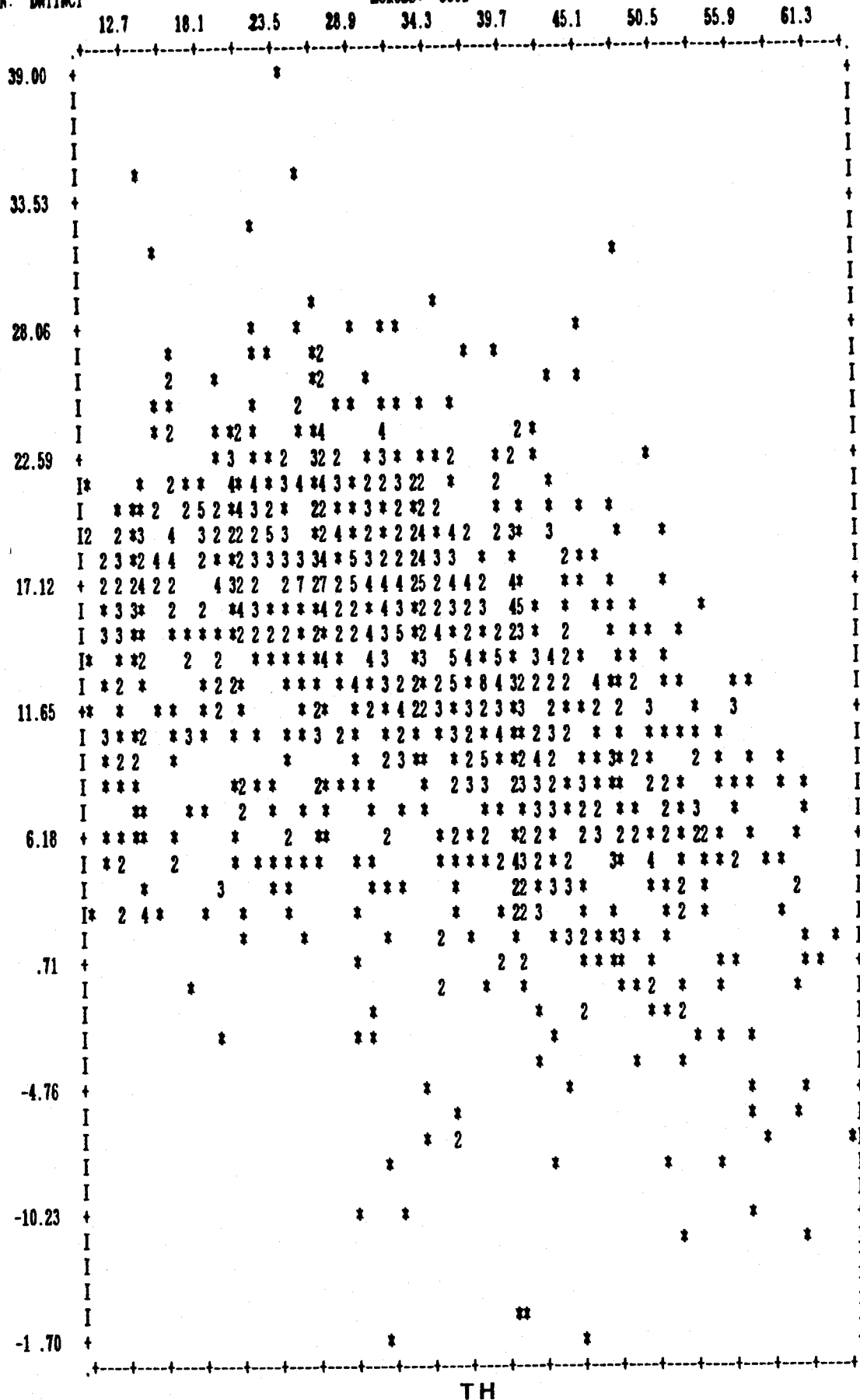


Figure 27. Scatterplot showing relationship between culmen length (OCUL, cm X 10) and daily growth rate (DWTINC1, g/d X 10) for Little Blue Herons.

DOWN: DWTINCI

ACROSS: OCUL

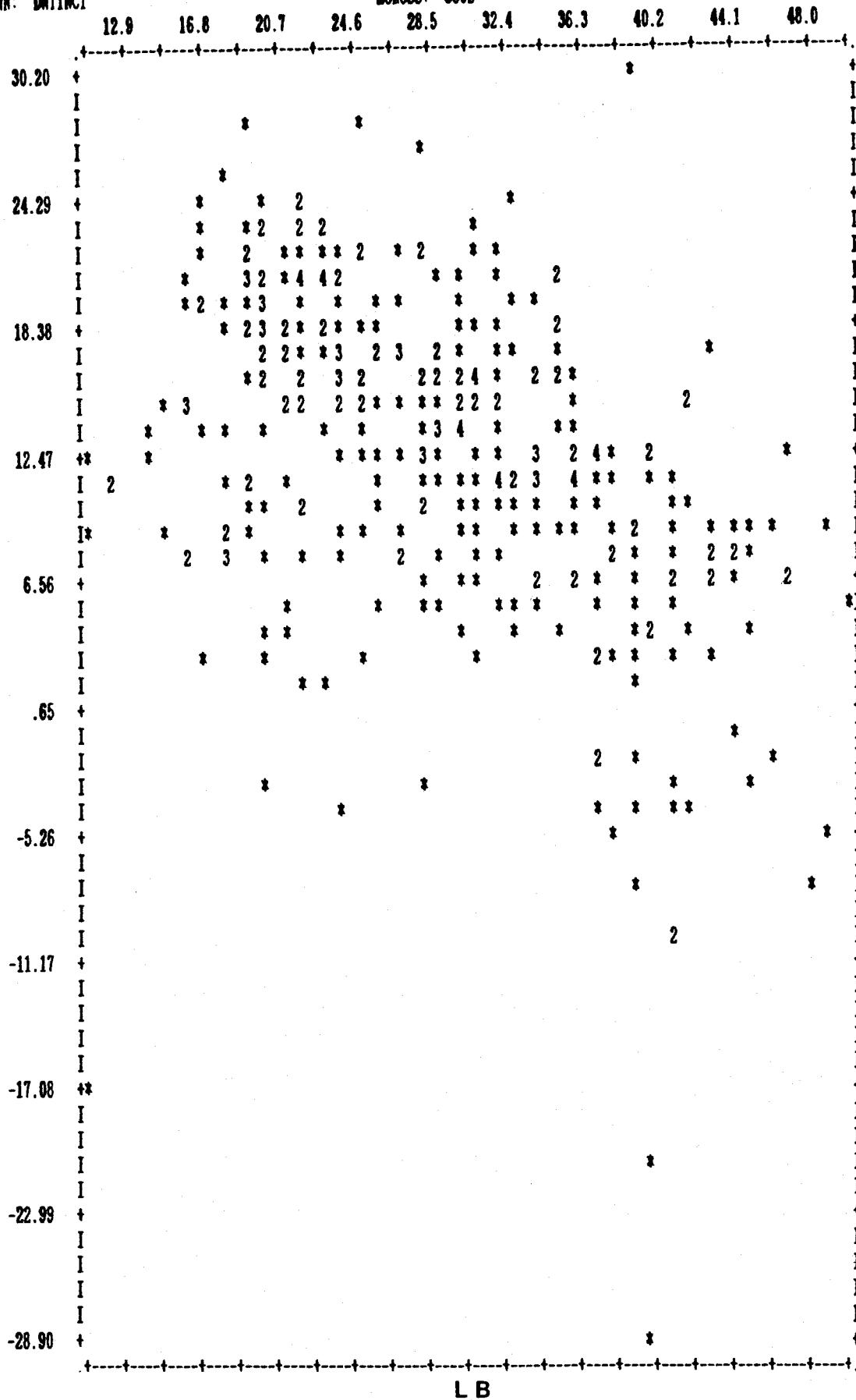


Table 23. Results of stepwise regression model of heron growth

Heron Species	¹ model	b	SE	F	P
Great Egret	Intercept	-6.838	2.2231	-3.076	0.002
	OCUL	1.931	0.1190	16.227	<0.0001
	OCULSQ	-0.026	0.0015	-17.591	<0.0001
² Model F = 169.17, P<0.0001, R = .24					
Snowy Egret	Intercept	12.172	1.5666	60.362	<0.0001
	OCULSQ	-0.018	0.0023	62.930	<0.0001
	OCUL	0.633	0.1198	27.908	<0.0001
	HTCHSEQ	-0.842	0.2321	13.145	0.0003
² Model F = 75.09, P<0.0001, R = .18					
Tricolored Heron	Intercept	11.452	1.3992	66.990	<0.0001
	OCULSQ	-0.010	0.0011	85.075	<0.0001
	OCUL	0.595	0.0956	38.802	0.0010
	HTCHSEQ	-0.797	0.2406	10.973	0.0027
	OWT	-0.023	0.0077	9.044	<0.0001
² Model F = 94.78, P<0.0001, R = .25					
Little Blue Heron	Intercept	4.361	4.0330	1.169	0.2803
	OCULSQ	-0.023	0.0044	28.253	<0.0001
	OCUL	1.269	0.2833	20.057	<0.0001
	OWT	-0.043	0.0140	9.550	0.0022
	HTCHSEQ	-0.808	1.3979	4.123	0.1430
² Model F = 35.52, P<0.0001, R = .28					

¹

Model predicts daily growth increase (gms) using the following variables:

²

OCUL = culmen length (cm) at first measurement; OCULSQ = (OCUL) ;

OWT = weight at first measurement (gm), HTCHSEQ = order of hatching (1,2,3).

conditions or the competitive environment, affects the growth of Great Egrets. Position in the clutch has an effect on the smaller species, although in no case did the current competitive situation with respect to siblings have an effect. Previous growth conditions did affect the current growth of Tricolored and Little Blue Herons.

Multivariable equations, using these variables, model the inherent growth pattern of the species during our study period. Residual variation around the model may reflect differing environmental conditions. Standardization of the residuals for individual birds, linearizes the scatter plot (Figs. 28 - 31) allowing comparisons among individuals and therefore nesting episodes irrespective of the developmental stage of the birds when they were studied. Figure 32 shows the success of standardization in normalizing the residuals; in each case the residuals are not normally distributed.

We tested the hypothesis that residual variation was related to environmental conditions by evaluating the variation among nesting episodes within species. In confirmation of this hypothesis, we found that the standardized residuals differed significantly among nesting episodes (Table 24).

It is likely therefore that residuals can be used to reflect differences in the success of nesting episodes. These mean episodic residuals are shown in Table 25. The results of Duncan range tests are also displayed and based on those results nesting episodes were assigned to categories representing high, intermediate, and low growth rates as indicated in Table 26. In

Figure 28. Scatterplot showing relationship between culmen length (OCUL, cm X 10) and z-transformed residuals of daily growth (ZRDWT) for the Great Egret. ZRDWT are residuals from the multivariate model of biomass growth against culmen and culmen squared (see Table 23).

DOWN: ZRDW7

ACROSS: OCUL

	15.1	21.4	27.7	34.0	40.3	46.6	52.9	59.2	65.5	71.8	
2.879205	+	*	*								+
I	I			*					*		I
I	I		*								I
I	I										I
I	I			**		* 2					I
2.277045	+		*				*				+
I	I		*		**	*			**		I
I	I		*	**	** *						I
I	I			*		*		*			I
I	I	*		* 2	*			*	*		I
1.674884	+	*	*	2	3	**		*	*	*	+
I	I		2		** *	*	*	*	**		I
I	I		**	** *	* 2*	**	*		**	*	I
I	I	*	**	*	* 2	** *	2	*	*		I
I	I	*	*	2*	* 4	**	3	**	*	**	I
1.072723	+	**	*	3	4*	24	** 2	*	*	*	+
I	I	*	2	**	* 3	**	3	22	* 2	**	I
I	I	**	*	* 2	**	2	**	**	* 3	2	I
I	I	*	** 3	*	**	2*	2	5	2	* 2	I
I	I	**	*	* 2	**	2	32	2	2*	2	I
.470563	+	2	2	4*	*	2	* 2	* 2	* 4	22	+
I	I	2	5*	3	2*	2*	**	3*	* 2*	2	I
I	I	* 2*	*	**	2	2	* 2	**	* 2	33	I
I	I	* 3	* 2	* 2*	*	* 2	32	**	**	32	I
I	I	2	* 2	**	**	3	22	**	* 3	22	I
-1.131598	+	*	**	**	3*	2	3	*	*	*	+
I	I	**	**	*	*	*	*	*	*	*	I
I	I	*	*	2	*	*	*	*	*	*	I
I	I	2	3	2	2*	*	*	*	*	*	I
I	I	*	*	*	*	*	*	*	*	*	I
-1.733758	+	* 3	2	**	* 2	2	2	**	*	*	+
I	I	* 2	*	*	* 2*	**	**	* 2*	* 2*	3	I
I	I	* 2	2*	**	*	**	*	*	*	*	I
I	I	*	*	2*	22	*	2	*	3*		I
I	I	**	*	**	2	*	*	*	*	*	I
-1.335919	+	**	*	**	2	2	*	*	*	*	+
I	I	2	*	*	*	*	2	*	*	*	I
I	I	*	* 2	**	*	**	2	*	*	*	I
I	I	*	*	*	*	*	2	**	*	*	I
-1.938080	+			2		*	*	*	*	*	+
I	I	2	*	*	**	*	*	*	*	*	I
I	I	*	*	*	*	*	*	*	*	*	I
I	I	*	*	*	*	*	*	*	*	*	I
-2.540240	+				*	*	*	*	**	*	+
I	I				*	*	*	*	*	*	I
I	I		*		*	*	*	*	*	*	I
I	I		*		*	*	*	*	*	*	I
-3.142401	+		*								+

GE

Figure 29. Scatterplot showing relationship between culmen length (OCUL, cm X 10) and z-transformed residuals of daily growth (ZRDWT) for the Snowy Egret. ZRDWT are residuals from the multivariate model of biomass growth against culmen, culmen squared and hatching order (see Table 23).

DOWN: ZRDWT

ACROSS: OCUL

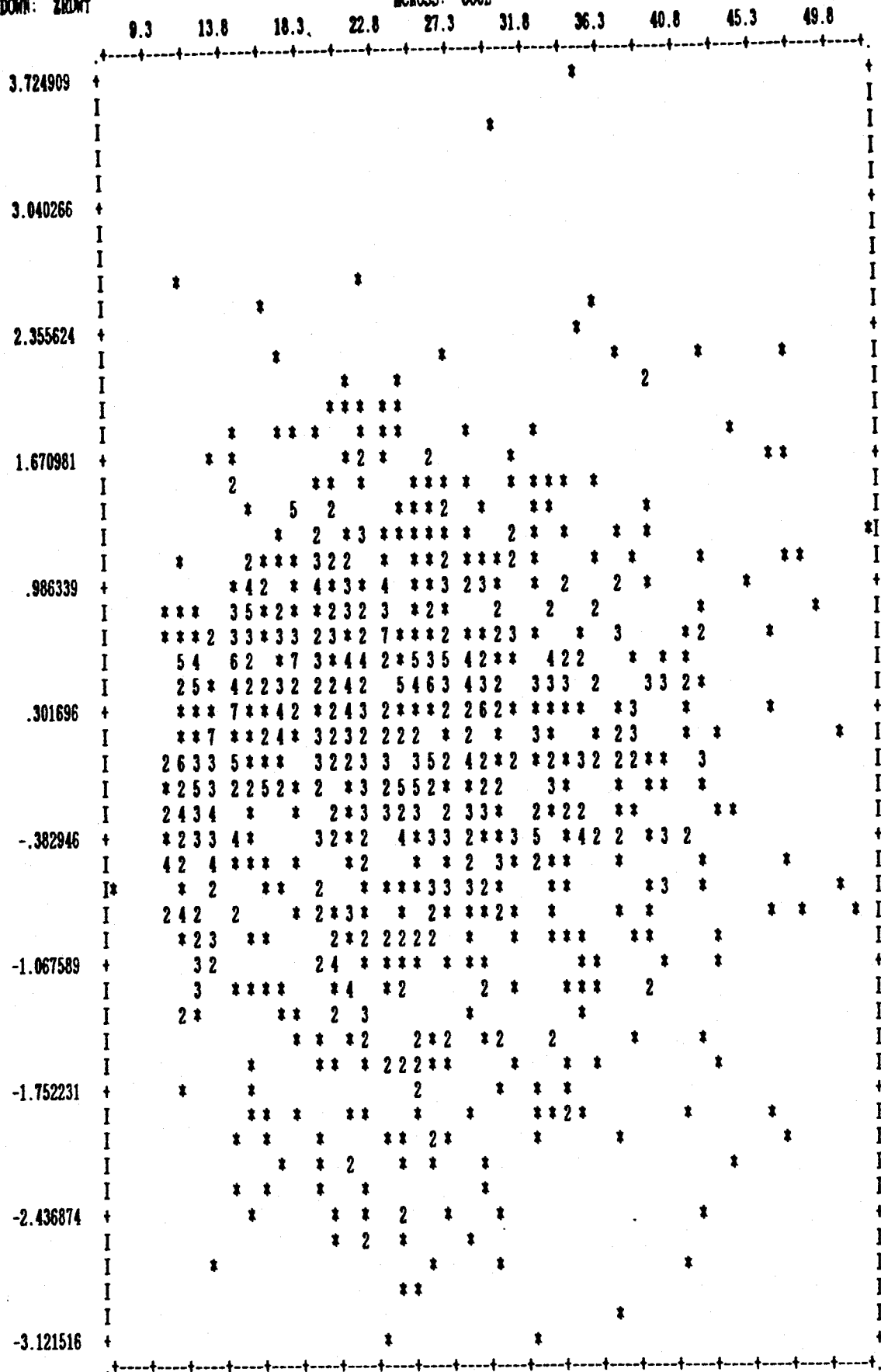


Figure 30. Scatterplot showing relationship between culmen length (OCUL, cm X 10) and z-transformed residuals of daily growth (ZRDWT) for the Tricolored Heron. ZRDWT are residuals from the multivariate model of biomass growth against culmen, culmen squared, hatching order, and original weight (see Table 23).

ACROSS: OCUL

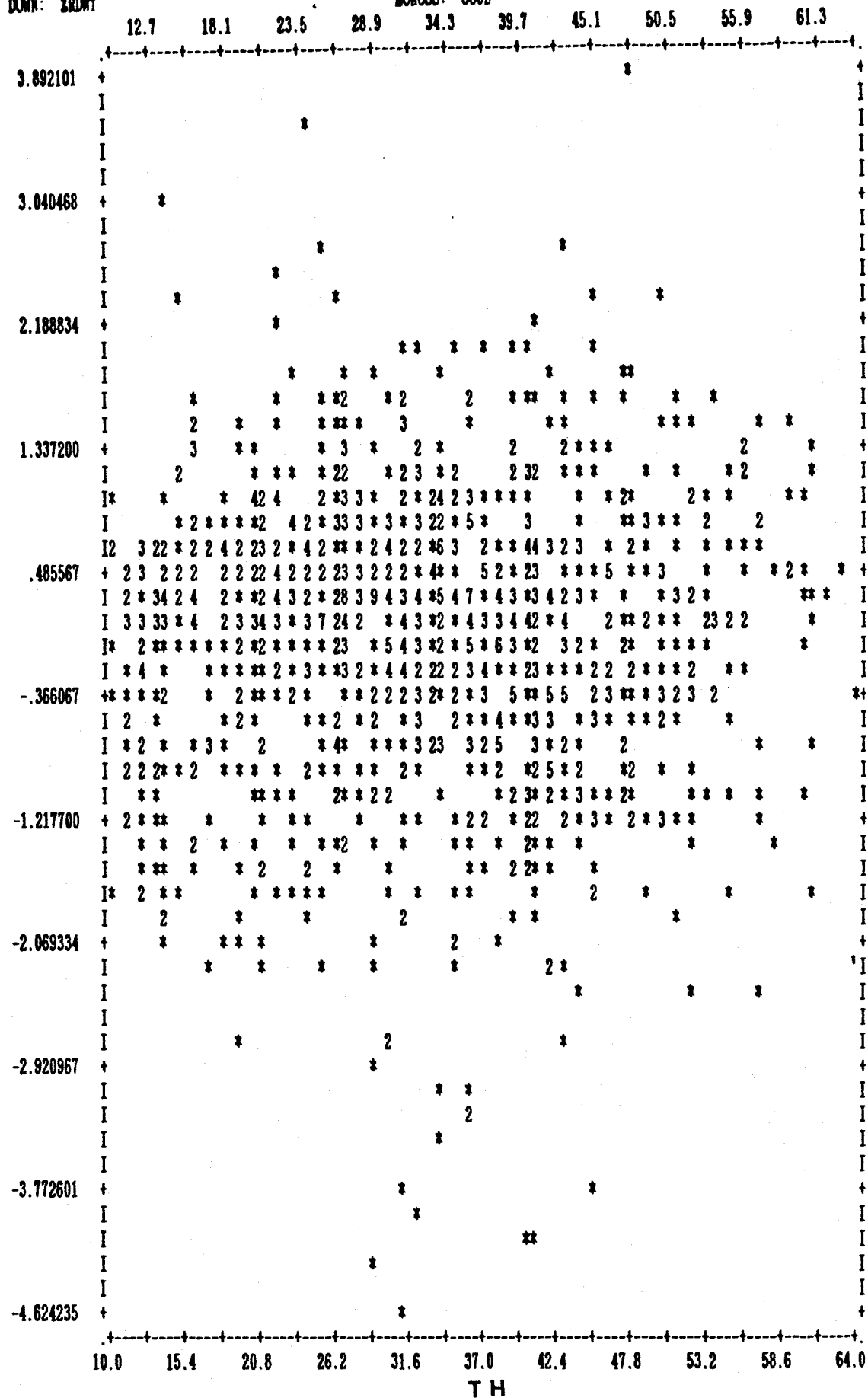


Figure 31. Scatterplot showing relationship between culmen length (OCUL, cm X 10) and z-transformed residuals of daily growth (ZRDWT) for the Little Blue Heron. ZRDWT are residuals from the multivariate model of biomass growth against culmen, culmen squared, hatching order, and original weight (see Table 23).

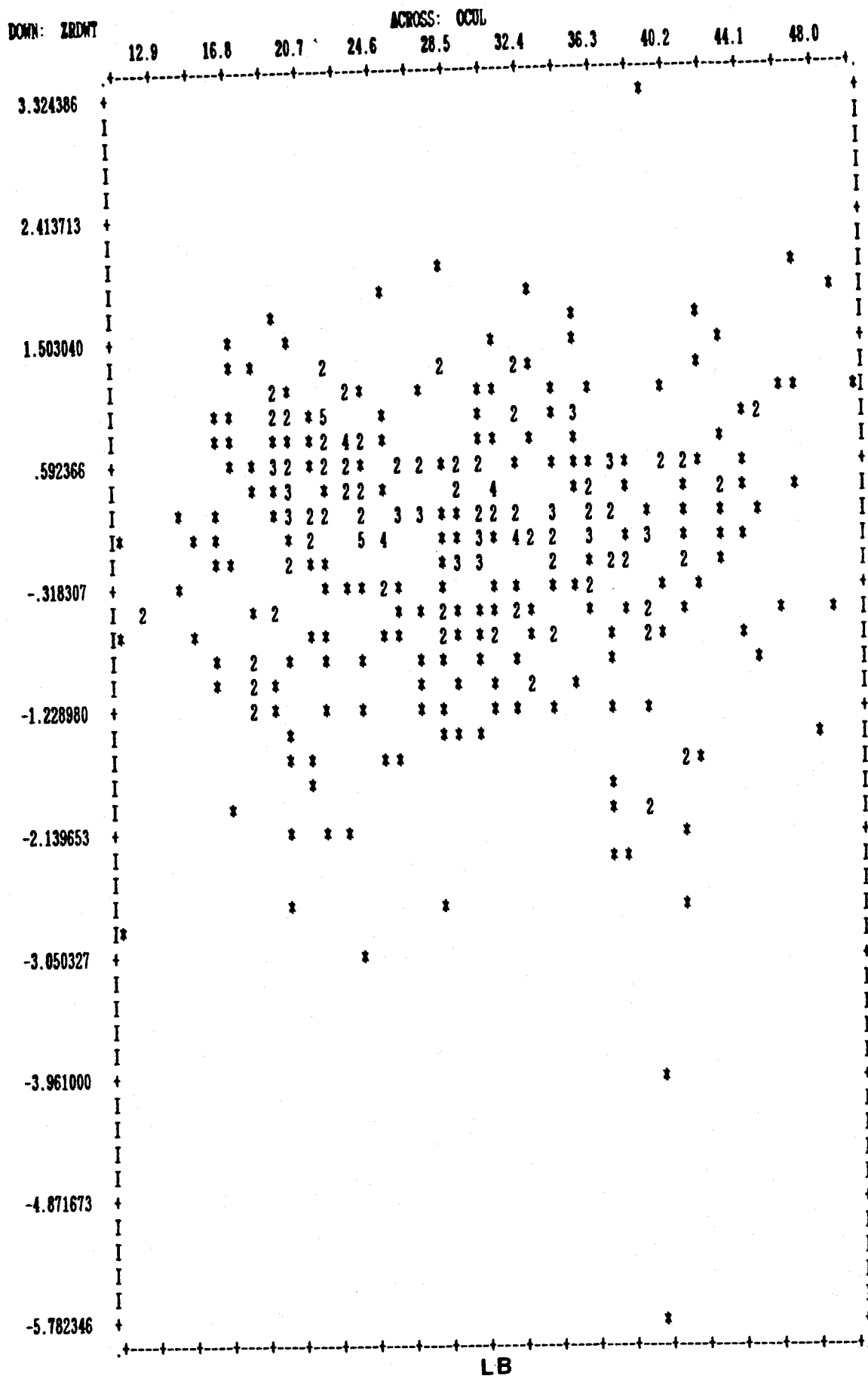
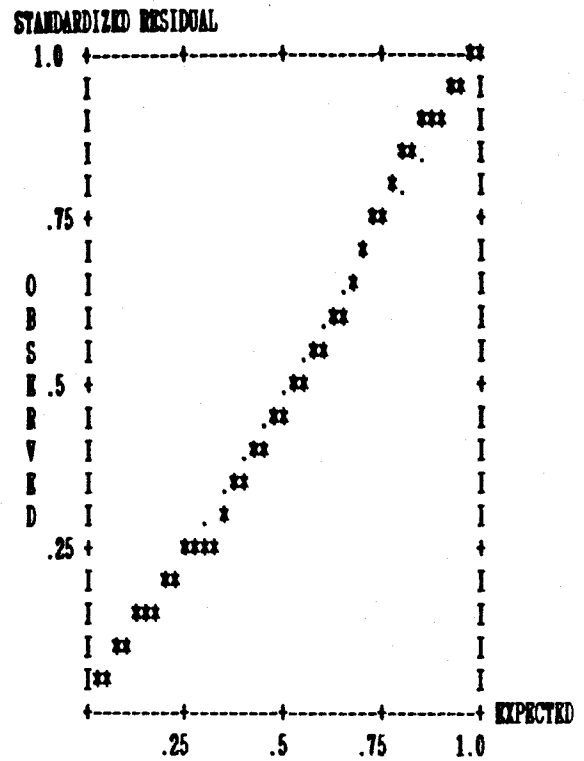


Figure 32. Plots demonstrating the normalization of growth residuals by z-transformation. Observed residuals are plotted against residuals expected from a normal distribution. Normality is shown the linearity of the plot.

SE



TH

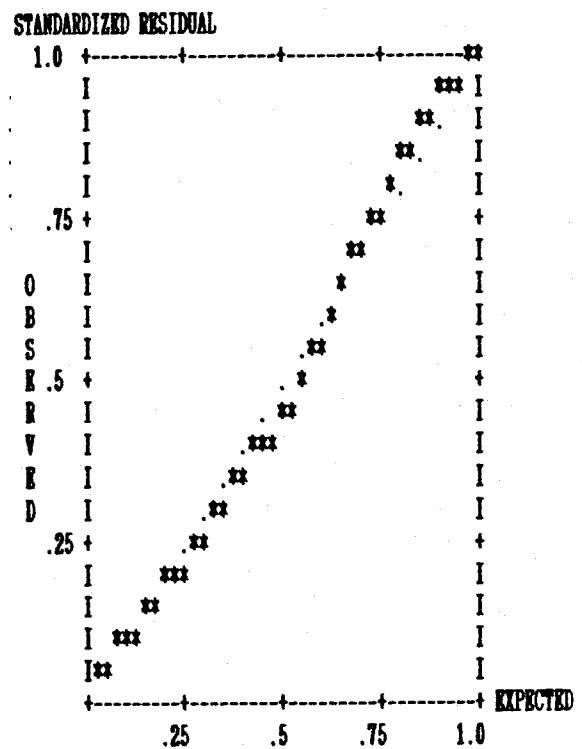


Table 24. Number of cases (N), mean and standard duration (s.d.) of standard residual of daily weight increase among herons and nesting episodes. Vertical bars connect means which are not significant at $\alpha=0.05$ using Duncan procedure.

Heron Species	Nesting Episode	Standardized Residuals		
		mean	s.d.	N

Great Egret

LA79A	.396	.8731	139
AN81	.361	.860	129
RO79A	.343	.7135	129
RO78A	.294	.8162	120
AN79A	.090	.9305	160
LA78	-.314	.7162	40
FR78B	-.355	.9260	51
RO80	-.392	1.0619	84
FR78A	-.562	.7780	112
AN79B	-.618	.9982	50
LA80	-.845	.9722	160

Snowy Egret

AN81	.691	.7190	135
LA79A	.320	.6661	50
FR79	.311	.8300	80
RO78A	.177	.6979	220
LA78	.029	1.0004	75
AN79B	-.015	.9671	51
RO79A	-.017	.7797	84
LA80	-.356	.8934	62
RO81	-.396	.9786	148
FR78A	-.443	.9160	64
FR78B	-.527	.6546	9
LA79B	-.742	1.2631	17
RO78B	-1.362	.7229	17

Tricolored Heron

AN81	.744	.7292	126
RO79A	.356	.6649	99
FR79	.351	.8093	84
LA79A	.294	.6686	35
RP79	.092	.3459	13
RO78A	.084	.6432	17
RO80	.041	.7940	104
AN79A	-.044	.4830	27
AN80	-.048	.7891	154
LA78	-.076	.8903	131
LA80	-.085	.9370	64
LA78	-.092	.5243	48
HH80	-.193	.9835	68
RO79B	-.265	1.0460	17
HH79	-.336	.6642	21
AN79B	-.585	.8395	58
RO78B	-.778	.8579	45
LA79B	-.838	1.1954	24

Little Blue Heron

AN81	.504	.6419	94
HH79	.240	.8470	27
FR79	.187	.7280	86
RO78	.100	.7736	42
RP79	-.210	.9185	41
HH80	-.504	.9686	34
OW78	-.556	.5599	17
LA78A	-.633	.9652	16

139

individuals
on 139
X 139

Table 25. Within species comparisons of the mean standardized residuals for different nesting episodes using one-way analyses of variance.

Species	MS Groups	df	MS Error	df	F	P Level
GE	16.5260	10	.7573	1034	21.8232	< 0.001
SE	14.2321	12	.7037	999	20.2241	< 0.001
TH	9.6856	17	.6459	1117	14.9950	< 0.001
LB	7.1149	7	.5999	349	11.8605	< 0.001

Table 26. Groupings of nesting episodes.

Heron Species	Success	Nesting Episode	
		Mortality	Growth
GE	Higher	LA79A	LA79A
		AN81	AN81
		RO79A	RO79A
		RO78A	RO78A
	Intermediate		AN79A
		AN79A	RO80
		FR78B	FR78B
		FR78A	LA78
	Lower	RO80	
		LA78	FR78A
		AN79B	AN79B
		LA80	LA80
SE	Higher	AN81	AN81
		LA79A	LA79A
		FR79	FR79
		RO78A	RO78A
	Intermediate	AN79B	
		RO79A	
		LA78	LA78
		RO78B	AN79B
	Lower	FR78B	RO79
		LA80	LA80
		RO80	RO81
		FR78B	FR78A
TH	Higher	LA79B	FR78B
			RO78b
			LA79B
		AN81	AN81
	Intermediate	HH79	RO79A
		RO79B	FR79
		RP79	LA79A
		RO78B	RP79
	Lower	LA78	RO78A
		RO78A	RO80
		AN79B	AN79A
		LA79A	AN80
LB	Higher	RO79A	LA78
		AN79A	LA80
		FR79	SA78
		HH80	HH80
	Intermediate	SA78	RO79B
		LA80	HH79
		RO80	AN79B
		AN80	RO78B
	Lower	LA79B	LA79B
		AN81	AN81
		HH79	HH79
		FR79	FR79
	Higher	OW78	
		RO78A	
		RP79	RP79
		HH80	HH80
	Intermediate	LA78	LA78
	Lower		

all cases nesting episodes in the higher categories exhibited positive residuals (ie, greater than the average represented by the regression model. The lower category represented negative residuals. The intermediate category also represented negative residuals, with the exception of LA78 for Snowy Egrets. These results suggest that analyses of residual growth rates may be used to evaluate the success of nesting.

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The growth rate categories show a remarkable general agreement with similar categories erected based on mortality data (Table 26). For Great Egrets, Snowy Egrets, and Little Blue Herons, the few nesting episodes not classified in the same way were shifted between the adjacent category, and the growth rates associated with them were not significantly different from those in both adjacent categories. Given the tenuousness of the mortality data and the small sample size from some nesting episodes the agreement is encouraging. Unfortunately this is not the case for Tricolored Herons, which show considerable divergence between classifications schemes. Small sample size, the inclusion of a numberd small nesting episodes, late nesting, and the substantial overlap of groups of growth rates that are not significantly different from each other all may have lead to the difficulty in distinguishing among categories. Also the intermediate categories for Tricolored Herons were characterized by both low growth rates (negative residuals - Table 26) and relatively low measured mortality.

high

The results obtained from analyses of mortality and growth of Everglades herons suggest that considerable variability existed among nesting episodes. The results obtained from consideration of hydrology, food availability, and food consumption suggest that environmental conditions appear to impact growth and nesting success.

We investigated these potential inter-relationship by examining the correlations between daily growth rates and 23 variables representing several aspects of the environment affecting heron nesting success in the Everglades. Growth rates were described by the mean standardized residuals, as discussed above. Four groups of variables represented both hydrology (water depth and recession rates) and food (availability and consumption). The overall correlation matrix is given in Table 27.

Water depth variables included current water depth at the guaging station (on the same date as growth data were collected, STADEP) and the water depth at the food availability station (YDEPTH). Other stage variables were the average monthly station water depth in February, March, April, and May (YFEB, YMAR, YAPR, YMAY). We also looked at average water depth in May and at the food station after z-transformation to the mean water depth February-July (ZMAY, ZSTADEP). This was done in an attempt to make the stage fluctuations at various stations more equivalent. Although correlations were high, interpretation is difficult

Table 27. Correlation matrix of environmental variables versus mean standardized residual growth rate.

Environmental Parameter	Variable	Correlation Coefficient			
		GE	SE	TH	LB
Water Depth	YFEB	-0.271	0.088	-0.114	0.210
	YMAR	-0.408	-0.024	-0.225	-0.253
Recession Rates	YAPR	-0.539	-0.157	-0.273	-0.426
	YHAY	-0.469	-0.360	-0.561	-0.521
	ZHAY	0.505	0.434	0.468	0.497
	ZSTADP	0.681	0.560	0.372	0.436
	YDEPTH	-0.048	-0.074	-0.086	-0.024
	STADP	-0.630	-0.399	-0.455	-0.502
	REC7	-0.347	-0.394	-0.288	-0.360
	YRECFM	-0.355	-0.035	-0.163	-0.433
	YRECHAR	-0.562	-0.296	-0.386	-0.604
	YRECAPR	-0.560	-0.456	-0.438	-0.594
Food Avail- ability	YRECHAY	-0.015	-0.259	-0.380	-0.427
	DISTANCE	-0.085	-0.001	-0.089	-0.263
	LOGFISH	0.597	0.318	0.468	0.558
	LOGMASS	0.483	0.595	0.531	0.431
Food Eaten	YLGLN	-0.020	0.528	0.288	0.087
	MEANLLN	0.383	-0.154	-0.387	-0.452
	MEANLWT	0.363	-0.331	-0.407	-0.462
	ASP 1	-0.224	0.227	-0.392	0.210
	ASP 2	-0.406	-0.031	0.121	---
	ASP 3	---	-0.505	-0.185	---
	ASP 4	---	---	-0.331	---
	ASP 6	---	---	---	0.429
	ASP 21	---	---	---	-0.413
	ASP 22	-0.224	0.262	---	0.467
	ASP 41	0.293	---	---	---

because standardization rendered absolute depth changes incomparable among stations (ie, a 1 cm fall at one station no longer represented 1 cm fall at another),

In general, station water depth variables were negatively correlated with growth rates. This indicates that the shallower the water depth in the Everglades during nesting the better the nesting success. Current station depth was highly correlated with growth, indicating an important real time component to the beneficial impact of shallow water levels (low stages). That is shallow depths create concurrent high growth rates. February water depth was not highly correlated, because it was prior to nesting and also because relatively high water prevailed prior to nesting during most years of the study. Only the water depths associated with the AN81 nesting episode were relatively low, and correlated with the best nesting episode recorded.

The growth of Great Egrets was highly correlated with low water depths in April whereas Tricolored and Little Blue heron growth was correlated with low water depths in May. This result reflects the earlier nesting of Great Egrets. Depths at the food station did not correlate highly, because the depths chosen by feeding herons were uniformly shallow and minimally variable.

Shallow water depths are caused by the drop of water levels, so we investigated the correlations of several recession rates: the mean recession during the seven days preceeding collection of growth data (REC7); the mean recession rate from February through May, the usual drying season (YRECFM); and the mean recession rates in each month February through May (YRECFEB, YRECMAR,

YRECAPR, YRECMAY). All recession rates were negatively correlated with heron growth. The faster the drying, the better the nesting. Which rates were most important varied among species. For Great Egrets recession rates in March and April were most important, reflecting their early nesting. May recession rate was not highly correlated because in years of high growth rates nesting was completed by May. The highest correlations for Snowy Egrets and Tricolored Herons were for April, indicating the importance of this part of the dry season for these species. All recession rates were highly correlated with growth of Little Blue Herons, which not only indicates the importance of drying to that species but also reflects its extended nesting season.

Food availability was measured by the distance for the feeding site from the colony (DISTANCE), the mean number of prey per m² (LOGFISH), the mean biomass per m³ (LOGMASS), and mean length of fish (YLGLN), the latter three log transformed for normality. The number and biomass of available food were highly correlated with growth rates of Great Egrets, Tricolored Herons, and Little Blue Herons. The greater the number and biomass of food available the greater the growth rates. Biomass and prey length available correlated most highly with growth of Snowy Egrets. The small negative correlation between fish length and the growth of Great Egrets suggests that large fishes do not enhance nesting success of this species. This is important because this heron can eat relatively large prey.

Distance between the colony and the feeding site was not correlated with growth rates. Thus this does not seem to be an important factor in the nesting of Everglades herons. Presumably,

the distances traveled (which can be over 30 km) did not affect 126
nesting.

The effect of the diet actually consumed by herons was evaluated using several variables. Overall diet quality was evaluated by mean length of prey items and mean weight of prey items taken (MEANLLN, MEANLWT), both log transformed. Additionally we evaluated the proportion of the total daily diet composed of the four prey most important in the overall diet, evaluated by biomass. All proportions were arcsine transformed for normality. For the Great Egret the species were mosquitofish (ASP1), sailfin molly (ASP2), prawns (ASP22), and spotted sunfish (ASP41). For the Snowy Egret, the prey species were mosquitofish, sailfin molly, sheepshead minnow (ASP3), and prawns. For the Tricolored Heron, the species were mosquitofish, sailfin molly, sheepshead minnow (ASP3), marsh killifish (ASP4). For the Little Blue Heron, the species were mosquitofish, least killifish (ASP6), crayfish (ASP21), and prawns.

The growth of Great Egrets was most highly correlated, negatively, with sailfin mollies and was also negatively correlated with prawns. Although these species made up important components of the diet, the Great Egrets did better when they were not abundant. Sailfin molly numbers were inversely correlated with sunfish numbers, suggesting that they did better where sunfish were taken, and in such places sailfin mollies and prawns were not taken or not available. Similarly the growth of Snowy Egrets were negatively correlated with proportion of sailfin mollies in the diet, again suggesting that this species represented relatively poor feeding conditions. Tricolored Heron

growth was negatively correlated with the proportion of marsh killifish in the diet. Little Blue Heron growth was negatively correlated with the proportion of least killifish and negatively correlated with the proportion of crayfish.

These correlations reveal much about the conditions necessary for high growth rates, and therefore successful nesting, in the Everglades. The bivariate correlations best demonstrate the independent relationships of each variable with growth rates. However it is useful to try to reduce the number of variables by eliminating co-correlations that arise because some of the variables inevitably vary together and so explain similar amounts of the residual variability of growth rates. To reduce covariation, we performed a series of stepwise multivariate regressions. For each heron species, four regressions were run, each on the variables within each of the four environmental categories (Table 28). Four regressions were run per species in order to maximize the number of cases used in that not all variables were available for all cases. For water depth, the contemporaneous water depth at the reference station was entered to provide an indication of present conditions, and then the more general and historical variables of monthly mean depth were entered based on their calculated tolerances in a stepwise fashion. Depth at the food availability site was not run owing to its poor bivariate correlation. For recession rates, the seven day rate was entered to account for present conditions, then the means over longer periods were entered stepwise according to tolerances. For food availability, mass was entered because it is the most encompassing variable, being composed of a combination of prey numbers and prey size. The other variables were then allowed

Table 28. Results of discriminant analyses for classification of the nesting episodes of four species of herons by mortality. Table shows the canonical correlation and significance for discriminant functions derived from the total set of environmental variables. Each analyses achieved 100% correct discrimination.

Heron Species	DF1					DF2				
	% Var.	Canonical Corr.	χ^2	df	p	% Var.	Canonical Corr.	χ^2	df	p
SE	66.64	0.991	143.34	32	<0.0001	33.36	0.982	65.09	15	<0.0001
GE	91.84	0.993	111.05	32	<0.0001	8.16	0.932	35.46	15	<0.01
TH	67.19	0.952	103.13	34	<0.0001	32.81	0.909	43.77	16	<0.001
LB	100.00	0.959	7.54	6	ns					

to enter if they explained additional variation. For food consumed, all variables were entered stepwise according to their tolerances. 129

The resulting regression equations provide an indication of the primary set of environmental variables that explain most of the residual variation of growth rates. The variables and their loading order are shown in Table 29. Variation in the growth of Great Egrets is best explained by current water depth, the current recession rate, March recession rate, the mass and number of prey available, and the proportion of sailfin mollies. Variation in the growth of Snowy Egrets is best explained by the current water depth, the mean water depth in May, the current recession rate, the recession rates in April, May, and in February-May, and biomass available and mean biomass of prey items consumed. Variation in the growth of Tricolored Herons is explained by the current water depth, the mean water depth in April, the current recession rate, the recession rates in April, May, and February-May, the proportion of marsh killifish in the diet, and the mean biomass of prey. Variation in the growth of Little Blue Herons is explained by the current water depth, the current recession rate, the recession rate in March, the biomass available, and the proportion of prawns consumed.

not
sign.

Thus overall the variation in growth rates of herons in the Everglades can be explained by current hydrological conditions (current depth and current recession rate), the biomass per cubic meter of prey available, and additional variables that include additional drying periods, and the species and length of prey consumed. These variables indicate the important environmental

Table 29. Results of multiple regression model of primary environmental variables on heron growth.

Heron Species	model ¹	b	SE	F	P
Great Egret	Intercept	-0.360	0.3468	-1.039	0.3101
	ASP2	-0.648	0.2690	-2.407	0.0249
	LOGFISH	0.379	0.1300	2.914	0.0081
	REC7	-0.250	0.1004	2.489	0.0209
	YRECHAR	-0.124	0.2402	-0.517	0.6104
	STADPE	0.006	0.0067	0.950	0.3522
	LOGHASS	-0.168	0.0776	-2.162	0.0418
2					
Model F = 5.76, P < 0.001, R = 0.61					
Snowy Egret	Intercept	-1.415	1.9930	-0.710	0.4857
	MEANLWT	-2.610	4.0298	-0.648	0.5242
	YRECAPR	0.034	0.3370	0.100	0.9214
	REC7	0.012	0.1804	0.066	0.9476
	YLGLN	0.630	0.6180	1.020	0.3194
	ASP3	-0.810	0.3669	-2.209	0.0384
	YMAR	0.020	0.0122	1.655	0.1127
	LOGHASS	0.028	0.1067	-0.261	0.7969
	STADPE	0.029	0.0160	-1.777	0.0900
2					
Model F = 3.79, P < 0.01, R = 0.59					
Tricolored Heron	Intercept	-0.075	0.3276	-0.229	0.8203
	MEANLWT	-2.262	2.2117	-1.023	0.3159
	YRECFM	-0.195	0.1587	-1.228	0.2305
	ASP4	0.190	0.2763	0.688	0.4978
	REC7	0.081	0.1064	-0.764	0.4516
	LOGHASS	0.045	0.0606	0.738	0.4672
	YMAI	-0.012	0.0113	-1.117	0.2742
	YRECAPR	0.007	0.2447	0.029	0.9772
	YRECHAY	-0.121	0.2638	-0.459	0.6502
	STADPE	0.008	0.0120	0.726	0.4743
2					
Model F = 4.30, P < 0.01, R = 0.60					
Little Blue Heron	Intercept	-0.425	1.2529	-0.339	0.7669
	ASP22	1.822	3.2412	0.562	0.6307
	YRECHAR	-2.268	0.9520	-2.382	0.1401
	REC7	0.918	0.5247	1.749	0.2223
	STADPE	0.022	0.0577	0.258	0.8204
	LOGHASS	0.027	1.2529	0.080	0.9438
2					
Model F = 2.62, P > 0.05, R = 0.87					

¹ Model predicts standardized residual (sresid) of daily growth increase using the primary environmental variables.

conditions required for successful nesting of herons in the Everglades and explain about 60% of the residual variability in growth rates (Table 29). Given the differing biology of the four species, it is encouraging that the same several hydrology and food availability variables correlate with a quantitative measure of nesting success. 131

The success of environmental variables in predicting nesting success can be assessed directly through discriminant function analysis. As an overall test of the hypothesis that environmental conditions can be used to predict nesting success, discriminant functions were developed using the entire array of environmental variables. Figures 33-35 provide representative results in discriminating among categories of nesting episodes classified by nestling mortality. The environmental variables provide 100% correct classification of episodes, proving conclusively that environmental determine nesting success. (Little Blue Herons were not run because of the small sample size relative to variables.)

To reduce the adverse analytical effects of attempting to load a large number of variables, we compressed the number of variables need to representing those conditions. We used the primary set of variables developed from within-category regression analyses. The discriminate functions loaded variables according to tolerances. The resulting two discriminate functions (one in the case of Little Blue Herons) clearly separated the nesting episodes classified either by mortality (Fig. 36-38, 42) or by growth residuals (Fig. 39-41, 42; Tables 30-33). In all cases the environmental variables correctly classified nearly all nesting episodes with respect to their nesting success. The

classification rates for growth categories were 94% for Great Egrets, 96.7% for Snowy Egrets, 88.9% for Tricolored Herons, and 100% for Little Blue Herons. The correct classification rates for mortality categories were 96.4% for Great Egrets, 90% for Snowy Egrets, 94.4% for Tricolored Herons, and 100% for Little Blue Herons.

The discriminating power of the environmental variables is impressive. Seldom has it been possible to be able to define so thoroughly the physical and biological conditions necessary for reproductive success. It is clear from our results that water conditions and the resulting pattern of food availability determine the nesting success of herons in the Everglades.

Figure 33. Plot of the values of two canonical discriminant function scores for Great Egret nesting episodes. Cases are identified by their mortality classification group (1-3). Asterisks indicate a group centroid. Numbers may represent more than one case. Analyses are based on the entire set of environmental variables.

CANONICAL DISCRIMINANT FUNCTION 1

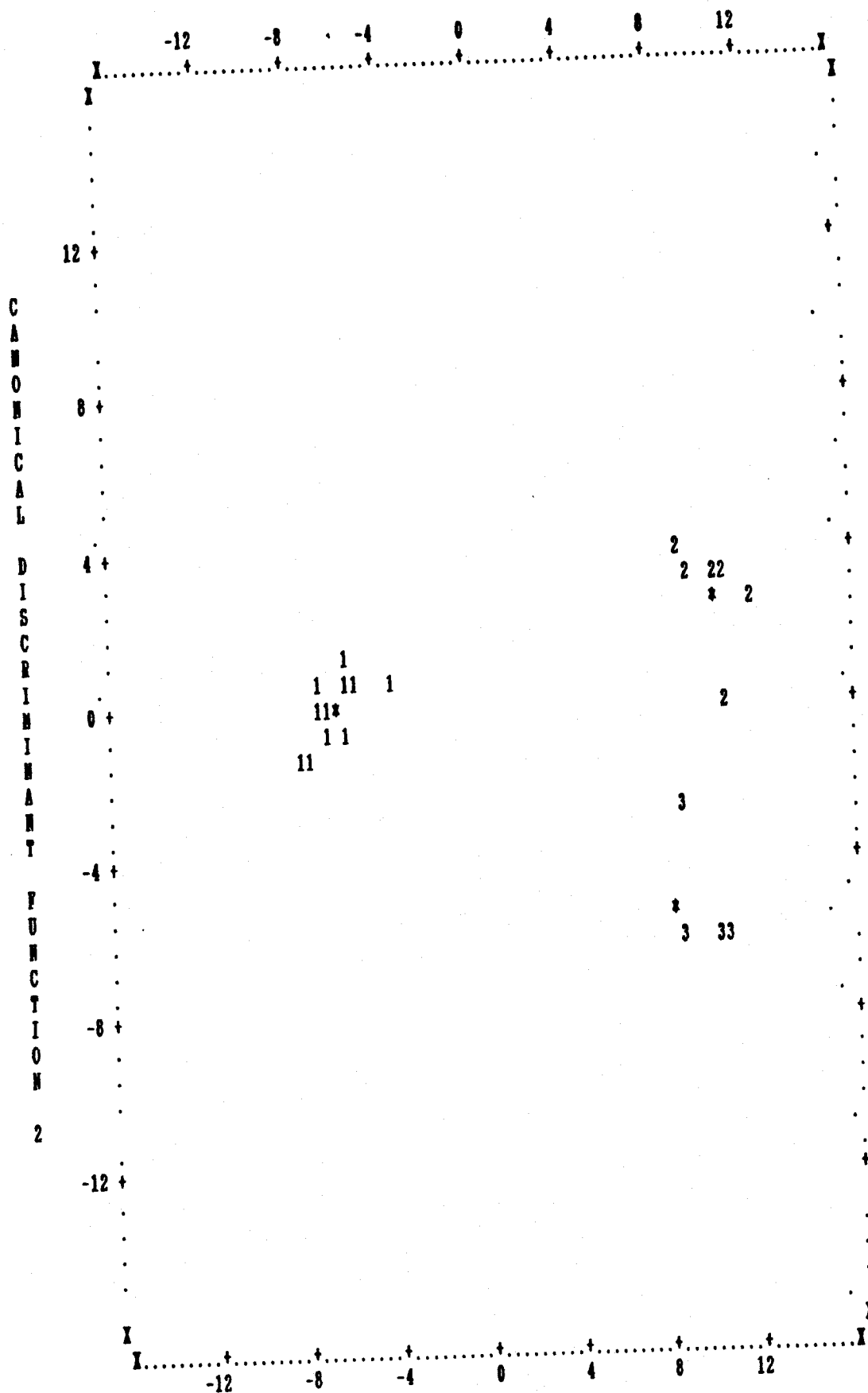


Figure 34. Plot of the values of two canonical discriminant function scores for Snowy Egret nesting episodes. Cases are identified by their mortality classification group (1-3). Asterisks indicate a group centroid. Numbers may represent more than one case. Analyses are based on the entire set of environmental variables.

CANONICAL DISCRIMINANT FUNCTION 1

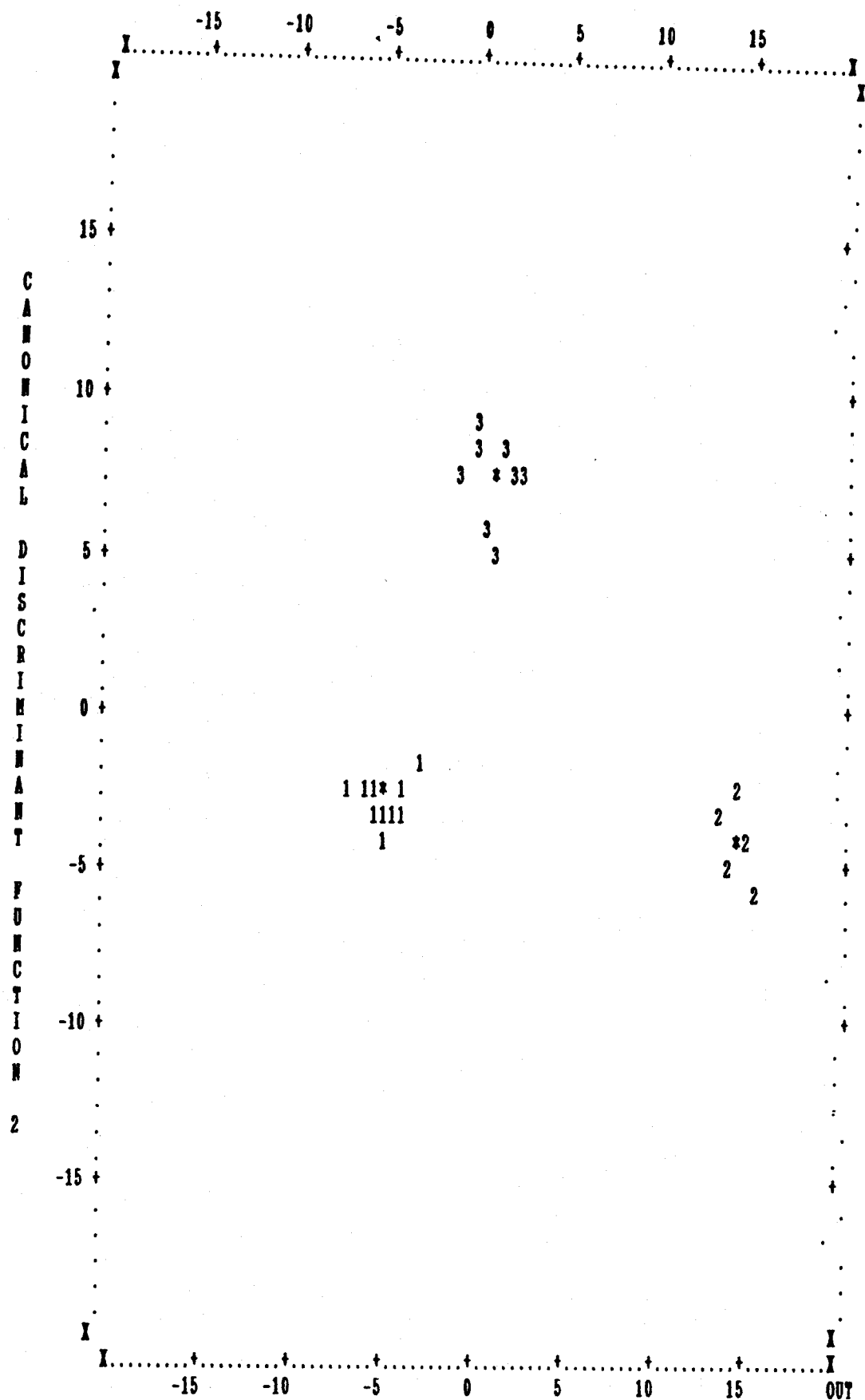


Figure 35. Plot of the values of two canonical discriminant function scores for Tricolored Heron nesting episodes. Cases are identified by their mortality classification group (1-3). Asterisks indicate a group centroid. Numbers may represent more than one case. Analyses are based on the entire set of environmental variables.

CANONICAL DISCRIMINANT FUNCTION 2

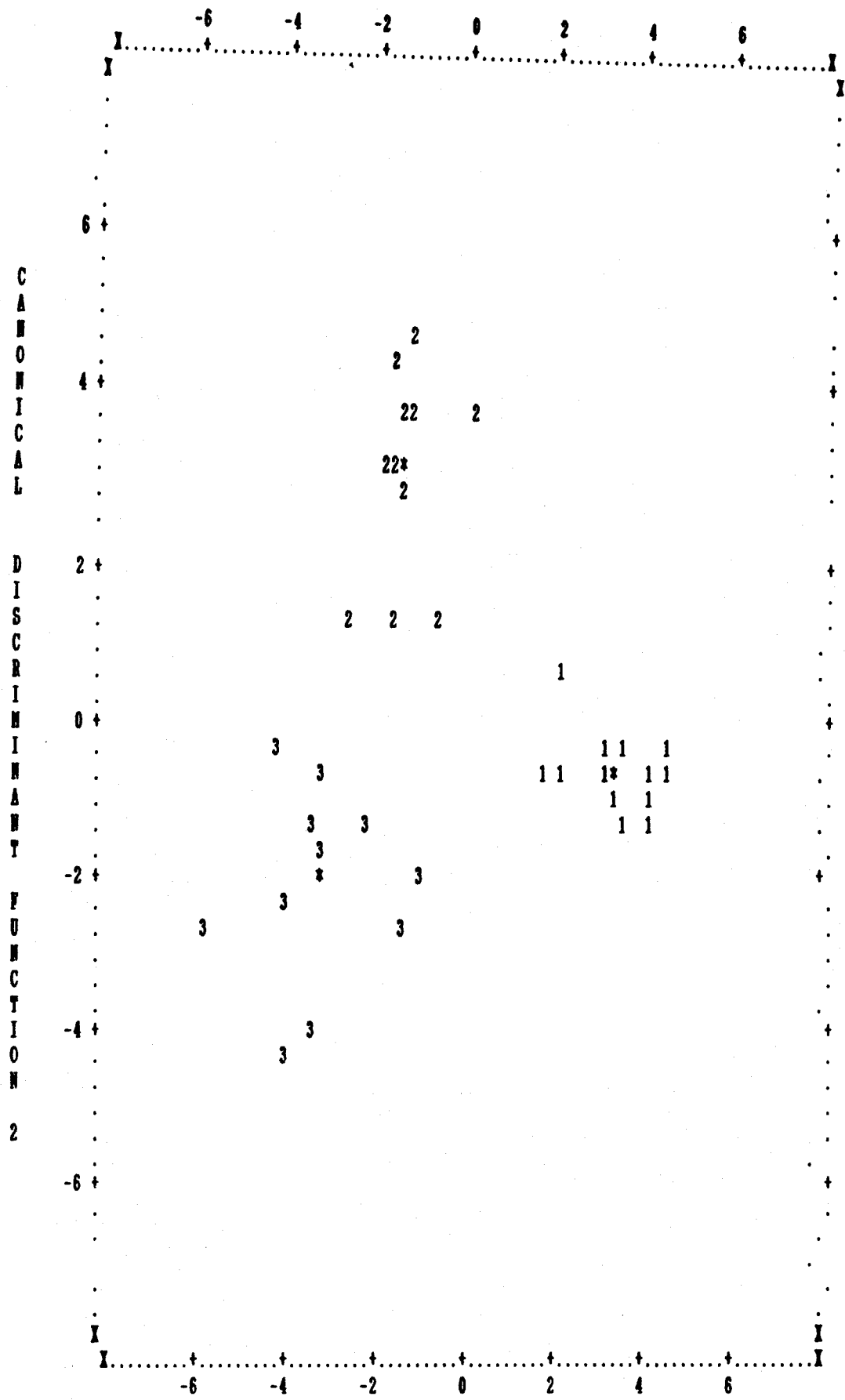


Figure 36. Plot of the values of two canonical discriminant function scores for Great Egret nesting episodes. Cases are identified by their mortality classification group (1-3). Asterisks indicate a group centroid. Numbers may represent more than one case. Analyses are based on the primary set of environmental variables.

CANONICAL DISCRIMINANT FUNCTION 1

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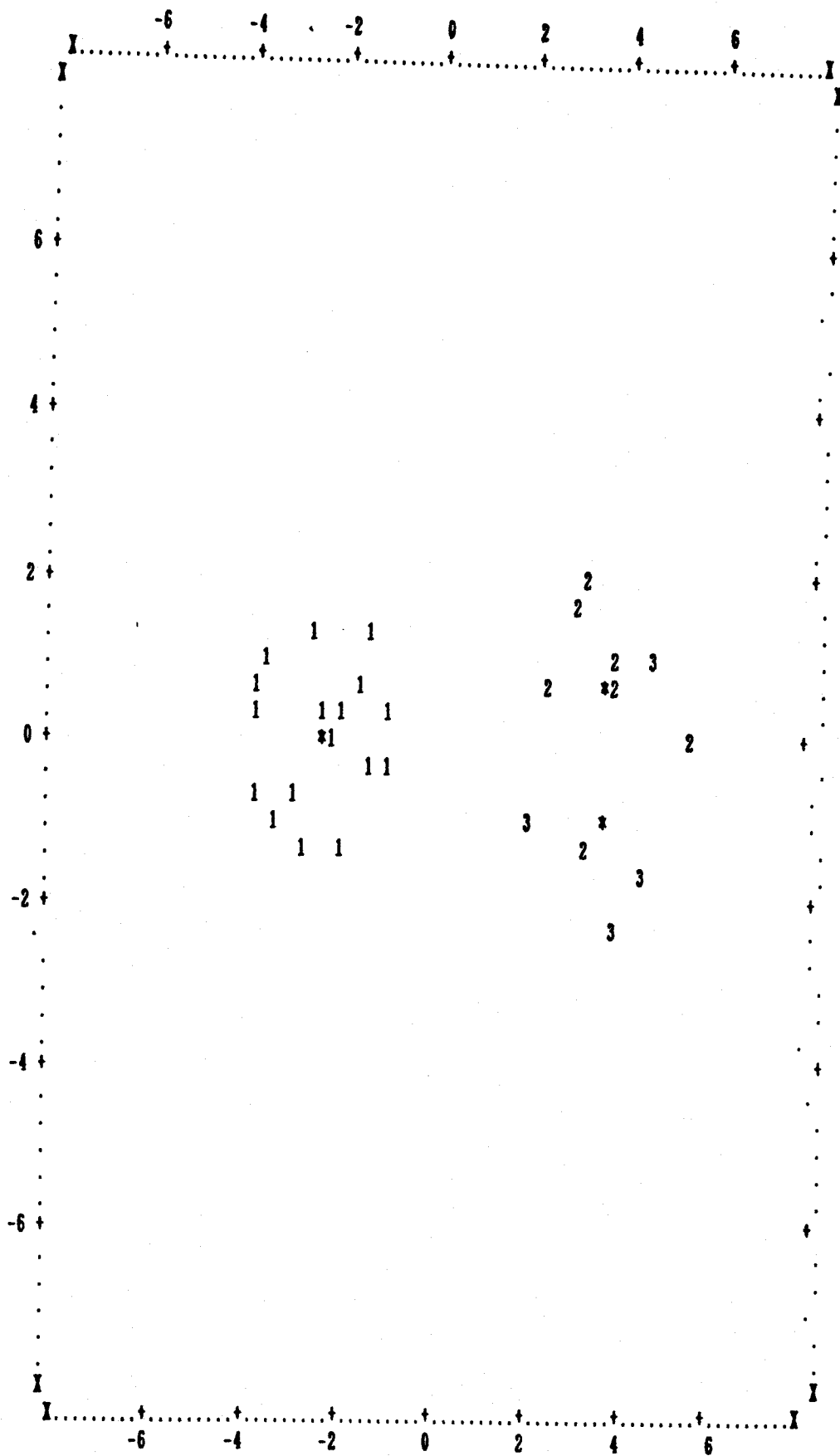


Figure 37. Plot of the values of two canonical discriminant function scores for Snowy Egret nesting episodes. Cases are identified by their mortality classification group (1-3). Asterisks indicate a group centroid. Numbers may represent more than one case. Analyses are based on the primary set of environmental variables.

CANONICAL DISCRIMINANT FUNCTION 1

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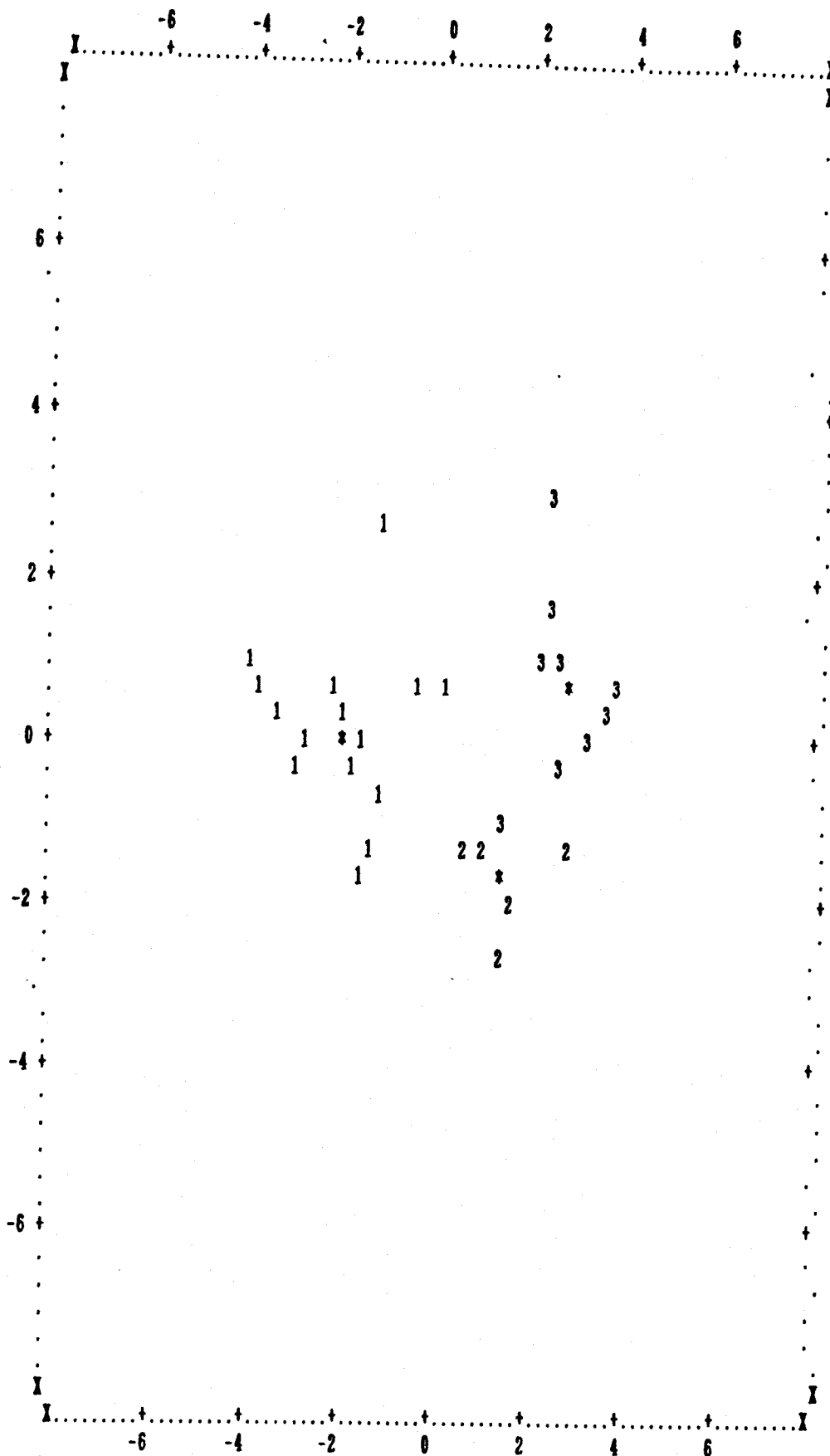


Figure 38. Plot of the values of two canonical discriminant function scores for Tricolored Heron nesting episodes. Cases are identified by their mortality classification group (1-3). Asterisks indicate a group centroid. Numbers may represent more than one case. Analyses are based on the primary set of environmental variables.

CANONICAL DISCRIMINANT FUNCTION 1

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N
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2

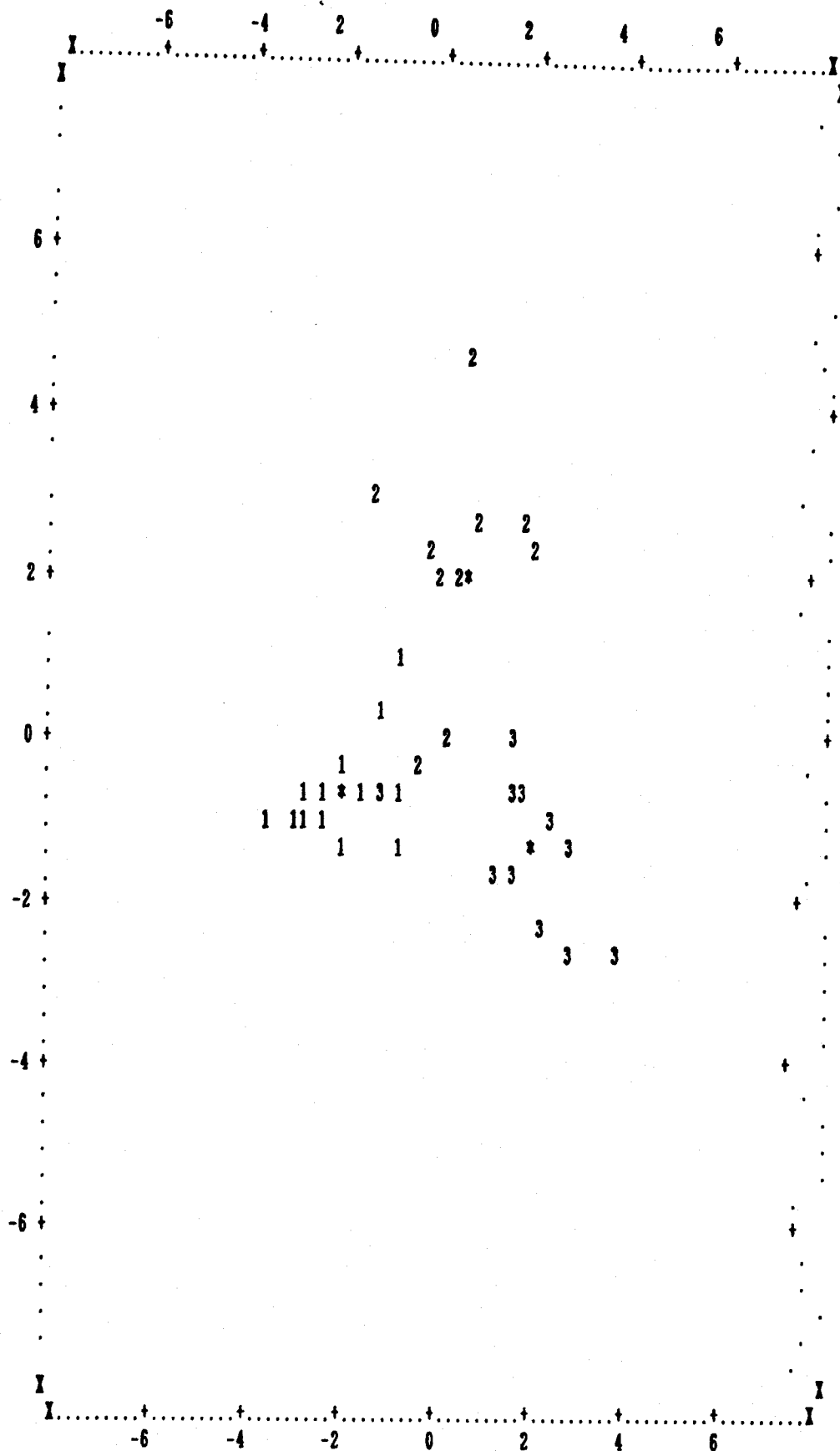


Figure 39. Plot of the values of two canonical discriminant function scores for Great Egret nesting episodes. Cases are identified by their growth residual classification group (1-3). Asterisks indicate a group centroid. Numbers may represent more than one case. Analyses are based on the primary set of environmental variables.

CANONICAL DISCRIMINANT FUNCTION 1

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2

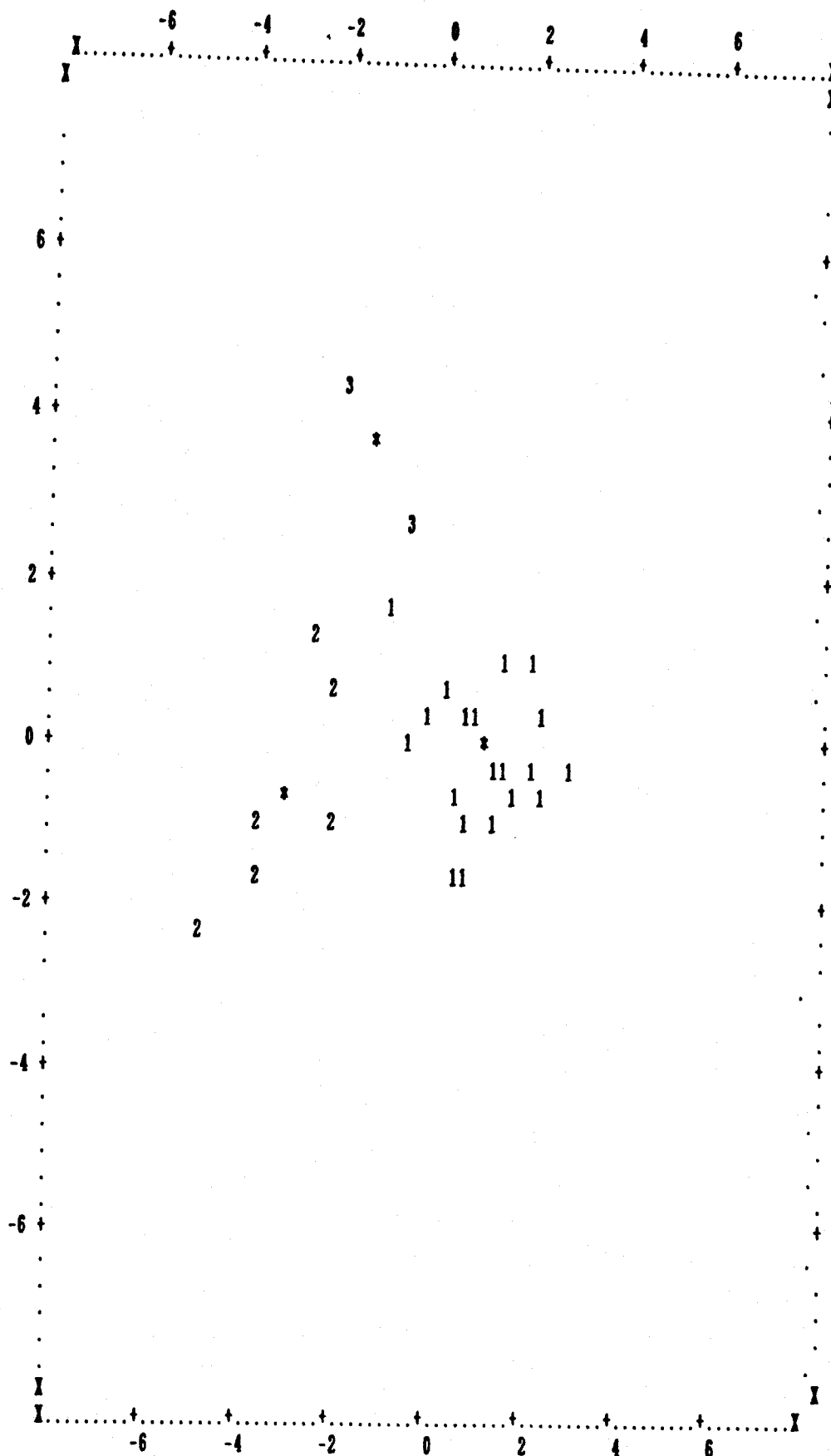


Figure 40. Plot of the values of two canonical discriminant function scores for Snowy Egret nesting episodes. Cases are identified by their growth residual classification group (1-3). Asterisks indicate a group centroid. Numbers may represent more than one case. Analyses are based on the primary set of environmental variables.

CANONICAL DISCRIMINANT FUNCTION 1

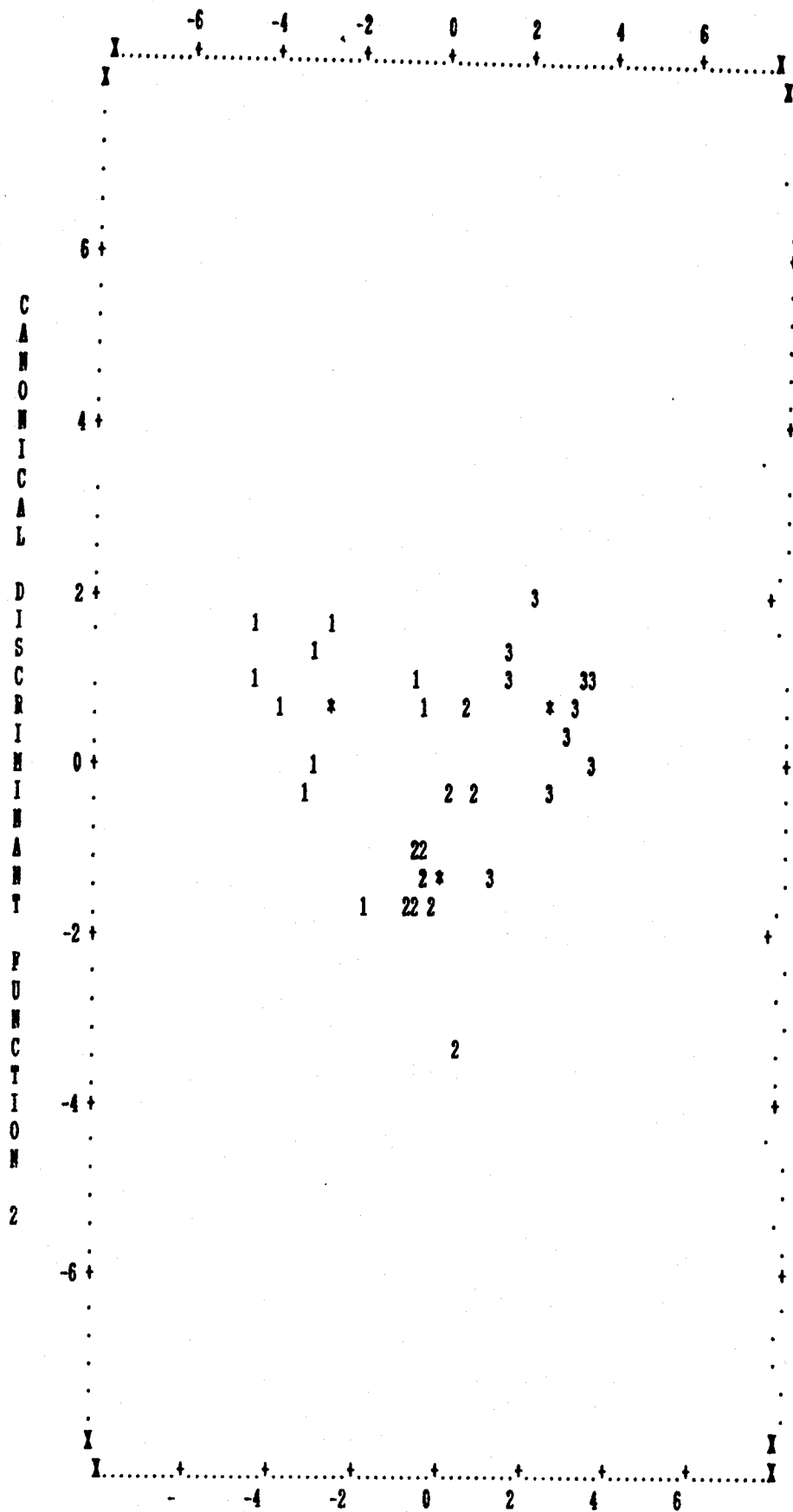


Figure 41. Plot of the values of two canonical discriminant function scores for Tricolored Heron nesting episodes. Cases are identified by their growth residual classification group (1-3). Asterisks indicate a group centroid. Numbers may represent more than one case. Analyses are based on the primary set of environmental variables.

CANONICAL DISCRIMINANT FUNCTION 2

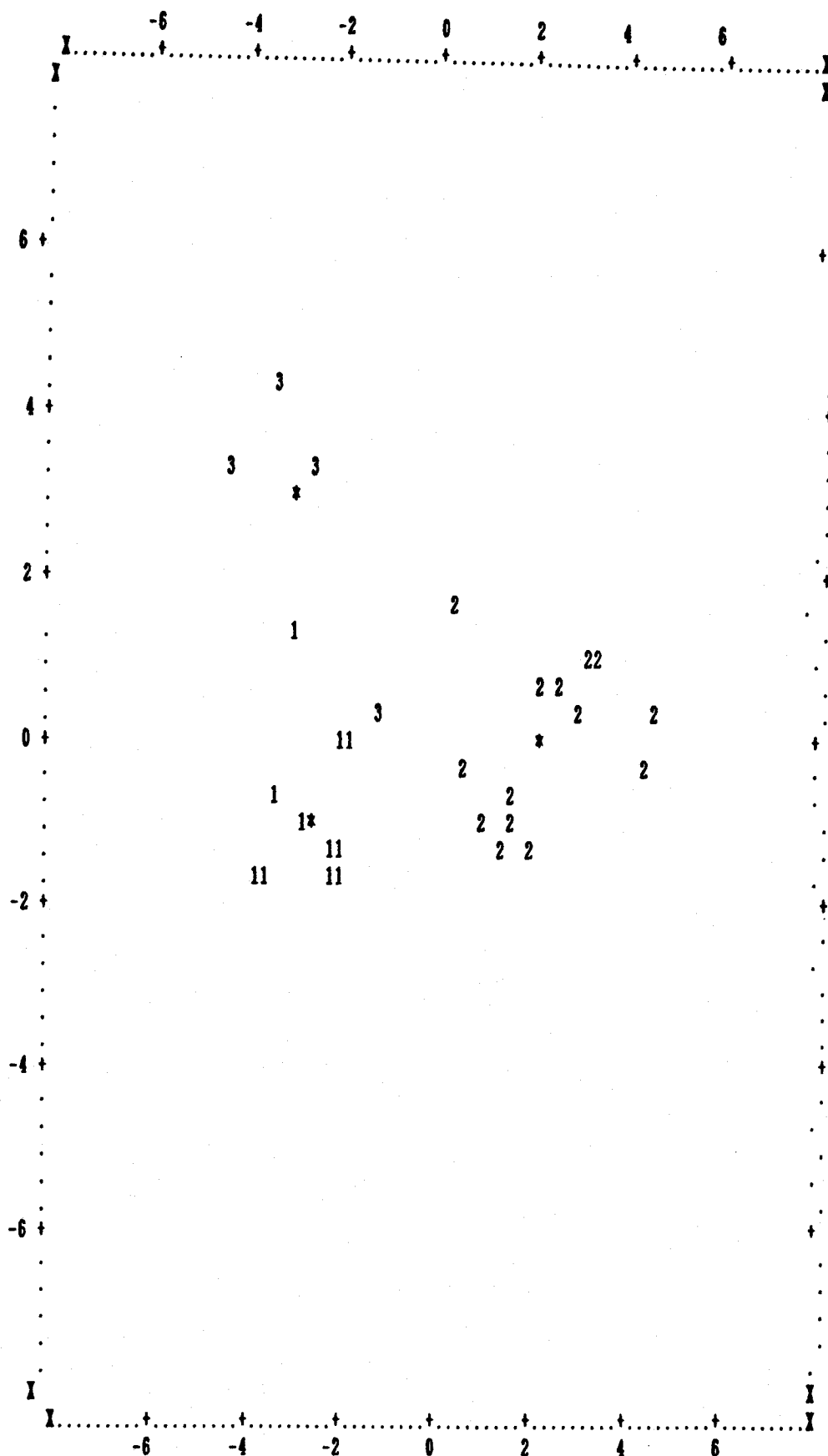
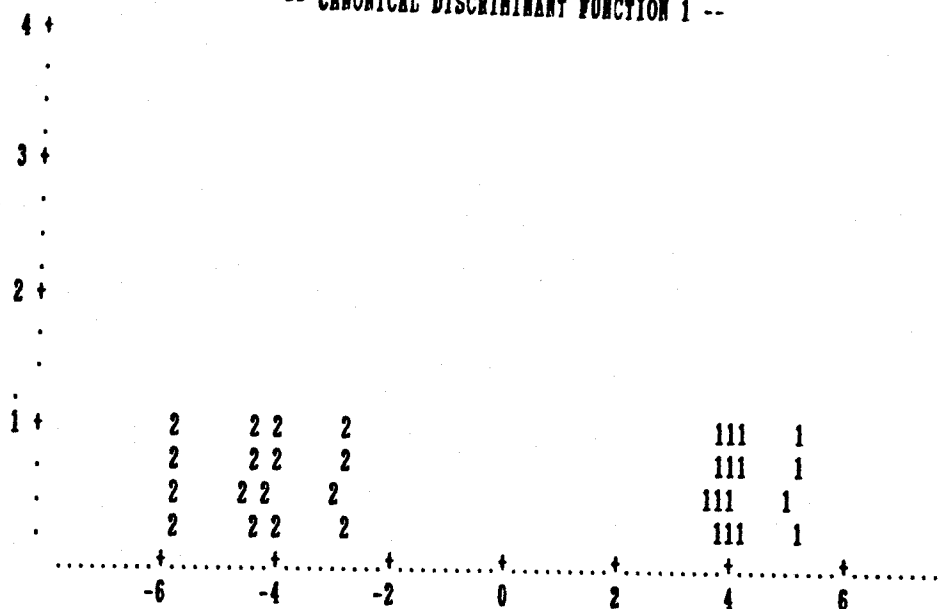


Figure 42. Plot of the value of one canonical discriminant function score for Little Blue Heron nesting episodes. Cases are identified by their growth residual classification group. Analyses are based on the primary set of environmental variables. Top: separation based on mortality classification. Bottom: separation based on growth residual classification.

-- CANONICAL DISCRIMINANT FUNCTION 1 --

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-- CANONICAL DISCRIMINANT FUNCTION 1 --

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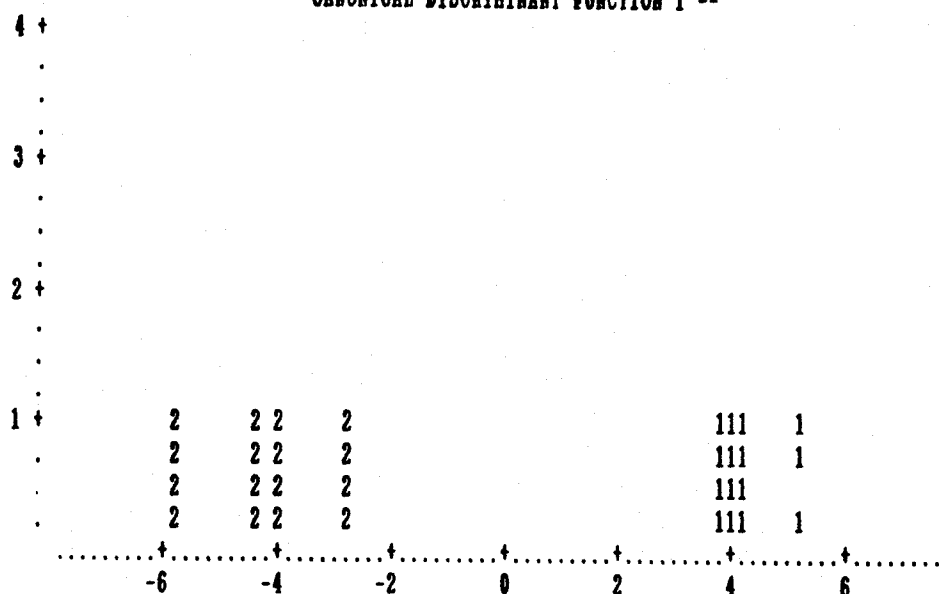


Table 30. Results of discriminant analyses for classification of Snowy Egret nesting episodes by mortality and by growth residuals. Table shows canonical correlations of each of the primary environmental variables that loaded significantly on the discriminant functions.

Variables	DF1		DF2	
	coeff.	corr.	coeff.	corr.
Growth Residuals				
YRECAPR	0.71135	0.47097	0.43519	0.11380
ASP3	0.32417	0.20618	0.78193	0.13217
LOGMASS	-0.00485	-0.46921	1.22621	0.50901
STADFP	2.16735	0.33108	0.22883	0.11503
YHAR	-2.06668	0.05587	0.15995	0.21776
YLGLN	0.12006	-0.12105	-0.04079	0.00976
MEANLWT	0.22903	0.19670	0.83023	0.12392
REC7	-0.25756	0.14269	-0.30673	-0.19346
% Variance	86.51		13.49	
Canonical corr.	0.916		0.670	
2				
X	56.99		14.01	
df	16		7	
P	<0.0001		<0.05	
Mortality				
YRECAPR	0.98979	0.77013	-0.03756	0.12401
ASP3	1.56506	0.31759	0.20969	-0.23316
LOGMASS	0.01702	-0.44208	0.96021	0.58407
STADFP	0.39448	0.25981	2.03313	0.37682
YHAR	-0.46161	0.10043	-1.12010	0.34229
YLGLN	0.28112	-0.12637	-0.16257	0.23130
MEANLWT	0.46344	0.11219	-0.16905	-0.17864
REC7	-0.16250	0.04187	-0.72841	-0.16116
% Variance	88.48		11.52	
Canonical corr.	0.920		0.646	
2				
X	56.81		12.74	
df	16		7	
P	<0.0001		ns	

Table 31. Results of discriminant analyses for classification of Tricolored Heron nesting episodes by mortality and by growth residuals. Table shows canonical correclations of each of the primary environmental variables that loaded significantly on the discriminant functions.

Variables	DF1		DF2	
	coeff.	corr.	coeff.	corr.
Growth Residuals				
STADBP	0.55347	0.24329	0.72456	0.86924
YNAY	-1.04267	0.26145	0.31829	0.75193
REC7	1.02447	0.11767	-0.37714	0.19375
YRECAPR	1.79671	0.57521	-0.51109	0.27498
YRECHAY	-0.50002	-0.00958	0.41541	0.15762
YRECFH	-0.94380	0.09664	0.50507	0.26020
LOGHASS	-0.04680	-0.22355	-0.16950	-0.24269
ASP4	0.27398	0.15633	0.04925	0.23183
MEANLWT	-0.41069	-0.04149	0.27842	0.34114
% variance		83.14		16.86
Canonical corr.		0.934		0.764
2				
X		85.47		25.43
df		18		8
P		<0.0001		<0.01
Mortality				
STADBP	1.09364	0.44821	-0.31738	0.00702
YNAY	-0.40752	0.60602	0.73979	0.12003
REC7	-0.29959	0.08396	-0.05017	0.17374
YRECAPR	1.30089	0.44593	-1.35914	-0.38783
YRECHAY	1.62863	0.22676	0.54027	0.42251
YRECFH	0.38193	0.08814	0.38579	-0.23492
LOGHASS	1.40905	-0.09954	0.15680	0.07602
ASP4	-0.31649	0.19531	0.83996	0.27162
MEANLWT	-0.13032	-0.00716	0.10394	0.16673
% variance		56.18		43.82
Canonical corr.		0.863		0.834
2				
X		74.28		34.54
df		18		8
P		<0.0001		<0.0001

Table 32. Results of discriminant analyses for classification of Little Blue Heron nesting episodes by mortality and by growth residuals. Table shows canonical correctations of each of the primary environmental variables that loaded significantly on the discriminant functions.

Variables	DF1	
	coeff.	corr.
Growth Residuals		
STADBP	5.40116	-0.18187
REC7	4.11731	-0.04912
YRECHAR	-2.27667	-0.19646
LOGNASS	5.51190	0.20749
ASP22	2.65675	0.22343
% variance	100	
Canonical corr.	0.980	
2		
X	11.32	
df	5	
p	<0.05	
Mortality		
STADBP	5.40116	0.18187
REC7	4.11731	-0.04912
YRECHAR	-2.27667	-0.19646
LOGNASS	5.51190	0.20749
ASP22	2.65675	0.22343
% variance	100	
Canonical corr.	0.980	
2		
X	11.32	
df	5	
p	<0.05	

Table 33. Results of discriminant analyses for classification of Great Egret nesting episodes by mortality and by growth residuals. Table shows canonical correclations of each of the primary environmental variables that loaded significantly on the discriminant functions.

Variables	DF1		DF2	
	coeff.	corr.	coeff.	corr.
Growth Residuals				
STADBP	0.63148	-0.29320	1.21180	0.47648
REC7	0.26463	-0.01426	-0.25064	0.23593
YRECHAR	-1.77825	-0.53792	-0.69480	0.04436
LOGFISH	0.89077	0.49364	0.13955	0.01791
LOGHASS	0.33781	0.48108	0.35723	-0.03278
ASP2	-0.55677	-0.30184	0.87082	0.59932
% variance	75.48		24.52	
Canonical corr.	0.879		0.725	
2				
X	50.12		16.76	
df	12		5	
P	<0.0001		<0.01	
Mortality				
ADEP	0.79350	0.50338	0.58733	0.51938
REC7	-0.25678	0.08496	-0.06658	-0.04898
YRECHAR	0.43346	0.34236	0.20139	0.12202
LOGFISH	-0.54645	-0.46374	0.46418	-0.10974
LOGHASS	-0.53745	-0.30816	-0.02957	0.50957
ASP2	0.37011	0.14849	-1.02897	-0.71248
% variance	97.17		2.83	
Canonical corr.	0.954		0.476	
2				
X	59.89		5.78	
df	12		5	
P	<0.0001		ns	

POPULATIONS.-- Determining heron population levels was not a part of this study, but data were gathered on nesting numbers of herons in the major colony sites in Everglades National Park by ground censuses. Such data are substantially more accurate than the estimates arrived at by aerial surveys, especially for the smaller herons that nest under the canopy of trees and are invisible from the air. As a result the numbers we report are reasonably accurate. Robertson and Kushlan (1974) suggested that these species were decreasing, and although this seems likely, our data provide no quantitative documentation of a changing nesting status of these species. The most comparable data set available is that from a 1975 study sponsored by the US Fish and Wildlife Service (Kushlan and White 1977), in that both censuses were based on ground counts and colonies were active and produced young in both years. The maximum population present in the major park colonies during our study was higher than that in 1975 for two of three species that could be compared. In 1979, the numbers of Great Egrets in major park colonies were 150% that of 1975, and Snowy Egrets were 164% that of 1974. Tricolored Herons were 61.4% of the number that nested in 1975. Thus the comparable data are mixed with respect to any continuing nesting population declines. The population trend is best documented for the Wood Stork. The nesting population of this species has decreased markedly during the past 25 years (Kushlan and Frohring 1986, Ogden et al. 1987). In any case, the numbers of herons nesting in the Park appear to be below that which could be expected in such a large wetland.

And it is clear from our data that in some years, such as 1980, few individuals nest in colonies in the Park. But there is no reason to suspect that individuals are in any way permanently bound to a colony site, but rather move among available sites in different seasons. This understanding recently has been documented by Bancroft and co-workers (pers. comm.). Thus the regional populations of each species of heron includes the nesting and non-nesting residents of all of southern Florida, which suggests the need for regional management (Kushlan 1983).

Nonetheless the poor nesting effort and success in the National Park has critical implications for management. That the herons in many years choose to nest in other than the traditional sites in the Park is indicative of differing environmental conditions in the various management zones of the region, and reflects the existence of relatively poor nesting conditions in the Park during most of our study.

Our results have implications with respect to monitoring the regional populations of southern Florida herons. Of primary concern is securing reliable and timely information on the status of breeding populations. The pattern of seasonal change of the number of birds observable on feeding sites indicates that many of the herons present in southern Florida are not part of the nesting population. This indication has been proven in the case of Wood Storks (Coulter et al. 1987). More northerly nesting populations winter in southern Florida at the same time that the local population may be nesting. From the change in nesting numbers among years we documented, it is apparent that not all resident birds nest every year. Thus the only way to monitor the trend in nesting numbers is to census within the colony, rather than on the

feeding ground. Furthermore, because of summer nesting in small scattered colony sites throughout the interior, monitoring the number of birds in the spring nesting colonies alone would underestimate the population attempting to nest each year. Thus monitoring nesting numbers would require ground visits to all park colonies, including those that occur at odd times and places and in the summer. 149

Although such monitoring would provide information on nesting effort, even counting all the birds in the colony sites provides no information on nesting success, as there is no relation between nesting success and number of nesting wading birds (Rodgers et al. 1987). In this study we have engaged a statistically robust method for assessing nesting success, and this methodology can be recommended with confidence for monitoring purposes.

NOT
all
valid

The more usual methods of measuring nesting success, such as by estimating mortality or the number of young produced to some arbitrary time, have drawbacks. They require multiple visits to a colony over the entire nesting episode, from prehatching through fledging. Mortality is measured either as a percentage loss for the entire colony or loss per nest. Number of young produced is also measured on either a colony or a per nest basis. Growth measurements have the advantage of being measured on a per chick basis, which increases sample size - of crucial importance in statistical analysis. Growth rates can be determined with only a few visits, although a difficulty remains if the chicks measured are of different ages, as growth rates are not expected to be constant across growth stages, as we have verified.

This difficulty is overcome by using as a statistic the residual variation of a growth interval after the effects of age, history, and position in the clutch have been accounted for by a multivariate regression. This methodology permits the comparison of growth among colonies having differently aged chicks, enabling monitoring information to be collected over a short period of time. Such growth information can also be gathered during or after a change in environmental conditions to assess its effect. An additional advantage is that the model effectively accounts for or omits as unimportant historic conditions. This means the growth intervals of individual birds can be treated as being independent, and the sample size increases to encompass the collection of all growth intervals measured rather than the number of chicks measured. Standardization of the residuals normalizes the data, permitting the use of powerful parametric analysis in investigating differences among colonies, times, locations, or years. The growth analysis technique allows real time comparisons of nesting success among colonies and times in a manner that is sensitive, effective and inexpensive relative to repeated colony visits throughout the nesting season.

Evaluating growth rate data, we found that low growth rates were the rule in most nesting episodes during our study period, as was high mortality. We can conclude that most nesting episodes were unsuccessful from 1978 through 1981. These results indicate that environmental conditions in the park wetlands were not conducive to successful nesting. They also suggest that whatever population decreases might have occurred over the past decade were undoubtedly do in part to prolonged poor nesting success.

NESTING SUCCESS.-- Our data showing high mortality and slow growth rates during most nesting episodes suggest that recruitment was limited in most years from park colonies. Although a number of studies have documented mortality, survival, or growth of nestling herons, few have been able to document the populational impact of specific criteria of nesting success (Dusi and Dusi 1970, Siegfried 1972, Wiese 1978, Rodgers 1980, 1987, Pratt and Winkler 1985, McKilligan 1985). Unfortunately it is not known what levels of fledgling production are necessary to maintain population stability for most heron species. Henny (1972) in his study of Great Blue Herons indicated that an annual recruitment of 1.9 young per two adults is required for replacement. This value is 1.9 per two adults in the potentially breeding population, not just those appearing to nest in a given year. Subsequent studies supported this estimate (Forbes et al. 1985).

After our measurement period, considerable additional mortality typically occurs. Pratt (1970) demonstrated that mortality of Great Egret chicks increased in the third week, after we no longer were able to follow them. Furthermore, mortality subsequent to fledging appears to be high in species studied to date. Kahl (1963) found mortality in Great Egrets to be 76% in the first year and 26% thereafter. He also found that migration correlated with higher mortality in the first six months of life. Dusi (1963) found that Little Blue Herons had a mortality rate of 74% in the first year and 33% thereafter. Ryder (1978) found a 72% mortality for Snowy Egrets in the first year and 31% thereafter.

Our cluster analyses divided the nesting episodes of herons

into three categories on the bases of mortality rates of marked nestlings and residual growth rates. Given this level of mortality after nesting and the conservativeness of our estimates of mortality during nesting, it is likely that only our most successful categories could have produced replacements. The nesting episodes we categorized as having high mortality, 40-80% documentable losses, are clearly unsuccessful, and in some cases no fledging occurred. Nesting we classified as intermediate, having 15-40% documentable mortality, were likely also to have been unsuccessful from the point of view of population stability. If the documentable mortality were half of the actual mortality, this loss plus post-fledging mortality would certainly not permit population replacement. Only the several years having the lowest mortality and highest growth rates were clearly successful. These instances were relatively few during the four years and 50 nesting episodes (species-colony-time) during the study.

These classifications successfully categorized the nesting episodes, which were able to be discriminated on the basis of environmental conditions affecting food availability. Nesting success of Everglades herons is clearly related to environmental conditions at the time of nesting, especially those affecting food availability.

FOOD AVAILABILITY.-- The fundamental hypothesis tested in this study was that food availability determined nesting success of Everglades herons (for recent general discussion see Martin 1987). Much of the basic ecological and evolutionary strategy characteristic of herons lends support to this notion. It appears from recent studies that the most fundamental explanation for colonial nesting in herons is food finding (Krebs 1974, Krebs 1978, Kushlan 1981b, Burger 1981, Vessem and Draulans 1986). Aggregative foraging is similarly adaptive in increasing heron foraging effectiveness through several mechanisms (Krebs 1974, Kushlan 1978a, Des Granges 1979, Caldwell 1981). Feeding site selection is clearly related to food availability in herons, at least in a general sense (Owens 1955, Erwin 1984, Bateman 1970, Custer and Osborn 1978, Pratt 1980). However, the correlates of feeding site selection have been determined only approximately. Several studies have implicated the importance of water depth (Kushlan 1976, Custer and Osborn 1978). However detection of additional variables has been relatively unsuccessful, as the failure to find statistically significant correlations among a number of habitat variables has recently shown (Erwin et al. 1987). Few published studies have been able to document quantitatively the most difficult variable, food availability, the exceptions being studies that have followed the methodology developed in the present study. Hafner and Britton (1983), for example, were able to document that changing foraging sites were related to food availability. The results of the current study are by far the most exhaustive and definitive in demonstrating the crucial role of food availability.

In the Everglades, feeding sites selected by herons are those

shallow enough for wading and having appropriate food availability. The latter varies seasonally, being only 20 - 50 g/m³ during the nonnesting season. However availabilities of 200 - 2000 g/m³ are used during nesting, and it appears that for all species of herons availability must exceed about 300 g/m³ for successful nesting (ie low mortality rates).

All of the heron species have a diverse diet composed of most of the types of prey available in southern Florida. Such wide feeding niches are characteristic of herons (see summary in Kushlan 1978). Nonetheless, only a few prey types make up the bulk of the diet, calculated either by frequency of occurrence or biomass. High proportions of these heavily used prey types do not necessarily positively correlate with nesting success. This result suggests that many of the most abundantly taken prey during our study period may not have been optimal. Thus prawns, that make up a large portion of the diet of the Snowy Egret, are not indicative of good nesting - they are "filler food" used when other prey are not available. There is no indication that large size of prey is related to nesting success. In fact there is evidence to the contrary in the Great Egret. It nonetheless is likely that individual prey are captured on the basis of abundance, size, and behavior. The repeated correlations of site choice and food choice on the basis of biomass indicates the importance of energy availability to the nesting success of Everglades herons.

The finding that large fish do not contribute to the success of Great Egrets, Tricolored Herons, and Little Blue Herons is of some importance. Fishes and other prey items grow rapidly in the

Everglades. Concurrent studies showed that some of the most important prey species, such as mosquitofish, can mature within 2-3 months (Haake and Dean 1983). Thus individuals these species can grow quickly to a size herons eat, certainly within one annual cycle. Also the rapid growth and short life span means the populations turn over rapidly. Sunfish are among some of the larger fishes in the Everglades, but even these are consumed when relatively small. Thus there is no indication that the number, type, size, or biomass of prey are dependent on conditions in previous years, only on the way they are made available in the drying season. Water conditions during the nonnesting season does not seem to affect food abundance, although availability is better when the dry season starts from a relatively low stage at the beginning of the recession in February (as occurred near the Andytown site in 1981). The latter result relates to the pattern by which prey are made available, not to the sizes or total amounts present.

ENVIRONMENTAL CORRELATES.-- The success of herons nesting in the Everglades can be predicted and discriminated on the bases of several environmental variables. The most general of these among species are water depth and recession rate, both being negatively correlated. The shallower the water and faster the recession rate the more successful the nesting of herons in the Everglades. This can be seen clearly in the case of the nesting episode at Andytown colony site in 1981. For nearly all species, this episode had the highest growth rates and lowest mortality. It was characterized by having shallow water depths in February and dried down from there with an uninterrupted recession rate. It is such hydrological conditions that are required for the successful nesting of herons in the Everglades.

It is unlikely that similar results obtained from studies of the nesting ecology of Wood Storks in the Everglades are coincidence. The timing and success of stork nesting in traditional colony sites in the Everglades is correlated with a rapid drying rate (Kushlan et al. 1975). In fact the population decreases of this species can be attributed directly to the reduced nesting success brought about by high water levels in the usual drying season. That herons require both shallow water and rapid drying provides encouragement that provision of these conditions would positively affect the entire wading bird community (Kushlan 1986a).

The feeding and nesting ecology of six wading bird species have now been studied in detail in the Everglades and nearby freshwater wetlands: the Wood Stork by Kahl (1962, 1964), Kushlan et al. (1975), Ogden et al. (1976, 1978) and the White Ibis by

Kushlan (1977a,c,d, 1978b, 1979a, Kushlan and Kushlan 1975) and the four species studied in this report. The ecological relationships of these species have been discussed by Kushlan (1986, in press) and Ogden et al. (1980) and the management implications of the results by Kushlan (1979b, 1983, 1986b, 1987). For all six species, in previous and the current study, shallow water during the drying season was required for successful nesting. Furthermore, with the exception of the White Ibis, rapid recession rates have been shown to be required for successful nesting.

Overall we can conclude that the critical variable is the abundance of food available to the foraging birds, measured in biomass units of prey density and size. With the exception of the highly specialized Wood Stork and to a lesser extent the proclivity of Little Blue Herons for amphibians, all species tend to consume what is most readily available of their potential diet. For herons prey type does not seem limiting. Because any size of prey generally taken can be produced within a growing season, there appears to be no long term history to prey availability, and each drying season presents prey made available during that previous year. Nor is there any indication that absolute levels of prey abundance are too low. Low prey densities in the high water season become dense food concentrations upon drying throughout the Everglades and adjacent marshes. In this season the locations where food is sufficiently dense and water depths sufficiently shallow are used by nesting birds. The abundance and biomass of prey during concentration is critical. Such concentrations occur because of the recession of surface water. Thus drying is essential for successful nesting of herons in the

spring. The result of high recession rates is to achieve a water depth shallow enough for feeding and to concentrate the prey items to the degree that they can be effectively harvested. Such hydrological patterns determine the nesting success, and ultimately the population stability of Everglades herons.

One result of this analysis was to suggest that environmental factors that affect growth rates are current, which means that there is little history. In fact such variables as original clutch, current clutch size and past hydrological conditions seldom entered into discriminant analyses. To the extent that current rather than past conditions determine nesting success, management of those conditions becomes less complex.

On the other hand some variables were definitely not important to nesting success. These include the distance the birds had to fly to the foraging site. Given the long distances traversed, it is clear that the entire southern Everglades is open for feeding, so long as water levels are shallow enough. In the wet season, water depths are too great and food density too low to support large-scale heron feeding. However, during the study high water levels in the upper Shark Slough remained too deep through most of the year, owing primarily to the continual discharge of water into the Park from the north through the usual drying season. Thus much of the southern Everglades was unavailable for feeding because water depths were too high.

Given this understanding of the patterns of prey availability necessary for successful nesting, it is apparent why hydrological variables such as current water level, recession rates, and

biological variables such as biomass available most discriminate between successful and unsuccessful nesting episodes. The Everglades must be drying For successful nesting it is apparent that falling water levels must prevail in the Everglades marshes through the nesting season and that this recession must result in water depths shallow enough to concentrate fish and permit heron foraging.

It is concluded that:

1. The nesting success of herons in the Everglades can be evaluated through analysis of growth rates relative to an intrinsic model of daily growth.
2. The growth analysis methodology is appropriate for use in monitoring the reproductive success of Everglades colonies.
3. The growth analysis methodology is appropriate for use in assessing the results of environmental events, including hydrological conditions.
4. Nesting success is correlated with environmental conditions. Although each species is affected by a different array of variables, the common determinants of nesting success include water depth, current recession rate, and biomass of food available at foraging sites. Other depths and recession rates also are critical to success.
5. The hydrological correlations are negative. That is the shallower the water depths and faster the recession rate the greater the nesting success.
6. An example of hydrological conditions conducive to successful nesting is provided by water level fluctuations at guage G-33 in Conservation Area 3 in 1981. Low late winter water levels were followed by rapid and steady recession rates.

7. The finding of the importance of recession rates, shallow water depths, and high food density to nesting success is coherent with previous findings for the Wood Stork and the White Ibis in the Everglades. Therefore management action benefiting one will benefit all six species of wading birds that have been studied in the Everglades.

It is recommended that:

8. That discharge of water into Everglades National Park be managed so as to produce high recession rates during the usual Spring nesting season resulting in the availability of shallow feeding sites throughout the late Winter and Spring.

9. A monitoring program be developed that includes the assessment of nesting success through use of growth rates for all four species of herons.

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