The Auk 112(3):613-632, 1995

LONG-TERM POPULATION TRENDS OF COLONIAL WADING BIRDS IN THE SOUTHERN UNITED STATES: THE IMPACT OF CRAYFISH AQUACULTURE ON LOUISIANA POPULATIONS

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ABSTRACT.—Long-term population dynamics of colonial wading birds (Ciconiiformes) were examined using data from Audubon Christmas Bird Counts (CBC, 1949-1988) and Breeding Bird Surveys (BBS, 1966-1989). Winter populations of Louisiana wading birds increased dramatically over the 40-year period, with the sharpest increases occurring during the last 20 years. Several species populations grew exponentially from 1968 to 1988. High overall positive covariance was found in the abundance of the various species over time, and cluster analysis showed that the species with similar dietary requirements and foraging habits covaried most strongly and positively with each other. Trend analysis of CBC and BBS data from 1966-1989 and 1980-1989 showed a close correspondence between CBC and BBS trends in Louisiana. Most species increased in Louisiana at the same time as they declined in Florida and Texas. Several factors might explain increases in populations of wading birds in Louisiana, including long-term recovery from the effects of human exploitation, expansion of breeding populations in more northern states, changes in weather, recovery from DDT and similar pesticides, and regional movements due to habitat loss in other coastal states. These hypotheses are not mutually exclusive and merit further study. However, based on several inferential lines of evidence, increased acreage devoted to crayfish (*Procambarus*) aquaculture in Louisiana appears to be the most significant factor explaining observed population trends in the state. First, populations of colonial wading-bird species that use crayfish were correlated positively with the wild crayfish harvest in Louisiana, and even more strongly with commercial crayfish pond acreage. Second, the regularity with which these ponds are managed provides a more predictable foraging habitat than do corresponding natural areas. Third, the use of crayfish ponds by wading birds peaks during pond drawdowns, which may increase reproductive success by concentrating prey available to wading birds during their nesting season. Fourth, those species of wading birds that specialize on crayfish showed the greatest population increases and the strongest correlation with crayfish pond acreage. These findings have important implications for conservation and management of Louisiana's wading-bird populations. *Received 16 May 1994, accepted 5 September 1994.*

ALTHOUGH WE LACK reliable nineteenth century data on colonial wading-bird populations (order Ciconiiformes), accounts from pioneer naturalists like Audubon document enormous colonies throughout the southern swamps and estuaries (Bent 1926). By the end of the nineteenth century, plume hunting had reduced many species to near extinction. Legal protection began in 1900 with the Lacey Act, which prohibited interstate commerce in illegally killed animals, followed by the Migratory Bird Treaty in 1916. The establishment of wildlife refuges also helped protect wading-bird colonies (Parnell et al. 1988).

Since their protection from plume hunters, many species of colonial wading birds have steadily increased their North American populations, and expanded their ranges northward and inland (Ogden 1978, Ryder 1978). However, wading-bird increases have not occurred in all regions. Whereas populations have increased and ranges expanded in the past 30 years in some regions of the United States for species such as Snowy Egrets, Great Blue Herons, and Cattle Egrets (Bock and Lepthien 1976, Ryder 1978, McCrimmon 1982, Larson 1982; Table 1), regional declines characterize other species, such as the Reddish Egret and Roseate Spoonbill (Powell et al. 1989, but see Ogden 1991). Florida, for example, despite having a high historical population density of most species of colonial wading birds (Root 1988), has witnessed reduced wading-bird populations due to prolonged drought, estuarine degradation, and human-induced hydrological changes in and around the Everglades (Bancroft et al. 1988, Bancroft 1989). Ogden (1994) estimated that populations of five species of wading birds in the Florida Everglades declined by 93% between 1931-1946 and 1982-1989. Such conflicting trends in populations of colonial wading birds may even indicate large-scale shifts of regional population centers.

This diversity of population trends among regions and species indicates the need for increased monitoring, and for in-depth analyses at national and regional scales. This need is particularly apparent in Louisiana, where wading-bird population trends have been poorly documented in the past, with breeding-colony data only available for 1977, 1984, and 1990 (Portnoy 1977, 1978, Keller et al. 1984, Martin and Lester 1990, R. P. Martin 1991), and where wetland acreage is more abundant than in any other state.

We review population trends of 15 species of colonial wading birds in Louisiana over the past 40 years, using data extracted from Audubon Christmas Bird Counts (CBC). We compare and contrast these trends with state, regional, and national trends from Breeding Bird Survey (BBS) data. We use published data to discuss briefly and evaluate several such factors, namely long-term recovery from the effects of the plume trade and other human exploitation, increased winter populations due to expanded ranges of migratory wading birds in more northern states, effects of weather, recovery from heavy pesticide use, competition, predation, habitat loss, and land-use changes in Louisiana due to the growth of crayfish (*Procambarus*) aquaculture (note: in Louisiana, the common name "crawfish" is used instead of "crayfish").

Continued declines in the quality and quantity of foraging habitat in natural wetlands due to drainage, pollution, and other human influences highlight the importance of understanding how and why birds use artificial wetlands such as flooded fields or aquaculture ponds. The exponential growth of commercial crayfish pond acreage in Louisiana may have directly contributed to increases in Louisiana wading-bird populations by creating new high-quality foraging habitats. Maddock and Baxter (1991) suggested that food limitation is a critical factor in egret reproductive success.

The use of aquaculture ponds by wading birds also raises important legal and conservation issues, both locally and internationally. The problem of bird predation in aquaculture ponds involves: tropical-fish farms in Florida; catfish farms in California, Arkansas, and Mississippi; and fish farms in Europe (Draulans 1987b, Stickley and Andrews 1989, Boyd 1991, Cezilly 1992, Stickley et al. 1992). Wading birds currently are treated as agricultural pests under the Department of Agriculture's Animal Damage Control program. Depredation permits have been issued in several states for lethal control of several migratory bird species (including herons, egrets, pelicans, and cormorants) that feed at catfish farms and other aquaculture facilities. Increased populations of White Ibises and Yellow-crowned Night-Herons, which feed heavily on crayfish, are of particular concern to Louisiana wildlife biologists and farmers. Sound management policy for colonial wading birds in Louisiana will require detailed understanding of the relationship between wading-bird populations and crayfish aquaculture, towards which our analyses of wading bird population dynamics are an important first step.

TABLE 1. Species of Ciconiiformes regularly seen on 343 Louisiana Christmas Bird Counts 1949-1988, and average number observed per count.

Species	Average per count
American Bittern (*Botaurus lentiginosus*)	1.5
Least Bittern (*Ixobrychus exilis*)	0.1
Great Blue Heron (*Ardea herodias*)	41.3
Great Egret (*Casmerodius albus*)	122.8
Snowy Egret (*Egretta thula*)	118.3
Little Blue Heron (*E. caerulea*)	81.3
Tricolored Heron (*E. tricolor*)	50.4
Reddish Egret (*E. rufescens*)	0.2
Cattle Egret (*Bubulcus ibis*)	100.9
Green-backed Heron (*Butorides striatus*)	1.1
Black-crowned Night-Heron (*Nycticorax nycticorax*)	13.0
Yellow-crowned Night-Heron (*N. violaceus*)	0.3
White Ibis (*Eudocimus albus*)	256.5
Glossy and White-faced ibises (*Plegadis falcinellus* and *P. chihi*)	432.1
Roseate Spoonbill (*Ajaia ajaja*)	21.2

METHODS

CBC.—We used data from the annual Audubon Christmas Bird Count (CBC) to analyze winter ciconiiform population trends in Louisiana. CBCs are held on a single day between 15 December and 5 January. All birds seen within a 24.1-km (15-mi) diameter circle are tabulated. In addition, observer effort is gauged

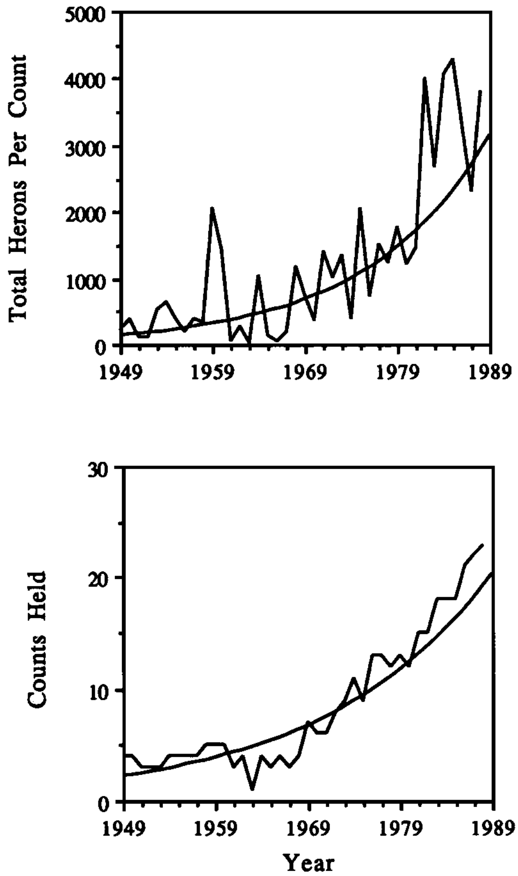

Fig. 1. Number of Christmas Bird Counts held and total colonial wading birds counted, 1949–1988 (see Table 1 for complete list of species).

by recording the total mileage covered and the total observation hours by all parties (party miles and party hours, respectively; Butcher 1990). We used abundance data for the 16 species of ciconiiforms regularly seen in Louisiana (Table 1), along with observer effort recorded for each count location. Analyses spanned the 40-year period from 1949, the first year in which three or more counts were regularly held statewide, through 1988, for a total of 343 individual counts (number of counts per year are summarized in Fig. 1).

Several methods have been used to normalize CBC data in order to minimize variation due to differences in observer effort. Initially, we examined trends standardized per 10 party-hours, per 100 party-miles, and per count for all wading bird species over the 40-year sample period, and found that the method of normalization had surprisingly little effect on the observed trends (unpubl. data). Given that colonial wading birds aggregate, changes in observer effort within a count circle would probably not influence numbers of birds counted as strongly as would the addition of new count circles in wetland areas (Raynor 1975, Morrison and Slack 1977, Bock and Root 1981). Therefore, we calculated the total number of birds observed divided by the number of counts held in that year.

There are several methodological problems with CBC data. CBC data are not truly random samples, since regions of high species density are favored in the selection of count areas (Drennan 1981). CBC counts also are subject to error due to year-to-year differences in weather and timing of the count (Falk 1979, Smith 1979, Rollfinke and Yahner 1990), and due to observer-reliability errors and volunteer turnover (Stewart 1954, Confer et al. 1979, Arbib 1981, Butcher 1990). CBC data are most meaningful when they cover many years and include a broad geographic area because annual variations in weather and observer reliability become relatively less important (Bock and Root 1981, Ferner 1984, Butcher et al. 1990).

The potential problem of species identification is not serious for wading birds, except for the difficulty of discriminating between Glossy and White-faced ibises. We pooled these species into a single category. Most CBC observations of dark ibises in Louisiana were reported as White-faced Ibises.

To provide an independent test of observed CBC trends, we analyzed Breeding Bird Survey (BBS) data for the same species for the periods 1966–1989 and 1980–1989 (1966 is the first year in which BBS trends were reported). BBS surveys are held in the summer, and reflect the population size of breeding birds, while winter populations (CBC) reflect a combination of remaining (resident) birds plus wintering migrants. Several studies have found close agreement between CBC and BBS data for a variety of species (Robbins and Bystrak 1974, Dunn 1986, Burdick et al. 1989, Butcher et al. 1990). Because BBS data are compiled by roadside census, they tend to underestimate population sizes of colonial wading birds (Bystrak 1981, Butcher 1990). Wading-bird colonies often are located in remote wetlands far from highways. Nonetheless, the BBS sample sizes for each species of wading bird usually exceeded the BBS minimum recommended size for data analysis, often by several orders of magnitude (10 routes minimum per species; S. Droege pers. comm.). We analyzed BBS survey results for Florida, Louisiana, Texas, and California, states which consistently recorded the highest wading-bird population densities in CBC counts (Root 1988).

Data analysis.—We calculated linear regressions and exponential curves for each species based on the annual number of birds per CBC count. Data series with zero values were transformed by adding 0.1 to each data point for testing with an exponential model. The use of regression to test hypotheses concerning statistical significance in autocorrelated data sets, such as annual censuses, violates the assumption of independence (Beal and Khamis 1990). Therefore, we use the regression data only to demonstrate the obvious

TABLE 2. Slope and error (R^2) values for linear and exponential best-fit regression models of Louisiana winter wading-bird populations, based on per-count Christmas Bird Count data, 1949-1988 (343 counts). Trends were not tested for significance (see text).

Species	1949-1988 linear	1968-1988 linear	1949-1988 exponential	1968-1988 exponential
American Bittern	−0.04 (0.09)	−0.05 (0.06)	0.00 (0.02)	0.00 (0.00)
Least Bittern	0.00 (0.00)	0.00 (0.02)	0.00 (0.02)	0.00 (0.01)
Great Blue Heron	1.15 (0.34)	3.87 (0.83)	0.01 (0.21)	0.04 (0.79)
Great Egret	6.86 (0.40)	14.47 (0.39)	0.03 (0.36)	0.04 (0.64)
Snowy Egret	8.61 (0.40)	18.55 (0.37)	0.04 (0.28)	0.05 (0.62)
Little Blue Heron	3.56 (0.09)	−8.65 (0.09)	0.05 (0.46)	−0.01 (0.02)
Tricolored Heron	1.93 (0.19)	2.90 (0.09)	0.02 (0.18)	0.02 (0.11)
Reddish Egret	0.02 (0.26)	0.03 (0.15)	0.02 (0.32)	0.03 (0.22)
Cattle Egret	8.71 (0.45)	12.03 (0.20)	0.11 (0.84)	0.05 (0.45)
Green-backed Heron	0.06 (0.35)	0.06 (0.07)	0.04 (0.59)	0.02 (0.24)
Black-crowned Night-Heron	0.80 (0.20)	3.02 (0.47)	0.02 (0.09)	0.10 (0.62)
Yellow-crowned Night-Heron	0.01 (0.10)	0.04 (0.36)	0.01 (0.14)	0.04 (0.41)
White Ibis	23.22 (0.49)	56.21 (0.59)	0.07 (0.48)	0.07 (0.66)
Glossy and White-faced ibises	22.92 (0.30)	55.21 (0.46)	0.05 (0.21)	0.06 (0.41)
Roseate Spoonbill	1.35 (0.29)	1.37 (0.07)	0.08 (0.56)	0.06 (0.24)

long-range trend in the population densities of these species, rather than to test hypotheses of statistical significance of trends. We smoothed population data with a three-year sliding average for graphic presentation only (Raynor 1975). The squared correlation coefficient of the fitted curve (R^2) for linear regressions of nonsmoothed data approached or exceeded 0.50 for the most abundant and rapidly increasing species (Table 2).

To allow direct comparison of BBS with CBC data, we calculated CBC trends (annual percent change per year) for each species for 1966-1989 and 1980-1989. These two periods represented the most recent BBS data available. BBS trends are calculated with a route-regression technique, which estimates median trends using a bootstrap analysis to estimate trends from random subset samples (Geissler and Noon 1981, Geissler 1984, Geissler and Sauer 1990). Our trend analysis of CBC data is based on one estimate of species abundance for each year (per-count data). We fitted a simple linear regression

$$\log_e (\text{count}_i + 0.5) = \text{year}_i(\log_e[b]) + \log_e(a), \quad (1)$$

where e is the base of the natural logarithms, count_i is the number of birds observed per count in year i, b is the slope of the fitted regression, and a is the y-intercept of the fitted regression. We added the constant 0.5 to insure a defined logarithm for counts of zero. We calculated the trend from the antilog of the slope in this regression (Holmes and Sherry 1988):

$$\text{Trend} = e^{(\log_e b - 0.5\text{SE})}, \quad (2)$$

where b is the slope and SE the standard error of the slope of the regression on logarithmic per count data. The SE term corrects for the asymmetry of the log-normal distribution (Geissler 1984). We then expressed the resulting trend as percent change per year (100[trend − 1]).

We assessed covariation of temporal trends among species for the 40-year CBC data set using Schluter's (1984) covariance test. This test is based on the ratio (V) of the variance in the total number of individuals per sample (S_T^2, all species combined) to the sum of the variances of the individual species densities ($\Sigma_i s_i^2$). By the null hypothesis of no covariation in population trends among species, the conditional expected value of S_T^2 is equal to $\Sigma_i s_i^2$, giving V the value of 1. In this case, the variance in total abundance for all species from year-to-year can be completely explained by the sum of the variances in density of each individual species.

We calculated Schluter's index of association (W), which is equal to VN (N equals the number of samples) and

$$W = VN = S_T^2 N \Big/ \sum_i s_i^2, \quad (3)$$

where

$$S_T^2 = (1/N) \sum_j^N (T_j - t)^2, \quad (4)$$

and

$$s_i^2 = (1/N) \sum_j^N (X_{ij} - t_i)^2. \quad (5)$$

T_j is the total density of birds in year j, t is the mean density of total birds across all j years, X_{ij} equals the density of species i in year j, and t_i equals the observed mean density of species i among all j years. If the ratio V is greater than one, species tend to covary positively and, if V is less than one, species tend to covary negatively. W is approximately chi-square distributed, with n degrees of freedom (Schluter 1984).

We calculated Pearson correlation coefficients for each possible pair of species over the 40-year CBC data set. We then clustered all species on the basis of their correlation coefficients, using a maximum-linkage algorithm to summarize similarities in abundance patterns.

Results

Sixteen colonial wading bird species were observed regularly on Louisiana Christmas counts (Table 1). Winter population sizes for most species increased (Table 2) based on per count CBC data smoothed with a three-year sliding average (Fig. 2). Slopes of linear regressions (abundance per year) from 1949 to 1988, based on nonsmoothed per-count data, were positive for 13 of the 16 species (Table 2). Species with highest slopes were White Ibis, Glossy and White-faced ibises, Cattle Egret, Snowy Egret, and Great Egret; other species with positive slopes were Little Blue Heron, Tricolored Heron, Roseate Spoonbill, Great Blue Heron, and Black-crowned Night-Heron. Least Bitterns and American Bitterns had a slope near zero. The relative rarity of the Green-backed Heron, Reddish Egret, Yellow-crowned Night-Heron, American Bittern, and Least Bittern precludes drawing any firm conclusions regarding these species.

When we restricted analyses to the last 20 years (1969–1988), most species (11 of 16) increased exponentially, based on a somewhat better fit to an exponential than a linear regression (i.e. larger R^2; Table 2). In particular, populations of Great Blue Herons, White Ibises, Great Egrets, Black-crowned Night-Herons, Snowy Egrets, Cattle Egrets, Yellow-crowned Night-Herons, and Glossy and White-faced ibises increased dramatically from 1968 to 1988 (Fig. 3).

Comparison of CBC and BBS trends in Louisiana.—Most Louisiana BBS trends closely paralleled Louisiana CBC trends during the 1966–1989 time period in terms of their magnitude and direction (Table 3). Both BBS and CBC trends show that most Louisiana populations increased from 1966 to 1989, especially White Ibises, Glossy and White-faced ibises, Roseate Spoonbills, Snowy Egrets, Cattle Egrets, and Great Egrets.

Not all Louisiana BBS trends corresponded with the CBC trends in these two time periods. For example, from 1966 to 1989, breeding populations (BBS trends) showed a higher rate of increase than did winter populations (CBC trends) in White-faced Ibises, Roseate Spoonbills, Snowy Egrets, Great Egrets, and Yellow-crowned Night-Herons, while CBC data indicated greater increases than BBS data for Black-crowned Night-Herons and Great Blue Herons.

BBS trends by state.—A comparison of Louisiana BBS trends with those of other states containing large wading bird populations (Florida, Texas, and California) revealed regional differences in population trends during the past two decades (Table 3). Florida's wading-bird populations, unlike those in Louisiana, appear to be declining. Only the Snowy Egret, Little Blue Heron, and Green-backed Heron populations increased from 1980–1989. Colony census data, however, indicate that Florida's Snowy Egret population may have declined sharply during this period (Ogden 1994). Furthermore, populations of 10 Florida species declined more rapidly from 1980–1989 than 1966–1989. Most species of Texas wading birds also declined, especially in the last decade. Several of the species that remained stable or declined from 1980–1989 in Florida or Texas simultaneously increased in Louisiana, namely the White Ibises, Glossy Ibises, White-faced Ibises, Yellow-crowned Night-Herons, Black-crowned Night-Herons, and Tricolored Herons. California wading-bird populations showed the largest number of significant increases of the states examined, particularly in 1980–1989 for the White-faced Ibises, Cattle Egrets, Snowy Egrets, Great Egrets, and Black-crowned Night-Herons.

Community-level analyses.—The Schluter (1984) covariance test assesses covariance within a community or assemblage. This test revealed a high degree of positive covariance in 40-year CBC population trends in Louisiana among all 16 species ($W = 127.15$, df $= 40$, $P < 0.001$). We believe that this covariance reflects a similar response among species pairs to changing ecological conditions, particularly the quality of foraging habitat (see Discussion).

We clustered species based on species pairwise correlation coefficients of population sizes over time, using a complete-linkage method (Sneath and Sokal 1973, Bock and Root 1981, Holmes et al. 1986). The resulting tree diagram (Fig. 4) shows that the Great and Snowy egrets (diurnal visual feeders on primarily fish and crayfish) clustered most closely with one an-

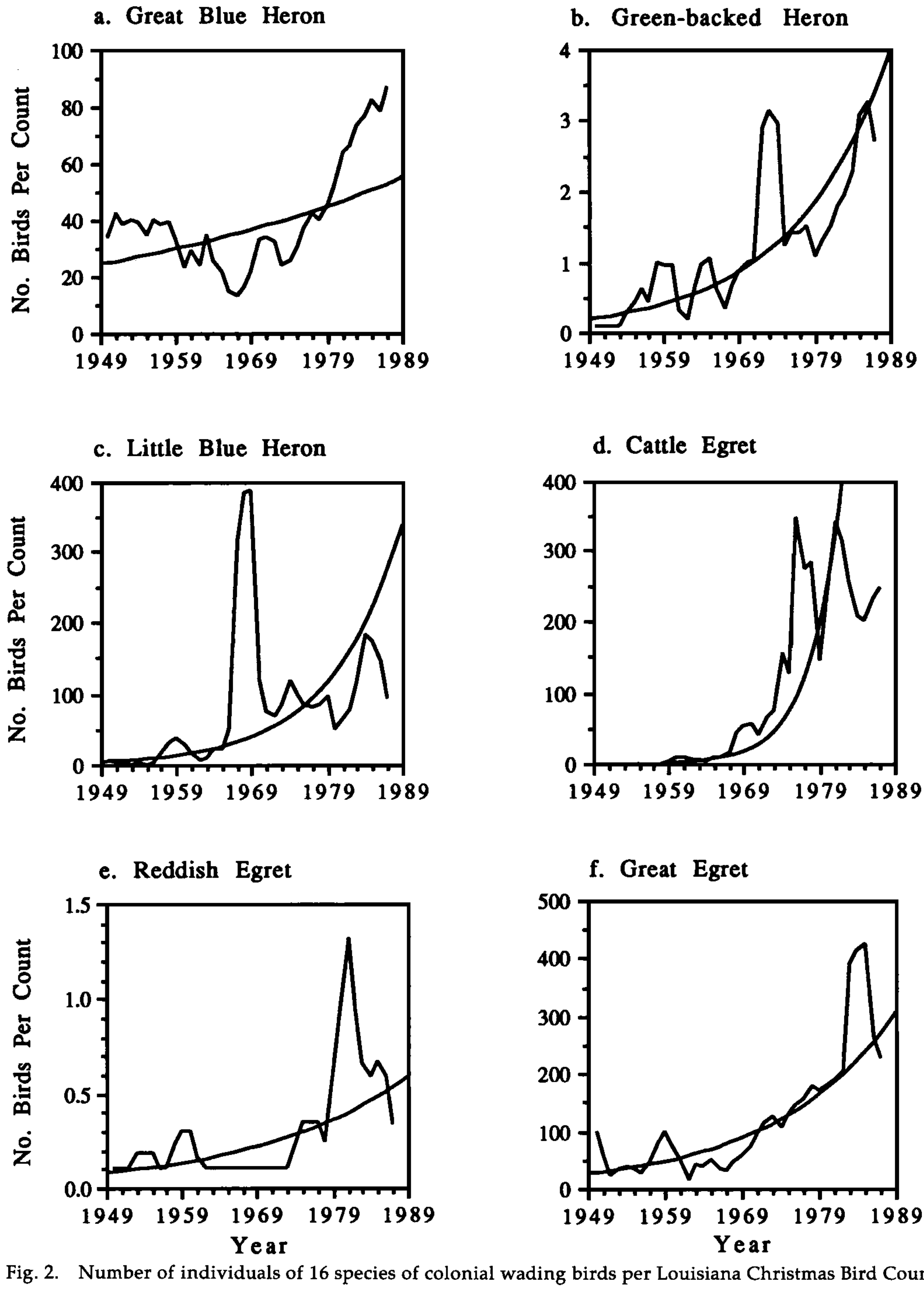

Fig. 2. Number of individuals of 16 species of colonial wading birds per Louisiana Christmas Bird Count, 1949-1988. Curves are least-squares exponential functions fit to smoothed per-count data.

other, indicating greatest similarity of population trends. The ibises (diurnal tactile feeders on primarily crayfish) also were closely correlated with one another, as were the two night-heron species (nocturnal visual feeders on primarily crayfish). The Great Blue Heron clustered most closely with the ibises and egrets. The Little Blue Heron and the two bitterns were dissimilar from the other species in population changes within Louisiana.

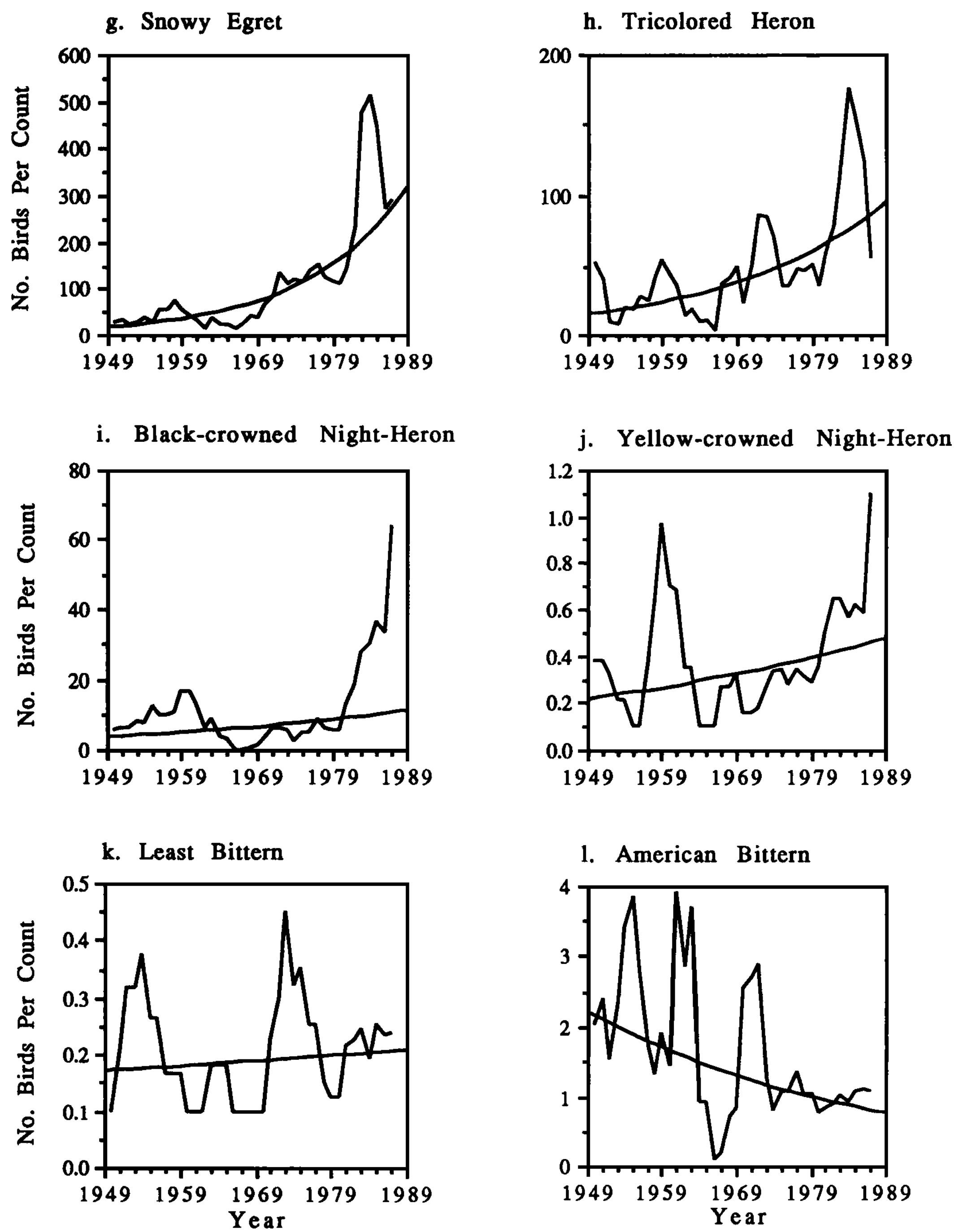

Fig. 2. Continued.

Discussion

Louisiana wading-bird population trends.—CBC data show increasing winter populations of most species of Louisiana wading birds. The increases demonstrated by CBC data were not an artifact of data-collection methods. The use of the per-count method for normalizing CBC data for colonial wading birds only removed the exponential trend shown in observer effort over

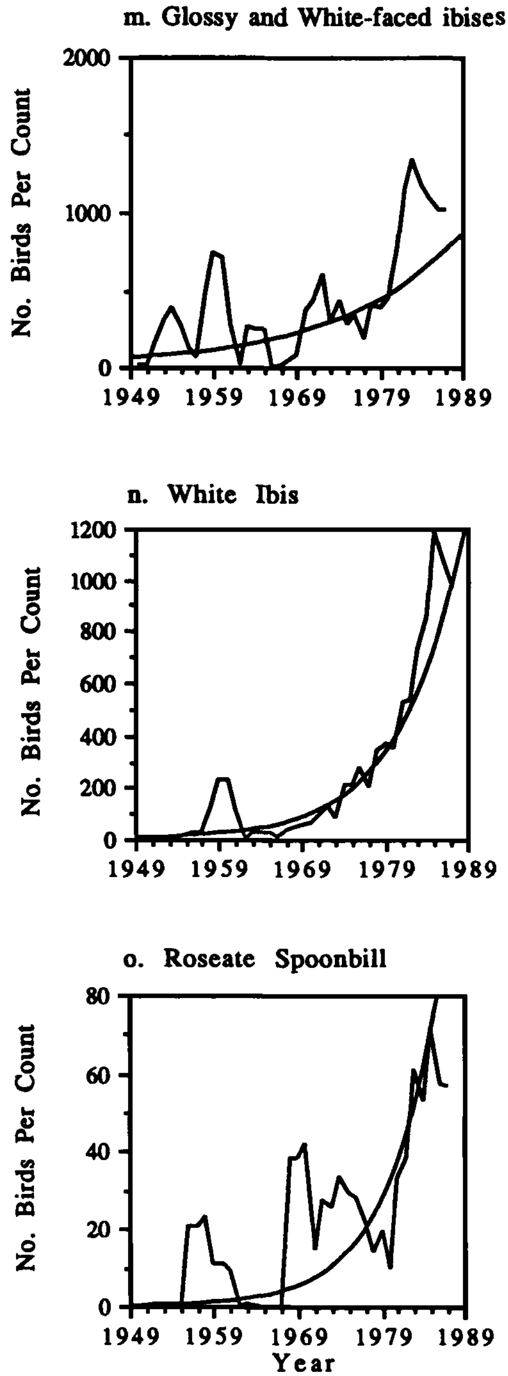

Fig. 2. Continued.

the same time period (Fig. 1). Some CBC counts added in the last decade are in areas of high bird density and, therefore, might affect the calculated trends. A separate analysis of six high-density species, however, in two individual counts at opposite ends of the state (New Orleans and Sabine NWR) from 1954 to 1988 showed the same trends as in the complete data set (Fleury unpubl. data). Furthermore, Louisiana BBS trends generally support the observed CBC trends for the same time periods (Table 3).

The Schluter covariance test suggests that some ecological factors were affecting most species similarly, resulting in a strong and positive covariance between them. Closely related species, however, need not covary in their population fluctuations, and BBS data from areas outside of Louisiana suggest different population trends even in congeneric pairs of species (Table 3). Interspecific competition is one cause of negative values of W in some communities (Schluter 1984), but the positive value of W in our data indicate that interspecific competition was not an important factor influencing population trends in these wading-bird species. Moreover, these species clusters are similar to those proposed by Kushlan (1978) based on resource partitioning in South Florida wading-bird communities. Many environmental factors could account for the trends we have documented. As we argue below, however, the most likely single factor is variation in food supply.

State and regional population trends.—Analyses of BBS data proved useful here in corroborating many CBC trends (Table 3), and suggested a complex regional pattern of shifting ranges and population centers for colonial wading birds. Our study suggests the possibility of large-scale regional changes in population centers of wading birds along the Gulf Coast. Many of the decreases in wading-bird populations in Texas and Florida indicated by BBS data were contemporaneous with increases in Louisiana populations of these species. Frederick and Spalding (1994) described a general pattern of population shifts of White Ibises from Florida to other areas in the Southeast. A decline in nesting White Ibis in the Carolinas also seems to parallel gains in Louisiana's White Ibis population (Frederick et al. in press). R. P. Martin (1991) noted that for 8 of the 11 wading-bird species known to nest in the Louisiana coastal zone, the state now accounts for over 25% of the known U.S. coastal breeding populations. Further study will be needed to determine whether the observed patterns are caused by regional population shifts, or are the result of complex local population changes.

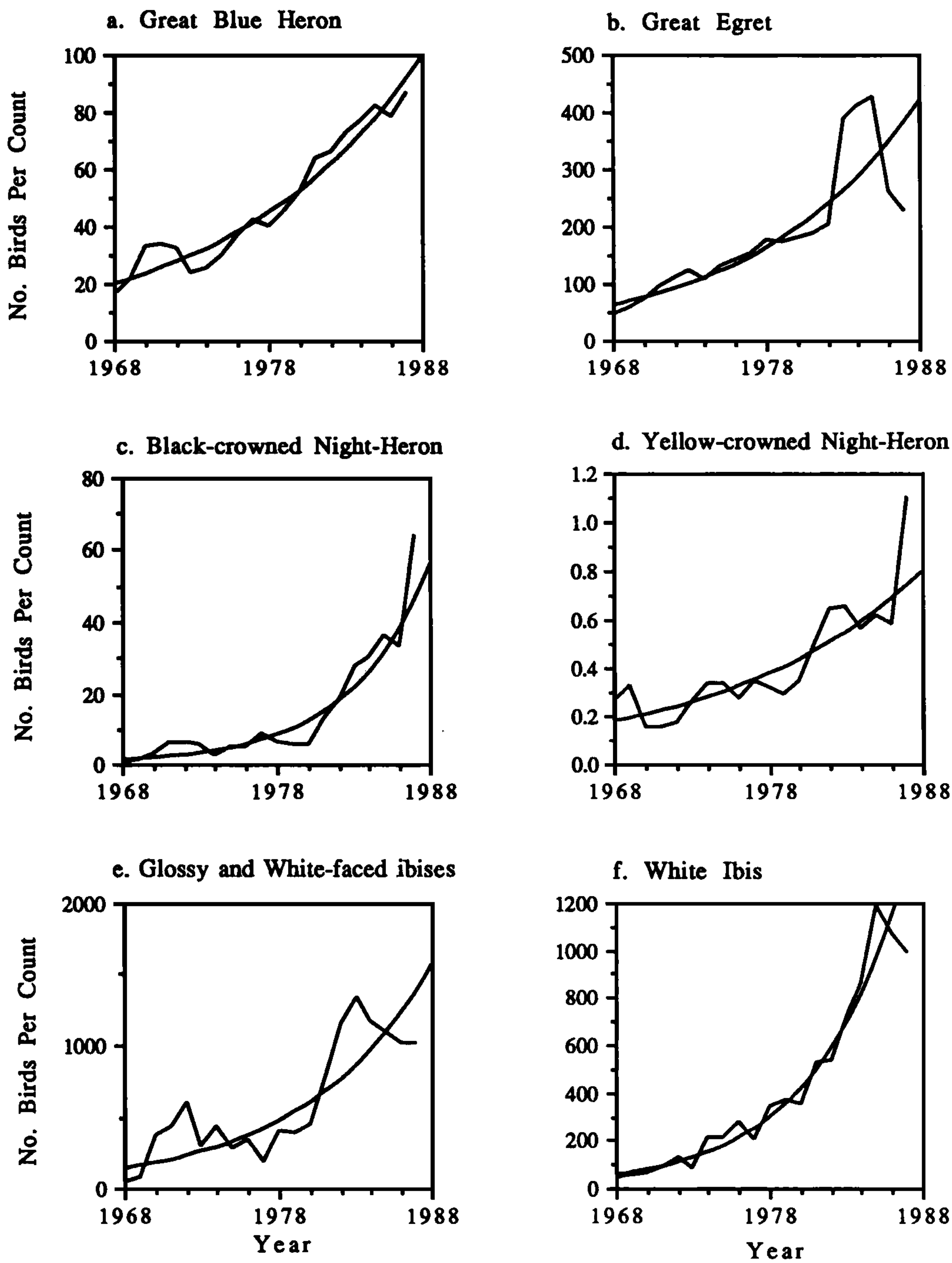

Fig. 3. Exponential-growth models of selected species of colonial wading birds in Louisiana Christmas Bird Counts, 1968–1987 (number per count, smoothed).

Wading birds and crayfish ponds.—We found a strong positive correlation between several species populations of wading birds and the availability of both wild and pond-raised crayfish between 1968 and 1987. We list several lines of evidence below to support the hypothesis that increased acreage devoted to crayfish aquaculture is a dominant ecological factor influencing

TABLE 3. Christmas Bird Count (CBC) trends for Louisiana, and Breeding Bird Survey (BBS) trends for Louisiana, Florida, Texas, and California (percent annual change). Dash (—) indicates no data reported.

Species	Louisiana CBC	Louisiana BBS	Florida BBS	Texas BBS	California BBS
		1966–1989			
American Bittern	0.4	—	−0.2	1.1	3.2
Least Bittern	0.4	1.7	0.9	0.6	—
Great Blue Heron	8.8	1.7	−1.1	3.6**	1.9
Great Egret	9.7	15.5*	−9.4	0.4	12.4***
Snowy Egret	15.1	24.8	17.0	0.7	11.1***
Little Blue Heron	1.2	−2.2	−2.0	−2.3	—
Tricolored Heron	7.7	8.4	−1.2	−0.1	—
Reddish Egret	3.0	—	−0.8	0.0	—
Cattle Egret	11.1	12.3***	1.2	2.7	19.1*
Green-backed Heron	4.0	2.0	−2.7	1.0	5.7***
Black-crowned Night-Heron	20.3	3.3	−11.6	−0.2	11.1
Yellow-crowned Night-Heron	4.0	9.1	0.2	−0.2	—
White Ibis	25.4	18.5	−1.2	10.1**	—
White-faced Ibis	24.9[a]	58.8	—	−0.9	26.8***
Glossy Ibis	24.9[a]	—	−8.9	—	—
Roseate Spoonbill	17.5	36.4	132.3	1.3	—
		1980–1989			
American Bittern	−3.3	—	—	—	1.0
Least Bittern	−0.6	—	−15.0	−2.7	—
Great Blue Heron	4.8	−2.4	−7.0*	4.2	−3.1
Great Egret	3.7	10.6	−9.7	10.1	12.3***
Snowy Egret	7.5	49.6	6.9	8.9*	13.0***
Little Blue Heron	−0.7	6.6	3.4	−6.5	—
Tricolored Heron	−2.0	6.1	−3.2	−10.8**	—
Reddish Egret	−11.4	—	−16.8***	—	—
Cattle Egret	−11.0	1.1	−1.0	−3.0	25.4*
Green-backed Heron	1.0	−5.6	3.2	−4.7	2.6
Black-crowned Night-Heron	18.3	5.8	−15.1	−3.9	21.9
Yellow-crowned Night-Heron	7.7	21.2**	−1.2	2.5	—
White Ibis	13.5	2.2	−3.3	0.9	—
White-faced Ibis	8.0[a]	4.7	—	−21.2***	44.9***
Glossy Ibis	8.0[a]	—	−20.5	0.9	—
Roseate Spoonbill	16.6	14.6	0.9	−16.9**	—

*, $P < 0.10$; **, $P < 0.05$; ***, $P < 0.01$.

[a] Combined data for Glossy and White-faced ibises. Most birds reported as White-faced Ibis.

the strong recent growth trends of many Louisiana populations of wading birds.

The Atchafalaya basin provides abundant fish, crayfish, frogs, and other prey for wading birds (Blades 1974, Gary 1974a). This rich food supply, however, fluctuates sharply from year to year depending on weather (McSherry 1982, Huner 1990). The crayfish-aquaculture industry provides farmers with a reliable alternative to an unpredictable swamp harvest (Gary 1974b, McSherry 1982), and the regularity with which ponds are managed also makes crayfish ponds a more predictable food source for wading birds than comparable natural foraging areas. Well-managed ponds mimic the natural hydrologic patterns that promote crayfish growth in the extensive marshes of southern Louisiana. The hydrological cycle in crayfish ponds is managed slightly out of phase with, and ahead of, the natural wetlands hydrological cycle (Fig. 5). This minimizes the overlap between the pond harvest and the wild harvest, and prevents an overabundance of marketable crayfish, which would significantly reduce the market price (Martin 1979, McSherry 1982, Huner and Romaire 1990).

Louisiana crayfish landings from 1949 to 1987 were significantly and positively correlated with populations of Great Blue Herons, Yellow-crowned Night-Herons, Black-crowned Night-Herons, Great Egrets, Snowy Egrets, White Ibises, and Glossy and White-faced ibises (Table 4). All of these species are known to feed on crayfish (Table 5).

We found correlations nearly twice as high,

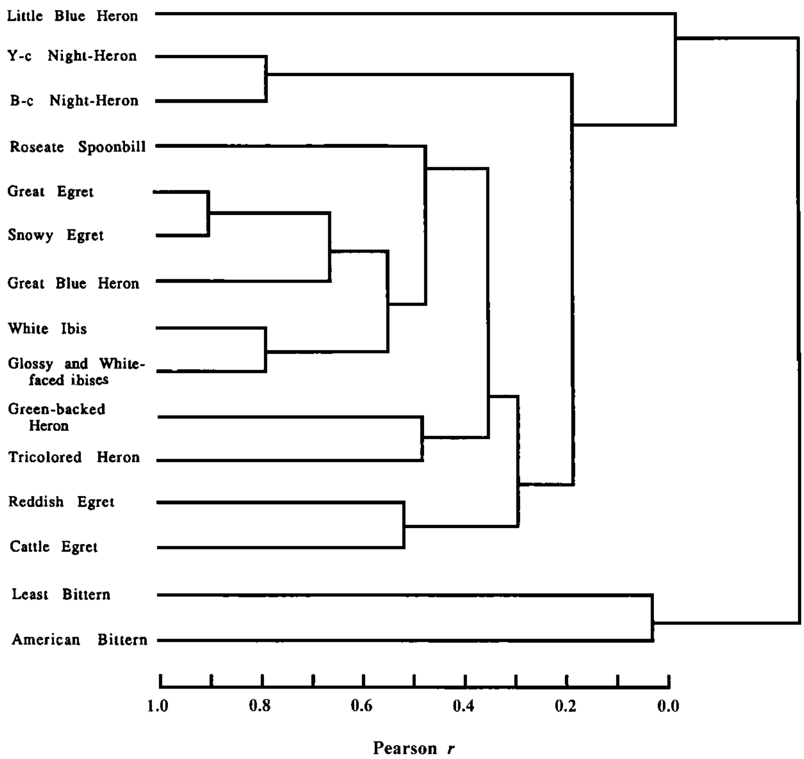

Fig. 4. Cluster analysis of species pairwise correlation coefficients based on per-count CBC data, 1949–1988.

however, between these same species of wading birds and the total acreage devoted to commercial crayfish ponds in Louisiana. Crayfish farm ponds increased from 99 ha in 1949 to over 284, 165 ha in 1991 (W. Lorio pers. comm.), but reliable data for crayfish ponds are only available from 1968 to date (Table 4). Many species of wading birds feed regularly in crayfish ponds, especially Yellow-crowned Night-Herons, White Ibises, Great Egrets, Snowy Egrets, and Little Blue Herons (Table 6; Huner 1994, Martin and Hamilton 1985; Huner 1976 presentation at Ecological Society of America; Fleury pers. obs.).

More importantly, species-specific dietary patterns of Louisiana wading birds support the hypothesis that crayfish aquaculture and wading-bird population increases are causally related (Table 5). Population growth of species that rarely feed on crayfish, including Cattle Egrets and Roseate Spoonbills, are poorly correlated with crayfish pond acreage (Tables 4 and 5). Wading-bird species whose population increases from 1969–1989 correlated most highly with crayfish acreage were the Great Blue Heron, Black-crowned Night-Heron, Yellow-crowned Night-Heron, White Ibis, Glossy and White-faced ibises, Great Egrets, and Snowy Egrets (Table 4). These same species had the highest proportion of crayfish in their adult or nestling diets, and were among those increasing most rapidly in Louisiana CBC or BBS trends

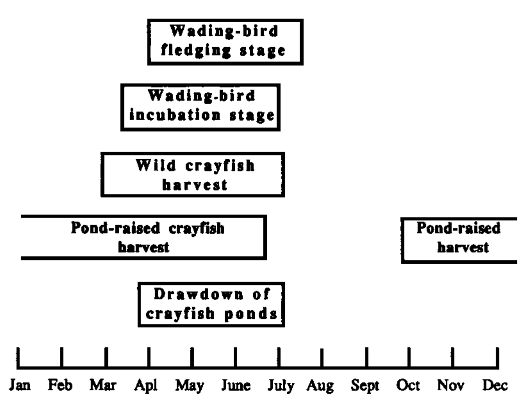

Fig. 5. Temporal relationship between wading-bird breeding cycle, crayfish pond harvest, and crayfish pond drawdown.

TABLE 4. Pearson product-moment correlation of wading-bird populations (per count CBC, 1968–1987) with crayfish aquaculture pond acreage, wild crayfish harvest (in pounds), and rice field acreage (harvested).[a]

Species	1968–1987 crayfish (df = 18) Pond	Wild	1949–1987 wild crayfish (df = 37)	1968–1987 rice
American Bittern	−0.20	−0.12	−0.21	−0.14
Least Bittern	0.10	−0.01	0.08	−0.02
Great Blue Heron	0.90**	0.45*	0.52**	−0.55
Great Egret	0.63**	0.35	0.56**	−0.30
Snowy Egret	0.63**	0.44	0.61**	−0.37
Little Blue Heron	−0.26	−0.17	0.18	0.33
Tricolored Heron	0.44	0.25	0.44**	−0.18
Reddish Egret	0.46*	0.02	0.29	0.19
Cattle Egret	0.38	−0.02	0.39*	−0.21
Green-backed Heron	0.40	0.32	0.55**	−0.24
Black-crowned Night-Heron	0.89**	0.56*	0.47**	−0.59
Yellow-crowned Night-Heron	0.68**	0.45*	0.25	−0.07
White Ibis	0.72**	0.42	0.44**	−0.45
Glossy and White-faced ibises	0.75**	0.34	0.60**	−0.40
Roseate Spoonbill	0.35	0.31	0.53**	−0.14

*, $P < 0.05$; **, $P < 0.01$.

[a] Crayfish pond acreage data from W. Lorio (pers. comm.) and J. Huner (pers. comm.). Data for wild-crayfish landing data from the National Marine Fisheries Service. Rice-acreage data from Fielder and Nelson (1982) and University of New Orleans (1990).

from 1966 to 1989 (Tables 3 and 5). A few species are exceptions to this pattern. Great Blue Herons, for example, consume relatively few crayfish, but their numbers correlate strongly with crayfish pond acreage. They may benefit from other prey, such as the abundant small fish found in most farm ponds.

Seasonal patterns of crayfish-pond usage by Louisiana wading birds also strongly support the hypothesis that crayfish ponds contribute to population growth by increasing reproductive success (Fig. 5). Wading birds use crayfish ponds throughout the year, but usage peaks twice annually (Huner 1983, Martin and Hamilton 1985). The first peak occurs in winter, when the ponds are filled and adult crayfish emerge from their burrows with broodstock. A much higher peak occurs in May and June, when ponds are drained following the commercial harvest and wading birds are establishing nests and feeding nestlings (Martin 1979; Fig. 5 and Table 6).

Crayfish pond drawdown simulates the drying of surface water in natural wetlands, and consequent concentration of prey, although the drying period in crayfish ponds is relatively short. During the pond-drawdown phase, crayfish that have not yet burrowed are concentrated in shallow water, along with other crustaceans, fish, amphibians, and aquatic insects (Huner 1983, 1994). The natural concentration of prey in shallow water, governed by the seasonal drying rate, is an important requirement for efficient wading bird foraging in the Everglades, particularly for tactile feeders (Kushlan et al. 1975). A rapid drying rate ensures that prey items will be concentrated in sufficient density in small pools (Bancroft et al. 1988). While this relationship may not hold generally for wading birds outside the Everglades (Frederick and Spalding 1994), the timing of breeding cycle and pond drawdown in Louisiana suggests a similar pattern, particularly for the White Ibis. White Ibises rely heavily on crayfish for their nestling diet (Bildstein et al. 1990, Bildstein 1993), and abandonment and failure of White Ibis nests is closely related to low prey density and excessive rainfall (Frederick and Collopy 1989b).

Because drawdowns occur at different times on different farms throughout southern Louisiana, crayfish farms create a landscape-level series of patches of high prey density. These landscape-level patches are analogous to those tracked by wading birds foraging in natural wetlands. Colonial wading birds are well adapted behaviorally to track spatially and temporally patchy food supplies (Kushlan 1976, Erwin 1983, Kushlan 1986, Bancroft et al. 1994). If wading-bird populations are ultimately food limited, the addition of a new source of prey that is readily available as well as spatially and tem-

TABLE 5. Percentage of crayfish and other crustaceans in diets of colonial wading birds. Where range is given, first reference cited corresponds to lower value, with "ad" referring to adult bird diet, and "j" referring to juvenile bird diet. Percent values represent ratios of numbers of crayfish to total number of prey items. Values marked "mass" represent dietary percentage by mass or volume.

Species	Percent crayfish in diet of		Source
	Adult	Juvenile	
American Bittern	19–25	—	Palmer 1962 (ad), Sprunt and Chamberlain 1949 (ad)
Least Bittern	10[a]	—	Palmer 1962 (ad)
Great Blue Heron	9–14[a]	—	Palmer 1962 (ad), Sprunt and Chamberlain 1949 (ad)
Great Egret	9 (mass)[a,b]	30	Recher and Recher 1980 (ad), Howell 1932 (j)
Snowy Egret	16 (mass)–39	0.7–3	Recher and Recher 1980 (ad), Telfair 1981 (ad), Jenni 1969 (j), Howell 1932 (j)
Little Blue Heron	11–73	5–8	Niethammer and Kaiser 1983 (ad), Telfair 1981 (ad), Howell 1932 (j), Rodgers 1982 (j)
Tricolored Heron	2[a]–20	0–2	Sprunt and Chamberlain 1949 (ad), Palmer 1962 (ad), Jenni 1969 (j), Howell 1932 (j)
Reddish Egret	2 (mass)[c]	—[c]	Recher and Recher 1980 (ad)
Cattle Egret	0	0	Palmer 1962 (ad), Telfair 1981 (ad), Jenni 1969,1973 (j)
Green-backed Heron	1–20	—	Niethammer and Kaiser 1983 (ad), Palmer 1962 (ad)
Black-crowned Night-Heron	22	8	Palmer 1962 (ad), Howell 1932 (j)
Yellow-crowned Night-Heron	74–97[a]	—	Niethammer and Kaiser 1983 (ad), Riegner 1982 (ad)
White Ibis	52–72 (mass)	46	Kushlan and Kushlan 1975 (ad), Kushlan 1979 (ad), Howell 1932 (j)
Glossy Ibis	—[d]	37–40	Sprunt and Chamberlain 1949 (ad), Baynard 1913 (j), Howell 1932 (ad,j)
White-faced Ibis	35	—	Palmer 1962 (ad)
Roseate Spoonbill	—[c]	—[c]	Palmer 1962

[a] Dietary reports include other crustaceans in total.
[b] Diet reported as 100% prawns.
[c] For these species, Palmer (1962) described diet as mainly fish, with a few crayfish or other crustaceans.
[d] Sprunt and Chamberlain (1949) described diet as "for the most part" crayfish and grasshoppers. Howell (1932) noted that crayfish comprised a "considerable percentage" of the diet.

porally staggered from natural food sources should have a substantial impact on reproductive success of species using this resource. Double-crested Cormorants (*Phalacrocorax auritus*), for example, winter in ever-increasing numbers to feed in 222,390 ha of catfish farm ponds scattered across Mississippi's Delta region. This new foraging habitat may have contributed to a 25%

TABLE 6. Wading birds observed during drawdown of crayfish ponds at the University of Southwestern Louisiana's Crawfish Research Center, 1992–1995. Annual census is taken near end of drawdown when pond bottoms partly exposed, and represents peak annual bird count recorded on 20-ha farm-pond complex.

Species	1992	1993	1994	1995
Great Blue Heron	0	2	1	0
Great Egret	211	26	499	84
Snowy Egret	445	192	273	439
Little Blue Heron	4	4	18	42
Tricolored Heron	2	2	—	5
Black-crowned Night-Heron	—	2	—	—
Yellow-crowned Night-Heron	—	1	8	1
White Ibis	104	0	225	85
Total	766	229	1,024	656

increase in the species' northern Great Lakes breeding population (Conniff 1991, A. May pers. comm.). The explosive growth of California's White-faced Ibis population (Table 3) may be attributable to its ability to forage successfully in the irrigated fields that have largely replaced its former foraging habitat of backwater sloughs and flooded meadows (Bent 1926, Small 1975, Bray and Klebenow 1988).

Food limitation may be especially critical during the nestling phase of the annual breeding cycle (Rodgers and Nesbitt 1979, Newton 1980, T. E. Martin 1987, 1991). Mortality in wading birds peaks in the first two weeks of life, and remains high for fledglings (Kushlan 1978). Kahl (1963) reviewed mortality in several wading-bird species, and found that first year mortality ranged from 61 to 78%. Abundant food supply may affect population growth by improving the survivorship of both nestlings and newly fledged young (Powell 1983, Mock et al. 1987). Crayfish ponds also may increase fledgling survival by assuring inexperienced fledglings a steady supply of easily captured prey while they learn to forage. Juvenile wading birds are less effective foragers than adults in the same habitat (Recher and Recher 1969, Bildstein 1983, 1993, Draulans 1987a, Cezilly and Boy 1988, Frederick and Spalding 1994). Farm ponds also have fewer alligators (*Alligator mississippiensis*) and other avian predators than natural wetlands, perhaps because there is little or no cover around farm ponds where predators can hide (Fleury pers. obs.). As a result, birds require less vigilance when foraging in farm ponds, and may experience lower mortality from predation while foraging.

Our data support the hypothesis of food limitation for populations of colonial wading birds breeding in Louisiana, but further work is needed to establish the mechanism involved. Because we cannot determine the extent to which local population increases are due to immigration at the regional level versus local recruitment, we cannot unambiguously demonstrate the role of food limitation in Louisiana wading birds.

Possible alternative hypotheses.—We briefly consider below several alternative hypotheses for the observed trends in populations of Louisiana wading birds. These hypotheses, which are not mutually exclusive, include a long-term recovery from the effects of the plume trade, range expansion of wading-bird species in northern states, recovery from the effects of DDT and other pesticides, competition, predation, a response to changing weather, and changes in habitat.

The AOU calculated that some 5,000,000 birds of all species were killed each year by plume hunters for the fashion trade from about 1875 through the early 1900s (Buchheister and Graham 1973), although the questionable accuracy of early population estimates makes it difficult to judge the true impact of the plume trade on wading birds (Robertson and Kushlan 1974, Frohring et al. 1988, Ogden 1994). Exploitation of wading birds for plumes, eggs, and food was an important source of mortality throughout the southern United States as late as the 1930s for several species (Powell et al. 1989), and some illegal harvesting probably continues to this day. Most wading-bird species, at least in the Gulf coast states, had probably recovered from plume hunting by the 1930s (Ogden 1978, Bancroft 1989). Therefore, it is unlikely that the post-1940s increases we have documented are primarily the result of recovery from the plume trade or other human exploitation.

Could the observed population increases reflect expanding ranges of migratory wading birds outside of Louisiana? Great and Snowy egrets are expanding their ranges to the north, possibly reoccupying portions of their range occupied prior to plume hunting (Ogden 1978, Ryder 1978). Great Blue Herons have increased in northern New York, perhaps in response to reforestation of abandoned farmland (McCrimmon 1982). The Glossy Ibis and White Ibis also have expanded their ranges along the Atlantic coast, and the White-faced Ibis has been extending its range steadily eastward in Louisiana. Many wading birds that breed in more northern regions are known to winter in Louisiana and elsewhere along the Gulf coast (Byrd 1978, Hancock and Kushlan 1984, Root 1988). Detailed banding studies will be required to determine what proportion of Louisiana's winter populations are resident birds as opposed to migrants. Emigration from neighboring states into Louisiana may explain some of the observed increases, but in the absence of historic data and relevant data from band recoveries, we cannot fully evaluate this hypothesis (Frederick et al. in press).

Could population increases be due to a release from heavy pesticide contamination in the 1950s and 1960s? Per-count data for all species show relatively flat population curves from 1949 to 1960, followed by a general decline beginning about 1960 and continuing through about 1970 (Fig. 2). CBC efforts during this period generally were stable or increasing (except for 1963) in number of counts, party-hours, and party-miles (Fig. 1). The timing of the declines in Louisiana wading-bird populations corresponds with similar pesticide-related declines noted for cormorants (Morrison and Slack 1977), Brown Pelicans (*Pelecanus occidentalis;* Schreiber and Mock 1987), and raptors (Bednarz et al. 1990). Recovery coincides with the banning of DDT in 1972. We conclude, therefore, that some of the population increases we have documented (Fig. 2) could have resulted from recovery of populations following the banning of DDT and other pesticides. However, not all the post-1970 population changes are attributable to release from pesticide effects, because this hypothesis predicts rangewide increases, and these are not observed in Florida and Texas (Table 3).

Competition does not appear to be a major limiting factor for colonial wading-bird populations, at least at present population densities. The high positive covariance of wading-bird populations in our study argues against a strong competitive interaction among species of Louisiana wading birds (Schluter 1984). The birds are highly social, breeding and feeding together in large numbers, with a well-defined partitioning of resources (Burger 1978, Kushlan 1978).

Predation is an important limiting factor for some avian populations, but there is no evidence to suggest that predation has decreased sufficiently to release wading-bird populations. Frederick and Collopy (1989a) observed that 43% of wading-bird nest loss in the Everglades was due primarily to predation by snakes or raccoons (*Procyon lotor*). Both these predators are abundant in Louisiana as well, and probably account for a significant proportion of nest failure. We have seen no evidence that these predators have decreased significantly over the study period. Snake populations have declined locally in areas of severely disturbed habitat, but there has been no noticeable change in total populations (B. Prima pers. comm.). Crows also prey on wading-bird nests (Frederick and Collopy 1989a). Analyses of 1949–1988 CBC data for Fish Crows (*Corvus ossifragus*) and American Crows (*C. brachyrhynchos*) show increasing populations that peak in 1982 and decline thereafter (B. Fleury unpubl. data).

Weather conditions can affect reproductive success of many species in a particular year, and also affect CBC counts by depressing volunteer efforts. Severe winter weather in 1962, 1963, and 1968, for example, caused Cattle Egrets to decline in both Florida and national CBC counts (Bock and Lepthien 1976, Larson 1982), and 1963 winter storms reduced CBC efforts in Louisiana to a single count. Although weather fluctuations may explain at least part of the annual variation in population size, they cannot account for the long-term exponential growth of some Louisiana wading-bird populations.

Habitat destruction and degradation due to water management, urban development, impoundment, and wetland drainage, coupled with several years of drought, have contributed to the precipitous decline of wading-bird populations in southern Florida and California (Small 1975, Kushlan and White 1977, Bancroft 1989, Ogden 1994). Louisiana also has experienced a significant loss of inland wetland habitats during the past 40 years (R. P. Martin 1991), but an abundance of suitable wading-bird habitat remains. Forested wetlands in Louisiana comprise about 7,400,000 ha, with an additional 8,400,000 ha of nonforested wetlands (Williams and Chabreck 1986). Louisiana wading birds do not seem to be limited by the availability of suitable nesting sites, and a recent survey of wading-bird colonies in southern and coastal Louisiana found little change in the number and turnover rate of colonies from the previous census (Keller et al. 1984, Martin and Lester 1990). Aquaculture ponds have not significantly altered the quantity of foraging habitat, but have provided a new and higher-quality habitat in terms of predictability in space and time, as well as high densities of preferred prey.

Not all flooded fields provide high-quality foraging habitats. Crayfish ponds frequently are reflooded after drawdown and seeded with rice (Huner 1990, Huner and Romaire 1990). Wading birds frequently forage in these flooded rice fields (Cardiff and Smalley 1989, Remsen et al. 1991). Although rice fields in Italy provide critical foraging habitat for Black-crowned Night-Herons and Little Egrets (*Egretta garzetta;* Fasola 1983, 1986), we found no significant positive correlation between any wading-bird populations and changes in rice-field acreage in Louisiana (Table 4; Fielder and Nelson 1982, University of New Orleans 1990). Use of a wide variety of powerful pesticides in Louisiana rice fields may depress populations of fish, crayfish, and other invertebrate prey species (Louisiana

TABLE 7. Total United States Animal Damage Control depredation permit kills authorized and reported in 1991 (compiled by U.S. Fish and Wildlife Service).

Group	Authorized	Reported
Egrets	2,766	1,174
Herons	4,300	2,400
Night-herons	175	243
Cormorants	10,814	6,789
Pelicans	50	43
Kingfishers	216	126
Gulls	1,338	561
Coots	200	134
Anhingas	0	19
Grebes	70	336
Ducks	110	20
Miscellaneous	4,665	1,483
Total	24,704	13,328

State University Agricultural Center 1987). Pesticide use in French rice fields adversely affected Little Egret foraging (Hafner et al. 1986)

To summarize our evidence for the hypothesis that crayfish aquaculture is the primary factor causing the dramatic increases in wading-bird populations in Louisiana, the highest wading-bird population increases occurred during the 20-year period in which the crayfish industry was expanding. Increased pond acreage correlates best with the abundances of those species known to prey most heavily on crayfish. Pond drawdowns may influence population growth by providing a predictable and readily available food resource during the incubation, nestling and fledging periods. Finally, the alternative hypotheses are not compelling.

Conservation and management implications.—Our findings have important implications for the conservation and management of wading birds. The increases in several species wintering in Louisiana and corresponding increases in breeding-bird populations suggest that Louisiana will continue to provide critically important habitat for wintering and breeding North American colonial wading birds. Current wetlands management often is aimed exclusively at enhancing duck habitat, particularly in national wildlife refuges, and these management policies need to be reevaluated for their possible impact on colonial wading-bird habitat requirements.

The strong positive population increases that we have documented in many Louisiana populations of colonial wading birds also indicate that the conflict between aquaculture farmers and state and federal wildlife officials is likely to increase (Boyd 1991). Current aquaculture farm-management policies are focused on scaring birds from ponds with a variety of nonlethal methods such as pyrotechnics (butane cannons, "screamer" shotgun shells, etc.), and screening ponds to limit access by birds. When nonlethal methods fail to reduce bird predation, U.S. Department of Agriculture (USDA) permits allow limited taking of wading birds (Stickley and Andrews 1989, Littauer 1990a, 1990b, Boyd 1991). Reported bird kills in 1991 under USDA depredation permits, issued mainly to Mississippi catfish farmers, included 2,400 herons and 1,174 egrets (Table 7), and the National Audubon Society also has documented extensive illegal killing of wading birds (Williams 1992). Avian predators on crayfish farms actually may have a minimal effect on the final harvest (Huner 1976, 1983). Martin (1979) estimated that wading birds consumed only about 1% of the total commercial harvest, and Martin and Hamilton (1985) estimated consumption at less than 2% of the commercial harvest. Because high crayfish density results in reduced average crayfish size, limited predation by birds actually may benefit crayfish farmers by reducing the level of intraspecific competition among crayfish. The timing and duration of crayfish farm drawdown and flooding periods across the state, and their relation to the reproductive cycle of colonial wading birds need further investigation, as do the effects on bird populations of farmers eliminating access to aquaculture ponds. Good documentation of avian population trends, predation rates, and the actual impact of wading birds on commercial crops are needed to establish sound management practices. Our study represents an early step towards that goal.

ACKNOWLEDGMENTS

We thank Jay Huner for his invaluable assistance, and Tom Bancroft, Peter Frederick, Fran James, Jim Kushlan, John Ogden, and Allan Strong for reviewing various drafts of this manuscript. Our research is presently supported by the Louisiana Crawfish Promotion and Research Board.

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