POPULATION ENERGETICS OF THE
AMERICAN WHITE IBIS

James A. Kushlan

ABSTRACT.—The White Ibis population nesting in the fluctuating water ecosystem of southern Florida numbered up to 62,000 birds and used several nesting habitats including islands in large lakes, the vast freshwater marshes of the Everglades, and coastal estuaries. Periodic reproduction at large inland colonies, accounting for 93–98% of the nesting birds, sustains the population at its current level, but smaller, more consistently successful coastal colonies provide recruitment during years of inland nesting failure. Clutch size, brood reduction pattern, and energy requirements showed intraregional variation. Clutch size differences may be related to habitat, with lowered clutch sizes along the coast. Despite clutch size differences, the number of young fledged was similar in different colonies. Intraregional variation in timing of brood reduction resulted in differences in the energy required for nesting. The daily energy expenditure of White Ibis was estimated from the time-activity budget and multiples of measured metabolic rates. Although existence metabolism was similar to that predicted by Kendeigh's (1970) regression, daily energy expenditure was considerably below that predicted by extrapolating King's (1974) regression, suggesting a slower increase of DEE at higher body weights. The White Ibis consumed about 21% of its body weight daily, similar to that found in other studies of ciconiiformes. The energy required to raise a brood of young was $9.2–9.9 \times 10^3$ kcal. The nesting population expended 930 and 640×10^6 kcal during 1972 and 1973 respectively. Over 70% of this energy was derived from the Everglades and over 90% from inland habitats. Contrasted with the Wood Stork, the smaller size and shorter nesting cycle enables nesting White Ibis to support 11 times the population on 1.1 times the energy. The ability of smaller birds to maintain higher populations on a given resource base may supply a competitive advantage during times of intense resource-based selection. Together the south Florida populations of White Ibis and Wood Storks require 1.9 billion kilocalories per nesting season and are important determinants of energy flow in the wetland ecosystem.—*U.S. National Park Service, Everglades National Park, Homestead, Florida 33030*. Accepted 17 May 1976. (This paper was subsidized by the United States Department of the Interior, National Park Service.)

THE dynamics and energetics of bird populations are central to much of current ecological theory. Information on the bioenergetic demands of bird populations is of particular value in considerations of community energetics and ecosystem modeling. The available data on small- and medium-sized birds from such autecological studies as those of West (1960), Kale (1965), Zimmerman (1965), Schartz and Zimmerman (1971), and Kendeigh (1972) and from syntheses such as those of Lasiewski and Dawson (1967) and Kendeigh (1970) have been extensively used to estimate energy demands of bird communities (Karr 1971, Holmes and Sturgess 1973, Weins and Innis 1974, Weins and Nussbaum 1975). The data base on large-sized, wide-ranging bird species is more scanty because of the difficulty in obtaining empirical data. Thus large mobile species have seldom been studied on a regional basis, a necessity in determining patterns of energy use within the population. The possibility that important population characteristics such as clutch size, growth patterns, energy use, and ecological impact may exhibit intraregional variation has been little examined. Populations of wading bird species may be significant components of certain regional ecosystems (Kushlan 1976). Thus regional population and energetics information on wading bird species is of considerable value in understanding the patterns of energy flow in highly productive marshland ecosystems worldwide.

This paper discusses the population energetics of the White Ibis (*Eudocimus albus*) in southern Florida. Emphasis is placed on estimating the energy required for nesting

and the relation between intraregional variation in nesting parameters and the bioenergetic demands of nesting. These data are contrasted with some similar information available from Kahl's (1964) study of the Wood Stork (*Mycteria americana*) in southern Florida, one of the few previous attempts at a regional analysis of the energy demands of a wading bird population. This comparison suggests a role of body size in the comparative ecology of species adapted to a particular habitat.

<div align="center">METHODS</div>

The numbers of birds in colonies were determined by aerial photographs supplemented by nest counts made from the ground. Time-budget was determined by watching birds at a colony and on their feeding grounds. Clutch sizes were measured by ground counts of recently completed clutches. Survival of nestlings was determined by periodic censuses of marked nestlings and also, later in development, by the number of juveniles fed by an adult. Energy required for growth and maintenance of young was determined by measuring metabolized energy at 32–35°C, following Kendeigh's (1970) method, using nestlings taken from the nest as pipped eggs. Existence metabolism of adults was measured over 3-day periods of $0.5 \times 0.5 \times 1.1$ m cages. Birds averaged 948 g and varied less than 5% in body weight. Wild birds averaged 881 g. I also measured the energy required for adults to exist in a $3 \times 3 \times 2$ m aviary where activities such as foraging, short flight, fighting, wading, and walking were possible. I call this parameter "aviary existence metabolism." Nestlings were initially fed a mixture of two parts shrimp (*Penaeus duorarum*) and one part sardines (*Harengula pensacolae*). Older birds were fed shrimp, sardines, or anchovies (*Anchoa mitchilli*). Availability of food in habitats was measured with 1-m² throw traps. Prey organisms, food, and excreta were analyzed for calorific value in a Parr adiabatic calorimeter. All excreta were collected and analyzed during the nesting period and the metabolized energy of nestlings was determined by subtracting energy value of feces from energy value of food. All existence metabolism data were obtained during the usual inland nesting season, March–June 1972, at ambient southern Florida temperatures. The temperatures during EM experiments averaged 24.0°C, range 22–27°C. Ambient temperatures during the nesting season averaged 24.3°C, range 11–32°C. Thus the data obtained on these temperature-dependent physiological measurements were similar between wild and captive ibis.

<div align="center">RESULTS</div>

Population and nesting parameters.—In this paper, I consider the southern Florida nesting population of White Ibis to be those birds breeding in and south of Lake Istokpoga. They nested at 14 locations from 1971 through 1973, although not at every site each year (Fig. 1). Lake colonies were on islands in Lake Istokpoga and Lake Okeechobee. Everglades colonies were located in the central Everglades and at the headwaters of coastal rivers in the southern Everglades. Coastal colonies were on mangrove islands in estuaries and coastal bays. The numbers of White Ibis nesting in southern Flordia varied from year to year. Only 1,650 nested in the drought year of 1971, but 62,300 nested in 1972 and 43,200 in 1973. In the years (1972 and 1973) when all colonies were successful, 22 and 21% nested in lake colonies, 76 and 72% in Everglades colonies, and the remainder in coastal colonies (Fig. 1).

Mean clutch size ranged from 2.20 in coast colonies to 2.49 in lake colonies and differed significantly between coastal colonies and the two types of inland colonies (*t*-tests, $P < 0.05$) (Table 1). There were no differences between the years 1972 and 1973 within colony type or between Everglades and lakes colonies (*t*-tests, $P > 0.05$). Because eggs were laid at 1- to 3-day intervals and incubation, which lasted 21 days, began soon after the first egg was deposited, eggs hatched at intervals of less than 1 to 3 days apart. Newly hatched nestlings averaged about 35 g (n = 16, range 30.1–41.0 g). Adults began feeding young soon after hatching. After later chicks hatched, the largest, oldest chick was fed first 95% of the time (n = 35). As a result of asynchronous hatching and differential feeding, siblings differed in size and vigor. During the
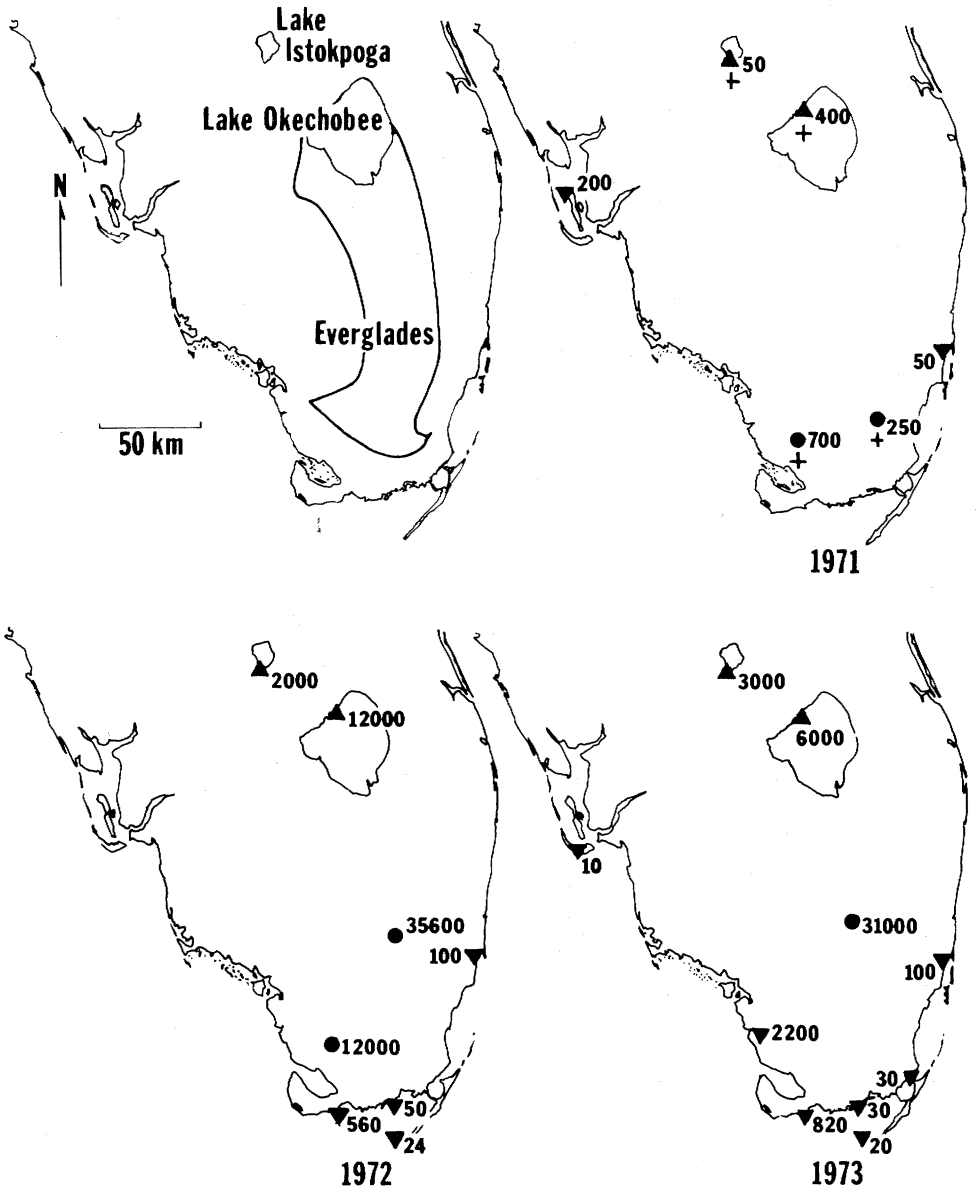
Fig. 1. Location of nesting colonies and numbers of individual White Ibises nesting in southern Florida in 1971–73. Lakes colonies are marked with upward pointing triangles. Everglades colonies are marked with circles. Coastal colonies are marked with downward pointing triangles. Unsuccessful colonies are marked with a plus sign in yearly maps.

first 2 weeks, the second chicks averaged 68% (n = 12) and the third chicks 27% (n = 12) the weight of the oldest chicks in 3 chick nests, and the second chicks averaged 58% (n = 17) of the first chicks in 2 chick nests. As a consequence, brood reduction was severe and differed at different colonies through the first 20 days (Table 1). The number of nestlings reared to fledging averaged a little over 1 per nest, with no significant differences among colonies (t-tests, $P > 0.05$) (Table 1). Juveniles left the nesting colony, i.e. "fledged," in from 40 to 50 days. I found no

TABLE 1

MEAN CLUTCH SIZE, YOUNG PER NEST, AND ENERGY REQUIREMENTS FOR YOUNG
PER NEST OF WHITE IBIS IN SOUTHERN FLORIDA[1]

Colonies	Clutch size	Young per nest		Kcal per nest		
		@ 20 days	@ 40 days	1–20 days	20–40 days	Total
Lake	2.49 ± .56 (202)	1.25 ± .43 (133)	1.03 ± .16 (121)	3,375	6,098	9,473
Everglades	2.45 ± .67 (51)	1.38 ± .49 (53)	1.05 ± .22 (42)	3,726	6,216	9,942
Coastal	2.20 ± .64 (290)	1.14 ± .45 (64)	1.03 ± .18 (93)	3,078	6,098	9,176

[1] Nesting data collected 1972 and 1973 and given ± SD; number of samples given in parentheses.

evidence of parental feeding after young left the nesting colony. Thus the time from egg laying to independence of young was a minimum of 61 days.

Energy requirements.—Basal metabolic rate (BMR) of the White Ibis averaged 85 kcal/day (n = 3,944 kg, range 81–88 kcal/day) (Benedict and Fox 1927). This is an hourly rate of 3.54 kcal/h and a weight specific energy requirement of 0.09 kcal/g/day. Existence metabolism (EM) averaged 113.8 kcal/day (n = 3, range 107.3–123.7 kcal/day). Assimilation efficiency of captive adults averaged 79.7% (n = 22, range 54.9 to 91.6%). The hourly rate was 4.74 kcal/h and the weight specific energy requirement was 0.12 kcal/g/day. Existence metabolism was approximately 1.3 times basal metabolic rate. Aviary existence metabolism was 138.7 kcal/day or 5.77 kcal/h. This was 1.22 times usual existence metabolism and 1.63 times basal metabolism.

The daily time-activity budget of an adult during the latter part of the nesting period when young were being fed was 13 hours inactivity including roosting, resting, and nest attentiveness, 0.75 hours flying, 10.25 hours foraging. Foraging for both itself and young comprised 42% of the budget. I estimated the daily energy requirement for a free-living ibis from this time-activity budget. Roosting and resting were estimated by EM, as the cage activity of ibises during EM studies was low. Foraging was estimated by 1.2 times aviary existence metabolism. This assumes that there is little additional energy expended in foraging for young other than the increased time alloted to foraging. This is reasonable in a bird that has a limited repertoire of feeding behavior and that shows no apparent feeding behavior change during nesting unlike some other species (Davies and Green 1976). The energy cost of flight was estimated at 12 times BMR, based on the results of Utter and LeFebvre (1970) for other nonpasserines. The total daily energy expenditure (DEE) of an adult White Ibis during nesting was calculated by multiplying the daily time spent in an activity by the hourly energetic cost of the activity estimated by the metabolic parameters. Thus DEE was estimated to be 164.6 kcal/bird/day.

The caloric content of the food of the White Ibis in southern Florida averaged 4.05 kcal/g dry weight (average energy value of 90% of the food, primarily invertebrates, White Ibis consumed in southern Florida—Kushlan and Kushlan 1975). Using the mean assimilation efficiency and the average ratio of wet to dry weight of prey of 4:1, an adult White Ibis required about 203 g food per day or about 21% body weight. DEE/EM ratio is 1.5 and DEE/BMR ratio is 1.9. At an estimated daily expenditure of 329 kcal, 2 pair required 20,080 kcal during the minimum 61-day nesting period. These calculations assume that any energy increment for egg production, incubation, nest-building, or courtship activities was relatively small in relation to the total energy used for maintenance and activity of such a relatively large bird over a 2-month nesting period.

TABLE 2
Food Energy Used for Nesting by White Ibis in Southern Florida

	Number of nests		Total energy used kcal × 10⁶		Total food used (metric ton, wet wgt.)	
	1972	1973	1972	1973	1972	1973
Lake colonies	7,000	4,500	206.9	133.0	254.9	164.6
Everglades colonies	23,800	15,500	713.1	464.4	882.5	574.7
Coastal colonies	367	1,605	10.7	46.9	13.2	58.0
Total	31,167	21,605	930.7	644.3	1150.6	797.3

   Based on measurements of metabolized energy, I estimated that the energy re-
quirements for a wild nestling were 2,700 kcal to day 20 and 8,620 kcal to fledging on
day 40 (Kushlan 1977). To account for the young that died before fledging, I assumed
that the daily energy use of these nestlings was similar to surviving siblings and that
it could be estimated by applying the data for number of young per nest at 20 days,
midway through nesting (Table 1). The first assumption overestimates energy use as
siblings that die do so primarily because they obtain less food. This overestimate
should be balanced by ignoring the proportion of young not surviving to day 20 and
those surviving for some period thereafter but dying before fledging. As the brood
reduction pattern differed among colony types, energy use of each was calculated
separately. Using 2,700 kcal for a bird surviving through day 20, and 5,920 kcal for a
bird surviving day 20 through fledging results in energy requirements ranging from
approximately 9,180 kcal per nest on the coast to 9,940 kcal per nest in the
Everglades (Table 1). The energy use of a clutch ranged from 6–15% above the
energy used by a single nestling that survived to fledging. Adding the total mainte-
nance requirements for two adults for the minimum nesting period resulted in a total
energy use of 29,260 kcal per nest in coastal colonies, 29,550 kcal in lakes colonies,
and 30,020 kcal in Everglades colonies. The energy used for nestling growth and
maintenance was less than 50% of the total energy adults used during the nesting
season.
   I estimated the energy required for nesting of the southern Florida population,
based on the nesting distribution shown in Fig. 1, to be 930 million kilocalories in
1972 and 640 million kilocalories in 1973 (Table 2). Ibis nesting in the Everglades
accounted for 77% and 72% of the total energy used for nesting in 1972 and 1973
respectively, and all inland colonies together used 99% and 93% of energy those years.

DISCUSSION

   Energy of free existence.—The accuracy of applying the results of energy require-
ment studies of captive birds to wild birds is constrained by assumptions made in the
extrapolation. Existence metabolism (EM) is an often used and ecologically pertinent
laboratory measurement because it contains all components of daily metabolism,
differing from the energy requirements of wild birds only in the magnitude of activity
components, and is also a close approximation of the energy requirements of inactive
wild birds at similar temperatures. EM measured for the White Ibis was 113.8
kcal/day, not very different from the 95.3 kcal/day calculated by Kendeigh's (1970)
regression for nonpasserines, which was based on an experimental temperature of 30°
C, approximately 6°C above the mean ambient temperature during the present

study. The differences in temperature may account for the entire discrepancy be-
tween predicted and measured EM, indicating close agreement between the two.
Existence metabolism plus an estimate of the energetic cost of activity during free
existence have been used to generate yearly energy budgets for several small
passerines (West 1960, Schartz and Zimmerman 1971, Kendeigh 1972). More simply,
free activity of small passerines has been estimated at 2 EM (Odum et al. 1962) an 1.3
EM (foraging only—Kale 1965).

   In some of the few studies of large birds, comparable to the White Ibis, Kahl (1964)
and later Siegfried (1969) estimated simply that the energy requirements of wild
Wood Storks and Cattle Egrets (*Bubulcus ibis*) were 1.5 measured EM. Kahl mea-
sured existence metabolism by feeding storks at 3-day intervals in a large aviary and
did not collect feces, an experimental situation less precise than is usually the case in
EM studies. Under conditions similar to Kahl's, a male ibis required 1.22 times as
much energy for existence as it did in a standard experimental chamber. However
such aviary existence metabolism is closer to the metabolic requirements of wild
birds than is simple existence metabolism and can be used to calculate the energy cost
of free existence. Thus to estimate the energy required for a free living adult ibis, I
included measures of existence metabolism, large aviary existence metabolism, and
basal metabolic rate applied to the time activity budget of ibises during nesting. Such
a component approach produced a daily energy requirement of 1.5 EM, which is
the same that Kahl (1964) and Siegfried (1969) estimated in a less precise fashion.

   The energy cost of free existence in a White Ibis was about 40% greater than for
captive existence. The daily energy expenditure was considerably below the 300 kcal
extrapolated for a bird this weight from King's (1974) regression that was based on
studies of smaller birds. This deviation may suggest that increase in DEE is rela-
tively slower at higher body weights. The DEE/BMR ratio of 1.9 is at the low end of
the range of this parameter in other birds (King 1974). The DEE of the White Ibis
requires an adult ibis to obtain about 21% of its body weight in food each day.
Similar figures were arrived at by Kahl (1964) (21%) and Junior (1972) (16%) for
other ciconiiformes.

   White Ibis nesting ecology.—Nesting White Ibis used three general types of forag-
ing grounds in southern Florida (Kushlan and Kushlan 1975). Birds from lake col-
onies fed in shallow marshes and flooded pastureland. Birds from coastal colonies fed
in mangrove swamps and coastal marshes. Birds from Everglades colonies fed in the
extensive marsh prairies of the Everglades that cover much of the interior of peninsu-
lar Florida. All habitats are affected by the yearly wet-dry cycle that concentrates
rain in the 6-month rainy season and leads to a seasonal fluctuation of water level.
Coastal marshes, although less affected by seasonal drought, also experience exten-
sive drying. Nesting parameters and the pattern of energy use differed among ibis
nesting and feeding in these three ecologically distinct areas.

   Clutch size differed between coastal and inland colonies (Table 1). It might be
suggested that lowered clutch size in coastal colonies is an adaptation to the greater
stability of such habitats, but there is no reason to suspect that the ibises in the three
groups of colonies were reproductively isolated from each other. To the contrary,
year-to-year shifts in numbers of nesting birds suggest considerable interchange
among colonies. Thus necessary conditions for evolution of intraregional genetic
differences in clutch size probably do not prevail. An alternative explanation is that
clutch size differences directly reflect differences in food availability. This may not be

likely as available data suggest that differences in energy available at foraging sites in the principal feeding areas of the different colonies are not great, ranging from 6.0–7.2 kcal/m² (Kushlan MS). Preliminary evidence suggests lower clutch size of coastal as contrasted with inland nesting subpopulations may be a phenomenon common to other wading bird species in southern Florida. If this is true, the cause should be sought in factors commonly affecting all species. If food supplies are not involved, the cause may be a greater physiological stress and therefore caloric requirement associated with the marine environment. The need to excrete salt is one possibility. This pattern of intraregional clutch size variation assumes additional importance because of data from various species that suggest geographic variation in clutch size. In Florida, at least, variation appears to be inland vs coastal sites rather than latitudinal.

Despite the existence or possible cause of these small but statistically significant differences in clutch size between coastal and inland colonies, they are not of sufficient magnitude to be of biological importance to the population because all colonies had identical fledging rates of a little over one bird per nest (Table 1). Second and third chicks usually received little food and died before fledging, so final output was independent of initial clutch size. The pattern of brood reduction did differ among colony types. Such wastage of reproductive effort appears to go beyond mere provision of a replacement chick and thus appears maladaptive, especially if clutch size were evolved to match the maximal number of young that parents can raise (Lack 1954). The younger chicks may be fledged in years when feeding conditions are particularly good. It is also important to consider that regional clutch sizes may have evolved in response to a pristine, unaltered environment when hundreds of thousands of ibises nested in extreme southern Florida. Such high population levels prior to their decline over the past several decades demonstrate that a more highly productive system occurred then than now. Thus possibly some population parameters measured today may reflect adaptation to past rather than present conditions.

Over 70% of the 930 to 640 × 10⁶ kcal required by the southern Florida White Ibis population was derived from the fresh water marshes of the Everglades, demonstrating the energetic importance of these habitats to the population. Although all colonies were successful in 1972 and 1973, coastal colonies were successful in the dry year of 1971 when the inland colonies failed (Fig 1). Thus the periodic large scale reproduction in inland marshes sustains the population at its current level, and the relatively small, more stable coastal colonies serve as a buffer that maintains minimal recruitment between times of high inland reproduction. The boom or bust cycle of the variable freshwater wetlands contrasts markedly with the more stable but smaller colonies of the coast. Thus the colonies in marine and freshwater habitats respond differently to year-to-year variation of environmental conditions and function differently in maintaining the regional population.

Ibises and storks.—The energy required by White Ibis for reproduction can be contrasted with similar information available for the Wood Stork (Kahl 1964), using two recent years in which the entire potential reproducing populations of these species tried to nest and were generally successful, 1972 for the White Ibis and 1974 for the Wood Stork. The Wood Stork is larger than the White Ibis, weighing about 2.5 kg (Kahl 1964). The regional population level is lower than in the White Ibis with 5,800 storks (14,500 kg) nesting during 1974 (Robertson and Kushlan 1974). The 1972 White Ibis nesting population was about 11 times and the standing crop 4

times that of the Wood Stork. Based on Kahl's (1964) data, the Wood Stork population required 6.38×10^8 kcal for nesting in 1974. In contrast, in 1972 the White Ibis population required about 9.3×10^8 kcal. Thus the southern Florida White Ibis population required only about 1.1 times as much energy for nesting as did the Wood Stork population even though the ibis population was 11 times as large. The relatively low energy requirement of the ibis population was due to the smaller family size and weight. Less energy is required for total biomass growth of a smaller bird, and smaller size also permits a shorter period of growth and development, decreasing the energy needed to maintain both adults and young.

Thus the smaller size of the White Ibis, as contrasted with a larger bird having a similar developmental system, requires a shorter nesting cycle, lower energy cost for nesting, and permits a greater population level to be maintained on a given energy resource base. This may be particularly important for populations under the stress of changing environmental conditions, such as have occurred in southern Florida. Lower energy requirements for nesting may enable the smaller species to maintain larger population levels thus avoiding an irreversible population decline during successive years of nesting failure. This may be one of several reasons why the southern Florida White Ibis population has not yet become threatened with extirpation despite an 80–90% population decline over a 30- to 40-year period. It remains today the most numerous wading bird in southern Florida.

This phenomenon may have application beyond the specific case noted above. In the example of two competitors, which the ibis and stork are not, it seems possible that both may coexist on a single resource base during periods of resource abundance with their population levels determined by body size restrictions on the energy requirements of reproduction. Perturbations in the environment or other random events that prevent successful nesting may force the population of larger animals below the level where rebound is possible, whereas the smaller species, starting from a higher initial population, can recover. So the larger species may be extirpated while the smaller competitor may persist through such periods of intense selection.

Impact of energy requirements.—The present southern Florida White Ibis population's energy requirements for nesting are substantial. The total food requirements of the White Ibis can be estimated by considering the average caloric value of food (4.05 kcal/dry g), assimilation efficiency, and requirements of each colony (Table 2). Thus I estimate that White Ibis required 1150 and 780 metric tons of food for the 1972 and 1973 nesting seasons respectively (Table 2). Similarly based on Kahl's (1964) data Wood Storks required about 510 metric tons of food in 1974. The impact of the predation necessary to obtain this energy must be considerable. If the total reproductively active population of White Ibis and Wood Storks nested successfully in the same year, their total food requirements would equal 1.9 billion kilocalories. Unfortunately as these are some of the few data available on energy flow in the complex wetland ecosystem of southern Florida, little can be said at present about how these flows contribute to energy movement in the total system.

It should be noted that these are only 2 of 15 species of wading birds that nest in southern Florida and utilize these same aquatic habitats. Their combined pressure on most prey populations can only be surmised on a regional basis. In a specific case, I found in a previous study of wading bird predation that wading birds consumed 75% of the biomass of fish concentrated in a pond in less than a week (Kushlan 1976). The resiliency of aquatic prey species from one season to the next appears to be one of the

most important functioning aspects of the southern Florida ecosystem. The White Ibis population, including its subpopulational components, is undoubtedly an important determinant of the pathways and control of energy flow in the Everglades and coastal wetlands ecosystems of southern Florida.

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