

the female continuously until she starts to incubate (Tsuneki 1961; Newton 1972, pers. comm.). One possible explanation for the results on canaries is that selective breeding during the period of domestication (ca. 350 yr; Dodwell 1986) has produced incidentally a well-developed sperm storage ability (Clayton 1972, Lake 1975). This idea is plausible because breeders have undoubtedly selected for individuals that bred successfully in captivity, and prolonged sperm storage contributes to successful breeding. In addition, sperm storage durations differ significantly between different strains of chickens selected for different traits (Taneja and Gowe 1961), indicating that sperm storage duration has a genetic basis. Another explanation for these results is that they represent a few very rare occurrences at the extreme end of the distribution of sperm storage duration in canaries. A systematic study of sperm storage in canaries and other passerines, particularly wild species, might be interesting.

I am extremely grateful to the individuals who provided information on which this note is based: J. Maylan, R. Moat, T. Roberts, J. Robson, K. Swann, and A. C. Wyatt. I also thank Drs. M. de L. Brooke, K. M. Cheng, A. P. Møller, and I. Newton for commenting on the manuscript.

LITERATURE CITED

- BANNERMAN, D. A., & W. M. BANNERMAN. 1968. Birds of the Atlantic islands. Edinburgh.
- BIRKHEAD, T. R. 1982. Timing and duration of mate guarding in Magpies *Pica pica*. *Anim. Behav.* 30: 277-283.
- . 1987. Behavioural aspects of sperm competition in birds. *Adv. Stud. Behav.* in press.
- , L. ATKIN, & A. P. MØLLER. 1987. Copulation behaviour in birds. *Behaviour* 101: 101-138.
- CARR, V. A. V. 1959. Mule and hybrid birds. London, Cage Birds.
- CLAYTON, G. A. 1972. Effects of selection on reproduction in avian species. *J. Reprod. Fert. Suppl.* 15: 1-21.
- DODWELL, G. T. 1986. The complete book of canaries. London, Merehurst Press.
- HATCH, S. A. 1983. Mechanism and ecological significance of sperm storage in the Northern Fulmar with reference to its occurrence in other birds. *Auk* 100: 593-600.
- . 1987. Copulation and mate guarding in the Northern Fulmar. *Auk* 104: 450-461.
- IMBER, M. J. 1976. Breeding biology of the Grey-faced Petrel *Pterodroma macroptera gouldi*. *Ibis* 118: 51-64.
- LAKE, P. E. 1975. Gamete production and the fertile period with particular reference to domesticated birds. *Symp. Zool. Soc. London* 35: 225-244.
- LORENZ, F. W. 1950. Onset and duration of fertility in turkeys. *Poultry Sci.* 29: 20-26.
- NEWTON, I. 1972. Finches. London, Collins.
- PERRINS, C. M., & M. DE L. BROOKE. 1976. Manx Shearwaters in the Bay of Biscay. *Bird Study* 23: 295-299.
- TANEJA, G. C., & R. S. GOWE. 1961. Effect of varying doses of undiluted semen on fertility in the domestic fowl. *Nature London* 191: 828-829.
- TSUNEKI, K. 1961. Territory in flocks of the caged canaries, with special reference to its causation and defence. *Japanese J. Ecol.* 11: 19-26.

Received 28 January 1987, accepted 22 April 1987.

Energetic Consequences of Sexual Size Dimorphism in White Ibises (*Eudocimus albus*)

KEITH L. BILDSTEIN

Department of Biology, Winthrop College, Rock Hill, South Carolina 29733 USA, and
Belle W. Baruch Institute for Marine Biology, University of South Carolina,
Columbia, South Carolina 29208 USA

Sexual dimorphism is pronounced in White Ibises (*Eudocimus albus*): males are heavier than females, and they have substantially longer tarsi, bills, and wing chords (Kushlan 1977a). Sexual size dimorphism may result either from natural selection acting to reduce intersexual food competition or to increase clutch size in females (cf. Carothers 1984), or from sexual selection acting to enhance the mating success of appropriately sized individuals. Kushlan (1977a) proposed that the size dimorphism he reported for White Ibises resulted from sexual selection acting to increase body size and bill length in males.

Male ibises use their bills during courtship, when

males and females intertwine their bills and necks during pair formation (Palmer 1962, Rudegear 1975), and during copulation, when males extend their bills over females and engage in twig pulling (Rudegear 1975). A larger bill and body in males undoubtedly is also important for intrasexual fighting during courtship, mating, and nest building, when males fight over mates and attempt nest-site takeovers (Rudegear 1975, Frederick 1986). Fighting ability in males has also been linked to increased extrapair copulations in this sometimes promiscuous species (Frederick 1985a). Although female ibises participate in aggressive interactions at the colony site, female aggression is con-

siderably less intense, and females rarely fight in the absence of their mates (Rudegeair 1975).

Although the larger bill and body size of male ibises appears to be advantageous during courtship and mating, its effect on foraging behavior has not been examined in detail (Kushlan 1977a). I examined the feeding behavior of male and female ibises and estimated the energetic consequences of sexual size dimorphism in the species. I confirm that male ibises are larger than their female counterparts, and that they have disproportionately longer bills. Despite this difference in bill size, males and females capture prey at approximately the same rate, and, as a consequence of their larger body size, males must spend considerably more time feeding each day to maintain their daily energy balance.

Methods.—I measured the bill length (measured from distal edge of the nares to the tip of bill), bill chord, bill depth at the nares, and wing chord of 26 adult male and 22 adult female specimens at the American Museum of Natural History, New York, New York. Gender-related differences in size were analyzed using *t*-tests (Sokal and Rohlf 1969).

Field observations of ibises feeding on fiddler crabs (*Uca* spp.) were made along the Bly Creek drainage of the North Inlet Marsh, Hobcaw Barony, approximately 6 km east of Georgetown, South Carolina. The site is 5 km north of Pumpkinseed Island in Winyah Bay, where 2,000–20,000 pairs of ibises breed annually (unpubl. data). From mid-March through mid-September large numbers of ibises from this colony site feed on exposed portions of the drainage on fiddler crabs (Bildstein 1983). For a full description of the area and its birds, see Christy et al. (1981).

On 16 days during May–July 1985 and 8 days during May–August 1986, I used a 15–60× spotting scope atop an 18.5-m tower at the marsh edge to observe the foraging behavior of males and females feeding together in mixed flocks. Data on males and females were collected in a pairwise fashion throughout the day, but most observations were made between 0800 and 1600. For each paired observation I first watched either a male or female ibis for 4 min and then watched an individual of the other gender for 4 min. This sampling scheme enabled me to compare the behavior of birds under similar conditions, thus minimizing variance in environmental factors that might have influenced feeding rates (Petit and Bildstein 1987). Ibises fed on the drainage in stands of *Salicornia*, *Distichlis*, and *Spartina*, as well as along drained creek banks. I standardized habitat effects on feeding behavior (cf. Henderson 1981) by limiting my observations to birds feeding in stands of short *Spartina* away from creek-bank edges. To control for a “flock” effect on foraging behavior, I analyzed pairs of birds feeding at the peripheries of larger flocks or in small flocks separately from those feeding in the centers of large flocks. Ibises feeding alone, in small flocks (<15 birds), and on the perimeter of large flocks (>15 birds)

probe more and step less than do birds feeding in the center of large flocks (Petit and Bildstein 1987). This shift in behavior apparently is a response to the depressed availability of surface crabs as a result of the movement of a flock of ibises over an area. Although the capture rates of birds feeding in the center of large flocks do not differ from that of other individuals, almost all of the crabs caught by central birds are taken from burrows, whereas birds feeding elsewhere take crabs both from burrows and from the surface (Petit and Bildstein 1987). As the consequences of gender-related differences in bill length might differ for “central” and “peripheral” birds, I divided my observations equally between pairs of birds in these two situations.

I dictated into a cassette recorder the number of times the bird stepped, looked-up (i.e. stopped walking and cocked its head upward), probed into crab burrows or picked crabs from the surface, or captured prey. I later transcribed tapes for analyses. Foraging behavior and success of males and females were compared using Wilcoxon matched-pairs signed-rank tests (Sokal and Rohlf 1969).

The results of the feeding observations were used in combination with the mean masses of adult males and females (Kushlan 1977a), the dry-mass caloric content of fiddler crabs collected on the marsh (2.3 kcal/g; J. Johnston pers. comm.), an estimated digestive efficiency of 70% (Kale 1965), a time-activity budget for ibises (Kushlan 1977b), and existence metabolism equations of Wiens and Dyer (1977) to determine the amount of feeding time required by adult males and females to maintain energetic equilibrium.

Results.—Adult male White Ibises had significantly longer and deeper bills as well as significantly longer wing chords than did female ibises, but the bill length to bill chord ratio (a measure of the curvature of the bill) did not differ between the sexes (Table 1). Bill length and bill chord averaged 27% and 26% greater in males, respectively. In contrast, the wing chords of males averaged only 11% longer than those of females, and, using mass data given by Kushlan (1977a), the cube root of male body mass (a value comparable to linear measures [Amadon 1943]) also was only 11% greater than that of females (Table 1). Thus, adult male ibises not only are larger than adult females, they have disproportionately longer bills than do adult female ibises. (Although none of Kushlan's birds or the museum specimens I examined were collected at the North Inlet Marsh, 8 hand-reared individuals from the site exhibited a similar nonoverlapping bimodal pattern of bill, wing chord, and body size dimorphism.)

Adult male ibises hunting alone in small flocks and on the perimeters of large flocks caught prey at only 87%, and those in the centers of large flocks at only 90%, of the rate of their female counterparts. Neither of the differences, however, was significant (Table 2). Nor were there any significant gender-related differ-

TABLE 1. Sexual size dimorphism (mean \pm SD) of 26 male and 22 female White Ibises.

Morphometric character	Females	Males	Male/ female ratio	P^a
Bill chord (mm)	107.5 \pm 5.06 (22)	136.1 \pm 5.97 (26)	1.27	<0.001
Bill length (mm)	112.4 \pm 5.59 (21)	142.0 \pm 6.23 (24)	1.26	<0.001
Bill chord/bill length	0.954 \pm 0.008 (21)	0.958 \pm 0.009 (24)	1.00	>0.10
Bill depth (mm)	16.0 \pm 0.62 (22)	18.4 \pm 0.87 (26)	1.15	<0.001
Wing chord (mm)	265.5 \pm 6.82 (21)	295.0 \pm 5.59 (26)	1.11	<0.001
Bill length/wing chord	0.475 \pm 0.027 (21)	0.531 \pm 0.021 (26)	1.13	<0.001

^a Based on two-tailed *t*-tests.

ences in any of the other foraging parameters, or in the amount of time males and females spent looking up (presumably for aerial predators). There was also no difference in any of the parameters when data from the two foraging situations were pooled for analyses (all comparisons $P > 0.10$).

I did not collect quantitative data on the sex ratios of birds feeding on the marsh, but it appeared to be close to 1:1 during my observations. Similarly, there was no apparent variance from a 1:1 ratio in the numbers of males and females in the centers or on the perimeters of large flocks, in small flocks, or hunting alone. To facilitate collecting data, however, I conducted most observations when large numbers of ibises fed on the marsh, and the ratio of male to female ibises may have differed when fewer birds fed in the area. There was no indication that males dominated females during feeding. Indeed, I saw no aggressive interactions during my observations of feeding ibises.

None of the fiddler crabs caught by ibises were subsequently rejected by any birds, and male and female ibises appeared to capture male and female crabs of similar sizes. Although I could not determine the gender of the smaller crabs that the birds fed on, when ibises captured larger (>2 cm) male crabs they usually spent more time manipulating them, and they often broke the large cheliped from the body before consuming, in many instances, both pieces. Based on the male and female capture rates I observed, and on an estimated average daily energy expenditure of 178.2 kcal·bird⁻¹·day⁻¹ for males and 146.9 kcal·bird⁻¹·day⁻¹ for females, I estimate that male ibises needed to spend approximately 37% more time feeding on the marsh per day than did female ibises (3 h, 28 min vs. 2 h, 32 min).

Discussion.—Sexual dimorphism resulting from sexual selection often is assumed to represent a trade-off between reproductive success and survivorship (e.g. Zahavi 1975, Andersson 1982). More recently, however, researchers have suggested that traits such as large body and bill size may increase overall fitness in nonreproductive as well as in reproductive situations (Kodric-Brown and Brown 1984). For example, in White Ibis breeding colonies males are more likely to pirate prey, and are less likely to be victims of

piracy, than are females; presumably, this is because they are better able to intimidate their victims (Frederick 1985b). If such gender-related behavioral dominance also occurs in the large foraging flocks typical of the species (Kushlan 1977c), males might be expected to be more efficient foragers. In addition, the larger bills and tarsi of male ibises might enable them to probe more deeply in search of prey than could females (Kushlan 1977a), potentially further increasing the foraging effectiveness of males as well as permitting them to forage in deeper water. On the other hand, large males might be less fit overall than smaller males because they exceed an optimal size for foraging efficiency (Selander 1965) or because they require substantially more food to support their larger body size (Fiala and Congdon 1983). Either or both of these latter circumstances could lead to higher male mortality rates during times of food scarcity (Clutton-Brock et al. 1985).

Based on the above hypothetical considerations, male White Ibises could have been expected to secure prey at rates that were higher, lower, or (presuming male behavioral dominance was counterbalanced by decreased foraging efficiency) equal to that of their female counterparts. My observations of adult male and female White Ibises feeding side by side on fiddler crabs indicate that, at least in this situation, males capture prey at rates similar to those of females.

Adult male ibises use their disproportionately larger bills and larger bodies to secure mates as well as prey. Although there is considerable uncertainty inherent in my calculations of daily energy requirements, my data, together with those on ibis courtship and mating (e.g. Rudegeair 1975, Frederick 1985a), indicate that what is beneficial during courtship and mating may not be without cost when birds are foraging. My data also support Kushlan's (1977a) suggestion that sexual size dimorphism in White Ibises results from sexual selection acting during courtship and mating, rather than from natural selection acting to increase the foraging success of males.

The question of whether or not adult males are more efficient foragers in circumstances other than those in which I observed them deserves further study. Ibises feed in a variety of habitats in addition to salt

TABLE 2. Foraging behavior (mean \pm SD) of adult male and female White Ibises feeding in mixed-sex flocks on the Bly Creek drainage, Hobcaw Barony, South Carolina.

Foraging parameter	Females	Males	Male/female ratio	P ^a
Peripheral birds ^b (n = 25 pairs)				
Steps/min	44.4 \pm 14.7	42.9 \pm 19.2	0.97	>0.10
Look-ups/min	1.05 \pm 0.79	1.13 \pm 0.79	1.08	>0.10
Seconds looking up/min	3.37 \pm 3.26	3.56 \pm 2.82	1.06	>0.10
Probes/min	13.0 \pm 4.70	11.6 \pm 5.10	0.89	>0.10
Captures/min	2.09 \pm 0.79	1.81 \pm 0.82	0.87	<0.10, >0.05
Steps/probe	1.07 \pm 0.72	1.33 \pm 1.22	1.24	>0.10
Probes/capture	1.77 \pm 1.03	1.85 \pm 1.10	1.05	>0.10
Central birds (n = 25 pairs)				
Steps/min	39.8 \pm 16.4	41.6 \pm 18.6	1.05	>0.10
Look-ups/min	0.64 \pm 0.54	1.00 \pm 0.71	1.56	<0.10, >0.05
Seconds looking up/min	2.29 \pm 3.13	5.59 \pm 8.25	2.44	<0.10, >0.05
Probes/min	12.1 \pm 3.55	11.7 \pm 4.10	0.97	>0.10
Captures/min	1.73 \pm 0.90	1.56 \pm 0.77	0.90	>0.10
Steps/probe	0.96 \pm 0.62	0.95 \pm 0.59	0.99	>0.10
Probes/capture	2.14 \pm 1.21	2.26 \pm 1.40	1.06	>0.10

^a Based on two-tailed Wilcoxon's matched-pairs signed-rank tests.

^b Includes peripheral birds in large flocks (>15 individuals) and small flocks (<15 individuals).

marshes, and on a variety of prey (Kushlan 1977a). Present evidence, however, indicates that male and female ibises exhibit little, if any, of the differences in diet and feeding-habitat use (Kushlan 1977a) that are typical of other species of sexually size dimorphic birds such as raptors (cf. Newton 1979).

I observed the feeding behavior of male and female ibises during only two breeding seasons, one of which (1985) was especially dry (USDC 1985-1986), and under other environmental conditions male ibises may capture fiddler crabs at significantly higher rates than do female ibises (cf. Boag and Grant 1981). Nevertheless, and although I have not measured the effect of sexual size dimorphism on the overall fitness of male and female White Ibises directly, the daily energy expenditures presented above suggest that selection for the disproportionately larger bill and larger body size of adult males may be constrained by the increased time needed to secure sufficient prey.

I thank G. Caldwell, C. Marsh, P. Gowaty, and an anonymous referee for helpful comments on earlier drafts of this paper. My research on ibises has been supported by the Winthrop College Arts and Sciences Faculty Development Fund, the Whitehall Foundation, and NSF grant BSR-8119752 to the Belle W. Baruch Institute for Marine Biology and Coastal Research. This is contribution No. 690 of The Baruch Institute.

LITERATURE CITED

- AMADON, D. 1943. Bird weights as an aid in taxonomy. *Wilson Bull.* 55: 164-177.
- ANDERSSON, M. 1982. Sexual selection, natural selection and quality advertisement. *Biol. J. Linn. Soc.* 17: 375-393.
- BILDSTEIN, K. L. 1983. Age-related differences in the flocking and foraging behavior of White Ibises in a South Carolina salt marsh. *Colonial Waterbirds* 6: 45-53.
- BOAG, P. T., & P. R. GRANT. 1981. Intense natural selection in a population of Darwin's finches (Geospizinae) in the Galapagos. *Science* 214: 82-85.
- CAROTHERS, J. H. 1984. Sexual selection and sexual dimorphism in some herbivorous lizards. *Amer. Natur.* 124: 244-254.
- CHRISTY, R. L., K. L. BILDSTEIN, & P. DECOURSEY. 1981. A preliminary analysis of energy flow in a South Carolina salt marsh: wading birds. *Colonial Waterbirds* 4: 96-103.
- CLUTTON-BROCK, T. N., S. D. ALBAN, & F. E. GUINNESS. 1985. Parental investment and sex differences in juvenile mortality in birds and mammals. *Nature* 313: 131-133.
- FIALA, K. L., & J. D. CONGDON. 1983. Energetic consequences of sexual size dimorphism in Red-winged Blackbirds. *Ecology* 64: 642-647.
- FREDERICK, P. 1985a. Mating strategies of White Ibises (*Eudocimus albus*). Ph.D. dissertation, Chapel Hill, Univ. North Carolina.
- . 1985b. Intraspecific food piracy in White Ibises. *J. Field Ornithol.* 56: 413-414.
- . 1986. Conspecific nest takeovers and egg destruction by White Ibises. *Wilson Bull.* 98: 156-157.

- HENDERSON, E. G. 1981. Behavioral ecology of the searching behavior of the White Ibis (*Eudocimus albus*). M.S. thesis, Columbia, Univ. South Carolina.
- KALE, H. W., II. 1965. Ecology and bioenergetics of the Long-billed Marsh Wren in Georgia salt marshes. Publ. Nuttall Ornithol. Club No. 5.
- KODRIC-BROWN, A., & J. H. BROWN. 1984. Truth in advertising: the kinds of traits favored by sexual selection. *Amer. Natur.* 124: 309-323.
- KUSHLAN, J. A. 1977a. Sexual dimorphism in the White Ibis. *Wilson Bull.* 89: 92-98.
- . 1977b. Population energetics of the American White Ibis. *Auk* 94: 114-122.
- . 1977c. The significance of plumage colour in the formation of feeding aggregations of ciconiiforms. *Ibis* 119: 361-364.
- NEWTON, I. 1979. Population ecology of raptors. Vermillion, South Dakota, Buteo.
- PALMER, R. S. 1962. Handbook of North American birds, vol. 1. New Haven, Connecticut, Yale Univ. Press.
- PETIT, D. R., & K. L. BILDSTEIN. 1987. Effect of group size and location within the group on the foraging behavior of White Ibises. *Condor* 89: 602-609.
- RUDEGEAIR, T. J., JR. 1975. The reproductive behavior and ecology of the White Ibis (*Eudocimus albus*). Ph.D. dissertation, Gainesville, Univ. Florida.
- SELANDER, R. K. 1965. On mating systems and sexual selection. *Amer. Natur.* 99: 129-141.
- SOKAL, R. R., & F. J. ROHLF. 1969. *Biometry*. San Francisco, Freeman.
- U.S. DEPARTMENT OF COMMERCE. 1985-1986. Local climatological data: South Carolina, vols. 88-89. Washington, D.C., U.S. Dept. Commerce.
- WIENS, J. A., & M. I. DYER. 1977. Assessing the potential impact of granivorous birds in ecosystems. Pp. 205-266 in *Granivorous birds in ecosystems* (J. Pinowski and S. C. Kendeigh, Eds.). Cambridge, England, Cambridge, Univ. Press.
- ZAHAVI, A. 1975. Mate selection—a selection for a handicap. *J. Theor. Biol.* 53: 205-214.

Received 13 January 1987, accepted 23 April 1987.

Intraspecific Avoidance and Interspecific Overlap of Song Series in the Eastern Meadowlark

RICHARD W. KNAPTON

Department of Zoology, University of Manitoba, Winnipeg, Manitoba R3T 2N2, Canada

Communication and transfer of information by song is best achieved by minimal interference from features of the habitat and from vocalizations of other animals. Song transmission in birds is influenced by environmental variables that result in sound degradation and attenuation (Morton 1975, Roberts et al. 1981, Cosens and Falls 1984). Acoustic interference also may occur if another individual of the same or a different species sings simultaneously. Avoidance of acoustic interference has been achieved in neighboring Bewick's Wrens (*Thryomanes bewickii*) and Wrentits (*Chamaea fasciata*) by using different diurnal singing cycles (Cody and Brown 1969, Fleischer et al. 1985) and in individuals of the same or different species singing asynchronously at the same time of day, with one individual singing immediately after another has stopped (Wasserman 1977, Gochfeld 1978 on the same species; Ficken et al. 1974, Popp et al. 1985 on assemblages of different species).

The studies on short-term temporal avoidance of interspecific acoustic interference by Ficken et al. (1974) and Popp et al. (1985) were conducted on bird pairs and communities in forests, a habitat in which sound attenuates quickly. I investigated temporal patterns of singing behavior of Eastern Meadowlarks (*Sturnella magna*), which occupy an open-country hab-

itat that is shared with several other species. I attempted to find if an Eastern Meadowlark avoided singing when its nearest neighbor was in song, and if there was interspecific avoidance of song overlap with other species of open-country birds. Clearly, if such avoidance of song overlap occurs, then rate of song delivery could be affected by the singing behavior of other species, and avoidance results because of overlap in song structure among different species.

I studied songs in old fields and abandoned vineyards in the Short Hills Provincial Park Reserve, Regional Municipality of Niagara, Ontario (43°00'N, 79°10'W). The old fields were dominated by various grasses and were bisected frequently by old fence lines, which were used as song perches. Abandoned vineyards had grasses and forbs growing among rows of old posts, wire, and dead cultivated grape stalks.

Eastern Meadowlarks were mist-netted and color-banded for individual recognition, primarily in March and April. Tape recordings were made in the open from concealed locations during the period 29 April to 26 May 1984 and 1985, between 0600 and 1000, with a Uher 4000 Report Monitor tape recorder and a Turner SE14 microphone. Spectrograms of songs were made on a Kay Electric 7029A Sonagraph.

Recording sessions of 10 different singing males