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Feeding ecology of Chesapeake Bay Ospreys and growth and behavior of their young.— As the Chesapeake Bay's fish population has declined, food may have become more limiting to the bay's Ospreys (*Pandion haliaetus*) (Rothschild et al. 1981, Thompson 1984, Bird 1985). In 1985, we studied Ospreys in southwestern Chesapeake Bay. During this study, it appeared that there was increased sibling aggression, brood reduction, and decreased growth of the young compared with 1975 (Stinson 1976, 1977). This paper examines those differences and their apparent cause.

Methods.—Seven Osprey nests in Mathews and Lancaster counties, Virginia, were studied 21 May–25 July 1985. All nests were approximately 25–125 m from shore and accessible by boat. At most study locations, the Ospreys experienced various amounts of human activity (including our own), but they appeared to habituate to disturbance. Ospreys were observed four days per week. Each day included two, 7.5 h observation periods (0530–1300; 1300–2030 h DST) which were arranged systematically such that we spent 15 h/wk at each nest. We used 20×60 , 40×60 and 40×80 scopes for observation. We estimated the size of the fish brought to each nest by comparing them with 48-cm wooden rods graduated at 12-cm intervals affixed to each nest; we used the adult Osprey's tarsus for reference as well.

Fish lengths were converted to grams using length-weight relationships specific for each fish species (McLean 1986). We recorded the number of bites of fish eaten by the nest occupants during three, randomly selected, one-minute periods. We also noted the amount of time each male spent perched near the nest.

We visited the nests twice a week for approximately 10 min per visit to weigh and mark young and to measure lengths of their longitudinal body axis, tail, culmen, and tarsus. Masses were measured with 1000- and 2000-g Pesola spring scales. Crop fullness was estimated by palpation. The ages of the young were known within one day, and, in some cases, the exact date of hatching was noted. In nearly all cases, sex was determined by tail length (MacNamara 1977), behavior (MacNamara 1977), and feather color (Jamieson 1979, Jamieson et al. 1982). Red nail polish was applied to the middle toe of the largest sibling of the brood, and later, picric acid (a harmless dye) was applied to the neck and upper breast feathers to help identify individual young. Once the chicks were several weeks old, they were banded with U.S. Fish and Wildlife Service aluminum leg bands and with unique combinations of colored leg bands for positive identification; band masses were subtracted from all subsequent body mass measurements.

In July 1985, we visited local fish markets to collect samples of the bay's fish included in the Ospreys' diets. Samples were dried for 10 days at temperatures of 55–60°C, ground in a Wiley mill, and pelletized. We used a Phillipson oxygen microbomb calorimeter to determine cal/mg dry weight per sample.

Growth rates of the young were calculated based on logistic models (Ricklefs 1967). We also calculated the inverse of growth, t_{10-90} (days) = 1.098/(dw/dt), which represents the time required to grow from 10 to 90% of its asymptotic weight (Ricklefs 1976). We used one-way ANOVA to test for significant differences among means. Student-Newman-Keuls multiple range tests were used to compare fledging times between broods. All statistical analysis used the SPSSX (SPSSX 1983) and Minitab (Ryan et al. 1985) software packages.

Results.—The male Osprey did virtually all of the hunting and delivered 0.35 ± 0.14 fish/hour (mean \pm SD, N = 52). Adult males spent an average of 29.9% \pm 15.0 of daylight hours perched near the nest (inactive time).

We observed 32 incidents of sibling aggression in over 640 h of observation. All but one of the multi-young broods had at least one such incident, and eight and 18 aggressive actions occurred in Nests 5 and 7, respectively. Aggression commonly was a peck or a blow delivered to the back of the neck, head, or tail. Such behavior was noted throughout the nestling and fledgling periods. Thirty of the 32 attacks occurred during feeding. Once the aggressive chick appeared to have a full crop, the aggression would usually cease. The aggressor was nearly always the heaviest young, with the exception of the male of Nest 7. Victims of the aggression incurred substantial feather and epidermis injury, loss of access to food, and retardation of growth. In 35 of 48 feedings, the subordinate young in Nests 5 and 7 received no food at all. Such food deprivation likely was responsible for the early death of the smaller young of Nests 5 and 6. In general, a marked disparity was evident between the dominant and subordinate young in terms of size, mass and overall appearance of health (see below).

Sibling aggression (the number of blows) was not correlated significantly with the wet mass (g) of prey delivered to the nest (r = 0.665, df = 5, P > 0.05). However, sibling aggression and the caloric value of delivered prey were significantly correlated (r = 0.754, df = 5, P = 0.05).

To compare growth rates of Ospreys with those calculated by Stinson (1977), asymptotic values were calculated. Because asymptotic mass near fledging time is inversely proportional to brood size (Stinson 1977), the mean mass of the largest nestling of each brood size was used to represent the asymptote (Stinson 1977). Using 1700, 1605, and 1717 g as the asymptotic weights of one-, two-, and three-young broods, respectively, the growth rate (K) of the 14 young was 0.13 ± 0.04 (N = 14). The time required for the young to grow from

Variable	1975	1985
Total number of young	22	16
Total number of nests	10	7
Acts of sibling aggression	0	32
Cases of brood reduction	0	2
Percentage of empty crops	0	55
Sequential feeding of young	yes	no
Rank of young changes	yes	no
Adult males feed young	yes	no
Adult females hunt during nestling period	no	yes
Growth rate (K)	0.12	0.13 (0.043, 14) ^c
t_{10-90} (d)	36.7	37.2 (11.456, 14)
Mean asymptotic weight (g)	1587	1564 (195.2, 14)
Mean fledging age (d)	51.0	51.96 (3.82, 14)
Inactive time (%)	43.0 (6.2, 69)	29.9 ^d (14.9, 52)
Fish delivery rate (fish/h)	0.527 (0.06, 69)	0.351 ^d (0.14, 52)
Mean fish size (g)	237.1 (160, 145)	156.9 ^a (167, 254)

TABLE 1

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^a From Stinson (1976, 1977, 1978).

^b From McLean (1986).

^c Mean (SD, N).

^d Denotes pairs of values that are significantly different (P < 0.001).

10 to 90% of the asymptotic weight was 37.23 ± 11.5 days (N = 14). Growth rates as derived above (Ricklefs 1967, 1968, 1976; Stinson 1977) reflect the rate of growth as a percentage of the asymptote. Because male and female asymptotic weights differed significantly (male: 1365 \pm 90.62 g, N = 5, female: 1645 \pm 148.6 g, N = 5, P = 0.007), and because both sexes took about the same time to fledge (male: 51.0 ± 5.3 days, N = 5, female: 50.6 ± 2.9 days, N = 5; P = 0.886) the absolute rate of growth must be higher for females.

Examination among and within broods revealed a disparity in growth and fledging times between dominant and subordinate young. Among broods, the young of Nests 5, 6, and 7 took significantly longer to fledge than the young in some of the other nests. Within-brood comparisons showed that the lighter young of Broods 5 and 7 took significantly longer to fledge (57.5 \pm 3.5 days, N = 2, P = 0.017) than the other young (50.9 \pm 3.1 days, N = 12). Also, the lighter young (male) of Brood 5 was at least six days older than the other males at the last weighing before fledging, yet it had the lowest asymptotic weight and the shortest body length (43.2 cm) of all other Osprey young (mean = 50.1 cm).

Nestling deaths occurred in two of the seven broods. One of the chicks died at approximately six days of age and another was 10 days old at death. Both bodies were found in their nests, with little evidence of external injury. Necropsies performed by a local veterinarian indicated malnutrition as the probable cause of death.

Discussion.-Sibling aggression in 1985 was common among nestling Ospreys in southwestern Chesapeake Bay. Roberts (1982) documented aggression between siblings of two nests in the bay. In one case, the adults abandoned two young, 18 and 19 days old (Roberts, pers. comm.). Spitzer (unpubl. data) has monitored Osprey productivity in several areas of the bay's eastern shore and has noted brood reduction in approximately 75% of the nests in at least one area. However, there have been no published reports of sibling aggression or brood reduction among Chesapeake Bay Ospreys. In fact, Stinson (1976, 1977) found no signs of sibling aggression during his 1975 study of the reproductive behavior of Ospreys inhabiting the western shore of the bay. The adult Ospreys appeared to feed all young, and crops that were examined were never empty (Stinson 1976). In 1985, we observed 32 sibling attacks, and threatening postures and kleptoparasitism among siblings were common. Typically, more than half of the nestlings' crops were empty during our visits. In 1975, the young were fed sequentially (Stinson 1976). In 1985, in many instances, the young dominated each other through aggression and/or posturing and, as a consequence, feeding of the young was often nonsequential. Heavier young were fed repeatedly and lighter young were often ignored.

In 1985, the amount of time the male spent perched near the nest and the delivery of fish to the nest significantly decreased compared to 10 years earlier (Table 1). In 1975, the males spent about 43% of the day near the nest (Stinson 1976) in contrast to less than 30% in 1985. The delivery rate significantly declined from over 0.5 fish/hour in 1975 (Stinson 1976) to about 0.3 fish/hour in 1985. Also, the average size of the fish delivered to the nest was significantly greater in 1975 than in 1985. In 1985, Chesapeake Bay Ospreys apparently hunted more and delivered fewer fish than they did 10 years earlier.

There were several other striking differences between the data of 1975 and 1985 (Table 1). Although Stinson found the mass-rank of a chick changed from one weighing period to the next, all but one of the young studied in 1985 maintained rank consistently. In the exceptional case (Nest 7), change in rank was likely due to the sex of the young; the male's weight was exceeded by that of his two younger, female nestmates. Stinson (1977) noted that males often fed the young. In 1985, we never saw males feed young. Furthermore, none of the adult females of the 1975 study contributed to the hunting efforts until the fledgling period, as is typical of female Ospreys (Bent 1937). In 1985, one of the seven females hunted and this female began hunting three weeks into the nestling period—five weeks before the young had fledged.

In reviewing 1975 and 1985 data, the lack of a large difference in some of the values is puzzling (Table 1). If less food was being delivered in 1985 than in 1975, one might expect a lower growth rate, a lower average asymptotic weight and a greater t_{10-90} value and a greater average fledging age. We found no differences in any of these parameters. The small and unequal sample sizes in the two studies (Stinson 1977: five, one-young, one, two-young, two, three-young, one, four-young, and one, five-young broods; McLean 1986: one, one-young, five, two-young and one, three-young broods) may explain why the values are so comparable. Also, Stinson (1977) did not distinguish between sexes; the proportion of male and female young studied would affect the average asymptotic weight.

Other studies (Knight 1932, Poole 1979, Judge 1981, Jamieson et al. 1983) have noted the incidence of sibling aggression, and one report (Poole 1982) has implicated food shortage as the probable cause of sibling aggression and subsequent brood reduction. Knight (1932) noted one brief occurrence of aggression between two very young Osprey chicks. In Canada, 18 incidents of aggression were recorded during 449 h of observation of eight nests during the summers of 1978 and 1980 (Jamieson et al. 1983). There, aggression was noted to be more common later in the nestling period (when young were approximately four to five weeks old) and more prevalent in three-young than two-young broods. There appeared to be no fish shortage in the study area and the average rate of delivery of fish (0.48 fish/h) was similar to that found by Stinson (1976), but greater than the rate found in 1985. Jamieson et al. (1983) concluded that because most aggression was observed in these three-young broods, then competition for food, even if relatively abundant, results in aggression. In Florida Bay, Poole (1979) documented the constant aggression of one nestling against its nestmate. Measurements gathered in the days during and after observing the aggression

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showed a significant difference in size and weight between the aggressor and the intimidated sibling — differences very similar to those we observed in Chesapeake Bay Osprey young in 1985. Poole (1982) noted that sibling aggression could be turned on and off with the degree of hunger of the dominant young, which argues that food availability does, in fact, influence this behavior. The aggressive young nearly always ceased aggression after satiation — a finding identical to ours. Hatching asynchrony, as well, might have influenced the incidence of sibling aggression and the subsequent brood reduction observed in the Florida Bay Ospreys (Poole 1982). Third chicks in food-stressed colonies grew significantly slower than their siblings (Poole 1982). In short, Poole (1979, 1982) offered evidence to suggest that sibling aggression is due to food scarcity and, to a lesser degree, hatching asynchrony. Aggression was integral to brood reduction; subordinate siblings were forced out of the nest, or, more commonly, denied access to food.

Some of our results are easily explained, but others are seemingly paradoxical. Young in Nests 5, 6, and 7 took significantly longer to fledge than the other young. This delay in fledging times coincided with a substantial amount of sibling aggression and/or brood reduction observed in these nests. These results, then, imply delayed maturation as a result of sibling aggression. Yet, at these same nests, the occupants were the recipients of the greatest amount of fish. Such a result is contrary to expectation, particularly if sibling aggression and brood reduction are associated with food scarcity.

But a closer examination within broods is revealing. Although the occupants of Nest 5 received a large amount of fish, some was left uneaten, and a disproportionate share was eaten by the adult female and the dominant young. Based on our bite-counts, the dominant young of this nest ate twice as much as the subordinate young. Because the subordinate young was intimidated from eating, begging calls from it and subsequently from the adult female appear to have resulted in more fish being delivered to the nest. Also, of all adult females of the two-young broods, this female ate proportionately more than her young (34 vs 22%). It is conceivable her energetic demands were greater than others due to a host of factors including body size, quality of feeding during courtship, or demands of egg laying (cf Poole 1985). In Nest 7, a three-young brood may have been the stimulus for more fish delivered. Indeed, the male of this nest was the most active (inactive time = 12.7%) and had the highest rate of delivery of fish (0.421 fish/h) of any adult male. The young of this nest were vocal as well, and it was our impression that the subordinate young was inordinately vocal; this young was often neglected during feeding either through intimidation by the heavier siblings or by inaccessibility to the adult female when she distributed the food. Even though a substantial amount of energy was being delivered to these nests, in at least two cases (Nests 5 and 7) the young were receiving unequal shares.

Sex of the hatchlings and hatching asynchrony appear important in facilitating aggression and brood reduction. Male and female young differ in both asymptotic weights and absolute growth rates. Females grow faster and become heavier than males. However, being hatched a day or two before a nestmate confers an advantage as well. In brood 7, the male was hatched a day before one female and two days before the other. This male was able to maintain dominance over the females even though the females eventually became heavier. The five-day difference in age of the two young of nest 6 was probably partially responsible for the death of the one at 10 days of age. This is consistent with Stinson's (1979) proposal that the predominance of siblicide in raptors is facilitated by asynchronous hatching; this usually permits the older chick to dominate the younger one.

However, the ultimate cause of sibling aggression and brood reduction is probably food shortage (O'Conner 1978, Stinson 1979, Mock 1984). Although there is a positive correlation between sibling aggression and energy delivered to the nest, such a relationship may be best explained by ultimate rather than proximate factors (Mock 1984). Mock argues that there

is no necessary relationship between the timing of sibling aggression and subsequent food shortages and that sibling aggression does not have to occur during feeding. In this study, not all of the attacks were during feeding. In fact, a number of the posturing behaviors occurred in the absence of food. Additionally, even though Broods 5, 6 and 7 received large amounts of fish, the average rate of delivery to these nests (0.424 ± 0.14 fish/h, N = 24) was still significantly less than the average rate of delivery in 1975 (P = 0.001, Table 1). Because the average size of fish delivered in 1985 was significantly less than that delivered in 1975 (Table 1), then obviously the males of these nests were delivering significantly less fish in 1985 than 10 years earlier.

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Intraspecific piracy in Ospreys.—Piracy is a common foraging tactic in birds. By stealing prey, pirates avoid incurring time and energy cost of locating, handling, and transporting prey but may risk injury if the owner defends the contested resource (Brockmann and Barnard 1979, Hansen 1986). Ospreys (*Pandion haliaetus*) are frequent victims of interspecific piracy (Bent 1937, Prevost 1979), since their conspicuous mode of prey transport and reduced flight agility when carrying prey make them easy targets, but intraspecific piracy is heretofore unreported.

I studied Ospreys in the Creston Valley of southeastern British Columbia particularly at a nest with two chicks on a bridge at the mouth of the Kootenay River (49°15'N, 116°41'W). On 13 July 1987, the chicks (28 and 24 days old) were nearly identical in mass (1205 vs 1180 g), and at feeding bouts that day received similar portions of food. A severe 3-day rainstorm began on 16 July, during which time no observations could be made at the rest. Strong winds and thunderstorms occurred continuously throughout this period. Nest-watches resumed on 19 July, when the storm had abated. At 1008 h the parent male delivered a black bullhead (Ictalurus melas) which the female fed to the chicks. Although no aggression occurred, the older chick ate 78% of the 83 bites eaten by the chicks. The younger chick appeared weakened, and by 1305 h was lying on its back making only feeble movements. At that time, the female parent left the nest and flew toward a second male from an adjacent nests which was standing on the riverbank with a live largescale sucker Catostomus macrocheilus; estimated mass 600 g). The female grabbed the caudal peduncle of the sucker, and a prolonged tug-of-war with the male ensued. The male resisted the female's attempts to take the fish until the female released the fish and attacked the male, biting his bill and head. The female then flew with the sucker to a site about 300 m north of the bridge. During this flight, she was attacked and struck twice by the victimized male. The male returned to its nest 300 m south of the bridge and the female ate the anterior portion of the fish over the next 31 min. At 1351 h she returned to the nest with the fish, and over the next 2 h and 27 min, at two feeding bouts, fed the older chick 544 bites. The hunger of the female