

GROWTH AND BROOD REDUCTION OF MID-ATLANTIC COAST OSPREYS

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ABSTRACT.—Ospreys (*Pandion haliaetus*) exhibit both large geographic differences in growth rate and variable levels of brood reduction, which are assumed dependent on local prey abundance. We examined Ospreys nesting along the mid-Atlantic coast to determine how growth rate and brood reduction were influenced by an abundant, available prey base. Growth rate was substantially higher than previously reported and best described by a logistic growth curve ($k = 0.173$). We found little or no difference in growth related to year, to brood size, or in broods with and without nestling loss. Brood reduction occurred in this area, despite an apparently ample prey base, and was more common in larger broods. Higher incidence of brood reduction in large broods was a function of larger disparities in within-brood nestling size, probably caused by inadequate food provisioning by males. We believe large intercolony differences in Osprey growth are primarily a function of local food abundance and availability, whereas intracolony variation—reflected in higher rates of brood reduction—may be a function of a male's ability, experience, or motivation to provide food to nestlings. Received 12 March 1990, accepted 29 October 1990.

INTRASPECIFIC variation in avian postnatal growth is influenced by an array of extrinsic and intrinsic factors (Ricklefs 1983: 58–63). Extrinsic factors, which include food quality and abundance, weather, and habitat quality, have previously explained differential nestling growth within a species (Lack and Lack 1951; Van Balen 1973; Bryant 1975, 1978; Dunn 1975; Ross 1980; Poole 1982). Intrinsic factors—which include components of a species' reproductive biology such as type of development (precocial, semiprecocial, or altricial), clutch size, hatching synchrony, and quality and amount of parental care—also affect growth (Ricklefs 1968; Klomp 1970; Howe 1976, 1978; Ricklefs and Peters 1981). Because growth within a single species is constrained by these intrinsic factors, variation in extrinsic factors such as food supply, weather, and parental care should account for differences observed in growth rate.

Growth rate and reproductive success of Ospreys (*Pandion haliaetus*) will vary with the amount of food supplied by adults to nestlings (Poole 1982). Because Ospreys hatch asynchronously, nestlings often compete with one another when prey is delivered at an insufficient

rate (Poole 1979, 1982; Jamieson et al. 1983; Hagan 1986). When sibling competition becomes severe, brood reduction—manifested through death of the youngest nestling—usually occurs in Ospreys as in many other species that hatch asynchronously (Ricklefs 1965, Meyburg 1974, Stinson 1980, Hahn 1981, Poole 1982, Hagan 1986). Although usually linked with reduced food supply (Newton 1977), sibling aggression has also been observed in Ospreys nesting near areas rich in available prey (Jamieson et al. 1983).

To determine growth rate and factors that affect brood reduction in an area rich in suitable prey, we investigated growth rates of Ospreys in an area with abundant prey, the effects of brood size on growth, and the frequency of brood reduction and its effect on growth. We examined why brood reduction in Ospreys occurs in an area with abundant prey.

METHODS

Study area and data collection.—Our study took place in southern New Jersey within a large population of nesting Ospreys. All nests studied were within 4 km of the Atlantic Ocean and in the northern portion of the Cape May peninsula. This area is a large, tidal estuary that supports typical salt-marsh vegetation dominated by salt-marsh cordgrass (*Spartina alterniflora*) and salt-meadow cordgrass (*S. patens*). Transparency of waters surrounding this colony ranged between 120 and 220 cm. During this study, nests

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were on man-made structures (87%) and in dead trees (13%). Reproductive success averaged 1.56 young fledged per occupied nest (Steidl 1990), well above levels thought necessary to maintain a stable population (Spitzer et al. 1983).

We visited a total of 38 Osprey nests every 5–8 days from egg laying through fledging in 1987 and 1988 combined. During visits, we weighed each nestling with Pesola spring scales (± 1 g or ± 3 g depending on nestling size and scale used); we usually kept adults away from nests for <3 min. In 1987, 18 pairs hatched 43 nestlings (1 pair hatched no young) that we weighed 1–4 times each season (mode = 3) until they reached 1,000 g (ca. 22–28 days). In 1988, 15 pairs hatched 31 nestlings (3 pairs hatched no young) that we weighed 1–6 times each season (mode = 6) until they reached or exceeded adult mass (ca. 35–40 days).

Measurements of Osprey growth can be influenced by hatching asynchrony (a single brood may contain young of various ages) and by the sex of nestlings. Sexual-size dimorphism appears in Osprey nestlings after approx. 1,000 g (McLean 1986), but because we did not attempt to sex nestlings, our results represent growth of all Osprey nestlings in this region. To avoid individually marking nestlings solely for aging, we assigned an age of zero to all nestlings in each brood at the midpoint of hatching.

Growth curve estimates and comparisons.—We fitted growth curves using a derivative-free, nonlinear least-squares regression routine (Proc NLIN; SAS Inst. Inc. 1988) to measured mass of nestlings. We examined three sigmoid growth models to determine which most accurately described growth of Osprey nestlings:

the logistic,

$$M(t) = a / \{1 + [(a - b)/b] \exp(-kt)\},$$

Gompertz,

$$M(t) = a \cdot \exp - [\ln(a) - \ln(b) \exp(-kt)],$$

and von Bertalanffy,

$$M(t) = a \cdot \{1 - [(a^{1/3} - b^{1/3})/b^{1/3}] \exp(-kt)\}^3,$$

where $M(t)$ is mass of a nestling at time t , and a , b , and k are constants proportional to asymptotic mass, initial mass, and growth rate, respectively. Richards' (1959) 4-parameter growth model can most accurately describe some growth relationships (White and Brisbin 1980), but it can also be severely restricted in its use and interpretation (Davies and Ku 1977, Zach 1988). Because our data fit the above 3-parameter curves so well, we restricted analyses to these simpler, more easily interpreted models.

We compared growth curves by several techniques, including (1) analysis of covariance (ANCOVA) after log transforming nestling mass and age (r^2 ranged from 0.86–0.98 with $P < 0.001$ in all instances), (2) an

F -test (White and Brisbin 1980), and (3) t -tests or one-way analysis of variance to compare mean mass within 5-day age intervals. All analyses yielded identical conclusions, so we report only ANCOVA results throughout. We also used ANCOVA to compare slopes of linear regressions calculated from linear periods of nestling growth (ages 5–28 days) determined from residual plots of regressions. Slopes are reported \pm SE.

RESULTS

Because we weighed nestlings only up to 1,000 g in 1987, we could not fit complete growth curves to these data. To determine if growth rates differed between years during this period of rapid growth, we compared 1987 data to an identical subset of 1988 data (nestling mass up to 1,000 g). Linear regressions calculated from nestling mass measured from 5–28 days were similar for both years (1987 slope = 42.5 ± 2.2 , $r^2 = 0.82$, $P < 0.0001$; 1988 slope = 43.0 ± 2.6 , $r^2 = 0.79$, $P < 0.0001$), which implies that growth of this Osprey population was uniform during both years ($F = 0.02$, $df = 1$, $P > 0.8$).

GROWTH OF OSPREY NESTLINGS

Although nestling growth was similar between years, we restricted sigmoidal growth-curve analyses to mass measured during 1988, when we had weighed nestlings throughout the entire nestling period. Nestling-mass data collected during both years were used for analyses restricted to earlier portions of the nestling period.

Comparison of growth models and growth among different brood sizes.—To determine which model best described Osprey growth, we fitted three growth models to data collected during 1988 (Table 1). All models fit the data well, but the logistic curve yielded the lowest residual mean square error and provided the most realistic parameter estimates. We used the logistic curve to perform the remainder of our analyses. Predicted mass generated by the logistic curve closely followed the observed data (Fig. 1).

To determine if growth differed among broods that hatched 1, 2, and 3 young, we calculated separate growth curves, the amount of mass gained per day, and the number of days required to grow from 10 to 90% of their asymptotic mass (t_{10-90}) and to one-half asymptotic mass ($t_{.5}$, inflection point of the logistic curve, calculated by nonlinear regression of $W(t) = a / \{1$

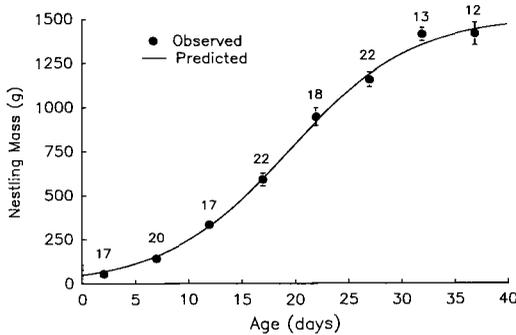


Fig. 1. Similarity of observed ($\bar{x} \pm SE$) and predicted logistic growth of Osprey nestlings, 1988. Sample sizes (above error bars) are number of nestlings weighed during each interval. Error bars were too narrow to show for all points.

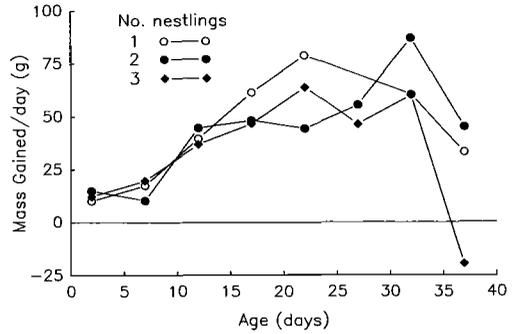


Fig. 2. Mass gained per day (\bar{x}) for different brood sizes.

+ $\exp[-k(\text{Age} - t_i)]$ from Ricklefs [1979]), for each of the three groups. Although broods of different sizes grew at slightly different rates (Table 2), the differences were not statistically significant ($F = 2.22$, $df = 2$, $P > 0.1$). For all broods combined, t_{10-90} was 26 days (range 25–29), and t_i was 19 days (19–20), with only minor differences between broods of different sizes. Mass gained per day was also similar for all brood sizes, which peaked between 20 and 35 days, and declined quickly thereafter (Fig. 2).

BROOD REDUCTION AND NESTLING GROWTH

For some broods there were large disparities in size among siblings. Periodically, the largest nestling in a brood dominated feedings or even battered its smaller sibling(s). We occasionally found nestlings dead in or under their nests, and at least twice we observed fratricide in 3-nestling broods.

Nestling loss and sibling competition.—To determine how brood reduction and sibling competition affected this population, for nests hatching ≥ 2 young we compared (1) nestling-

loss rates between 2- and 3-nestling broods, (2) growth of broods with and without nestling loss, and (3) within-brood mass differences between the largest and smallest siblings (called sibling weight difference by Poole [1982]).

For both years combined, 27 of 38 (71%) nests we visited hatched either 2 or 3 young. These nests produced a total of 68 young, 57 (84%) of which survived to fledge. Three of 13 (23%) nests that hatched 2 young and 5 of 14 (36%) nests that hatched 3 young lost ≥ 1 young before fledging (died or disappeared for an unknown reason). Although 3-nestling broods lost a higher percentage of nestlings than 2-nestling broods, timing of nestling loss was similar; most young died 2–3 weeks after hatching, as growth entered the steepest segment of the logistic growth curve (Fig. 3).

To determine if growth rate was influenced by brood reduction, we compared regression lines calculated from mass of 2- and 3-nestling broods with and without nestling loss. To compare nestling growth rates, we used linear regression for ages 5–28 days for 1987 and 1988 combined. Growth of multiple-nestling broods with nestling loss did not differ from those without (slope for broods with loss = 47.4 ± 3.2 , $r^2 = 0.86$, $P < 0.0001$; slope for broods with-

TABLE 1. Parameter estimates^a ($\pm SE$) of three sigmoid curves describing growth of Osprey nestlings in New Jersey, 1988. For all models, $r^2 > 0.97$.

Growth model	Growth rate (<i>k</i>)	Asymptotic mass (<i>a</i>)	Initial mass (<i>b</i>)
Logistic	0.173 \pm 0.013	1,508.2 \pm 49.8	50.3 \pm 10.3
Gompertz	0.095 \pm 0.009	1,705.2 \pm 93.1	6.8 \pm 4.7
von Bertalanffy	0.069 \pm 0.008	1,874.7 \pm 141.3	224.0 \pm 47.2

^a Estimates are not strictly comparable between curves.

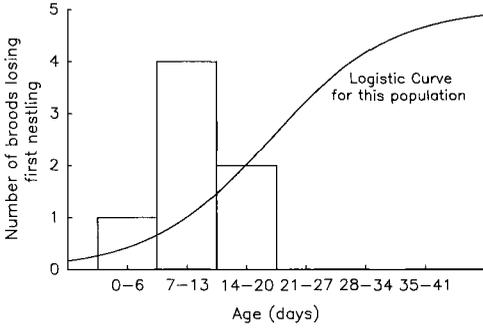


Fig. 3. Logistic growth curve and loss of Osprey nestlings in 1988. Loss of first nestling in multiple-nestling broods occurs during the period of most rapid growth.

out loss = 49.5 ± 1.8 , $r^2 = 0.84$, $P < 0.0001$; $F = 1.23$, $df = 1$, $P > 0.2$.

To examine why 3-nestling broods experienced greater brood reduction than 2-nestling broods, we compared sibling weight differences (Poole 1982) between these two groups. Actual sibling weight differences of 3-nestling broods increased while those of 2-nestling broods remained relatively constant as nestlings grew (Fig. 4). Percent sibling weight difference between the two groups was greatest from 15 to 20 days and subsequently decreased as nestlings approached fledging mass. This decrease probably results when the largest nestling within a brood nears adult size and requires less food for growth. Further, food demand is decreased for each brood where nestling mortality (due, in part, to sibling competition) reduces brood sizes. The high sibling weight difference in 3-nestling broods seems the probable cause of their higher nestling loss rates.

DISCUSSION

GROWTH CURVES

We recorded only slight variation in growth rate of broods hatching different numbers of young (Table 2). Poole (1982) found that growth during the first portion of the nestling period differed between broods of 1 and 3 nestlings in only 1 of 3 colonies he studied—the colony most food-stressed. In three species of terns, Dunn (1975) found only minor differences in growth attributable to brood size, and Dunn concluded that environmental factors such as wind and

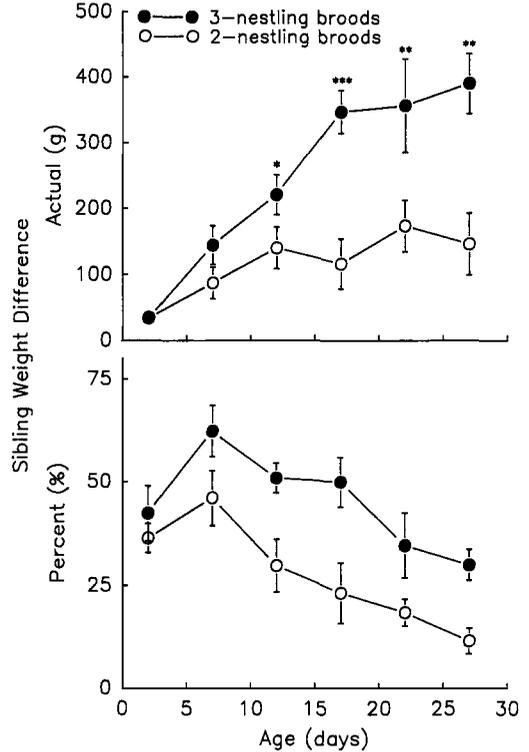


Fig. 4. Actual and percentage ($\bar{x} \pm SE$) sibling weight differences within broods of 2 and 3 nestlings. * = $P < 0.10$, ** = $0.01 < P < 0.05$, *** = $P < 0.005$.

weather influenced nestling growth because of their effect on foraging abilities of food-provisioning adults. Ospreys are also piscivorous and may have variable foraging success based on weather conditions (Grubb 1977, Ueoka and Koplín 1973, Stinson 1978), but the consistency of weather patterns and growth rates we observed suggest that these factors had little or no influence on growth during the two years of our study.

The growth of nestling Ospreys was more accurately described by the logistic growth curve than by the Gompertz and von Bertalanffy curves (Table 1). Stinson (1977) measured growth of nestling Ospreys in Chesapeake Bay as did Poole (1982) in two New York colonies and one Florida Bay colony. Only Stinson (1977) collected enough data to fit a logistic curve. He determined the growth rate (k) for Chesapeake Bay Ospreys to be only 0.12. This is 44% (95% CI = 23–65%) below the k of 0.173 we determined for Ospreys, and well above the 20% in-

TABLE 2. Logistic growth parameters (\pm SE) for different brood sizes.

Brood size	Growth rate (k)	Asymptotic mass (a)	Initial mass (b)
1	0.162 \pm 0.018	1,591.2 \pm 89.0	57.3 \pm 18.0
2	0.153 \pm 0.019	1,800.6 \pm 131.0	73.0 \pm 22.4
3	0.178 \pm 0.017	1,428.9 \pm 61.3	45.3 \pm 13.1

traspecific variation Ricklefs (1968) attributed to geographic differences while examining >150 bird species. Stinson (1977) also calculated t_{10-90} of 36.7 days for Chesapeake Bay Ospreys, which is 41% longer than the 26 days we calculated for this southern New Jersey colony.

Geographic variation in growth of Osprey nestlings from ages 5–27 days was reported by Poole (1982). We calculated linear regressions for the same period for two years, estimated similar values for Stinson (1977), and compared results among these previous studies (Table 3). During this portion of the nestling period, Ospreys exhibit considerable geographic differences in growth rate. These differences in growth are probably related to the amount of food supplied by adults to nestlings (Poole 1982), yet no study has examined food delivery of Ospreys with food abundance and availability in their foraging areas.

Differences in growth rate, brood reduction, and sibling aggression in Ospreys and other raptors have generally been related to food supply (Ingram 1959; Newton 1977; Stinson 1979; Poole 1982, 1989) and distance to foraging areas (Hagan 1986). The inconsistency we observed is that although Ospreys in southern New Jersey grew quite quickly—which implies an ample food supply—we still observed sibling aggression and brood reduction (as did Poole [1982] in food-stressed colonies). Ospreys in Chesapeake Bay grew considerably slower and displayed almost no sibling aggression or brood reduction (except possibly in an artificially large brood of 5; Stinson 1977), whereas Ospreys in Nova Scotia exhibited sibling aggression in an area of apparent food abundance (Jamieson et al. 1983).

BROOD REDUCTION

Ospreys in New Jersey underwent brood reduction primarily as nestlings entered the period of most rapid growth (Fig. 3). Hagan (1986)

TABLE 3. Geographic differences from Cape May, New Jersey, in growth of nestlings from ages 5–27 days, based on slopes from linear regressions.

Location	Slope	Difference (%)
Chesapeake Bay, VA ^a	29.7	64
Florida Bay, FL ^b	36.3	34
Gardiners Island, NY ^b	36.5	34
E. Long Island, NY ^b	45.3	8
Cape May, NJ ^c	48.8 (3.25) ^d	—

^a Estimated from Stinson (1977) by calculating a linear regression from values generated by fitting a logistic curve to Stinson's $k = 0.12$ and $a = 1,712.5$ for 2-nestling broods aged 5–27 days; initial mass, $b = 50.3$, was taken from this study.

^b Data from Poole (1982).

^c This study.

^d 95% CI.

found similar trends in a North Carolina colony and used O'Connor's (1978) brood reduction model to test his data. The model, as well as his observations, implied that fratricide, not infanticide or suicide, was the mechanism by which brood reduction in Ospreys should occur. In our colony, sibling aggression was common, and fratricide was observed in 3-nestling broods at least twice. Although nestlings from broods with and without brood reduction grew at similar rates, this may have occurred as growth rates became more similar after early nestling loss. We believe that brood reduction adjusted brood size to the amount of food delivered to nests.

We observed rates of brood reduction in 3-nestling broods that were higher than in 2-nestling broods. Jamieson et al. (1983) found that in 5 of 6 nests where sibling aggression occurred, there were 3-nestling broods. In their study colony, but not ours, all young lived to fledge.

In Ospreys, brood reduction through sibling aggression is facultative, usually a function of asynchronous hatching, reduced food supply, and subsequent disparity in nestling size within a brood. Striking contrasts observed in sibling weight difference between broods of 2 and 3 nestlings (Fig. 4) exemplify this size disparity. The greater difference in nestling mass of 3-versus 2-nestling broods fosters increased sibling competition and subsequent brood reduction observed in larger broods.

Brood reduction and food supply.—Along the Atlantic coast of southern New Jersey, Ospreys capitalize on the large numbers of menhaden (*Brevoortia tyrannus*) that spawn in and around

the estuarine waters where Ospreys nest (R. J. Steidl pers. obs.). These fish are brightly colored surface feeders that school (Rogers and Van Den Avyle 1989), which makes them easy prey for Ospreys.

Several factors support our contention that Ospreys nesting in southern New Jersey were not food limited. First, the growth rates for this population were the highest reported. Second, Osprey pairs that nest in this colony commonly fledge 3 and occasionally 4 young. Finally, decreasing age-related mass differences (percent sibling weight difference; Fig. 4) between siblings is indicative of well-fed colonies (Poole 1982). We suggest that the differences in brood reduction and subsequent differences in reproductive success are not determined solely by food abundance and availability.

We believe that differential brood reduction observed in this food-rich colony is due to differential male ability, experience, or motivation. Several authors have noted that male Ospreys, which provide nearly all the food to the female and nestlings, do not adjust their rate of food delivery according to the size of their brood (Stinson 1978, Poole 1982, Jamieson et al. 1983, Eriksson 1986). Males also spend only a small portion of their time foraging (Stinson 1978). The majority of their time is spent perched near the nest. The relatively fixed amount of prey males deliver to their nest is probably based on a combination of their foraging abilities and food abundance, not on brood size. Poole (1989) supports our hypothesis with four observations: (1) reproductive success of Ospreys increases with the experience and age of male parents, (2) earlier breeders have higher reproductive success (lower nestling-loss rates) than late breeders and tend to be older, more experienced birds, (3) more experienced birds bring more fish to nests than inexperienced birds, and (4) even in areas of apparent food stress, individual nests will fledge a full complement of young. Skagen (1988) showed experimentally that under conditions of abundant food, nestling Zebra Finches (*Poephila guttata*) raised by inexperienced parents grew more slowly and suffered higher mortality than did those raised by experienced parents.

There are common explanations for variation in growth rates: (1) environmental factors, including predation on nestlings, food availability, and sibling competition, (2) parental effort,

and (3) anatomical and physiological constraints of nestlings to convert energy into biomass (Ricklefs 1983: 66). From the nestlings' perspective, lack of parental foraging effort or ability does not differ from reduced environmental food supply. We believe differential foraging abilities in male Ospreys, probably based on age and foraging skill and not lack of available food, were responsible for larger sibling weight differences and subsequent brood reduction observed in some of the nests we studied. This hypothesis is consistent with the higher rate of brood reduction observed in 3-nestling broods because less experienced males are more capable of providing for smaller 2-nestling broods. Further investigation is needed to substantiate this male experience-brood reduction hypothesis.

Insight into how food abundance near Osprey colonies varies with the amount of food brought to nestlings by adults may help resolve geographic differences in observed growth rate, brood reduction, and sibling aggression. Based on our findings and others, we believe differences in local food abundance are responsible for intercolony differences in growth rate, while intracolony differences in brood reduction and sibling aggression may result from differential male ability, age, or experience. The lack of large differences in growth rate between broods of different sizes within colonies and differential rates of sibling competition and nestling loss observed also by Poole (1982) support our hypothesis. This explanation for differential nestling loss agrees with Lack's (1954, 1968) hypothesis, which links food supply and brood reduction, yet the explanation allows for instances of brood reduction in areas of high food abundance based on lower parental experience and ability.

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