

SEX-SPECIFIC GROWTH IN OSPREYS: THE ROLE OF SEXUAL SIZE DIMORPHISM

CHARLES P. SCHAADT¹ AND DAVID M. BIRD

Avian Science and Conservation Centre, Macdonald Campus of McGill University,
21,111 Lakeshore Road, Ste. Anne de Bellevue, Quebec H9X 3V9, Canada

ABSTRACT.—Sex-specific growth analyses were conducted for 20 male and 12 female Ospreys (*Pandion haliaetus*) in 19 broods in Nova Scotia, Canada during 1984–1986. The graphical methods of Ricklefs showed the logistic model to be most appropriate for mass increase with a growth-rate constant K of $0.18 \cdot \text{days}^{-1}$ for both sexes combined. The influence of sex on growth performance was also described using a reparameterized Richards model. Mass and tarsus length were the only variables to show well-defined asymptotes at fledging, although talon length, cranium width, and culmen length were within 10% of adult values. Males differed significantly from females in having lower asymptotes of mass and tarsus length, but did not differ in rate of growth. There was no difference in growth rates between individuals in broods of one, two or three nestlings, or within broods as a result of hatching-order asynchrony. Males and females showed no difference in age at time of feather emergence or in length of nestling period. Thus, because there was no evidence for rapid growth in males in order to compete with larger females for food resources at nests, we suggest that sexual size dimorphism may be independent of sibling competition in Ospreys. Received 8 May 1992, accepted 25 November 1992.

FISHER'S (1930) sex-ratio theory is based on the assumption that natural selection should favor parents who invest equally in male and female offspring, resulting in a population sex ratio of unity or 50:50. To test Fisher's theory, workers have turned to investigating sexually dimorphic species where sex ratios other than 1:1 can be predicted. To date, however, studies with sufficient sample size have discovered little evidence of sex-ratio deviation in either raptorial or passerine species (reviewed by Newton 1979, Clutton-Brock 1986, and Weatherhead and Teather 1991). An especially well-documented case of European Sparrowhawks (*Accipiter nisus*) was described by Newton and Marquiss (1979). Although this species is an extremely dimorphic raptor (females are twice as heavy as males), an analysis of 2,163 nestlings showed a sex ratio at unity. Clearly, it would be ill advised to assume unequal investment by parents of other species based solely on the production of dimorphic offspring (but see Bednarz and Hayden 1991, Wiebe and Bortolotti 1992).

This lack of consonance with predictions from theory has some implications: (1) selection may be ineffective in altering the sex ratio of birds;

(2) cost differences are substantially less than size differences (Slagsvold 1990, Drummond et al. 1991); or, as several authors have suggested, (3) sexually dimorphic growth patterns exist that equalize energetic expenditures on dimorphic offspring and maintain the sex ratio at unity during the nestling period (reviewed by Newton 1979, Richter 1983; see also Collopy 1986, Teather 1987, Drummond et al. 1991).

For species that show marked dimorphism at fledging, the smaller sex is thought to be at a relative disadvantage and must grow faster to compete with its larger nest mates for resources. To do this, the larger sex reportedly puts on mass while the smaller sex becomes feathered sooner, achieves asymptotic size more quickly, and leaves the nest earlier, regardless of which sex is larger. Because adult Ospreys (*Pandion haliaetus*) are markedly dimorphic in size (i.e. females are 15–18% heavier and have a wing length 4–5% longer than males), sexually dimorphic growth patterns could be expected to compensate for size differences among nestlings.

We present the results of a three-year investigation of sex-specific growth and asymptotic size of nestling Ospreys. Of particular interest was the fitting of growth models to individual birds so as to document the influence of sex on growth performance. Our objectives were: (1) to document the growth characteristics of mass,

¹ Present address: School of Forest Resources, The Pennsylvania State University, DuBois Campus, College Place, DuBois, Pennsylvania 15801, USA.

plumage and body size of male and female nestlings; (2) to assess the effects of hatch order and brood size on growth rates; and (3) to relate the patterns of sex-specific growth observed in Ospreys to evolutionary theory.

METHODS

Study area.—Growth of 32 Osprey nestlings from 19 nests was measured during the summers of 1984, 1985 and 1986 in Antigonish County in northeastern Nova Scotia. The watersheds of Antigonish and Pomquet estuaries, which empty into the Gulf of St. Lawrence, are characterized by broad-leafed and mixed forests in the highlands, whereas conifers dominate poorly drained areas and valley slopes. The majority of Ospreys forage in the estuaries, nesting in loose colonies on utility poles along power lines. Nests relocated on platforms erected adjacent to transmission poles (Bancroft and Toner 1986 unpubl. report) provided access to nestlings. All nests used in our study were located on platforms near Antigonish and Pomquet estuaries. Additional information on the study area and aspects of the population are provided by Prevost et al. (1978) and Jamieson et al. (1982).

Field methods.—We climbed to nests at 24- to 72-h intervals to document egg laying, clutch size, hatch interval, hatch order, nestling growth, and nestling survival. Prior to incubation, nests were entered to measure and mark eggs. Upon hatching (i.e. day one), neonates were marked on the head with a colored felt marker to assign each hatchling to the egg from which it came. This methodology provided hatching sequence and known ages for all nestlings.

Chicks were: (1) weighed to the nearest gram with Pesola spring scales. The young were measured with dial calipers to the nearest 0.1 mm for: (2) tarsal length, distance from heel to the joint between distal end of tarsometatarsus and third toe; (3) talon length (or hallux claw), distance between point where upper surface of claw emerges from skin to end of claw as measured across its arc; (4) cranium, distance between outer edges of supraorbital processes on each side of head; (5) culmen, from cere to tip of bill as measured across arc (mostly from Olendorff 1972); and (6) unflattened wing chord. To measure (7) eighth primary and (8) central rectrix as they emerged, we inserted a clear plastic ruler between the feathers up to the skin and held the feather flat against the ruler. The downy tuft at the end of the feather was not included in the measurement.

All measurements were performed by C.P.S. and consistently on the left side of the body. Measurements were taken every two days unless prevented by inclement weather. When chicks were young, measurements were taken in the nest within 15 min, but after 7 to 10 days of age, birds were lowered and measured on the ground. To prevent premature fledg-

ing, measurement of nestlings ended when the oldest in the brood reached 52 days of age.

Growth-curve analyses.—For most species, daily variations in food intake, activity or defecation should not significantly alter the characteristics of the growth curve calculated over the entire growth period. In large raptorial birds such as Ospreys, however, full or partially full crops lead to extreme variation in mass. Therefore, we evaluated crop content on a 1 (empty) to 4 (full) scale prior to weighing. Occasionally, during the course of the study, birds were weighed with full (or partially full) crops bracketed by days with empty crops, enabling us to evaluate crop content as a percent of body mass over all portions of the growth period. Net body masses for growth-curve analyses subsequently were calculated by subtracting crop content, as a percent of body mass, from gross mass on any given day. We consistently found nestlings near asymptote (i.e. >six weeks of age) to have more than 200 g of fish in full crops.

Growth data from individual birds were fitted to the logistic equation according to Ricklefs (1967). When fitting curves to mass and tarsus-length data (Table 1), points up to and including observed asymptotes were used (Ricklefs 1968). Asymptotes for the remaining six variables were estimated using simple linear regression.

The variable t_{10-90} was also calculated from the growth equation for individual birds. This inverse measure of growth rate represents the time it takes to grow from 10 to 90% of the asymptotic value. Because this section of the growth curve is approximately linear in all commonly used growth equations, it can be employed to compare species fitted to different curve shapes.

The logistic equation may be expressed as:

$$Y = W/[1 + e^{-K(x-t_i)}], \quad (1)$$

where Y is the value of the growth variable being studied (in grams or millimeters) at time x , K represents a constant proportional to overall growth rate (per day), t_i represents the age at which the curve attains the point of inflection (days), and W equals the asymptotic value of the growth curve (grams or millimeters).

To more thoroughly assess intraspecific comparisons, growth data for individual birds were also fitted to a reparameterized version of the Richards (1959) equation using the additive discrete derivation method of White and Brisbin (1980), rewritten by Brisbin et al. (1986). We used:

$$\frac{W_{i+1} - W_i}{t_{i+1} - t_i} = \frac{2(m+1)}{T(1-m)} (W^{1-m} W_i^m - W_i) + e_i, \quad (2)$$

where W_i is the value of the growth variable being studied at t_i , W is the asymptotic value of the variable being studied, T is the overall growing time indicative of growth rate, m is the Richards shape parameter, and e_i is the stochastic error at time t_i .

TABLE 1. Means of mass (grams) and tarsus length (millimeters) ± SD and sample size (in parentheses) of female and male Ospreys in Nova Scotia, Canada.

Age in days	Mass		Tarsus length	
	Females	Males	Females	Males
4	77.9 ± 10.5 (12)	82.9 ± 17.7 (20)	19.3 ± 1.4 (12)	18.9 ± 1.5 (20)
8	169.5 ± 26.0 (12)	170.6 ± 34.8 (20)	25.9 ± 2.2 (12)	26.0 ± 2.0 (20)
12	341.2 ± 34.9 (12)	331.5 ± 56.3 (20)	34.9 ± 2.7 (12)	35.6 ± 3.1 (20)
16	579.2 ± 62.1 (12)	559.7 ± 68.7 (20)	44.5 ± 3.2 (12)	45.4 ± 3.1 (20)
20	863.4 ± 74.3 (12)	797.8 ± 87.3 (20)	53.4 ± 3.2 (12)	54.4 ± 3.4 (20)
24	1,141.3 ± 78.8 (11)	1,026.7 ± 96.8 (20)	61.7 ± 1.9 (11)	60.5 ± 3.1 (20)
28	1,390.3 ± 67.5 (11)	1,213.6 ± 117.9 (20)	66.7 ± 1.6 (11)	64.7 ± 2.6 (20)
32	1,564.5 ± 54.6 (11)	1,346.7 ± 136.2 (19)	69.6 ± 1.5 (11)	67.3 ± 2.0 (19)
36	1,677.5 ± 31.7 (11)	1,417.2 ± 129.2 (15)	71.5 ± 1.5 (11)	68.7 ± 2.0 (15)
40	1,736.2 ± 32.6 (11)	1,461.2 ± 148.9 (15)	72.7 ± 1.5 (11)	69.9 ± 1.9 (15)
44	1,739.0 ± 48.1 (10)	1,438.9 ± 145.6 (15)	73.8 ± 1.9 (10)	71.1 ± 1.6 (15)
48	1,681.5 ± 43.7 (8)	1,418.1 ± 148.1 (14)	74.3 ± 1.8 (8)	71.1 ± 1.7 (14)
52	1,699.1 ± 22.6 (3)	1,441.5 ± 113.2 (4)	73.2 ± 0.9 (3)	71.5 ± 3.3 (4)

We used a nonlinear, derivative-free, regression routine to fit growth curves to the data set. Parameter estimates obtained from the Ricklefs (1967) method were used as initial starting values for each growth variable.

Data for nonlinear regression analyses were derived only from nestlings that survived to fledge and, as above, regressions for mass did not include values from the recession period of the curve. Because no recession was observed in the other variables, all data were included in the regression analyses.

Sex of individual nestlings was initially determined on the basis of the distinct mass classes that became apparent prior to fledging. The accuracy of these determinations was confirmed by a discriminant-function analysis based on the other constantly increasing variables and by karyotypic analysis of fibroblast tissue collected from a subsample of 17 nestlings (Kohler et al. 1989, Schaadt 1989). Data from birds of unknown sex were entered into the discriminant-function analysis and classified by comparison

with the 17 birds of known sex. A significant discriminant function was obtained ($P < 0.001$), based on the pooled covariance matrix, which enabled us to determine the sex of the unknowns on the basis of mass and tarsus asymptotes alone.

Other statistical tests are mentioned in the text where they are employed. Unless otherwise noted, means are given with standard errors.

RESULTS

We fitted Richards and logistic models to six morphometric characteristics and linear regression models to two feather variables for the 32 individuals. Table 2 summarizes growth parameters fitted with the logistic model, which we tested for year, sex, and their interaction by two-way ANOVA adjusted for unequal sample size (Sokal and Rohlf 1981). These tests revealed sig-

TABLE 2. Growth parameters of logistic equation for nestling Ospreys by sex. $\bar{x} \pm SD$.

Variable	Sex	n	Growth parameter		
			K	A	t_i
Mass	M	20	0.180 ± 0.006	1,499.5** ± 145.6	19.3 ± 1.1
	F	12	0.180 ± 0.007	1,790.0 ± 43.9	20.5 ± 1.1
Tarsus	M	20	0.143 ± 0.007	71.1** ± 1.5	12.0 ± 1.1
	F	12	0.142 ± 0.006	73.9 ± 1.6	12.9 ± 1.4
Talon	M	20	0.110 ± 0.006	30.1 ± 1.4	16.6* ± 1.2
	F	12	0.113 ± 0.006	31.3 ± 1.1	18.0 ± 1.2
Culmen	M	20	0.079** ± 0.005	31.8 ± 1.3	9.8 ± 1.7
	F	12	0.085 ± 0.006	32.7 ± 1.0	11.1 ± 1.4
Cranium	M	20	0.075** ± 0.004	43.4 ± 0.8	5.4 ± 0.9
	F	12	0.082 ± 0.005	44.0 ± 0.8	6.0 ± 1.1
Wing chord	M	20	0.099 ± 0.007	490.2 ± 23.9	30.8 ± 1.7
	F	12	0.098 ± 0.004	505.0 ± 5.2	31.5 ± 1.1

*, $P < 0.05$; **, $P < 0.01$. Significant difference between males and females.

TABLE 3. Growth parameters for Richards equation for nestling Ospreys by sex. $\bar{x} \pm SD$.

Variable	Sex	n	Growth parameter		
			m	W	T
Mass	M	20	1.23 ± 0.17	1,548.7* ± 168.3	36.5 ± 3.5
	F	12	1.26 ± 0.11	1,830.8 ± 76.9	36.0 ± 3.1
Tarsus	M	20	2.18 ± 0.54	71.0* ± 2.1	43.6 ± 3.7
	F	12	2.48 ± 0.48	73.6 ± 2.1	45.3 ± 4.0
Talon	M	20	1.47 ± 0.31	29.6 ± 1.5	50.8 ± 3.2
	F	12	1.80 ± 0.27	30.9 ± 0.9	48.9 ± 2.7
Culmen	M	20	1.90 ± 0.43	31.6 ± 1.9	69.6 ± 5.1
	F	12	2.41 ± 0.60	32.2 ± 1.1	70.9 ± 1.4
Wing chord	M	20	1.31 ± 0.16	456.6 ± 19.9	60.7 ± 4.7
	F	12	1.31 ± 0.18	471.9 ± 18.4	57.3 ± 5.9

* P < 0.01. Significant difference between males and females.

nificant sexual differences in growth rates for the cranium and culmen, in the asymptotes for mass and tarsus, and in the inflection point of the talon. There were no significant differences among years or interactions for any measure of growth.

Table 3 summarizes growth parameters estimated with the reparameterized Richards model also tested for year, sex and their interaction by two-way ANOVA adjusted for unequal sample size. These tests revealed no significant sexual differences in curve shape (m) but, as above, significant differences in asymptote for mass and tarsus. There were no significant differences among years or interactions for any variable.

To compare stages of growth to ultimate size,

adult Ospreys were captured and measured in the study area. Additional parameters of talon and culmen lengths were obtained from study skins of adults measured at the American Museum of Natural History, New York. The following results are compared to mean adult values for each sex obtained from these sources (Table 4).

The mass of nestlings on day 1 averaged 49.0 ± 2.1 g for males and 48.6 ± 2.4 g for females (Fig. 1A). Thus, male nestlings hatched at 3.3% of mean mass of adult males and female nestlings at 2.4% of mean mass of adult females. However, these values may not necessarily reflect true hatching mass, since it is possible that some neonates were fed prior to first weighing. Average mass of all day-1 nestlings combined

TABLE 4. Adult Osprey means compared to nestling means at 48 days of age (or at asymptote).

Variable	Sex	Adult		Nestling		
		\bar{x} (n)	Dimorphism index ^a	\bar{x} (n)	Dimorphism index	Percent of adult value
Mass	M	1,485.0 (8)	18.6	1,499.5 (20)	17.7	100.9
	F	1,790.0 (12)		1,790.0 (12)		100.0
Tarsus	M	71.0 (9)	2.2	71.1 (20)	2.2	100.1
	F	72.6 (10)		73.9 (12)		101.8
Talon	M	29.3 (9)	1.7	29.1 (13)	4.7	99.3
	F	29.8 (10)		30.5 (7)		102.3
Culmen	M	32.5 (8)	5.7	30.4 (13)	4.2	93.5
	F	34.4 (10)		31.7 (7)		92.2
Cranium	M	42.2 (7)	2.3	41.8 (13)	2.4	99.0
	F	43.2 (6)		42.8 (7)		99.1
Wing chord	M	494.5 (10)	4.2	378.7 (13)	2.5	76.6
	F	515.6 (10)		388.4 (7)		75.3
Eighth primary	M	337.0 (10)	3.8	241.1 (13)	1.6	71.5
	F	350.0 (10)		244.9 (7)		69.9
Central rectrix	M	207.0 (10)	4.5	158.4 (13)	0.9	76.5
	F	217.0 (10)		159.9 (7)		73.7

^a Dimorphism index = 100($\bar{x}_{females} - \bar{x}_{males}$)/(0.5 $\bar{x}_{females} + 0.5\bar{x}_{males}$) (Storer 1966).

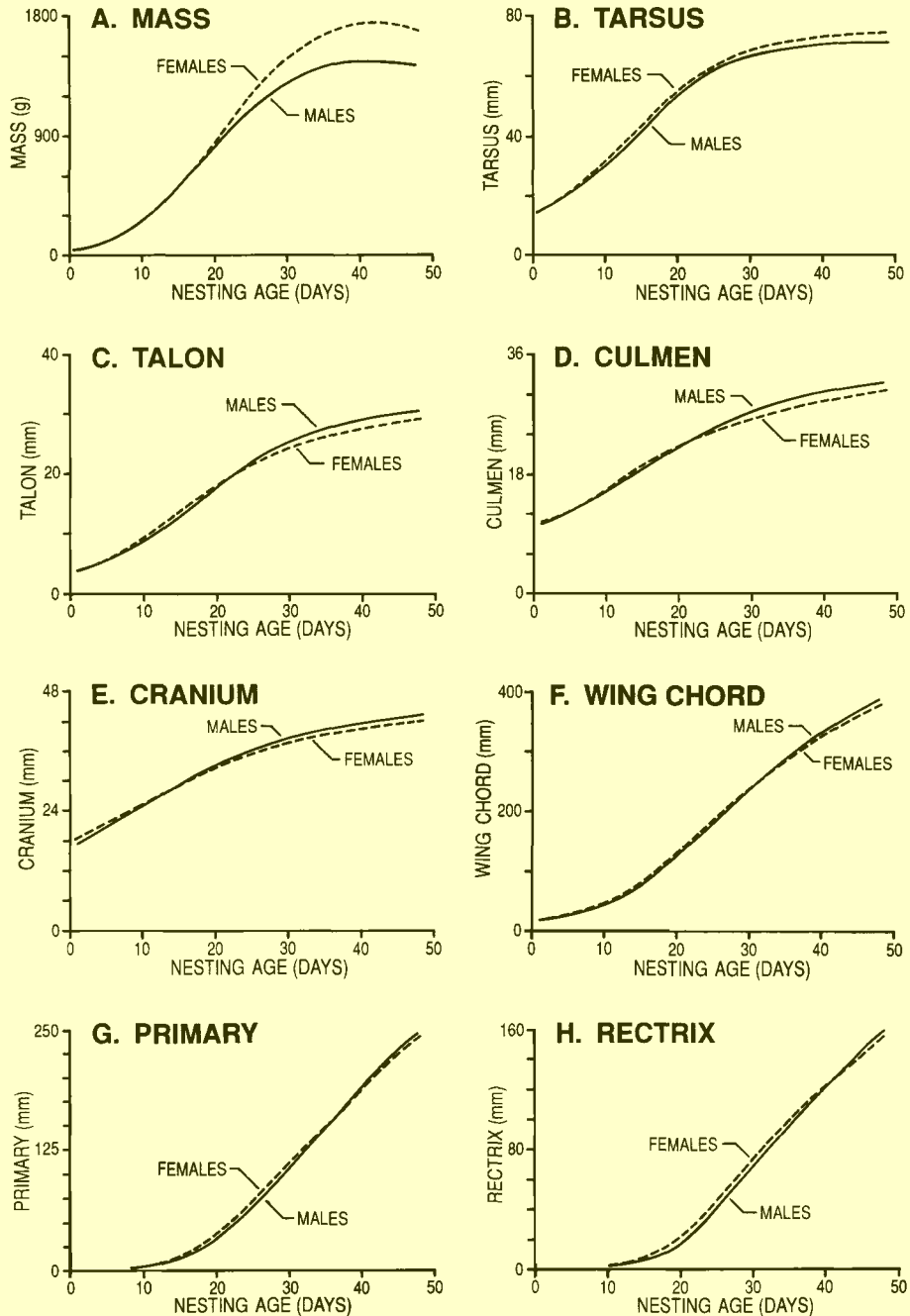


Fig. 1. Mean curves at four-day intervals of female (dashed line, $n = 12$) and male ($n = 20$) nestling Ospreys plotted against day at which growth occurred. Each chick measured on average 26 times (two-day intervals) throughout the eight-week nestling period, providing approximately 6,656 measurements to distinguish points of divergence for all variables in which they occurred. Variables were: (A) mass, (B) tarsus length, (C) talon, (D) culmen, (E) cranium, (F) wing chord, (G) eighth-primary length, and (H) central rectrix.

(48.8 ± 2.3 g) was 70.8% of the mass of the average fertile egg (68.9 ± 0.9 g) near the time of laying, comparable to the 76% reported by Bortolotti (1984) for Bald Eagles (*Haliaeetus leucocephalus*).

The masses of males and females increased at similar rates, but diverged near the point of inflection. Sexes differed in asymptote and had absolute growth rates at inflection ($dW/dt = KAW [1 - W]$, where W is 0.5 for the logistic equation; Ricklefs 1968) of 67.5 g/day for males and 80.5 g/day for females. Average daily growth rates for variables fitted with the Richards equation for male and female nestlings again showed significant differences for mass asymptotes, but no differences in curve shape (Fig. 2A).

The length of the tarsus increased at similar rates for both sexes well beyond the inflection point and differed only in asymptote at fledging (Figs. 1B and 2B). Talon length was the only variable to show significant difference at inflection. Again, the curves showed very similar growth well past the inflection point (Fig. 1C). No parameters of the Richards equation showed significant sexual differences for talon length.

The culmen was well developed at hatching and showed little of a sigmoid growth pattern posthatching (Fig. 1D). No differences were found for parameters of the Richards equation for culmen length. Cranium means did not exhibit a sigmoid shape posthatching (Fig. 1E). Like culmen, cranium growth constants differed between sexes. These data, however, must be viewed with caution because both structures are far from fully grown at fledging, and estimation of the asymptotic values required extrapolation from the growth equation. Furthermore, because cranium was well developed at hatching and convergence criteria for the Richards equation could not be met in all instances, mean curves for cranium width could not be generated.

Because male and female wing chords grew at similar rates until very near the end of the nestling period (Fig. 1F), this variable may prove to be the best criterion for aging nestling Ospreys. Wing chord was still increasing at fledging and asymptotes were estimated from the growth equation. There were no differences between sexes for any parameter of wing-chord growth using the Richards equation.

Feather growth was analyzed by comparing

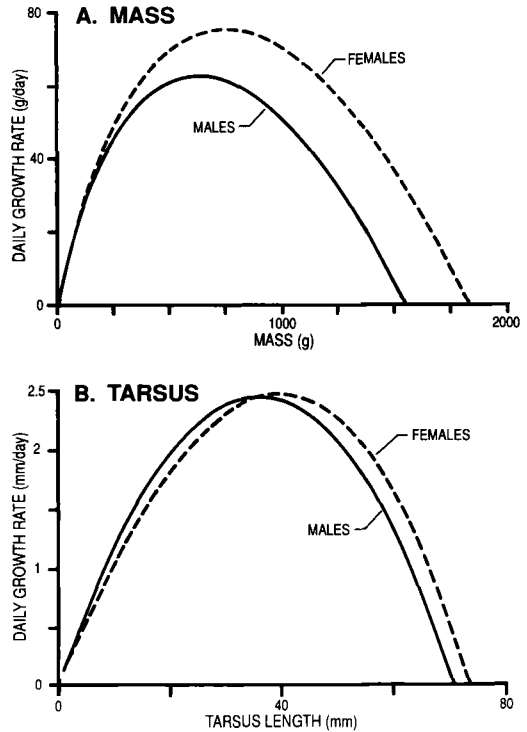


Fig. 2. Average daily growth rates for variables fitted with Richards equation for female (dashed line, $n = 12$) and male ($n = 20$) nestling Ospreys. Curves represent estimated average daily growth rates for (A) mass and (B) tarsus length.

regression lines during the linear period of growth beginning on day 20 (using methodology of Snedecor and Cochran 1978:432) because growth was too limited during the nestling period to generate growth curves. There was no significant difference ($P > 0.05$) between sexes or years in comparisons of slopes or evaluations (i.e. rate of growth) for eighth-primary or central-rectrix growth.

There were also no differences between sexes in the age at which the eighth primary first emerged from the skin (7.05 ± 0.19 days for males and 7.25 ± 0.25 days for females; Fig. 1G), or when the central rectrices began to emerge (9.25 ± 0.19 days for males and 9.50 ± 0.28 days for females; Fig. 1H). Furthermore, there were also no differences between the sexes in feather emergence among first-, second- and third-hatched nestlings (C1, C2 and C3, respectively; Wilcoxon signed-ranks matched-pairs test, $P > 0.05$). Thus, primaries and rectrices grew at sim-

ilar rates for both sexes during the nestling period, irrespective of hatching order, with no obvious divergence by time of last measurement.

Development at fledging.—The percent of nestling-to-adult values by sex (Table 4) provides an index of development at fledging. Mass and tarsus were the only variables to show well-defined asymptotes at fledging. Although talon length and cranium width were within adult range and culmen length was greater than 90% of adult values, no asymptote was obvious in the curves (Figs. 1C, 1D and 1E).

Wing chord, eighth-primary length, and central-rectrix length were 76, 71 and 75% of asymptotic size, respectively, at last measurement. Therefore, they probably were still growing at nest departure time.

Brood size and hatching order.—Analyses of brood size are complicated by loss of eggs during incubation and chick mortality during the nestling period. That is, should brood size be determined at egg laying, at hatching, midway through the nestling period or at fledging? Hence, tests were conducted on brood-size compositions at hatching and at fledging using Wilcoxon signed-ranks matched-pairs test.

First-, second- and third-hatched nestlings were compared within broods for fledging age and for mass parameters of growth. Comparisons were made for birds of same sex and for all birds in a brood regardless of sex. The tests revealed no significant difference for K or t_i ($P > 0.05$) between any of the pairs of C1, C2 and C3 nestlings, whether using compositions at hatching or at fledging. The consequence of failing to reject the null hypothesis (i.e. that growth is unaffected by hatching order) is that any bird within a brood is equally likely to have a positive or negative ranking regardless of sex.

There was also no difference in growth (mean K /brood) among broods of one, two or three nestlings. The growth rate (K) of broods of one averaged 0.1807 ± 0.0009 ($n = 6$), broods of two averaged 0.1798 ± 0.0017 ($n = 4$), and broods of three averaged 0.1808 ± 0.001 ($n = 6$).

Mean growth rate and relative growth.—Mean parameter estimates for growth curves of each sex obtained from a pooled sample of nestlings were generated for mass and tarsus length, and compared to means obtained from individual birds (Table 2). Values obtained from both methods were similar. The curve based on mean mass had values for K , A , and t_i equal to: 0.1789,

1,510 g, and 19.4 days for males; and 0.1793, 1,790 g, and 20.3 days for females, respectively. The curve based on mean tarsal length had values of: 0.1421, 71.6 mm, and 12.2 days for males; and 0.1438, 74.3 mm, and 12.4 days for females.

Because curves fitted to means of the observed data did not differ from the mean model parameters based on curves fitted to individuals, they were used to compare relative growth of mass and tarsus (variables that were significantly different by sex at asymptote). Mean mass and tarsus-length curves of male and female nestlings also were similar when compared using the growth index t_{10-50} (Ricklefs 1967), which represents the time required to grow from 10 to 50% of the asymptote.

Similar growth-rate constants (K) for mass between sexes were reflected in the time it takes to grow from 10 to 90% (t_{10-90}) of asymptotic mass (24.5 days for males and 24.4 days for females), even though females reached a significantly higher asymptote. Therefore, because the sexes hatched at equal mass, but attained asymptotic values 300 g apart in the same amount of time, females obviously accumulated tissue at a greater rate than males.

DISCUSSION

Growth rate.—In Ospreys, a curve shape for mass intermediate between the Gompertz ($m \rightarrow 1.0$) and logistic ($m = 2.0$) models was suggested by the mean Richards shape-parameter estimate m of 1.24 for birds of both sexes. Although more than one curve shape could fit a given data set in some individuals, the logistic model was appropriate in most cases for describing the growth of nestling Ospreys with a combined growth rate (K) of 0.180. The corresponding time of 24.4 days to grow from 10 to 90% of asymptote (t_{10-90}) represents about 45% of the overall nestling period.

A few data are available for comparison. Steidl and Griffin (1991) reported a similar K of 0.173 and a t_{10-90} of 26 days in a population of Ospreys in southern New Jersey. Stinson (1977), however, reported a considerably lower K of 0.120 and a t_{10-90} of 36.9 days for Chesapeake Bay Ospreys. Because he was not certain of the individual ages of chicks, Stinson calculated growth rates by correlating the average age of a brood (some of which were artificially increased) with the average mass of chicks in the brood measured on a weekly basis, with final measure-

ments of mass taken within one week of fledging. In a later study of the same population, McLean and Byrd (1991) calculated asymptotic values of broods of one, two and three nestlings and reported a similar K of 0.130 with a corresponding t_{10-90} of 37.2 days. We believe that the above methodologies of Stinson (1977) and McLean and Byrd (1991), in conjunction with sexual differences in asymptote, could underestimate Osprey growth rates by overestimating asymptotes. Therefore, the differences noted between these populations may not necessarily reflect geographic variation in growth rates.

Stinson (1977) reported the growth rate of Ospreys at the lower end of growth rates (0.078–0.257) of five falconiform species presented by Ricklefs (1968), with a t_{10-90} greater than all other raptors examined except for Golden Eagles (*Aquila chrysaetos*). Our study places the Osprey intermediate in this group, with a growth rate similar to that of a Red-tailed Hawk (*Buteo jaamaicensis*).

Comparing observed and predicted asymptotes, the logistic model produced higher estimates than the Richards model for all variables except female mass (Tables 2 and 3), even when characteristics were measured through the asymptotic period. The greatest disparity between the models was in wing-chord length, which achieved about 75% of adult size at last measurement. Logistic estimates were closer to recorded adult values than were Richards-model estimates, suggesting that the Richards model may have underestimated asymptotes, especially when the observed data did not include values leading up to and including the asymptote. Ricklefs et al. (1986) found that when the asymptote is not recorded, nonlinear curve-fitting techniques may overestimate the asymptote of growth curves and, as a result, underestimate the growth-rate constant because they are inversely related.

If the major determinant of growth rate in birds is that of body mass, Ospreys grow relatively fast. Using asymptotes of 1,500 g for males and 1,800 g for females, Ricklefs' (1968) model for temperate-zone passerines and raptors, which shows that growth rate is inversely related to body size by the equation

$$t_{10-90} = 3.98A^{0.278}, \quad (3)$$

predicts a rate of 30.6 days for males and 31.6 days for females, whereas the rates we obtained were 24.5 and 24.4 days, respectively. The re-

lationship between growth rate and nestling period (nestling period \times 0.57) predicts a nearly similar rate of 30.7 days for males and 31.0 days for females, again much slower than the observed values. Ospreys also grew much faster than predicted by Ricklefs' (1968) allometric equation for growth rate

$$K = 1.11A^{-0.278}, \quad (4)$$

which predicted values of 0.138 for males and 0.145 for females. The rate we calculated was 0.180.

Ricklefs (1968) found growth rate to be inversely related to body size interspecifically. However, this was not the case intraspecifically. In Ospreys, growth rate and inflection point apparently were unrelated to the large sexual differences in asymptote. Bortolotti (1984) reported a similar effect in Bald Eagle nestlings, and Ross (1980) noted that most studies of passerines failed to show distinct intraspecific relationships between growth rate and asymptote. O'Connor (1984) suggested that, intraspecifically, growth rate and asymptote are independent parameters of variation in growth that can be separately adjusted to ecological pressures.

Growth rates of morphometric characters for the logistic model were similar between sexes for all variables except culmen length and cranial width, both of which were well developed at hatching and showed little sigmoidal growth posthatching. Overall, the growth rate for mass was most rapid, followed by that for tarsal length, which in turn grew faster than did the talon, wing chord, cranium, and culmen. Growth was slowest in characteristics that were well developed at hatching, which provides support for Ricklefs' (1973) hypothesis that overall growth is a compromise between cellular growth and acquisition of mature function (i.e. mature tissues grow more slowly than those with less-developed function). This is concordant with O'Connor's (1977) suggestion that selection acts on a species' pattern of development such that the most important components develop earliest, possibly at the expense of overall growth rate. In our study, parts of the body that function early in feeding (i.e. culmen and cranium) were well developed at hatching.

Brood size.—No differences were found in growth rates among broods of one, two or three nestlings, or with respect to hatching order of birds within a brood. Klomp (1970) found ev-

idence both for and against a predicted negative effect of brood size on nestling growth. Ricklefs (1973), who argued that growth rates in birds are not adjusted to brood size, is supported by several studies (King and Hubbard 1981, Richter 1983, Ritter 1984, Moreno 1987), while others reported an effect of brood size on growth parameters (Ross 1980, Zach 1982, Zach and Mayoh 1982). Evidence of differential growth within broods of species hatching asynchronously often suggests that sibling competition inhibits the growth of the younger nestling, although it is difficult to separate the effects of genetics and environment from growth performance.

Among the hypotheses that have attempted to account for hatching asynchrony and brood reduction, Lack (1968) suggested that a "runt" system operates in birds of prey so that in times of food shortage the youngest and, therefore, weakest chick dies. An alternative to Lack's (1968) hypothesis is that later-hatched chicks are insurance against the loss of older siblings, which may have developed in response to accidental factors rather than in response to food supply (Hahn 1981; for a thorough review of hatching asynchrony and alternative explanations, see Magrath 1990).

Poole (1982) found food supply to be the major evolutionary factor selecting for brood size in Ospreys, which supports the food-shortage hypothesis. Additionally, Poole (1982) found third-chick survival to be common and loss of older chicks negligible in colonies with abundant food. Nestling mortality followed similar patterns here, suggesting food was readily available to birds in this colony, which is located in traditionally good habitat in terms of food supply (Prevost et al. 1978).

Sex-specific growth.—Several studies of growth of raptors (Newton 1978, 1979, Moss 1979, Bor-tolotti 1984) and passerines (for review, see Richter 1983) have shown sexual differences in growth dynamics where the smaller sex shows lower variability with relatively faster attainment of asymptote, earlier maturation of plumage, and earlier fledging age regardless of which sex is smallest. In Ospreys, the lack of significant differences in either growth rate (K) or growth-curve shape (m) between the sexes (Tables 2 and 3) suggests that males and females grew at similar rates. Although females added more body mass per day and had a significantly different asymptote of tarsal length than males, the sexes showed identical inflection points in

growth curves. When size difference was accounted for (i.e. relative growth), males and females showed very similar growth patterns. Males, however, showed a greater variability in growth than their larger sisters (Table 2). Bor-tolotti (1986) also found that growth in male Bald Eagle nestlings (the smaller sex) was more variable than in females.

Feather growth in Ospreys was found to be the least sexually dimorphic variable in growth performance (Figs. 1G and 1H). However, as Richter (1983) pointed out, because feather length was equal in size and growth rate between the sexes throughout most of the nestling period, and because males were smaller in other measured dimensions, their feathers were proportionally longer than those of females. Thus, males had relatively greater feather lengths than females for their size, at least during the second half of the nestling period. Males and females, however, did not differ in feather emergence times (which occurred on average on day 7 for the eighth primary and on day 9 for the central rectrix) or in fledging times.

Conclusions.—Our study did not support the prediction that males (the smaller sex) should develop feathers earlier and leave the nest sooner than females, nor did we find that females had more variability in growth. Appreciable size differences between the sexes did not develop in body and plumage components until growth had passed the inflection point of the growth curve, when food consumption was at its peak. Furthermore, Ospreys within a brood, separated by two-day intervals on average, were never observed to change rank (in terms of mass) in the nest until the end of the nestling period. Stinson (1977) reported weekly rank fluctuations within Osprey in two of six nests, but his data indicated this had occurred only after 90% (six weeks) of growth had been achieved, and sex and crop content was not even considered.

Competition for food was not based on sexual differences, but on hatching asynchrony (Schaadt 1989, but see Anderson et al. 1993). First-hatched chicks, regardless of sex, were usually fed first by locating themselves in the most advantageous position relative to the adult female unless they were satiated and not actively soliciting food. When nestlings did compete for food, first-hatched chicks being larger were dominant and forced later hatched siblings into subordinate feeding positions. Since food was generally abundant, however, there was no obvious advantage to being fed first.

Similar patterns were observed in all broods regardless of sex composition, suggesting that hatching asynchrony, if anything, had the greater potential to impose feeding disadvantages on later-hatched birds than did sexual size dimorphism.

Although our primary purpose was to describe sexual variation in growth and not speculate on its cause, the evidence reported here is not as clear as one would expect if sex-specific growth dynamics were the primary result of sexual size dimorphism and sibling competition. There was not evidence of sex-specific growth dynamics selecting for rapid growth in males to compete with the larger females for available food resources at the nest. The idea that male Ospreys are at a competitive disadvantage and should grow faster than females obviously needs to be examined in light of the much greater differences imposed by hatching asynchrony. Slagsvold (1990) argued that, in sexually dimorphic species, hatching asynchrony may have evolved specifically to prevent the larger sex from outcompeting the smaller to ensure equal expenditures on male and female offspring. Hence, in the Osprey, sexual size dimorphism appears to be independent of sibling competition.

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