Intraspecific Comparisons of Sexual and Geographic Variation in the Growth of Migratory and Sedentary Ospreys

by

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Throughout the 4 year course of this study my wife Debby has been my constant companion (and unpaid field assistant).

To her I dedicate this thesis.

THESIS ABSTRACT

Sex-specific growth analyses were conducted for 32 nestling ospreys (*Pandion haliaetus*) in a migratory population in Nova Scotia, Canada and for 31 nestling ospreys in a sedentary population in Sonora, Mexico. Eight variables including weight, body components and plumage characteristics were measured to document the influence of sex on growth performance. Within populations, males differed significantly from females in having lower weight and body component asymptotes but did not differ in plumage characteristics or growth rates. There was no difference in growth performance between individuals in broods of various sizes or within broods as a result of hatching order asynchrony. Comparisons of geographic variation showed that sedentary ospreys in Mexico had significantly higher weight and tarsus asymptotes, reduced growth rates, longer nestling periods and later emergence of flight feathers than migratory ospreys. Individual nestlings were initially identified by sex from karyotypic analysis of fibroblast tissue collected from a sample of 31 nestlings in the field. The karyotype is presented and growth performance is discussed within the framework of evolutionary theory.

RESUME

Une analyse de croissance en function du sexe a été conduite sur 32 nichées d'aigles pêcheurs (*Pandion haliaetus*) dans une population migratoire de Nouvelle Ecosse au Canada, et sur 31 nichées d'aigles pêcheurs dans une population résidente de Sonora, Mexique. Huit variables, incluant le poids, les composantes corporelles et les caractéristiques du plumage ont été mesurés pour documenter l'influence du sexe sur le taux de croissance. A l'intérieur de chaque population, les mâles se sont distingués des femelles en démontrant un poids inférieur et des composantes physiques asymptotiques mais n'ont pas montré de différences dans la qualité du plumage et dans le taux de croissance. Le taux de croissance n'a pas différé pour les individus d'une même portée, et ni d'une portée à l'autre en raison de l'éclosion asynchronisée. En tenant compte des variations géographiques, l'étude a démontré que les aigles pêcheurs résidents avaient un poids de beaucoup supérieur, des tarses asymptotiques, un taux de croissance réduit, une péreode passée au nid prolongée et une émergence tardive des plumes de vole comparativement aux aigles pêcheurs migratoires. Les niches individuelles ont été initialement identifiées en fonction du sexe par une analyse karyotypic de tissue fibroblast d'un échantillon de 30 nichées. Le karyotype ainsi que le taux de croissance sont discutés par rapport à la structure de la théorie de l'évolution.

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For growth is an increase... of the magnitude which is there already---that, indeed, is why the growing thing must possess some magnitude.

ARISTOTLE

PREFACE

Growth

During the past 2,000 years Aristotle's three axioms of growth *a) that every part of the growing magnitude is greater (for example, if flesh grows, every part of it grows); b) that it grows by the accession of something; c) that it grows because that which grows is preserved and persists,* (in Zeger and Harlow 1987) have caused philosophers and biologists alike to search for the fundamental truth or "law" underlying the force of growth. The search continued throughout the nineteenth century when mathematical tools for analyzing size and shape were developed making the quantitative study of growth a reality, thus with much debate, the role of mathematics in biology continues to grow well into the twentieth century. The context of mathematical growth models has changed however, from simply representing principles or "laws" of growth to being useful tools for addressing biological questions. It is not crucial that the function used be a "law" of growth; it need only be an adequate summary of the time course of size (Zeger and Harlow 1987). The result is not one or two isolated models but a box full of tools for summarizing growth data.

Avian growth

Avian growth and development, long a subject of concern to ornithology, was initially described simply by linking developmental processes in chronological order. It was soon recognized however, that growth patterns could be portrayed quantitatively and presented in terms of weight-versus-age curves which show a characteristic sigmoidal (or sshaped) form. In fact, many of the early growth equations which continue to influence current thought were initially developed to model the biological processes that underlie growth (Gompertz 1825, von Bertalanffy 1938, see also reviews by Pruitt et al. 1979 and Ricklefs 1983).

Modern treatment of ornithological growth analysis began with Ricklefs (1967) who presented a simplified method of making graphical fits to growth data in order to select the most appropriate of 3 commonly used fixed-growth-form models. This methodology, which has made a significant contribution to our understanding of interspecific variation in avian growth, evaluates fits to the von Bertalanffy, Gompertz and logistic growth models. These represent longer and more gradual approaches to asymptotic weight and have inflection points of about 30, 37 and 50 % of asymptote, respectively. The equations defining these growth models are as follows:

$$\text{Logistic model:} \quad Y = A/(1+e^{-K(x-t_i)})$$

$$\text{Gompertz Model:} \quad Y = Ae^{-e^{-K(x-t_i)}}$$

$$\text{von Bertalanffy Model:} \quad Y = A(1-1/3e^{-K(x-t_i)})^3$$

where *Y* equals the variable under study at age *x*, *K* represents a constant proportional to the overall growth rate, t_i represents the age at which the curve attains the point of inflection, *A* equals the asymptotic value of the growth curve, and *e* equals the base of natural logarithms. See Ricklefs (1967) for additional details of the models.

Growth models are a way of summarizing data, mathematical expressions which have the potential for bringing out relationships that are not obvious from the data alone. The above growth models are based on 3 growth parameters with associated biological meaning: 1) Asymptotic weight (A), an index of the maximal size that is attained by a growing individual which may or may not be achieved at fledging, dependent on species. 2) A growth-rate constant (K), which is proportional to the overall growth throughout the growth period. Ricklefs (1967) however, cautioned that K values are comparable only among species whose growth curves are fit by the same equation. He presented a formula to calculate a time interval for growth from 10 to 90% of asymptote. This interval is useful for making comparisons between species whose growth curves are fitted by different equations since the form of the 3 growth curves are reasonably similar during this period. 3) The point of inflection (t_i) is the age at which the organism's growth curve changes from convex to concave and represents the period of maximal rate of growth.

Recently, attempts have been made to incorporate a flexible growth curve developed by Richards (1959) as an alternative in avian growth analysis when the shape of the curve is unknown (Brisbin et al. 1986). The Richards equation may be considered a "parent" curve which, by varying the value of a shape parameter (m), can generate most of the commonly used sigmoid models. When $m = 0.67$ or 2.0, the Richards model is identical to the von Bertalanffy and logistic models, respectively, and as m approaches 1.0 the Richards model approaches the Gompertz model. Brisbin et al. (1987) considered the reparameterized version of this curve (White and Brisbin 1980, Brisbin et al. 1986), described in Chapter I, to be a new growth paradigm with a potential for detailed quantitative comparisons of growth in general and intraspecific comparisons of growth in particular. Gochfeld (1987) supported this view and noted that the shape of the curve has rarely been addressed in avian growth performance and in fact, deviations have generally been treated as noise rather than useful information. For an alternative view, see Zach (1988) who purported that growth-curve analysis is inappropriate for many studies and suggested that alternatives such as simple observed growth statistics may be more effective growth indicators.

Avian growth and development have been investigated for a wide variety of species (extensively reviewed by Lack 1968, Ricklefs 1968, 1973, 1983, Case 1978, O'Connor 1978, Drent and Daan 1980), but for few species of birds of prey. Very little data are available on the growth of young ospreys (*Pandion halieatus*). Those that are published are limited principally to gain in weight (Stinson 1977, Poole 1982) and there are no previously published reports of sexual growth variation in osprey. Thus, the data presented here are to facilitate studies on interspecific variation in the growth of raptorial species in general and intraspecific variation in the growth of ospreys in particular.

The purpose of this study was threefold: 1) to develop a method of sexually identifying osprey nestlings; 2) to examine the growth performance of sexually dimorphic osprey within an evolutionary context; and 3) to compare geographical variation in growth dynamics of a migratory population of ospreys in temperate Nova Scotia, Canada with those of a sedentary desert population in Sonora, Mexico.

Osprey natural history

The osprey is unique, the sole member of the family Pandionidae. This monotypic designation is merited by the species' morphological adaptations which show an evolution through a long course of specialization (Brown and Amadon 1968). One of the most widely distributed birds in the world, the osprey's range is nearly cosmopolitan. It is rarer in the southern hemisphere and does not breed there regularly except in Australia and adjacent islands (VanTyne and Berger 1976). Brown and Amadon (1968) described 5 geographical races (subspecies) which vary slightly in plumage and measurement. Prévost (1983) recognized only 4 subspecies corresponding to the Palearctic, North American, Bahamas and Australasia which he further divided into 2 groups: a Holarctic group consisting of Palearctic, North American and Bahamian ospreys, and the Australian ospreys.

In North America, the annual spring migration of ospreys from their wintering grounds in Mexico and South America begins in February with the birds arriving in the northern part of the continent during March and April (Bent 1937). In Nova Scotia, nest construction and repair begin in mid-April when the birds arrive, and copulations occur generally at the nest site. Egg laying begins at the end of April or early May and sometimes continues into June with a modal clutch size of 3. The female performs the majority of incubation duties, only occasionally relieved by the male. The incubation period ranges from 36 to 40 days. Hatching begins in mid-June and continues into July. The young begin flying in early August after a nestling period of 51 to 61 days. Some nests are already abandoned by mid-August and most birds have left the study area by early September to begin migration. In contrast, ospreys in Mexico (described in detail in Chapter II) are non-migratory and characterized by a highly asynchronous breeding period (pers. obs.).

Generally, ospreys are large, long-lived, fish-eating birds that feed primarily inshore and are the only hawks which dive completely into the water while hunting. They become sexually mature at 3-4 years of age and occur over most of the breeding range as single pairs returning with great fidelity to the same nest site year after year. In favored areas they nest in loose colonies near large bodies of water and along seacoasts and rivers. Finally, adult ospreys display very definite reversed sexual dimorphism with females in this study being approximately 300g heavier than males.

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THESIS STATEMENT

This thesis, as permitted by the Faculty of Graduate Studies and Research, includes the texts of three manuscripts to be subsequently submitted for publication. Chapter I describes sexual variations in growth patterns of nestling osprey within the framework of sex-ratio theory. Chapter II investigates geographical variation in growth rates and asymptotic size from sedentary and migratory populations which produce large differences in selective pressures on osprey reproductive adaptations. Chapter III presents a chromosome analysis of fibroblast cells obtained from skin tissue in the field which provided the basis for assigning gender to individual nestlings. Included are techniques used to identify sex chromosomes, the reliability and efficiency of the technique, and a discussion of karyological relationships within the Falconiformes.

Data collection, data analysis and manuscript preparation were conducted independently by the senior author. Manuscripts from Chapters I and II will be submitted for publication with my supervisor D. M. Bird as co-author. Regarding chromosome analysis in Chapter III, tissue samples were collected in the field and shipped to the Montreal Children's Hospital's cytogenetics lab where they were cultured and frozen for later analysis. Slide preparations and chromosome identification were subsequently accomplished with the assistance of Deborah Kohler who will co-author the paper on karyotypes.

REGULATION ON THESIS PRESENTATION

The following is presented in accordance with the regulations of the McGill University Faculty of Graduate Studies:

"The candidate has the option, subject to the approval of the Department, of including as part of the thesis the text, or duplicated published text (see below), of an original paper, or papers. In this case the thesis must still conform to all other requirements explained in Guidelines Concerning Thesis Preparation. Additional material (procedural and design data as well as description of equipment must be provided in sufficient detail (e.g. in appendices) to allow a clear and precise judgement to made of the importance and originality of the research reported. The thesis should be more than a mere collection of manuscripts published or to be published. It must include a general abstract, a full introduction and literature review and a final overall conclusion. Connecting texts which provide logical bridges between different manuscripts are usually desirable in the interests of cohesion.

It is acceptable for theses to include as chapters authentic copies of papers already published, provided these are duplicated clearly on regulation thesis stationery and bound as an integral part of the thesis. Photographs or other materials which do not duplicate well must be included in their original form. In such instances, connecting texts are mandatory and supplementary explanatory material is almost always necessary.

The inclusion of manuscripts co-authored by the candidate and others is acceptable but the candidate is required to make an explicit statement on who contributed to such work and to what extent, and supervisors must attest to the accuracy of the claims, e. g. before the Oral Committee. Since the task of the Examiners is made more difficult in these cases, it is in the candidate's interest to make the responsibilities of authors perfectly clear. Candidates following this option must inform the Department before it submits the thesis for review.

CHAPTER I. Sex-specific growth dynamics of nestling ospreys.

ABSTRACT

Sex-specific growth analyses were conducted for 32 nestling ospreys (*Pandion haliaetus*), 20 males and 12 females, in 17 broods in Nova Scotia, Canada during 1984-1986. The graphical methods of Ricklefs (1967, Ecology 48:978-983) showed the logistic model to be most appropriate for mass increase with a growth rate constant K of 0.18 days^{-1}. The influence of sex on growth performance was also documented using a reparameterized Richards model (Brisbin et al. 1986, Growth 50:1-11). Weight 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 weight and tarsus length but did not differ in rate of growth. There was no difference in growth rates between individuals in broods of various sizes or within broods as a result of hatching order asynchrony. Males and females showed no differences in feather emergence times or in fledging period. The eight variables presented within the framework of evolutionary theory suggest that, in ospreys, sex-specific growth patterns do not select for rapid growth in males in order to compete with larger females for nest resources.

INTRODUCTION

Sex ratio theory is based on the assumption that natural selection should favour parents who invest equally in male and female offspring resulting in a population sex ratio of unity (50:50) (Fisher 1930). It further assumes that if the sex ratio deviates from unity, natural selection should restore it by favouring genotypes which produce more of the rarer sex. However, if one sex costs less to raise, then an excess of that sex should be expected at the end of the parental care period. Such deviations from unity are suggested by sexual dimorphism among offspring in the expenditure they require of their parents, which should skew the sex ratio in favour of the cheaper sex, and by differential mortality (Fisher 1930, Leigh 1970, Maynard-Smith 1978). The mechanisms involved in the maintenance of equal sex ratios have been mathematically described by many authors (MacArthur 1965, Verner 1965, Leigh 1970, Fiala 1981).

Since theory argues that the ratio of expenditures on each sex should equal the inverse ratio of male and female progeny produced at the end of the parental care period, it becomes important to define the exact nature of expenditures. Although Trivers (1972) defined parental investment (PI) as "any investment by the parent in an individual offspring that increases the offspring's chance of surviving (and hence reproductive success) at the cost of the parents' ability to invest in other offspring", quantifying the "currencies" of PI continues to present problems of practical application. Knapton (1984) complained that investments by parents in terms of time, energy and risk factors can be of different units and therefore not additive. Unfortunately, the exact nature of expenditure continues to be ill-defined and hence, difficult to test in the field.

To test Fisher's theory therefore, workers have turned to investigating sexually dimorphic species where sex ratios other than 1:1 can be predicted. However, to date very little evidence of sex ratio deviation has been discovered in either raptorial or passerine species in studies with sufficient sample size (reviewed by Newton 1979 and Clutton-Brock 1986). One especially well documented case of European sparrowhawks (*Accipiter nisus*), for example, 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.

This lack of consonance with predictions from theory implies that either: 1) selection has been ineffective in altering the sex ratio of birds; 2) cost differences are substantially less than size differences; or, as several authors have recently suggested, 3) sexually dimorphic growth patterns exist which equalize energetic expenditures on dimorphic offspring and maintain the sex ratio at unity during the nestling period (reviewed by Newton 1979 and Richter 1983).

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

This paper presents the results of a 3 year investigation of sex-specific growth and asymptotic size of nestling ospreys. Of particular interest was the fitting of growth models to individual birds to document the influence of sex on growth performance. The objectives were: 1) to document the growth characteristics of weight, plumage and body size of male and female nestling; 2) to assess the effects of hatch order and brood size on individual growth rates and 3) to relate the patterns of sex-specific growth observed in ospreys to evolutionary theory.

METHODS

Study area

The growth of 32 nestling osprey from 19 nests was measured during the summers of 1984, 1985 and 1986 in Antigonish County (45°31'N, 62°57'W) in northeastern Nova Scotia. The watersheds of Antigonish and Pomquet estuaries which empty into the Gulf of St. Lawrence are characterized by broadleafed and mixed forests in the highlands while conifers dominate poorly drained areas and valley slopes. Ospreys nesting here use 2 types of habitat. The majority forage in the estuaries, nesting in loose colonies on utility poles along power lines, while the remainder are solitary and found inland near lakes and rivers and utilize natural nest sites. Some nests on the power lines have been recently relocated to platforms erected adjacent to transmission poles within the power line right-of-way (Bancroft and Toner 1986), thus providing access to nestlings. All nests used in this study were located on platforms near Antigonish and Pomquet estuaries. Additional information on the study area and aspects of the population are provided elsewhere by Prévost et al. (1978) and Jamieson et al. (1982).

Field methods

Behavioural observations were conducted to document interactions between siblings and between parents and offspring. A raptor actigram using an alphanumeric notation system adapted from Walter (1983) was employed to enhance the efficiency of recording and analyzing behavioural data. Observations were conducted on all nests during all daylight hours divided into four 3.5 hour periods; 0630-1000, 1000-1330, 1330-1700, and 1700-2330, and advanced by nest on a daily basis. Observations were made from blinds erected at vantage points 50-100 m from nests using 20-60x telescopes and 10x binoculars. Priority was given to recording and identifying prey deliveries to the nest and subsequent distribution of food among the young. I counted the number of pieces given to each nestling and the order (hierarchy) in which they were fed. Observations on parental and nestling behaviour were also recorded and will be published in a subsequent paper.

Nests were climbed at 24 to 72 hour intervals to document egg laying, egg measurement, clutch size, hatch interval, hatch order and nestling growth and survival. Prior to incubation, nests were entered to measure and mark eggs and thereafter, visited rarely to avoid unnecessary disturbances during the incubation period. Upon hatching (day = 1), 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 weighed to the nearest gram with pesola spring scales and measured with dial calipers to the nearest 0.1 mm for: *tarsal length*, the distance from the heel to the joint between the distal end of the tarso-metatarsus and the third toe; *talon length* (or hallux claw), the distance between the point where the upper surface of the claw emerges from the skin to the end of the claw as measured across its arc; *cranium*, distance between the outer edges of the supra-orbital processes on each side of the head; *culmen*, from the cere to the tip of the bill as measured across the arc (mostly from Olendorff 1972) and unflattened *wingchord*. To measure the *eighth primary* and the *central rectrix* as they emerged, I inserted a clear plastic ruler between the feathers up to the skin and held the feather flat against the rule. The downy tuft at the end of the feather was not included in the measurement.

All measurements were performed by the same individual and consistently from the left side of the body. They were conducted every two days unless prevented by inclement weather, since nest disturbance appeared to be minimal. Early on, measurements were taken in the nest to stay within a self-imposed time limit of 15 minutes, but after 7 to 10 days of growth the birds were lowered and measured on the ground. To prevent premature fledging, measurement of nestlings ended when the oldest in the brood reached 50 days of age. Measurements of the same variable were repeated several times over to assess the variance associated with our technique. The final result was a set of growth data on 8 variables for each individual bird from hatching to fledging.

Growth curve analysis

Daily variations in food intake, activity or defecation should not significantly alter the characteristics of the growth curve calculated over the entire growth period for most species. In large raptorial birds like ospreys however, full or partially full crops lead to extreme variation in mass, particularly in nestlings approaching asymptote. I therefore evaluated crop content on a 1 (empty) to 4 (full) scale prior to each weighing. Occasionally during the course of the study, birds were weighed with full (or partially full) crops bracketted by days with empty crops, enabling me to evaluate crop content as a percent of body weight over all portions of the growth period. Net body weights for growth curve analysis were subsequently arrived at by subtracting crop content, as a percent of body weight, from gross weight on any given day. I consistently found nestlings near asymptote, i.e. over 6 weeks of age, to have in excess of 200 g of fish in full crops.

Growth data from individual birds were fitted to log transformations of the logistic and Gompertz equations according to Ricklefs (1967). When fitting curves to weight and tarsus length data, points up to and including the observed asymptote were used (Ricklefs 1968). Asymptotes for the remaining variables were estimated from least squares regression fits to data.

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

In some instances, the log transformations of the logistic and Gompertz models showed little difference, suggesting that more than one model may fit a given set of data. When this occurred the logistic model was selected since parameters can be compared only when fitted to the same equation.

The logistic equation may be expressed as:

$$Y = A/(1+e^{-K(x-t_i)})$$

where, Y is the value of the growth variable being studied (g or mm) at time x, K represents a constant proportional to the overall growth rate (days^{-1}), t_i represents the age at which the curve attains the point of inflection (days), A equals the asymptotic value of the growth curve (g or mm), and e equals the base of natural logarithms.

Growth data for individual birds were also fitted to a reparameterized version of the Richards equation (Richards 1959) using the Additive Discrete Derivative method of White and Brisbin (1980) to more throughly assess intraspecific comparisons. The equation was recently rewritten by Brisbin et al. (1986) to eliminate n, a scaling factor, which is highly correlated with the other parameters and causes computer algorithms to arrive at least squares estimates inefficiently.

The present study used the following reparameterized form of the Richards growth equation:

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

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.

The NLIN procedure of SAS, version 82.4 (SAS 1982), a non-linear regression routine employing the Secant Method (DUD) of calculation, was used to fit the curve to the data set. Parameter estimates obtained from the Ricklefs (1967) method were used as initial starting values for each growth variable and allowed to proceed until convergence on a minimum value was achieved. Estimates thus obtained gave rapid convergence to a minimum error mean square.

Data for non-linear regression analysis were derived only from nestlings that survived to fledge and, as above, regressions for weight and tarsus did not include values from the recession period of the curve. Since no recession was observed in the other variables, all data were included in the regression analyses, i.e. maximal values were achieved on the last day of measurement.

Identification of sex

The sex of individual nestlings was initially determined on the basis of 2 distinct weight classes which appeared by fledging. The accuracy of these determinations were 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 in the field (see Ch. III). To do this, data from birds of unknown sex were entered into the discriminant function analysis and classified by comparison with the remaining birds all of known sex. For both groups a significant discriminant function was obtained ($P < 0.001$), based on the pooled covariance matrix, which enabled me to sex 100% of the unknowns on the basis of weight and tarsus asymptotes alone.

Other statistical tests are mentioned in the text where they are employed and were performed on an IBM XT personal computer using Statgraphics (Version 1.1, 1985, Statistical Graphics Corporation, Inc). and, unless otherwise noted, all means are quoted with standard errors (S.E.).

RESULTS

Reproduction data

Ospreys generally lay and hatch 3 eggs asynchronously within a 7 day period with incubation times ranging from 33-38 days (Godfrey 1966). In this study egg laying occurred between 30 April and 20 May and was highly synchronous between years. Eggs hatched between 6-26 June producing incubation times ranging from 36-40 days ($\overline{X} = 37.5 \pm 0.2$ days).

Clutch size ranged from 2-4 with eggs 1-2 and 2-3 having intervals of 1-3 days ($\overline{X} = 1.9 \pm 0.1$ days and $\overline{X} = 2.1 \pm 0.1$ days, respectively) while eggs 3-4 had consistent 2 day intervals. Hatching periods of 2 egg clutches varied from 1-2 days ($\overline{X}$ = 1.8 ± 0.2 days), 3 egg clutches, 3-6 days ($\overline{X}$ = 4.2 ± 0.2 days), and 4 egg clutches, 5-6 days ($\overline{X}$ =5.5 ± 0.3 days). Overall hatching period for all clutch sizes combined averaged 3.2 ± 0.3 days.

Reproduction data including clutch size and survival rate of nestlings are summarized in Table 1. The reproduction data presented here are similar to those recorded for the same population in recent years by Prévost et al. (1978) and the production of 1.7 young per active nest is well above the rate of 0.95-1.30 young per active nest regarded by Henny and Wight (1969) as required to maintain a stable population.

Collectively, during the 3-year period, 2 nests failed to hatch any eggs, 1 nest was abandoned prior to egg laying due to intense logging activity, no nests fledged 4 young, and on 1 occasion 2 eggs hatched on the same day but the second bird was abnormal and died at 30 days.

Characteristics of nestling growth

The Richards and logistic models fitted to 6 morphometric characteristics and linear regression models fitted to 2 feather variables for the 32 individuals provided a total of 448 parameters for comparison. Table 2 summarizes growth parameters of K (day^{-1}), A (g or mm) and ti (days) for variables fitted to the logistic equation and tested for year, sex and their interaction by 2-way ANOVA adjusted for unequal sample size (Sokal and Rohlf 1981). Sizes were considered significantly different if the probability of a larger F value was less than 0.05. The test revealed significant sexual differences in growth rate only for cranium and culmen, in asymptote for weight and tarsus and in the inflection point of talon. There were no significant differences among years or interactions for any measure of growth.

Table 3 summarizes growth parameters of *W* (asymptote), *m* (curve shape) and *T* (overall growing time) fitted with the reparameterized Richards model also tested for year, sex and their interaction by 2-way ANOVA adjusted for unequal sample size. The test revealed no significant sexual differences in curve shape but, as above, significant differences in asymptote for weight 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 in New York. The following results are compared to mean adult values for each sex obtained from these sources (listed in Table 4).

The weight of day 1 nestlings averaged 49.0 ± 2.1 g for males and 48.6 ± 2.4 g for females. Mean values for adult males and females were 1485 ± 28.9 g and 1790 ± 29.6 g, respectively (Table 4). Thus, male nestlings hatched at 3.3% of adult male mean and female nestlings at 2.4% of adult female mean. These values may not necessarily reflect true hatch weights however, since it is possible that some neonates were fed prior to first weighing. The average weight of all day-1 nestlings combined (48.8 ± 2.3 g) was 70.8% of the weight of the average fertile egg (68.9 ± 0.9 g) near the time of laying. The relationship between egg weight and hatching weight is comparable to the 76% reported by

Bortolotti (1984) for bald eagles (*Haliaeetus leucocephalus*).

The curves in Figs. 1 through 8 represent means at 4-day intervals obtained from the total sample of nestlings that survived to fledge for all variables analyzed. Since each chick was measured on average 26 times (2 day intervals) throughout the 8-week nestling period the curves represent an approximate total of 6,656 measurements for the 32 individuals (12 females and 20 males) that survived to fledge. This provided quantitative data to distinguish points of divergence for all variables in which they occur. Standard errors for weight and tarsus lengths (the only variables to show distinct asymptotes) are included in Figs. 2 and 3. Figs. 4-8 are presented without standard error bars for clarity of presentation.

Fig. 1 shows that the weights of males and females increased at similar rates but diverged near the point of inflection The sexes showed significant differences in asymptote and had absolute growth rates at inflection ($dW/dt = KAW\ (1-W)$, where $W = 0.5$ for the logistic equation, Ricklefs 1968) of 67.5 g/day for males and 80.5 g/day for females.

The curves in Figs. 9 through 13 represent average daily growth rates for variables fitted with the Richards equation for male and female nestlings. In Fig. 9 males and females showed significant differences for asymptote again only in mass (Table 3) and body weight curve shapes were similar.

Tarsal length at hatch averaged 14.5 ± 1.6 mm for males and 14.9 ± 0.7 mm for females representing 20.4% of adult male length (71.0 ± 1.6 mm) and 20.5% of adult female length (72.6 ± 1.7 mm). The length of the tarsus increased at similar rates for both sexes well beyond the inflection point and showed significant differences only in asymptote at fledging (Fig. 2, Table 2). Males showed maximal daily rate gain at inflection of 2.5 mm/day and females 2.6 mm/day.

Talon length at hatch averaged 4.2 ± 0.4 mm, 14.3% of adult value (29.3 ± 0.3) for males and 3.9 ± 0.3 mm, 13.4% of adult value (29.8 ± 0.4) for females (Fig. 3, Table 4). Talon length was the only variable that showed a significant difference at inflection (Table 2). Maximum daily growth for talon at inflection was 0.86 mm/day for males and 0.88 mm/day for females. Again, the curves showed very similar growth well past the inflection point. No parameters of the Richards equation showed significant sexual differences for talon length (Fig. 11, Table 3).

Culmen length at hatch averaged 10.7 ± 1.0 mm for males, 33% of adult length (32.5 ± 0.3 mm), and 10.3 ± 0.4 mm, 30% of adult length (34.4 ± 0.4) for females (Fig. 4, Table 4). It is obvious from Fig. 4 that the culmen was well developed at hatch and showed little sigmoid growth pattern post-hatch. Males achieved a maximal daily value at inflection for culmen growth of 0.63 mm/day compared to 0.69 mm/day for females. No differences were found for parameters of the Richards equation for culmen length (Fig. 12, Table 3).

Cranium widths at hatch averaged 18.4 ± 0.8 mm for males and 17.3 ± 2.4 mm for females representing 43.6% of adult male length (42.2 ± 0.3 mm) and 40% of adult female length (43.2 ± 0.4 mm). Cranium means also showed very little sigmoid shape post-hatch. (Fig. 5). Like culmen, cranium growth constants were significantly different (Table 2), However, these data must be viewed with caution since both variables are far from fully grown at fledging and estimation of the asymptotic values required extrapolation from the growth equation. Furthermore, since cranium was well developed at hatch and convergence criteria for the Richards equation could not be met in all instances, mean curves for cranium width could not be generated.

Wingchord and feather growth

Wingchord length at hatch averaged 20.0 ± 1.7 mm for males and 19.7 ± 1.4 mm for females, representing 4% of adult male length (494.5 ± 2.6 mm) and 3.8% of adult female length (515.6 ± 1.9). Since male and female wingchords grew at similar rates until very near the end of the nestling period (Fig. 6) this variable may prove to be the best criterion for aging nestling ospreys (Schaadt, in prep.). Wingchord was still increasing at fledging and asymptotes were estimated from the growth equation. Maximum daily gains at inflection averaged 12.1 mm/day for males and 12.4 for females. Again there were no significant differences for any parameters of wingchord growth using the Richards equation (Fig. 13, Table 3).

Feather growth was analyzed by comparing regression lines during the linear period of growth, beginning on day 20, since growth was too limited during the nestling period to generate growth curves (using the methodology of Snedecor and Cochran 1978, p. 432). There was no significant difference ($P > 0.05$ in all cases) between sexes or years in comparisons of slopes or elevations, i.e. rate of growth, for eighth primary or central rectrice growth.

There were also no differences by sex in the age at which the eighth primary first emerged from the skin, i.e. 7.05 ± 0.19 days for males and 7.25 ± 0.25 days for females (Fig. 7) or, when the central rectrices began to emerge on day 9.25 ± 0.19 for males and day 9.50 ± 0.28 for females (Fig. 8). There were also no differences between first (C1), second (C2) and third (C3) hatched nestlings (Wilcoxon signed-ranks matched-pairs test). Thus, primaries and rectrices grew at similar rates for both sexes during the nestling period irrespective of hatch order with no divergence obvious by time of last measurement.

Development at fledging

The ratio of adult to nestling values by sex (Table 4) provides an index of development at fledging. Weight 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. 3,4 and 5).

Wingchord, eighth primary and central rectrix lengths were about 76, 71 and 75% of asymptotic size, respectively, at last measurement, and therefore, were probably incomplete at nest departure time. Although it is unknown when adult values were achieved, the difference obviously does not affect flight capabilities as no birds were found to have difficulty making initial flights from the nest. In fact, Schaadt and Rymon (1983) documented an osprey, fledged from a hack tower, fishing successfully on the second and third day after first flight.

Brood size and hatch 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 hatch, 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.

Comparisons of C1, C2 and C3 nestlings were made within broods for fledging age and for mass parameters of growth for same sex birds and for the same parameters with asymptote eliminated (which was found to be significantly different between the sexes, Table 2) for all birds in a brood regardless of sex.

The tests revealed no significant difference between C1, C2 or C3 nestlings whether using compositions at hatching or at fledging. The consequence of accepting 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. Unfortunately, sufficient data to test the influence of brood sequence on growth parameters at egg laying were not available.

There was also no difference in growth (mean *K*/brood) between broods of 1, 2 or 3 nestlings. The growth rate (*K*) of single broods averaged 0.1807 ± 0.0009 (n = 6), broods of 2 averaged 0.1798 ± 0.0017 (n = 4) and broods of 3 averaged 0.1808 ± 0.001 (n = 6).

Mean growth rate and relative growth

Mean growth curves for each sex obtained from a pooled sample of nestlings were generated for weight and tarsus length and compared to the means of parameters for weight and tarsus length obtained from individual birds (Table 3). The parameters obtained from both methods were similar. The curve based on mean weights had parameter values for *K*, *A* and *ti* equal to 0.1789, 1510 g and 19.4 days for males and 0.1793, 1790 g and 20.3 days for females, respectively. The mean tarsal curve 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.

Since curves fitted to the means of the observed data were equivalent to the mean model parameters based on curves fitted to individual nestlings, they were used to compare relative growth of weight and tarsus, which were significantly different by sex at asymptote. Figures 14 and 15 show similar average weight and tarsus length curves of male and female nestlings when compared using the growth index (Ricklefs 1967). This is expressed in terms of growth units to either side of half growth and represents the time required to grow from 10 to 50% (t_{10-50}) of the asymptote.

The similar growth rate constants (*K*) for mass were reflected in the time it takes to grow from 10 to 90% (t_{10-90}) of asymptote, i.e. 24.5 days for males and 24.4 days for females, even though females reached a significantly higher asymptote. Therefore, since both sexes hatched at equal weights (Fig. 1), but attained asymptotic values 300 g apart, females obviously accumulated tissue at a much greater rate than males.

DISCUSSION

Growth rate

In ospreys, a curve shape for mass intermediate between the Gompertz (m = 1.0) and logistic (m = 2.0) models was suggested by the mean Richards shape parameter estimate of 1.24 for birds of both sexes. Although it was evident that more than one curve shape could fit a given data set the logistic model was most appropriate in most cases for describing the growth rate 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 represents about 45% of the overall nestling period.

Few data are available for comparison. Stinson (1977) reported a logistic growth rate of 0.120 and 36.9 days as the average length of time required to grow from 10 to 90% of asymptote during a study of ospreys in Chesapeake Bay. However, since 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 weight of the chicks in the brood measured on a weekly basis with final weights all taken within one week of fledging. This methodology, in conjunction with sexual differences in asymptotes, probably led him to underestimate osprey growth rates. Therefore, the difference noted in the two studies may not actually reflect geographic variation in growth rates between these populations. Stinson reported the growth rate of ospreys to be at the lower end of the spectrum of growth rates (0.078 - 0.257) of 5 falconiform species presented by Ricklefs (1968) with the length of time to grow from 10 to 90% of asymptotic weight greater than all corresponding times except for the golden eagle (*Aquila chrysaetos*). The current study places the osprey intermediate in this group with growth rates similar to those of the red-tailed hawk (*Buteo jamaicensis*).

To date, there have been no quantitative comparisons of differential growth of morphometric characteristics between male and female ospreys. Poole (1982) compared growth of nestling ospreys in 3 colonies during a study of brood reduction by comparing regression lines on average weights, within 5-day age intervals, but only during the first half of the nestling period (up to 30-days) when growth increased nearly linearly. However, since he did not fit growth curves or consider sexual growth differences his results cannot be compared directly to this study.

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 wingchord length which achieved about 75 % of adult size at last measurement. Here, as elsewhere, logistic estimates were closer to recorded adult values than were Richards model estimates, suggesting that the Richards model may have underestimated asymptote especially when the observed data did not include values leading up to and including the asymptote. Ricklefs et al.(1986), found that when asymptote is not recorded, nonlinear curve-fitting techniques may overestimate the asymptote of growth curves, and as a result, underestimate the growth rate constant since they are inversely related.

If the major determinant of growth rate in birds is that of body weight, ospreys grow relatively fast for their size. Based on asymptotes of 1500 g for males and 1800 g for females, Ricklefs' (1968) model for temperate zone passerines and raptors, which show growth rate to be inversely related to body size by the equation $t_{10-90} = 3.98A^{0.278}$, predicts a rate of 30.6 days for males and 31.6 days for females, whereas the observed rate was 24.5 and 24.4 days, respectively. The relationship between growth rate and nestling period (nestling period x 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 ($K = 1.11A^{-0.278}$) which predicted values of 0.138 for males and 0.145 for females. The observed rate was 0.180.

Ricklefs (1968) found growth rate to be inversely related to body size interspecifically. However, it is obvious that such was not the case intraspecifically. In ospreys, growth rate and point of inflection was 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 also fail 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 which can be separately adjusted to ecological pressures.

The growth rates of morphometric characters for the logistic model were similar between the sexes for all variables except culmen length and cranial width, both of which were well developed at hatch and showed little sigmoidal growth post-hatch. Overall, the growth rate for mass was most rapid, followed by tarsal length, which in turn grew faster than talon, wingchord, cranium and culmen. Growth was slowest in characteristics that were well developed at hatch, supporting Ricklefs' (1973) hypothesis that overall growth is a compromise between cellular growth and acquisition of mature function, that is, 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 this study parts of the body that function early in feeding, i.e. the culmen and cranium, were well developed at hatch.

Among passerines the ratio of adult weight to fledging weight is related to foraging behaviour (Ricklefs 1968). Ground feeders typically have ratios of less than 0.9 while ratios greater than 1.0 are found in species that spend a large proportion of foraging time in flight and whose young are capable of feeding themselves upon fledging. Ospreys, whose secure nesting places allow them to accept the long nestling periods necessary for flight muscles to mature, spend most of their foraging time in flight and conform to the general pattern by attaining weight asymptote ratios greater than 1.0 (Table 4).

Brood size

No differences were found in growth rates between broods of 1, 2, or 3 nestlings or between the hatch order of birds within a brood. In reviewing the literature, Klomp (1970) found evidence both for and against a predicted negative effect of brood size on nestling growth.

Ricklefs (1973), who argued against the hypothesis that growth rates in birds are adjusted to brood size, is supported by several recent 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 asynchronously hatching species 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.

Closely related to brood size is hatching asynchrony and brood reduction. Lack (1968) suggested that a runt system operates in birds of prey such 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 having developed in response to accidental factors rather than in response to food supply (Hahn 1981). Poole (1982) found food supply to be the major evolutionary factor selecting for brood size in ospreys in support of 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 supply. Nestling mortality followed similar patterns in the current study; only 1 of 6 chicks that died in the nest prior to fledging was a first hatched chick and it came from a single chick nest. The suggestion that a runt system operates in ospreys such that earliest birds are at an advantage relative to their siblings was further demonstrated in a 4 egg nest where the third egg failed to hatch. It is suspected that as the C1 and

C2 nestlings passed 6 weeks of age the C4 nestling was just approaching 5 weeks of age and was not yet adept at self-feeding. When parent birds placed prey in the nest without distributing it to the young, C4, unable to compete with the older siblings, subsequently starved.

It might be expected that females achieved higher asymptotes by being fed greater amounts of food. Such was not the case. Detailed observations showed no sexual preferences during feeding bouts. 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. Older birds frequently became satiated during a given feeding session, allowing younger birds to feed to satiation as well. As the female was feeding she would place food in the bill of the nestling most available at the time. If C1 was busy swallowing for instance, C2 or C3 would receive the bite instead. Thus, even when C1 nestlings were not fed to satiation, all birds generally received some food. 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 differences. Newton (1978) also found no differences in food consumption in European sparrowhawks despite great size differences between the sexes, and Poole (1982) reported, when food was abundant in his study, all chicks in a nest grew and fledged at no disadvantage relative to nestmates. The "runt" individual (Lack 1968) therefore enables brood size to be increased without increasing competitive liabilities for the rest of the brood when food sources are unpredictable. The establishment of a feeding hierarchy among young as the result of hatching asynchrony such that the youngest bird in the clutch has the highest probability of dying when competing for limited resources has been widely reported (Meyburg 1974, Procter 1975, Yom-Tov and Ollason 1976, Clark and Wilson 1981, Poole 1982, Edwards and Collopy 1983, Bortolotti 1986).

Sex ratio

It is tempting to speculate that the sex-ratio of nestlings within a brood may compensate for any competitive advantage one sibling may have over another. Offspring sex varying with hatch sequence has been shown for several non-raptorial species (Fiala 1981, Ankney 1982, Weatherhead 1985) and for bald eagles (Bortolotti 1986). Ryder (1983) proposed that for asynchronously hatching species which are sexually dimorphic it is adaptive for the larger sex to hatch first, thus enabling it to be better fed. Unfortunately, my data were not sufficient to test the idea of sex ratio variation within broods, differential mortality between sexes or the sex ratio at laying or fledging in ospreys.

Sex specific growth

Several studies of growth of raptors (Newton 1978, 1979, Moss 1979, Bortolotti 1984) and passerines (see Richter 1983 for a review) 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 an earlier fledging age regardless of which sex is smallest. In ospreys, the lack of significant difference in either growth rate (*K*) or growth curve shape (*m*) between the sexes (Tables 2 and 3) suggest that males and females grew at similar rates. Although females added more body weight per day and had a significantly different asymptote of tarsal length than males, they showed identical inflection points in growth curves. When size difference was accounted for (Figs. 14 and 15), males and females showed very similar growth patterns. Males however, showed a greater variability in growth than their larger sisters (Fig. 1, Table 2). Bortolotti (1986) also found males (the smaller sex) to be more variable in growth than female bald eagle nestlings. Richter (1983) argued that cost differences in sexually dimorphic species could be countered by feeding larger offspring extra food only when resources were abundant and therefore predicted the larger sex should show more variability in growth.

Feather growth in ospreys was found to be the least sexually dimorphic variable in growth performance (Figs. 6,7 and 8). However, as Richter (1983) pointed out, since feather length was equal in size and growth rate between the sexes throughout most of the nestling period, and since 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

Although my 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 sibling competition. The study did not support the prediction that males (the smaller sex) should develop feathers earlier and leave the nest sooner than females nor did it find the females to be more variable in growth. There was no evidence that males had faster skill development than females and competition for food was not based on sexual differences but on hatching asynchrony. Additionally, ospreys within a brood, separated by 2-day intervals on average, were never observed to change rank (weight relative to a sibling) in the nest until very late in the nestling period. Stinson (1977) reported weekly rank fluctuations within osprey broods (in 2 of 6 nests) but his data indicate that this occurred only after 90 % (6 weeks) of growth had been completed. Since sex and crop content (found here to be in excess of 200 g in older nestlings) was not considered in that study, it is difficult to assess the validity of this result.

The idea that males are at a competitive disadvantage and should grow faster than females seems maladaptive in ospreys in light of the much greater differences imposed by hatching asynchrony. Appreciable size differences between the sexes do not develop in most variables until growth has passed the inflection point of the growth curve, when food consumption is near its peak. When feeding the young parents discriminated only in relation to age related size differences and not by sex. Therefore, in ospreys there is no evidence of sex-specific growth dynamics selecting for rapid growth in males in order to compete with the larger females for nest resources.

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TABLE 1. Reproduction data for Nova Scotia ospreys in 1984 - 1986. Values are X ± S.D. (range).

	n	1984	n	1985	n	1986	n	Overall
No. nests laying (hatching)	6	(4)	7	(7)	6	(6)	19	(17)
clutch size (eggs laid/ nests)	17	2.8 ± 0.9 (2-4)	22	3.1 ± 0.3 (3-4)	18	3.0 ± 0.6 (2-4)	57	3.0 ± 0.6 (2-4)
No. young hatched	9	1.5 ± 1.3 (0-3)	15	2.1 ± 0.6 (1-3)	13	2.2 ± 0.9 (1-3)	37	1.9 ± 1.0 (0-3)
No. young fledged	8	1.3 ± 1.4 (2-3)	11	1.6 ± 0.7 (1-3)	13	2.1 ± 0.9 (1-3)	32	1.7 ± 1.1 (0-3)
% Nestling mortality		11.1		26.7		0		17.9
No. nests with clutch size =	1	0		0		0		0
	2	3		0		1		4
	3	1		6		4		11
	4	2		1		1		4
No. nests fledging young =	1	0		4		2		6
	2	1		2		1		4
	3	2		1		3		6
	4	0		0		0		0

TABLE 2. Growth parameters of logistic equation for nestling ospreys by sex. Values are means ± S.D. (range).

variable	sex	n	Growth parameter *K*	*A*	*ti*
Weight	M	20	0.180 ± 0.006 (0.168-0.190)	**1499.5± 145.6 (1190-1693)	19.3 ± 1.1 (17.2-21.3)
	F	12	0.180 ± 0.007 (0.170-0.187)	1790 ± 43.9 (1740-1880)	20.5 ± 1.1 (19.4-22.7)
Tarsus	M	20	0.143 ± 0.007 (0.126-0.158)	**71.1 ± 1.5 (68.8-74.0)	12.0 ± 1.1 (10.3-13.6)
	F	12	0.142 ± 0.006 (0.134-0.153)	73.9 ± 1.6 (72.0-76.9)	12.9 ± 1.4 (10.5-15.6)
Talon	M	20	0.110 ± 0.006 (0.101-0.123)	30.1 ± 1.4 (27.5-33.0)	*16.6 ± 1.2 (13.7-18.5)
	F	12	0.113 ± 0.006 (0.104-0.124)	31.3 ± 1.1 (29.0-33.0)	18.0 ± 1.2 (16.2-19.7)
Culmen	M	20	**0.079± 0.005 (0.072-0.090)	31.8 ± 1.3 (28.5-34.0)	9.8 ± 1.7 (6.4-11.9)
	F	12	0.085 ± 0.006 (0.078-0.096)	32.7 ± 1.0 (31.5-35.0)	11.1 ±1.4 (9.5-13.2)
Cranium	M	20	**0.075± 0.004 (0.068-0.084)	43.4 ± 0.8 (42.0-44.6)	5.4 ± 0.9 (3.8-6.1)
	F	12	0.082 ± 0.005 (0.071-0.091)	44.0 ± 0.8 (42.0-45.0)	6.0 ± 1.1 (3.9-6.4)
Wingchord	M	20	0.099 ± 0.007 (0.085-0.112)	490.2 ± 23.9 (400-510)	30.8 ± 1.7 (26.5-33.3)
	F	12	0.098 ± 0.004 (0.091-0.109)	505.0 ± 5.2 (500-510)	31.5 ± 1.1 (29.8-33.0)

* Males are significantly different from females, ANOVA *P* <0.05.
** Males are significantly different from females, ANOVA *P* <0.01.

TABLE 3. Growth parameters of Richards equation for nestling ospreys by sex. Values are means ± S.D. (range).

			Growth parameter		
variable	sex	n	m	W	T
Weight	M	20	1.23 ± 0.17 (0.87-1.68)	*1548.7 ± 168.3 (1187-1738)	36.5 ± 3.5 (31.3-47.1)
	F	12	1.26 ± 0.11 (1.06-1.43)	1830.8 ± 76.9 (1695-1956)	36.0 ± 3.1 (32.4-44.1)
Tarsus	M	20	2.18 ± 0.54 (0.88-3.41)	*71.0 ± 2.1 (68.0-75.2)	43.6 ± 3.7 (36.8-49.5)
	F	12	2.48 ± 0.48 (1.87-3.44)	73.6 ± 2.1 (69.0-76.6)	45.3 ± 4.0 (39.1-52.2)
Talon	M	20	1.47 ± 0.31 (0.96-2.09)	29.6 ± 1.5 (26.8-32.1)	50.8 ± 3.2 (45.7-55.9)
	F	12	1.80 ± 0.27 (1.39-2.41)	30.9 ± 0.9 (29.2-32.7)	48.9 ± 2.7 (45.5-52.7)
Culmen	M	20	1.90 ± 0.43 (1.09-2.63)	31.6 ± 1.9 (28.5-35.8)	69.6 ± 5.1 (61.1-79.3)
	F	12	2.41 ± 0.60 (1.34-3.10)	32.2 ± 1.1 (30.6-33.9)	70.9 ±1.4 (69.0-73.8)
Wingchord	M	20	1.31 ± 0.16 (1.07-1.59)	456.6 ± 19.9 (409.3-491.4)	60.7 ± 4.7 (52.3-68.1)
	F	12	1.31 ± 0.18 (1.02-1.74)	471.9 ± 18.4 (442.3-511.1)	57.3 ± 5.9 (48.1-65.2)

* Males are significantly different from females, ANOVA P <0.01.

Table 4. Adult means compared to nestling means at 48 days of growth (or at asymptote).

variable	sex	n	adults	d.i.*	n	nestlings	d.i.	% adult value
Weight	M	8	1485.0	-	20	1499.5	-	100.9
	F	12	1790.0	18.6	12	1790.0	17.7	100.0
Tarsus	M	9	71.0	-	20	71.1	-	100.1
	F	10	72.6	2.2	12	73.9	2.2	101.8
Talon	M	9	29.3	-	13	29.1	-	99.3
	F	10	29.8	1.7	7	30.5	4.7	102.3
Culmen	M	8	32.5	-	13	30.4	-	93.5
	F	10	34.4	5.7	7	31.7	4.2	92.2
Cranium	M	7	42.2	-	13	41.8	-	99.0
	F	6	43.2	2.3	7	42.8	2.4	99.1
Wingchord	M	10	494.5	-	13	378.7	-	76.6
	F	10	515.6	4.2	7	388.4	2.5	75.3
Primary	M	10	337.0	-	13	241.1	-	71.5
	F	10	350.0	3.8	7	244.9	1.6	69.9
Rectrice	M	10	207.0	-	13	158.4	-	76.5
	F	10	217.0	4.5	7	159.9	0.9	73.7

* Dimorphism index = mean females - mean males /((mean females / 2) + (mean males / 2)) X 100 (Storer 1966).

Fig. 1. Mean mass curves at 4 day intervals of male and female nestling ospreys plotted against day at which growth occurred.

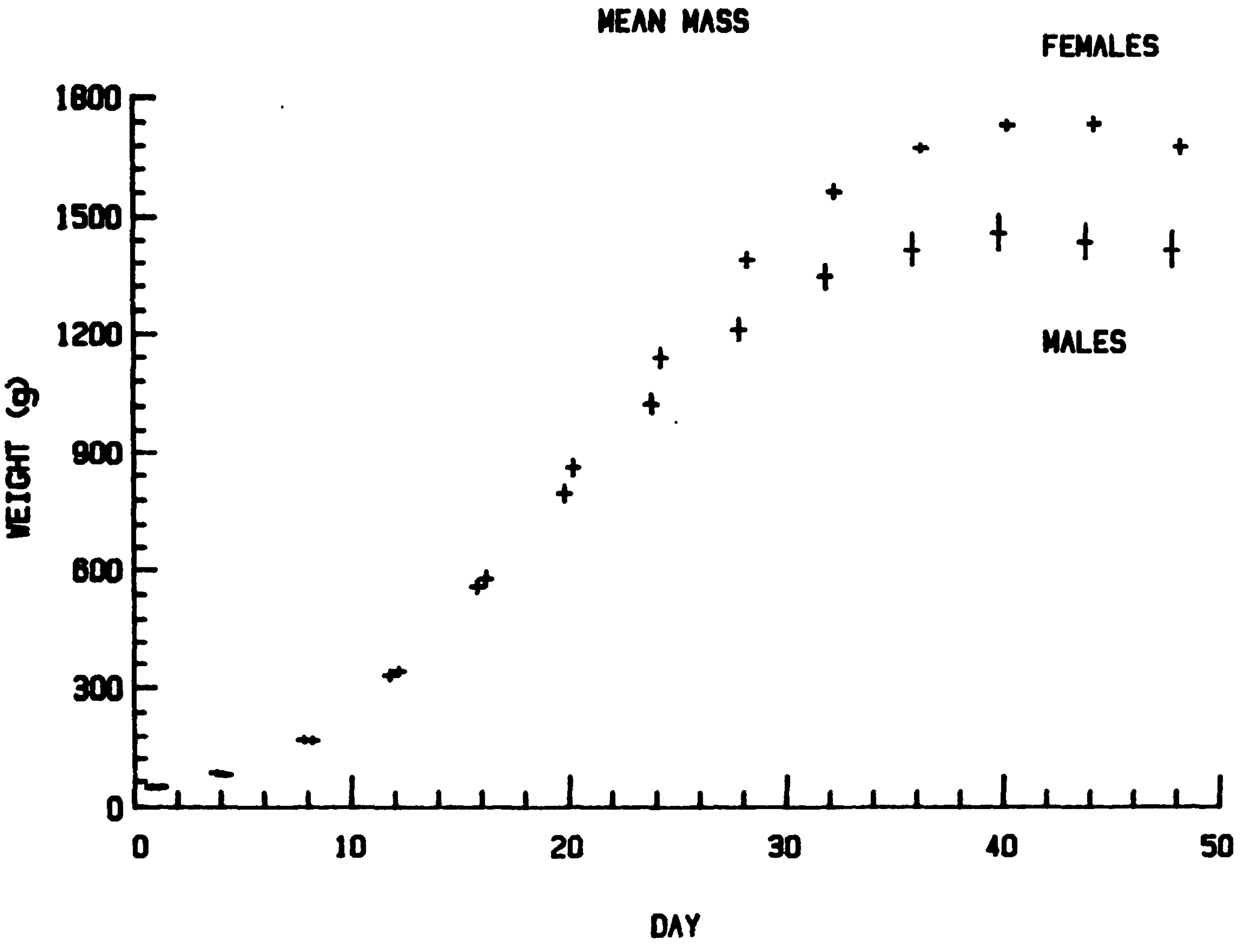
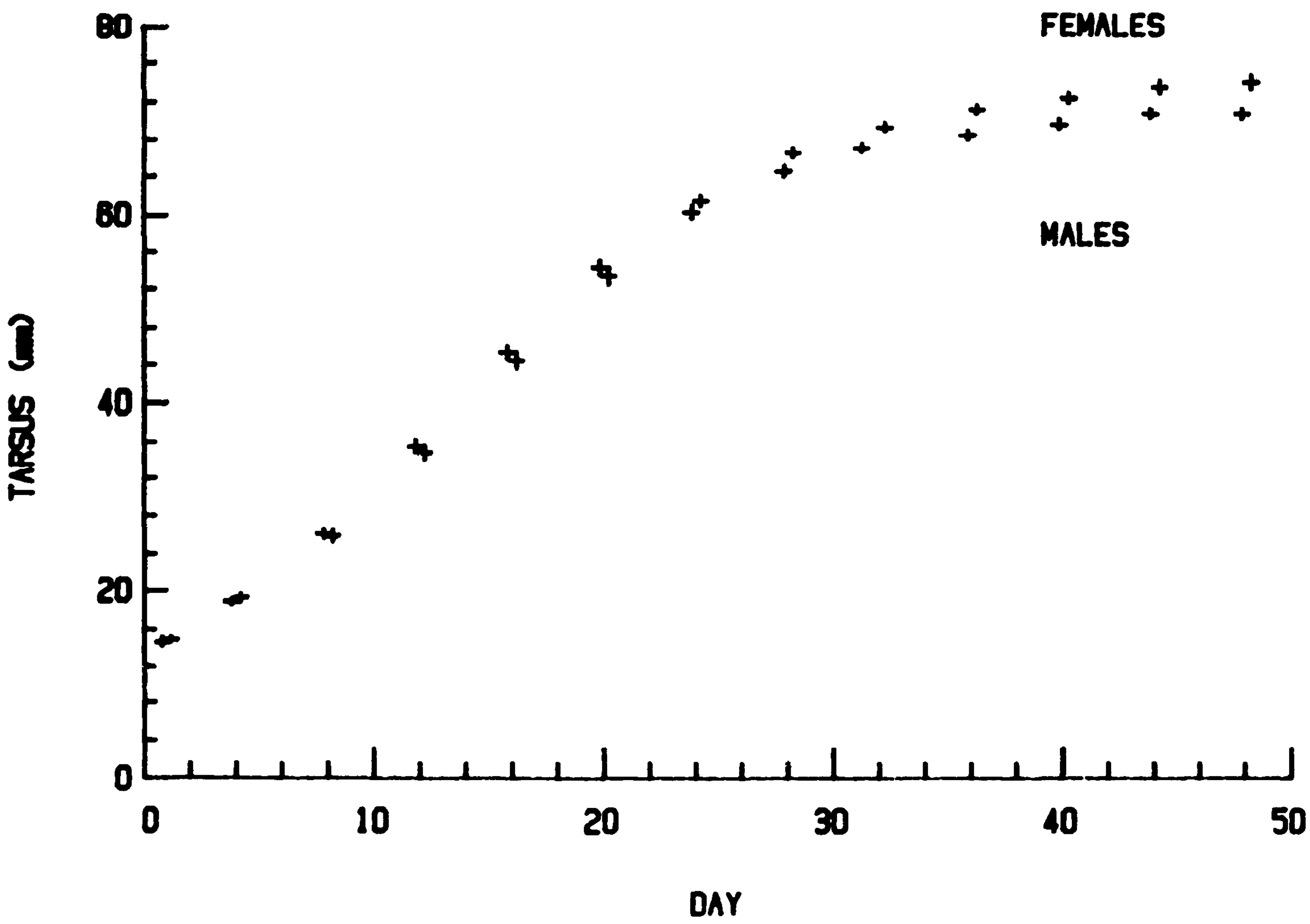

MEAN MASS
FEMALES
MALES
WEIGHT (g)
0
300
600
900
1200
1500
1800
DAY
0
10
20
30
40
50

Fig. 2. Mean tarsus length curves at 4 day intervals of male and female nestling ospreys plotted against day at which growth occurred.



MEAN TARSUS LENGTHS

Fig. 3. Mean talon length curves at 4 day intervals of male (dashed line) and female (solid line) nestling ospreys plotted against day at which growth occurred. (S.E. bars eliminated for clarity).

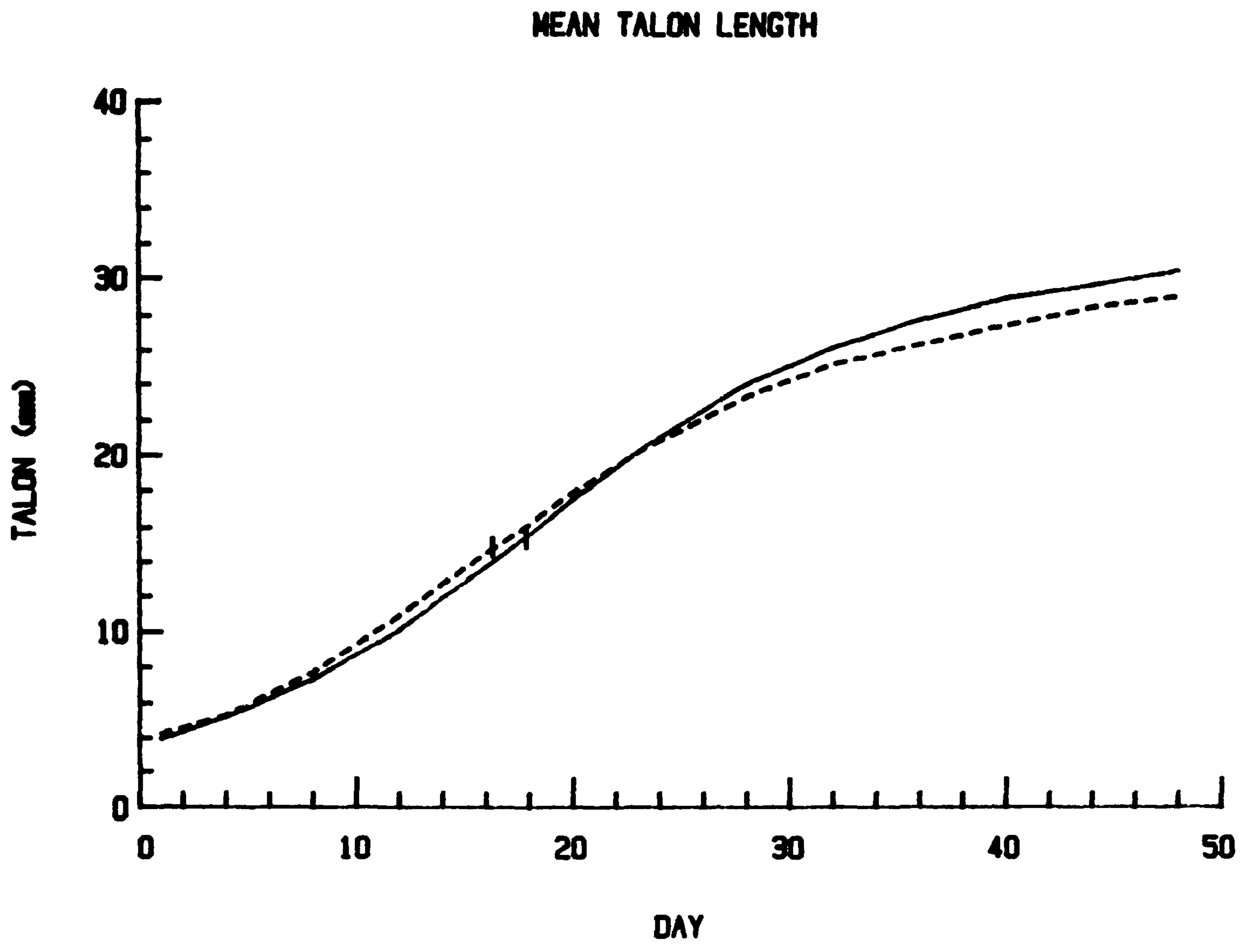

MEAN TALON LENGTH
TALON (mm)
40
30
20
10
0
0
10
20
30
40
50
DAY

Fig. 4. Mean culmen length curves at 4 day intervals of male (dashed line) and female (solid line) nestling ospreys plotted against day at which growth occurred. (S.E. bars eliminated for clarity).

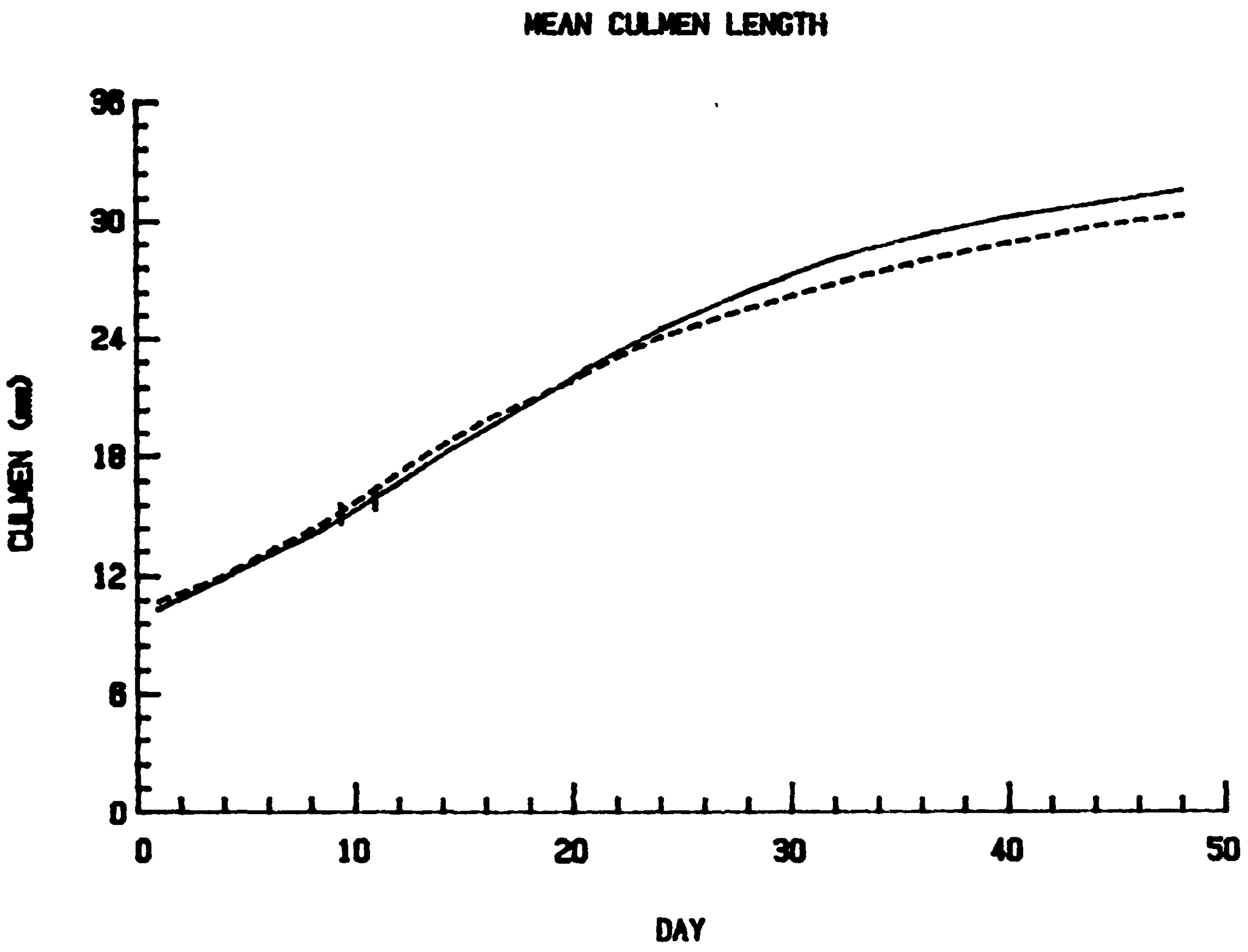
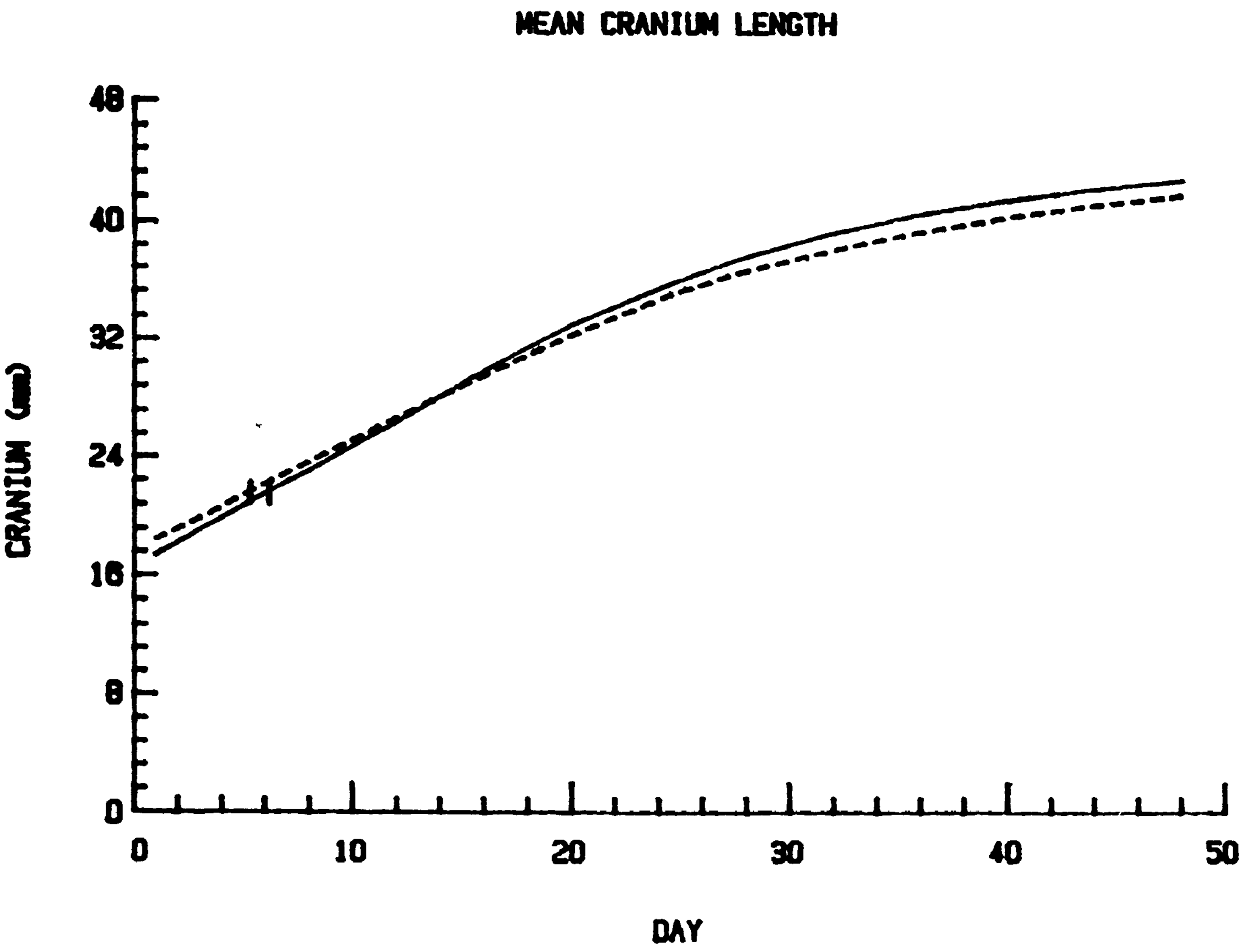

MEAN CULMEN LENGTH
CULMEN (mm)
36
30
24
18
12
6
0
0
10
20
30
40
50
DAY

Fig. 5. Mean cranium width curves at 4 day intervals of male (dashed line) and female (solid line) nestling ospreys plotted against day at which growth occurred. (S.E. bars eliminated for clarity).



MEAN CRANIUM LENGTH

Fig. 6. Mean wingchord length curves at 4 day intervals of male (dashed line) and female (solid line) nestling ospreys plotted against day at which growth occurred. (S.E. bars eliminated for clarity).

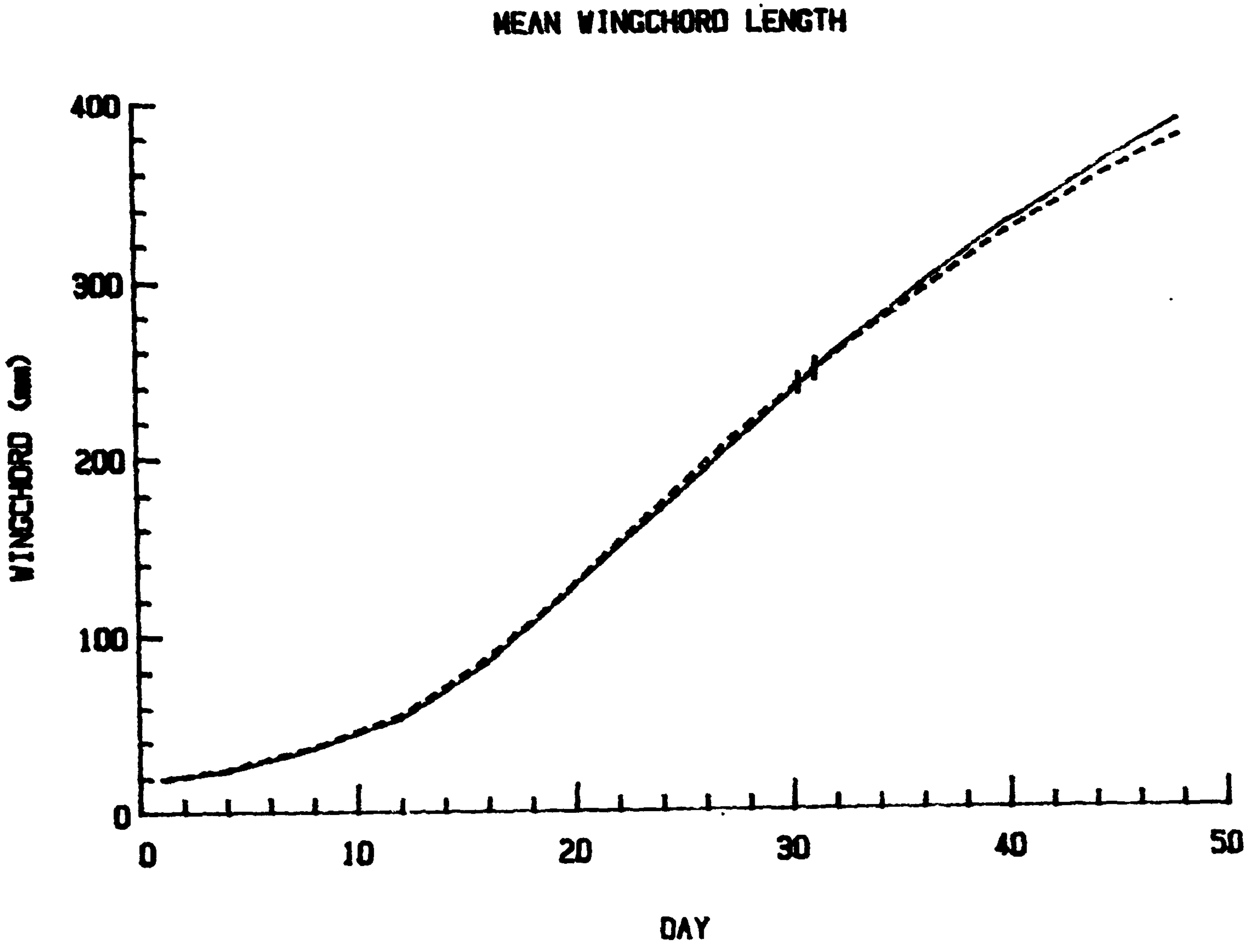
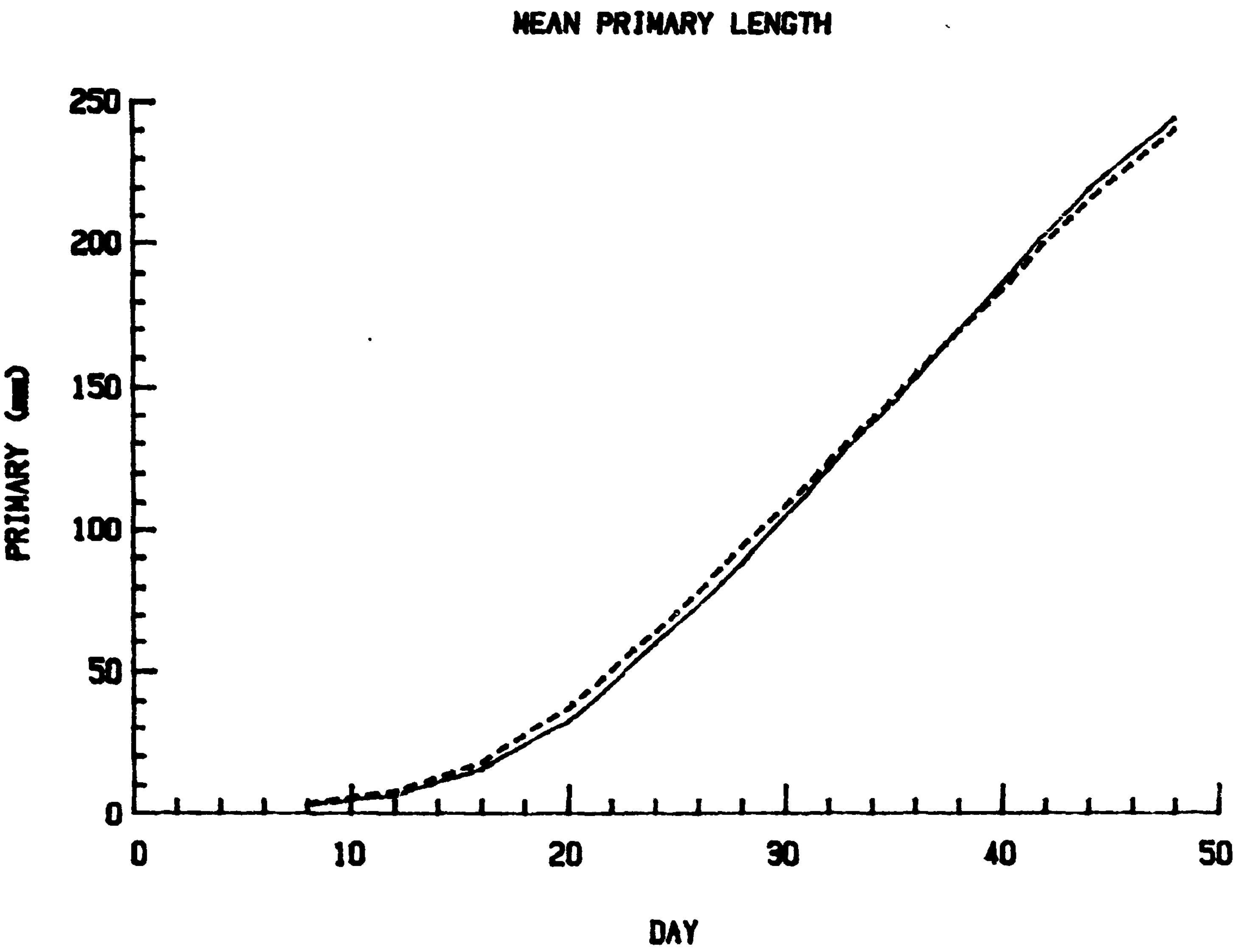

MEAN WINGCHORD LENGTH
WINGCHORD (mm)
400
300
200
100
0
0
10
20
30
40
50
DAY

Fig. 7. Mean primary length curves at 4 day intervals of male (dashed line) and female (solid line) nestling ospreys plotted against day at which growth occurred. (S.E. bars eliminated for clarity).



MEAN PRIMARY LENGTH

Fig. 8. Mean rectrix length curves at 4 day intervals of male (dashed line) and female (solid line) nestling ospreys plotted against day at which growth occurred. (S.E. bars eliminated for clarity).

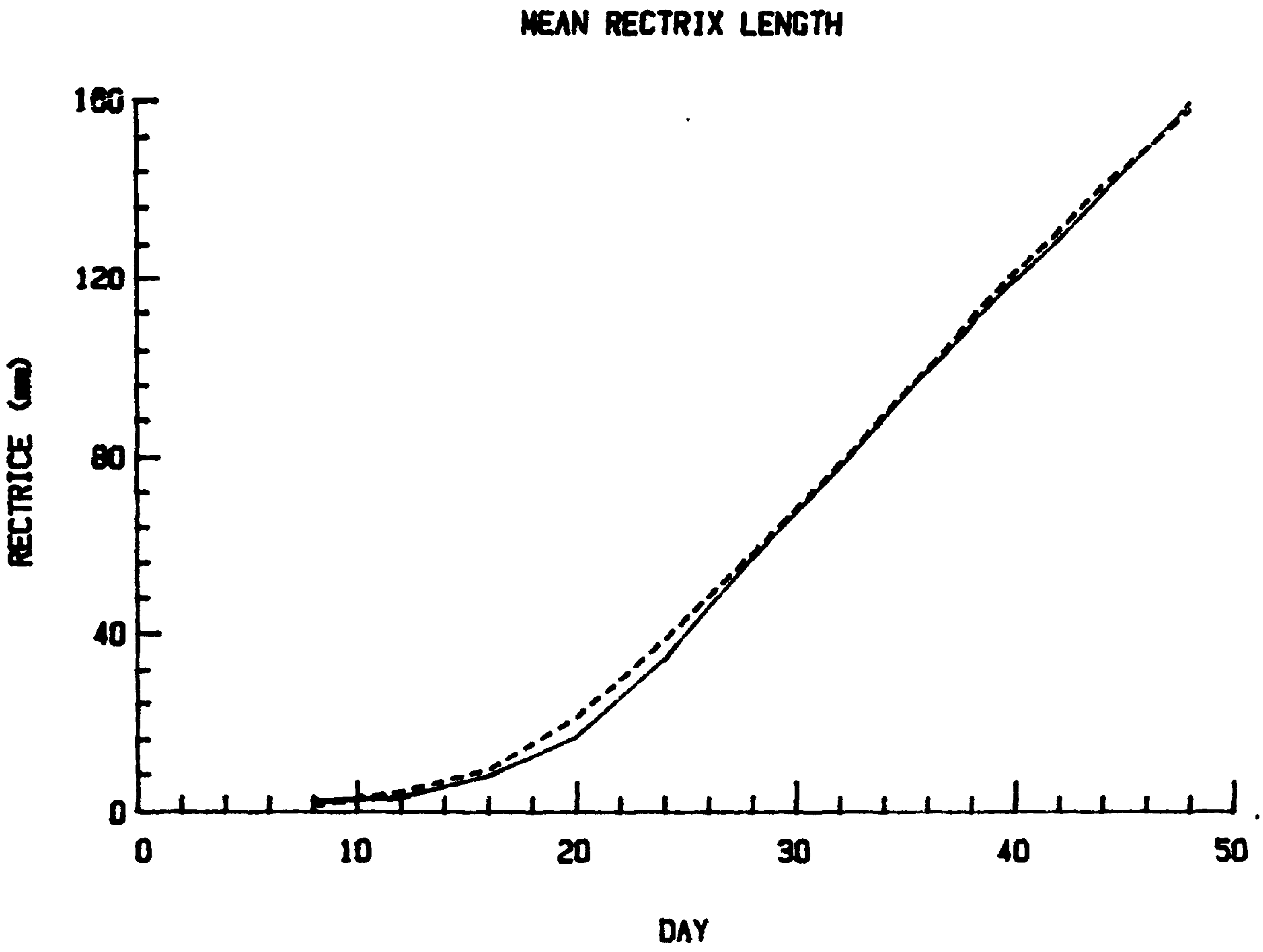

MEAN RECTRIX LENGTH
RECTRICE (mm)
0
40
80
120
160
0
10
20
30
40
50
DAY

Fig. 9. Estimated average daily growth rates for mass of male and female nestling ospreys plotted against weight at which growth rate occurred.

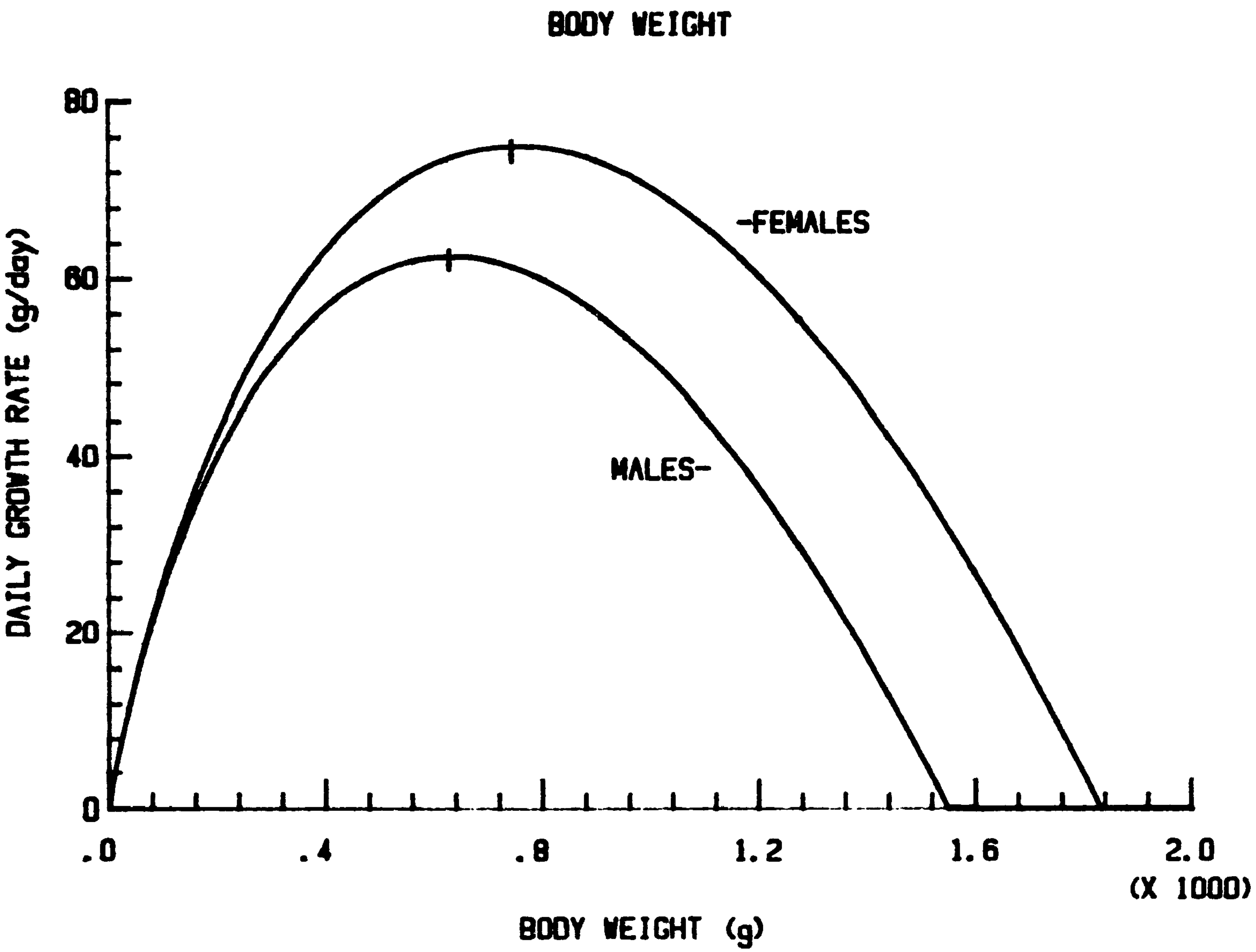
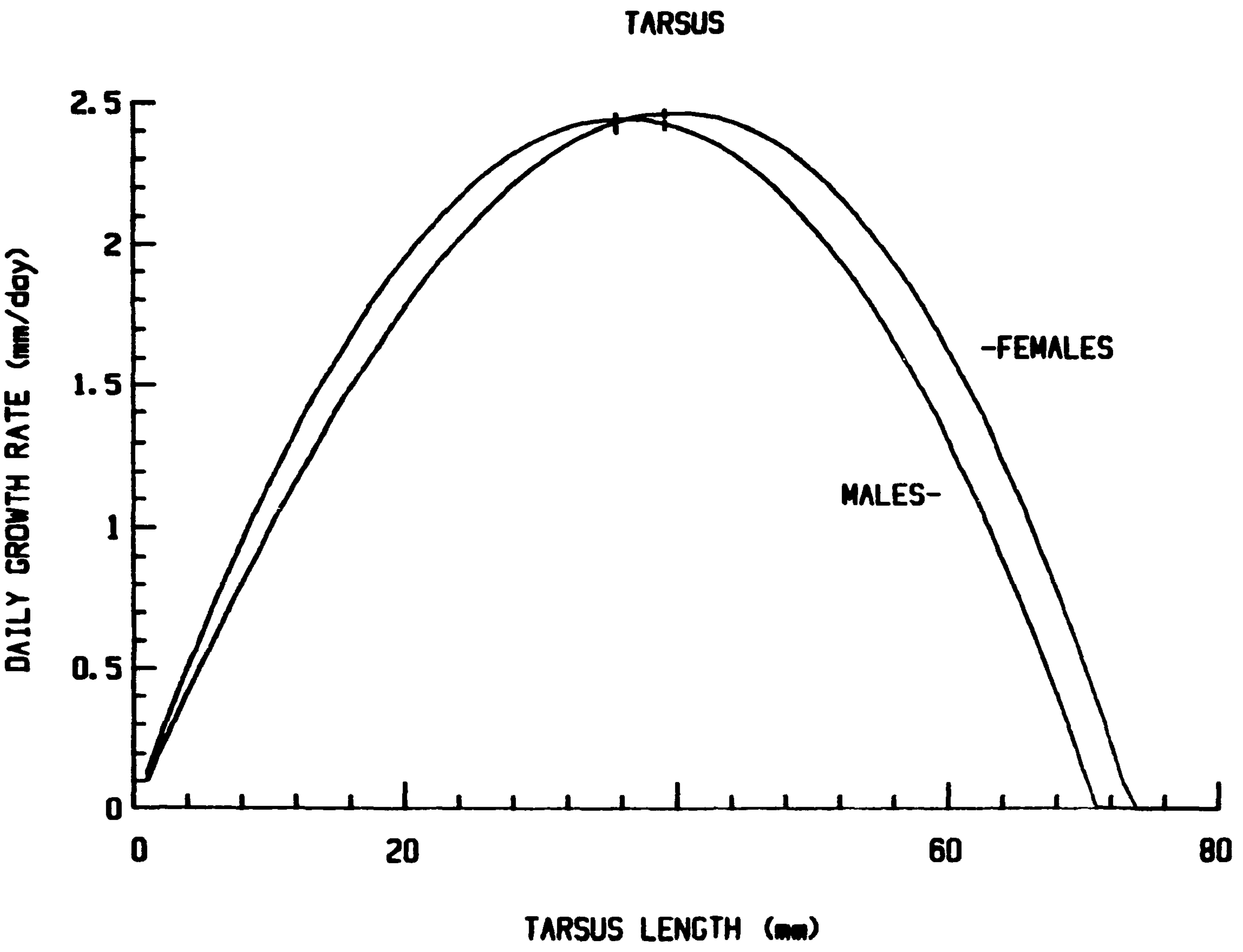

BODY WEIGHT
80
60
40
20
0
DAILY GROWTH RATE (g/day)
-FEMALES
MALES-
.0
.4
.8
1.2
1.6
2.0
(X 1000)
BODY WEIGHT (g)

Fig. 10. Estimated average daily growth rates for tarsus length of male and female nestling ospreys plotted against length at which growth rate occurred.



TARSUS

DAILY GROWTH RATE (mm/day)
2.5
2
1.5
1
0.5
0
-FEMALES
MALES-
0
20
60
80
TARSUS LENGTH (mm)

Fig. 11. Estimated average daily growth rates for talon length of male and female nestling ospreys plotted against length at which growth rate occurred.

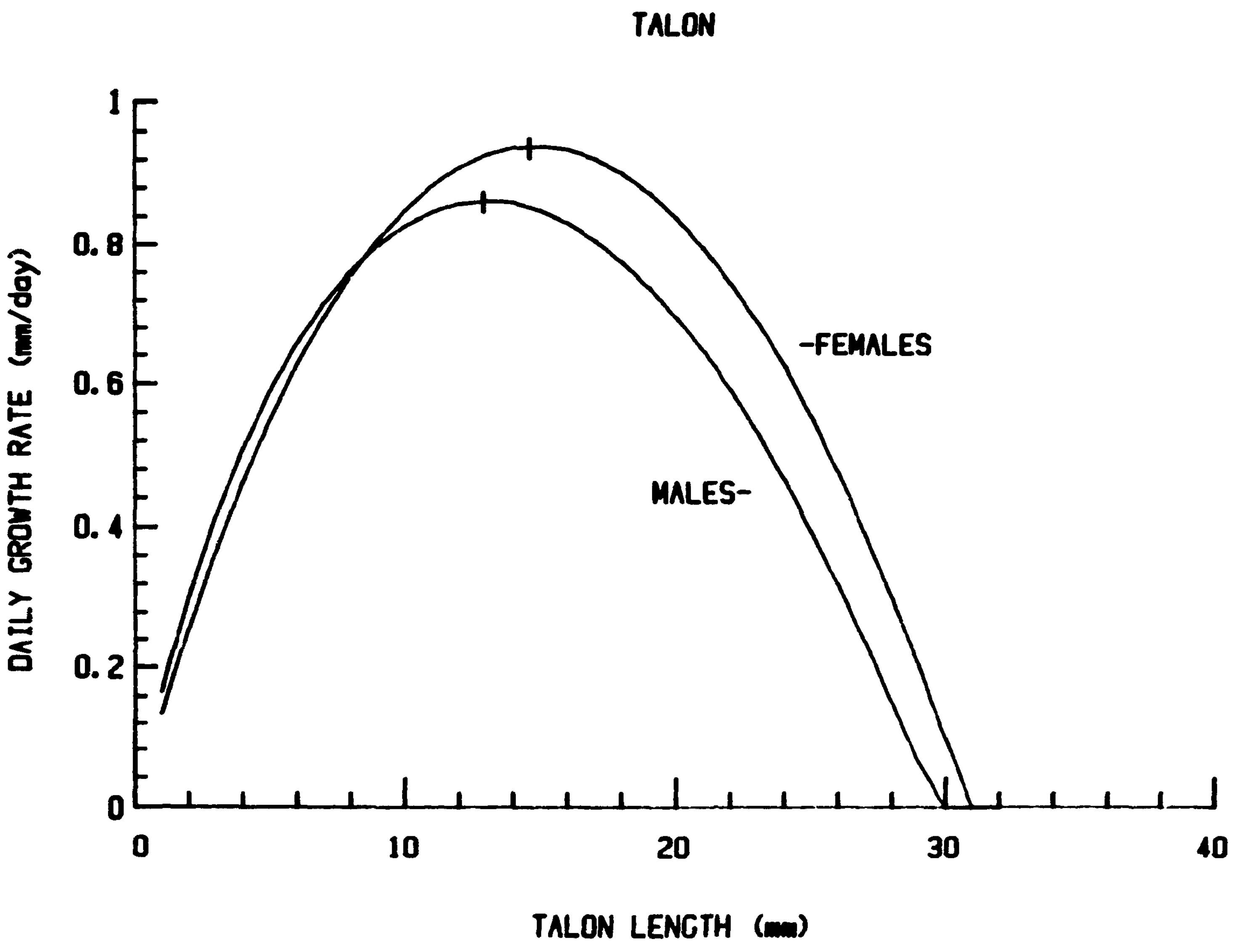

TALON
DAILY GROWTH RATE (mm/day)
1
0.8
0.6
0.4
0.2
0
0
10
20
30
40
TALON LENGTH (mm)
-FEMALES
MALES-

Fig. 12. Estimated average daily growth rates for culmen length of male and female nestling ospreys plotted against length at which growth rate occurred.

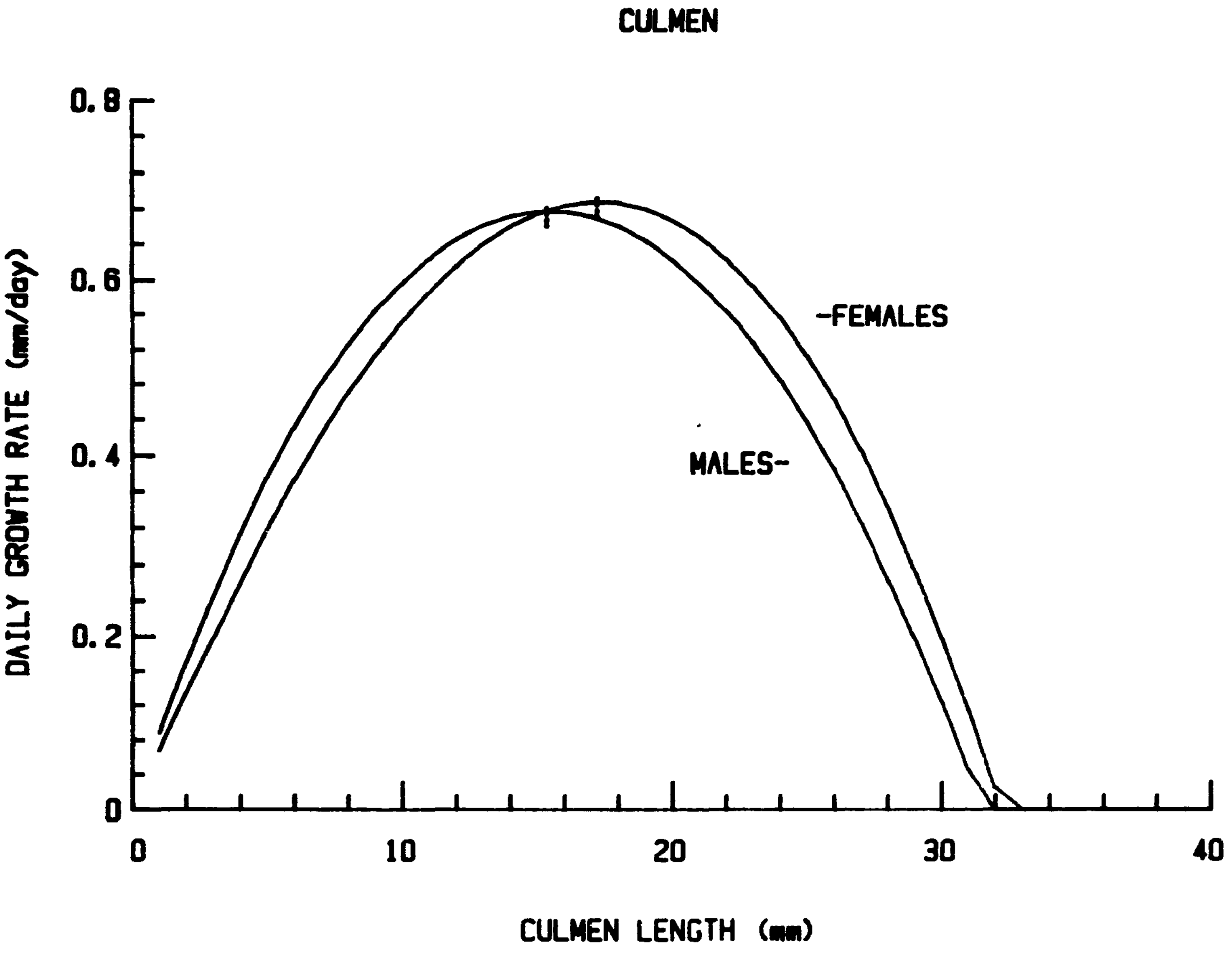

CULMEN
0.8
0.6
0.4
0.2
0
DAILY GROWTH RATE (mm/day)
-FEMALES
MALES-
0
10
20
30
40
CULMEN LENGTH (mm)

Fig. 13. Estimated average daily growth rates for wingchord lengths of male and female nestling ospreys plotted against length at which growth rate occurred.

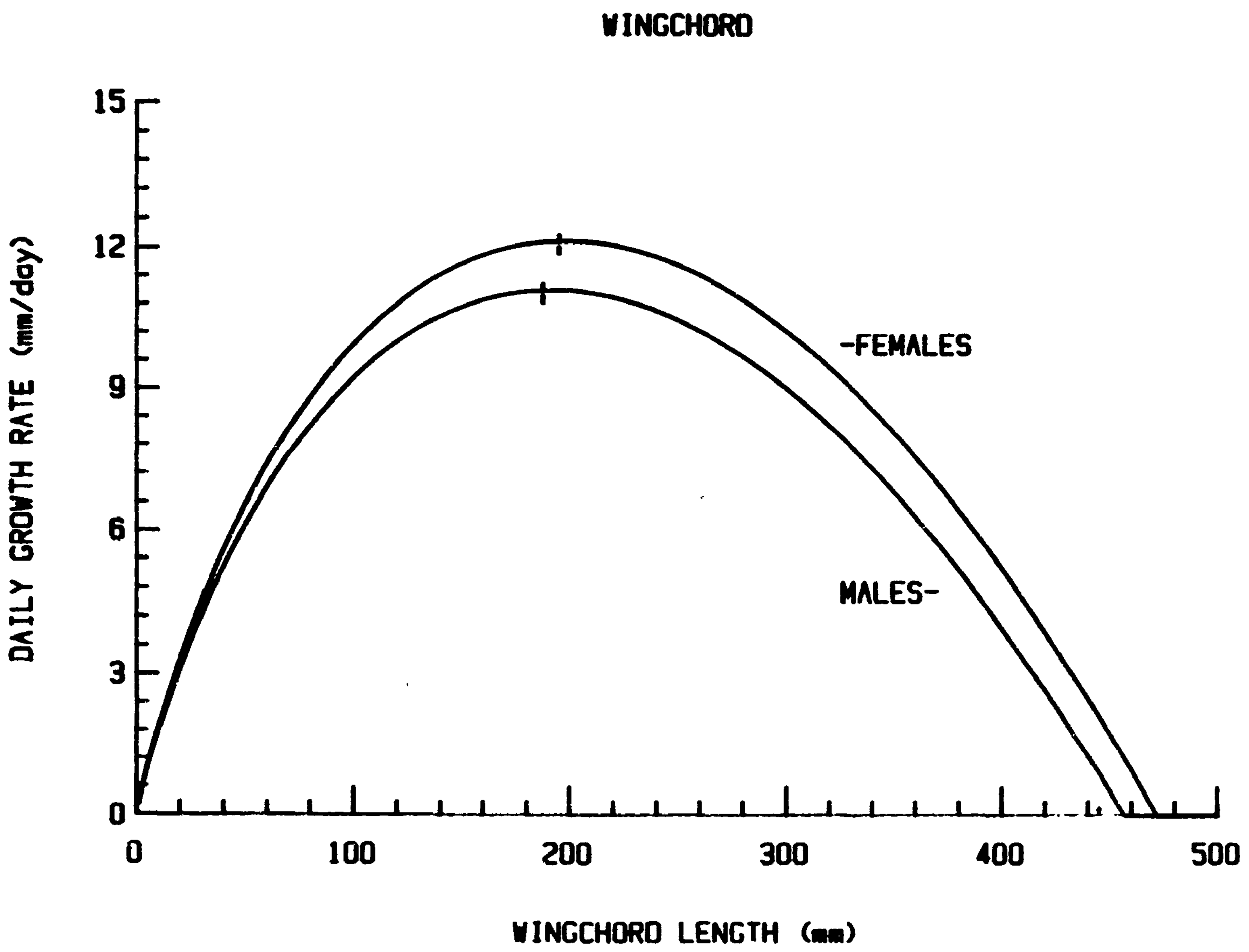

WINGCHORD
DAILY GROWTH RATE (mm/day)
15
12
9
6
3
0
0
100
200
300
400
500
WINGCHORD LENGTH (mm)
-FEMALES
MALES-

Fig. 14. Percent of mass asymptote attained in relation to the growth index (relative growth) for male (-) and female (.) nestling ospreys. Points represent means at each day of growth.

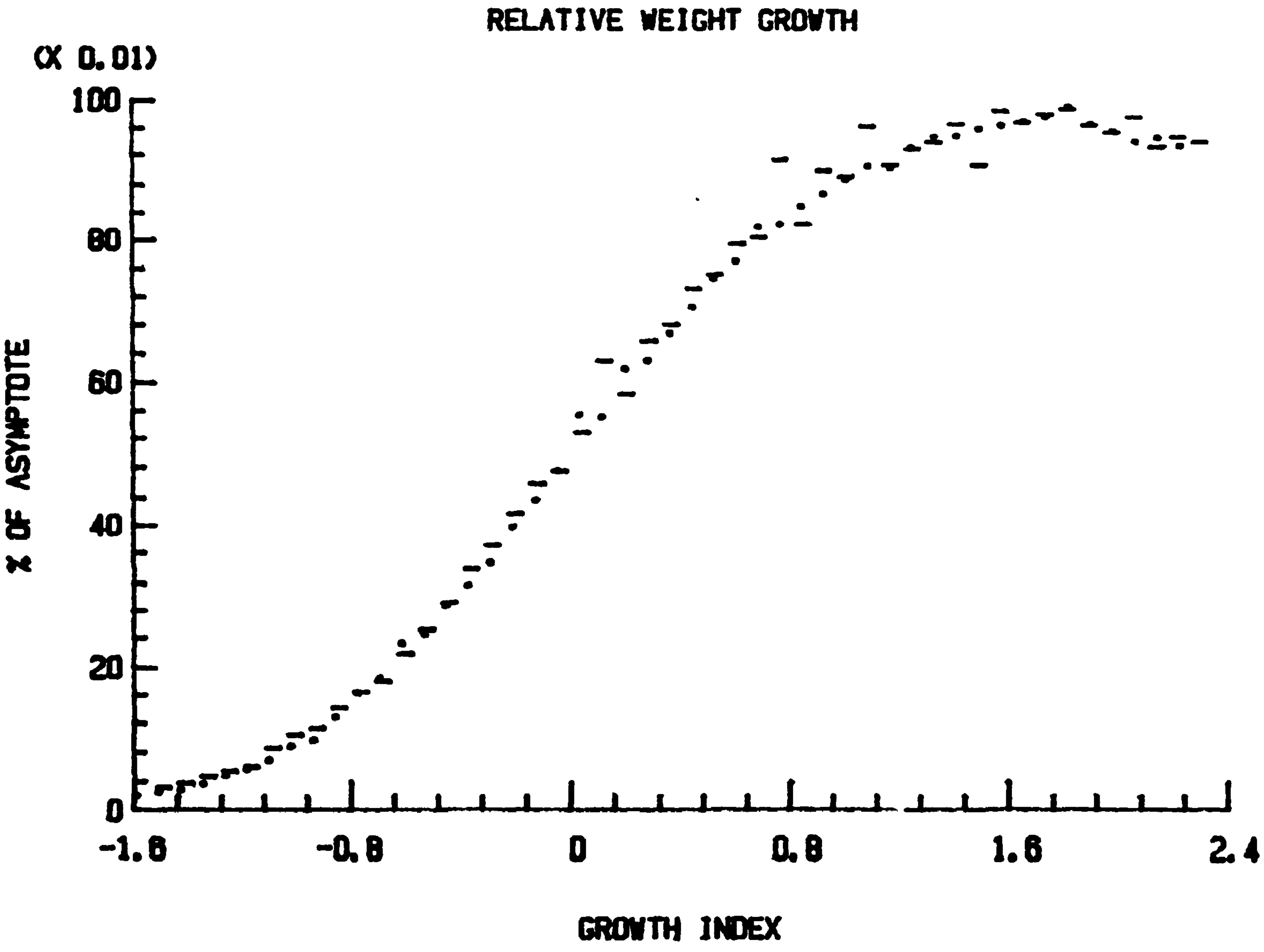
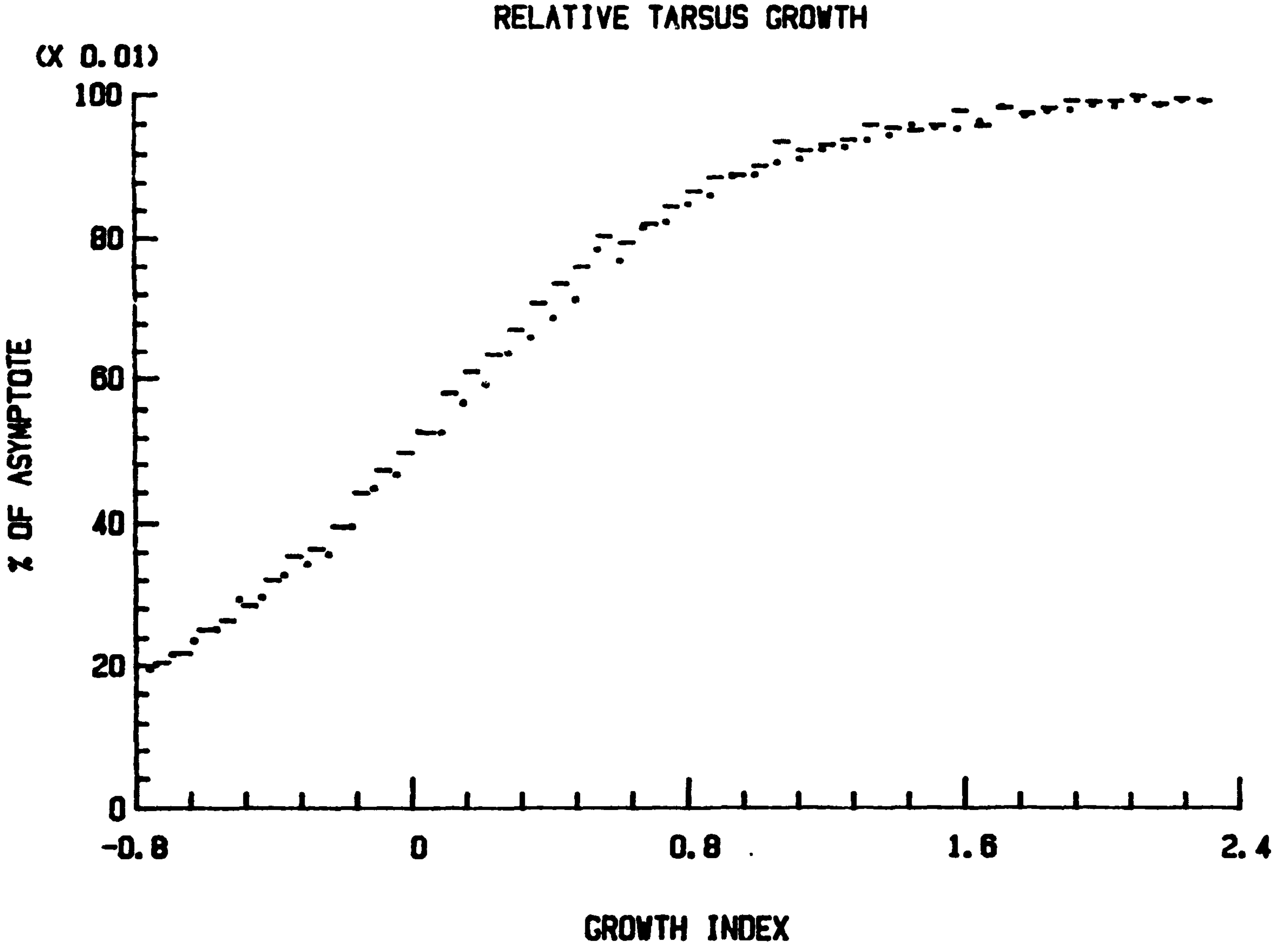

RELATIVE WEIGHT GROWTH
(X 0.01)
100
80
60
40
20
0
% OF ASYMPTOTE
-1.6
-0.8
0
0.8
1.6
2.4
GROWTH INDEX

Fig. 15. Percent of tarsus length asymptote attained in relation to the growth index (relative growth) for male (-) and female (.) nestling ospreys. Points represent means at each day of growth.


RELATIVE TARSUS GROWTH
(X 0.01)
% OF ASYMPTOTE
100
80
60
40
20
0
-0.8
0
0.8
1.6
2.4
GROWTH INDEX

CONNECTING STATEMENT

In Chapter I, I compared the growth of individual male and female nestlings in a migratory population of ospreys in Nova Scotia, Canada and found no significant differences in growth rates of weight, body components, or plumage characteristics.

In Chapter II, I evaluated the sex-specific growth performance of ospreys in a sedentary population in Sonora, Mexico and compared them to nestlings in Nova Scotia to investigate the extent of geographical variation in osprey populations.

CHAPTER II. Geographic variation in the growth of migratory and sedentary ospreys

ABSTRACT

Thirty-one nestling ospreys (*Pandion haliaetus*) evaluated for sex-specific growth performance within a sedentary population in Sonora, Mexico were compared with nestlings from a migratory population in Nova Scotia, Canada. Comparisons of geographic variation by sex showed that ospreys in the Sonoran desert had significantly higher weight asymptotes, reduced growth rates, longer nestling periods and later emergence of flight feathers than temperate migratory birds. We present a hypothesis that invokes phenotypic responses to external environmental conditions, namely, migratory habits (which are related to synchrony of the breeding season) and climate as possible factors accounting for differences in morphological features observed between the 2 populations. However, whether the geographic variation observed in growth rates represents an adaptation allowing growth to be optimized in regard to environmental factors remains a question to be answered.

INTRODUCTION

Lack (1968) proposed that growth rates in birds represent a compromise between fast growth to reduce the chicks' vulnerability to predation, and slower growth to allow the parents of altricial species to feed more nestlings. Ricklefs (1969, 1973, 1979) hypothesized that birds grow as fast as possible within limits imposed by constraints on tissue growth, that is at some physiologically maximal rate rather than optimized with regard to environmental factors. Alternatively, Case (1978) reasoned that since rapid growth required parents to spend more time in gathering food than in providing parental care, optimal growth should occur at intermediate values in response to such environmental factors as nest mortality and food availability. In a recent reexamination, Ricklefs (1984) concluded that these hypotheses, i.e. ecological optimization (Lack 1968, Case 1978) and physiological maximization are not necessarily incompatible when explaining variation in growth rates.

King and Hubbard (1981) tested the hypothesis that growth rates were physiologically maximized and hence, geographically invariant in the growth of nestling white-crowned sparrows (*Zonotrichia leucophrys*). Postnatal growth curves in 6 sample populations were "virtually congruent" and independent of mean brood size and locality. They concluded that if growth rates were submaximal and "optimized" in relation to the local environment there would have been a greater diversity of growth rates.

Since variation occurs not only within populations but also between populations, the effect of the local environment on the growth process of a single species should become obvious when viewed over a wide latitudinal distance. Factors favouring either rapid or slow growth should become apparent by comparative observation of geographically variable populations.

Although major differences may exist in the breeding strategies of sedentary and migratory populations, few studies have compared the growth performance of a single species in different portions of their range (King and Hubbard 1981, James 1983, Murphy 1983). Ospreys (*Pandion haliaetus*) show both sexual-size dimorphism and geographic variation in North America and are migratory except for sedentary populations in southern Florida and Mexico.

This study therefore, was an attempt to investigate geographical variation of growth parameters of nestling ospreys in populations separated by 16° latitude and 50° longitude. I was interested in answering the following questions: 1) Are growth rates in ospreys physiologically maximized and therefore geographically invariant? 2) If not, what is the extent of geographic variation in growth rate and asymptotic size between the 2 populations? 3) If variation does exist, how does it relate to the prevailing environmental conditions within the populations?

To answer these questions I compared sex-specific growth and asymptotic size of nestlings in a sedentary population of ospreys in Sonora, Mexico with those of a migratory population in temperate Nova Scotia, Canada, (see Ch. 1)

METHODS

Study area

In contrast to the intensively studied population in Nova Scotia, (Prévost 1977, Jamieson et al. 1982, Seymour and Bancroft 1983, Schaadt Ch. I) the historical distribution and abundance of ospreys in the Gulf of California are little known (Kenyon 1947, Jehl 1977). Recently, Henny and Anderson (1979) estimated the nesting population of ospreys in coastal Sonora, Mexico at 124 pairs.

This study was conducted during the breeding seasons of 1985 and 1987 in 2 locations along the Sonoran coast. In 1985 the northernmost study area was located within a Seri Indian reservation (Felger and Moser 1985) at Punta Sargento (29° 14'N, 112° 18'W) between Tiburon Island and El Desemboque (Fig. 1). Henny and Anderson (1979) described the area behind Punta Sargento, including the nearby flats along the east coast of Tiburon Island as containing the greatest concentration of breeding ospreys in the Gulf of California region. F. and F. Hamerstrom (pers. comm.) have mapped more than 100 osprey nest sites near Desemboque and estimated roughly one-third to be active at any one time. Over the 2 year period I located a total of 44 nests of which 27 (61%) were active.

For logistic reasons the study site was relocated further south in 1987 to Punta Baja (28°38'N, 111°47'W) between Kino Bay and Guaymas (Fig. 1), after a reconnaisance of the northern study area showed a majority of nests to be delayed in comparison to the 1985 season. Henny and Anderson (1979) estimated 46 pairs of ospreys nesting between Kino Bay and Guaymas. I found 24 nests there, 10 (42%) being active. Of the other 14 nests, 10 had birds associated with them but whether nestings were eventually attempted is not known. The additional 4 nests seemed unoccupied.

In both study areas nests were located on tall cacti, primarily cardon (*Pachycereus pringlei*) and occasionally saguaro (*Carnegiea gigantea*), 6 to 12 m above the ground. The presence of coyotes (*Canis latrans*) on the mainland prevents the ground and cliff nests common to island populations in the gulf (Judge 1983).

Field work was conducted between late February and early June. Fourteen nests with 17 nestlings that survived to fledge were studied for growth performance in the Desemboque study area in 1985. In the Punta Baja study area in 1987, 8 nests with 14 nestlings were examined for growth. Overall, 31 nestlings (13 males and 18 females) from 22 nests were measured for growth during the course of the study.

Field methods

The most striking feature of the breeding chronology of sedentary ospreys in the Sonoran desert is the high degree of asynchrony among nesting pairs compared to more northerly migratory populations. Kenyon (1947), for example, found 27 nests containing all stages from fresh eggs to flying young in late April. Judge (1983) reported the onset of egg laying to occur from early January through early March (9-10 weeks).

Therefore, upon arrival in the study area I initiated nest surveys (using a mirror pole) to identify nests containing eggs or chicks. When eggs were found, they were marked, measured and weighed and then observed on a daily basis to document hatching. When chicks were encountered, they were aged in comparison to known aged birds (primarily from average growth curves of linear measurements ± 1 day, Schaadt in prep.) and if used in the study, (i.e. less than 5 days of age), marked on the head with a colored felt marker for subsequent identification. As birds hatched (day=1) they were marked according to the egg from which they came and then weighed and measured at 2-3 day intervals for the remainder of the nestling period. This provided known ages and hatching sequence for all chicks included in the study.

Birds were weighed to the nearest gram with Pesola spring scales and measured for tarsus length, hallux claw (talon) length, cranium width, culmen length, unflattened wing chord, and as feathers emerged, eighth primary and central rectrix. The result is a set of longitudinal growth data on 8 variables for each nestling, 31 in all over the growth period.

Data analysis

Log transformations of the logistic equation according to Ricklefs (1967) were fitted to individual sets of growth data for all variables for the 31 birds. The parameters K (a constant proportional to the overall growth rate and measured in day $^{-1}$), A (asymptote in g or mm) and ti (the point of inflection in days) were determined from the curves of individual nestlings. The variable t_{10-90}, an inverse measure of the growth rate representing the time it takes to grow from 10 to 90% of the asymptotic value, was calculated for individual birds from the growth equation.

Growth data from individual birds were also fitted to a reparameterized version of the Richards equation (White and Brisbin

1980) rewritten by Brisbin et al. (1986), providing parameters of *m* (curve shape), *W* (asymptote) and *T* (overall growing time) using the NLIN procedure of SAS, version 82.4 (SAS 1982) to more thoroughly document intraspecific comparisons. Data for the above methods were derived only from nestlings that survived to fledge and incorporated all data points up to and including the asymptote. For variables in which no asymptote was achieved prior to fledging, all data were included in the analyses. Crop content, found to be in excess of 200 g in older nestlings (i.e. greater than 6 weeks in age, see Ch. I), was taken into consideration in the analysis of weight accumulation.

The sexing of individual nestlings was initially determined on the basis of 2 distinct weight classes which appear by fledging and confirmed by karyotypic analysis of fibroblast tissue (Ch. III) collected from a subsample of 14 birds in the field. Birds of unknown sex were then entered into a discriminant function analysis to be classified by comparisons with birds of known sex. A significant discriminant function ($P < 0.001$), based on the pooled covariance matrix, enabled me to sex all of the unknowns on the basis of weight and tarsus asymptotes alone. Detailed accounts of field methodology, growth curve analysis and sexing of nestlings can be found in Chapter I.

Statistical techniques are presented in the text where they are employed and were performed using Statgraphics (Version 1.1, 1985, Statistical Graphics Corporation, Inc) on an IBM XT personal computer. Unless otherwise noted, all means are quoted with standard errors (S.E.) and tests were considered significantly different if the probability of a larger F value was < 0.05.

RESULTS

Reproduction data

Egg laying during this study occurred from 18 January to 30 April and eggs hatched (based on an average incubation period of 38 days, pers. observ.), from 24 February to 6 June, providing a conservative estimate of an 101 day interval for the onset of egg laying. Data for 34 eggs from 14 nests in the Desemboque area show an average clutch size of 2.42 ± 0.2 (1-3). In the Punta Baja area I located 8 nests with 19 eggs for an average clutch size of 2.38 ± 0.1 (1-3). Overall clutch size for both study areas averaged 2.40 ± 0.2 (1-3).

Hatching intervals averaged 3.85 ± 0.2 (3-6) days for 3 egg clutches and 1.66 ± 0.3 (1-3) days for 2 egg clutches. There were no 4 egg clutches discovered during either breeding season. The data presented here for clutch size, laying intervals and hatch dates are not necessarily from the same nests used for nestling growth analysis due to the asynchrony of the breeding season.

Characteristics of nestling growth

Table 1 summarizes growth parameters of *K*, *A* and *ti* for the 31 birds fitted to the logistic growth equation (Ricklefs 1967) and tested for year, sex and their interaction by 2-way ANOVA adjusted for unequal sample size (Sokal and Rohlf 1981). The test revealed significant sexual differences in asymptote for mass, tarsus and culmen length and in the inflection point of culmen. There were no significant sexual differences in growth rate for any variable and no significant differences between years or interactions.

Table 2 summarizes growth parameters of *W*, *m* and *T* for the same individuals fitted with the Richards equation (Brisbin et al. 1986) and tested for year, sex and their interaction by 2-way ANOVA adjusted for unequal sample size. As above, the test revealed significant differences in asymptotes for mass, tarsus and culmen lengths and in overall growing time for tarsus length, but no significant sexual differences in curve shape (*m*) and no difference among years or interactions for any variable.

The curves in Figs. 2-8 represent means at 4-day intervals for all variables analyzed. The curves are based on an approximate total of 6,200 measurements of the 31 individuals (i.e. 8 measurements x 31 birds x 25 measurement days), providing quantitative data to distinguish points of divergence where they occur. Standard errors for weight and tarsus lengths (the only variables to show distinct asymptotes) are included in Figs. 2 and 3. Figs. 4-8 are presented without standard error bars for clarity of presentation.

Fig. 2 shows that the weights of male and female nestlings began to diverge prior to the inflection point. The sexes showed significant difference in asymptote and achieved absolute growth rates at inflection ($dW/dt = KAW(1-W)$, where $W = 0.5$ for the logistic equation, Ricklefs (1968) of 68.4 g for males and 79.6 g for females. The sexes did not differ significantly in the time to reach maximal observed weight with males averaging 45.4 ± 0.47 days and females, 46.1 ± 0.67 days.

Although female tarsal lengths remained slightly larger throughout the growth period (Fig. 3), actual divergence began past the inflection point. Males achieved absolute growth rates at inflection of 2.59 mm and females, 2.69 mm.

Talon length (Fig. 4) was remarkably similar between the sexes with no significant differences for any parameter of growth. Inflection occurred at about day 18 and the sexes first began to show divergence very late in the nestling period. Absolute growth at inflection averaged 0.89 mm for males and 0.88 mm for females.

Culmen lengths were significantly different by sex for asymptote and inflection (Fig. 5). Males achieved maximal daily growth rates of 0.66 mm and females 0.69 mm. Cranium width (Fig. 6) however, showed no differences for any parameter of growth and only began to diverge during the last quarter of the growth period. Male cranial growth had a maximal daily rate at inflection of 0.86 mm and females 0.89 mm.

Feather growth

Wingchord, eighth primary and central rectrix grew at similar rates throughout the nesting period (Figs. 7 and 8). Males had a maximal daily rate at inflection for wingchord of 11.7 mm while females averaged 12.1 mm.

The growth of primary and rectrix feathers (Fig. 8) were insufficient for growth curve analysis during the nestling period and were analyzed by comparing regression lines during the linear period of growth (i.e. beginning on day 20), following the methodology of Snedecor and Cochran (1978). Comparisons of slopes and elevations showed no significant difference between sexes or years for feather growth and no sexual difference in the age at which feathers first emerged (on day 9.02 ± 0.27 for males and day 9.08 ± 0.25 for females for eighth primary, and day 11.01 ± 0.22 and 10.83 ± 0.23 for central rectrice, respectively).

Brood size and hatch sequence were analyzed by comparing first (C1), second (C2) and third (C3) hatched chicks within each brood for fledging age, weight parameters of the logistic curve, (K, A and t_I), and feather emergence times for birds of the same sex. This procedure was repeated for the same parameters except weight asymptote for all birds in a brood, regardless of sex, using the Wilcoxon signed-ranks matched-pairs test. The test revealed no significant difference within broods for any measure of hatch sequence, with or without sexual considerations, or in growth parameters between broods of 1, 2 or 3 nestlings.

Geographic variation

Geographic variation was tested by comparing the means of weight and tarsus length growth parameters (the only 2 variables to show distinct asymptotes) by sex between the 2 populations. Since no significant year effects were detected in this population nor in the Nova Scotia population (Ch. I) I conducted *a priori* multiple comparisons by sex between populations using t-tests modified for equal and unequal variances, after testing each pair of samples with an F-statistic.

The results of differences from 9 comparisons (Table 3) showed that both males and females in the Mexican population reached significantly higher weight and tarsus asymptotes than the migratory Nova Scotia population. Growth rate constants and inflection points of both sexes were significantly different for weight but not tarsus length. Males and females in Mexico also took a significantly longer time to reach observed weight asymptotes and had significantly longer nestling periods than Nova Scotian ospreys.

Comparisons of the Richard's curve analysis for weight and tarsus length growth parameters (not presented here) produced similar results and showed an additional significant difference in the shape parameter (m) of male tarsus growth between populations.

Because weight specific growth did not vary between years or sexes in either population (ANOVA $P > 0.05$ in all cases, Ch. I), growth rate means were pooled, irrespective of sex, and compared between populations. Table 4 shows growth rate parameters of weight and tarsus length, for both logistic and Richards models, as well as fledging time and feather emergence time to be significantly different between the populations.

DISCUSSION

This study showed no significant difference between sexes in growth rate constants or curve shape parameters for any measure of growth within the Mexican population. The logistic model fitted to 31 nestlings showed a combined growth rate (K) for mass of 0.168 with a corresponding t_{10-90} of 26.2 days, representing 44% of the overall nestling period of 58.5 days. Stinson (1977) reported a logistic value of 0.120 for ospreys in the Chesapeake Bay, but he correlated the average age of a brood (some of which were artificially increased) with the average weight of chicks in the brood and may therefore have underestimated osprey growth rates (see Ch. I).

Schaadt (Ch. I) found only relative differences in the growth of male and female ospreys in Nova Scotia and suggested that sibling competition and hatching asynchrony had little effect in selecting for sex-specific growth within broods in that population. Sex-specific growth within this population also appears unrelated to sibling competition and hatching asynchrony as no differences were found in growth performance of chicks in broods of 1, 2 or 3 nestlings, regardless of sex composition, nor between these broods.

Several studies of growth of raptors (Newton 1979, Moss 1979, Bortolotti 1984a) and passerines (Richter 1983) have shown differences in growth dynamics of sexually dimorphic species where the smaller sex often shows earlier maturation of plumage and earlier fledging times. In this population, males and females grew at similar rates (Tables 2 and 3) and did not differ in feather emergence times or in fledging times.

Geographic variation

The pattern of growth exhibited between the sexes did not vary from the sex specific growth dynamics previously described for the Nova Scotia population (Ch. I). However, comparisons of the two osprey populations nesting at different latitudes showed significant difference in growth rate, asymptotic size and fledging time (Tables 3 and 4). Surprisingly, weight and tarsus length asymptotes of both sexes were significantly higher in the Mexican population which correspondingly showed reduced growth rate parameters for both logistic and Richards curve models (Table 4).

Few data exist for comparison. Poole (1982) compared 3 eastern

North American colonies (i.e. 1 sedentary colony located in Florida Bay and 2 migratory colonies on coastal Long Island, N. Y.) during a study of brood reduction, but did not fit growth curves to the growth data or consider sexual differences. Instead he compared slopes of regression lines of weight on age during the first half of the nestling period (from age 5 - 27 days) on birds grouped according to colony, brood size, and position in the hatch sequence. He found growth rates to be more variable between colonies than within nests and that the sedentary population grew significantly slower than one, but not both of the New York colonies. Poole attributed variation in growth to differences in food delivery rates between the colonies and to the "evolutionary pressures of sibling competition to equalize growth of nestlings".

Both osprey populations in this study are currently classified as the same subspecies by Prévost (1983) who described 4 subspecies worldwide. Prévost believed that morphological similarities between migrants and residents (based on museum specimens) suggest that this separation is more recent than the separation between North American and Palearctic ospreys and therefore prohibits the assignment of subspecies classification based solely on migratory habits.

Differences observed in growth rates may be allometrically related to the asymptotic size differences found between the populations. Ricklefs (1968) has shown that interspecifically, larger birds grow more slowly than smaller species. However, Schaadt (Ch. I) and Bortolotti (1984b) failed to show any relationship intraspecifically in ospreys and bald eagles (*Haliaeetus leucocephalus*) respectively, and Ross (1980) noted that most studies of passerines also failed to show a distinct relationship between growth rate and asymptote. It is doubtful therefore, that the difference in growth rates observed between the populations are a simple result of allometric scaling, although I have no data for adult body size in the Mexican population. O'Connor (1984) suggested that intraspecific growth rate and asymptote are independent variables which can be separately adjusted to ecological pressures.

Some of the variability observed in asymptotic size and possibly growth rate may be the result of phenotypic modifications in response to prevailing environmental conditions in the 2 populations. Several environmental factors which reflect differences in environmental conditions were evident between them, namely migratory habits (which are associated here with synchrony of the breeding season) and climatic factors. These conditions will be considered in terms of phenotypic adaptation and discussed in the context of ultimate factors relating to asymptotic size and possibly growth rate differences observed between the 2 populations.

Migratory versus sedentary habits

Implicit throughout this paper have been differences associated with migratory versus sedentary habits. In species with both migratory and sedentary populations, migratory individuals often have relatively longer wings and more pointed wingtips in relation to body size (Amadon 1943, Mayr 1963). Comparing osprey museum specimens, Prévost (1983) found that sedentary forms from the Red Sea and Bahamas populations had smaller wings and tails than their migratory counterparts, although the sample size was statistically too small. Consistent with this is the observation that male and female ospreys in Nova Scotia had significantly lower weight asymptotes than the non-migratory Mexican birds.

Mayr's suggestion (pers. comm. in Hamilton 1961) that a general reduction in body size would require less energy during migration and permit quicker restoration of expended fat deposits in migratory forms may also be related to the lower weight asymptotes found in the Nova Scotia population (Table 3).

Synchrony of the breeding season

Synchronous breeding, where individual pairs carry out stages of the reproductive cycle simultaneously, is characteristic of many colonial species, including migratory ospreys in coastal Nova Scotia (Prévost 1977, Schaadt Ch. I). Gochfeld (1980) suggested that the close association between spatial and temporal (synchronous) influence on nesting pairs should not be considered independent of coloniality. However, the spatial coloniality of ospreys in Mexico is independent of synchronous associations and may therefore be unrelated to the suggested adaptive advantages of coloniality such as reduced predation pressure or increased efficiency of food localization (Emlen and Demong 1975, Greene 1987). Populations in seasonal habitats may be highly synchronous simply because of limited time available for reproductive processes, which in this case does not confer a selective advantage (Findlay and Cooke 1982). Migratory ospreys at high latitudes are under considerable pressure to reproduce within well-defined reproductive seasons (Henny 1977), whereas sedentary ospreys in lower latitudes face much less pressure.

The idea that temporal synchrony of the reproductive period is an adaptation of birds nesting in seasonal habitats is supported by the fact that clutches in the migratory Nova Scotia population were all initiated within a 20 day period while those in Mexico were initiated during a minimum period of 101 days. Male and female nestlings in Nova Scotia also had significantly earlier emergence times for flight feathers and fledged from the nest earlier than Mexican birds (Table 3). Interspecifically, Bortolotti (1986) suggested that the short nestling periods in lesser spotted eagles (*Aquila pomarina*) may be associated with the degree of migratory movement and rapid growth observed in that species.

It is not known why lower-latitude ospreys nest during the winter and early spring months (Poole 1982, Judge 1983, this study). However, Suaretz (1983) speculated that for a sedentary population of ospreys nesting in desert conditions along the Red Sea, winter months provide optimal conditions for nesting with maximal temperatures below 30° C, although nighttime temperatures fall below 10° C. He believed that when hatching occurs in early March and April, day and night temperatures are most comfortable for nestling birds, whereas later hatched chicks experience temperatures over 40° C.

Climatic factors

There is some evidence of desert species not conforming to the general trends of Bergmann's rule (see Hamilton 1961), that intraspecifically, size increase is inversely correlated with temperature and therefore latitude (but see Geist (1987) for an alternative view). Ripley (1950, cited in Hamilton 1961) was first to note that birds from arid regions tend to be larger than those from more humid regions ("aridity effect" cited as Ripley's rule). Hamilton (1958) speculated that selection pressure for larger body size in birds in arid regions is due in part to the need to conserve water. Bartholomew and Dawson (1953) showed that respiratory water loss per unit body weight decreased with increased size in comparisons of several desert dwelling species. James (1970) believed that this "aridity effect" is operative at the intraspecific level and that the precise relationship between mean body size and the combined effects of temperature and moisture (and other climatic variables) may all be part of one complex phenomenon. Although the effects of aridity on geographic variation have not been fully studied, adaptation to desert conditions may contribute to the explanation of the higher nestling mass asymptotes found in desert ospreys in this study.

The large body size observed in sedentary ospreys may also be related to climatic factors in association with migratory habits. Since temperate zone ospreys spend the winter south of their sedentary conspecifics ("leapfrog migration"), the average annual temperature at which the northern-breeding birds live may be higher, and their body size therefore smaller, than sedentary birds at middle latitudes (Salomonsen 1955). This interpretation in support of Bergmann's rule illustrates the importance of considering factors affecting individuals year-round in studies of ecogeographical variation in species containing migratory and sedentary populations (Hamilton 1961).

Growth rates

Regarding the reduced growth rates observed in the Mexican population, O'Connor (1978) suggested that slow growth would be adaptive under conditions of varying food supply. I believe however, that the reduced growth rates (and possibly nesting asynchrony) observed in the Mexican population were unrelated to parental feeding abilities, primarily for the following reasons. 1) Growth rates within the population did not differ significantly between years. 2) Small fluctuations were observed in individual nestling weight growth curves. 3) Food is generally abundant and available in the subtropical Gulf of California (Thomson et al. 1979).

Sedinger (1986), in comparing geese that nest at different latitudes, suggested that growth rates may be related to daylength or the length of the growing season during broodrearing. Geese at lower latitudes grew considerably more slowly than those at higher latitudes. Daylength and growing season may similarly affect ospreys nesting at different latitudes in this study. There are of course many other possibilities such as nest mortality (for which I have no data) and predictability of the food supply (Case, 1978). It is indeed possible that intraspecific patterns of geographical variation detected here may not be adaptive in any sense (James 1983).

CONCLUSION

I have speculated that climatic factors in the sedentary, desert nesting population in Mexico and migratory habits (including time-limited synchronous breeding conditions) in the temperate Nova Scotia population may act in some way to account for size differences observed between the 2 populations.

I recognize the difficulties involved in assessing the significance of the small geographic variations observed in this study and that it is particularly difficult to attribute the patterns of growth directly to natural selection acting on growth itself (Bortolotti 1984b). However, natural selection does operate on morphological features, such as body size, which is an inevitable consequence of the geographical variation of the environment (Mayr 1963).

It is evident that ospreys must adapt themselves in different parts of their range to the demands of the local environment. The higher growth rates observed in Nova Scotia therefore, may reflect a maximum set by physiological constraints as suggested by Ricklefs (1969, 1973, 1979). The question remaining however, is whether the reduced growth rates observed in the Mexican population are an adaptation to which allow growth to be optimized with regard to the environmental factors found in that population, as was suggested by Lack (1968) and Case (1978).

Whatever the answer, this analysis should be considered as a plausible interpretation of the asymptotic size differences observed between the 2 populations and treated as a hypothesis stimulating further research into comparisons of intraspecific geographic variation in *Pandionidae*. Especially needed are further studies on food availability and adult body size from sedentary and migratory populations.

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TABLE 1. Growth parameters of logistic equation for nestling ospreys in Mexico by sex. Values are means ± S.D. (range).

			Growth parameter		
variable	sex	n	*K*	*A*	*ti*
Weight	M	13	0.167 ± 0.004 (0.162-0.173)	**1638.9 ± 30.9 (1581-1683)	21.5 ± 0.9 (20.4-22.9)
	F	18	0.169 ± 0.004 (0.164-0.176)	1885 ± 123.6 (1700-2105)	21.3 ± 0.9 (20.2-22.9)
Tarsus	M	13	0.142 ± 0.004 (0.136-0.149)	**73.1 ± 0.7 (71.9-74.7)	12.7 ± 1.1 (12.2-13.2)
	F	18	0.141 ± 0.006 (0.131-0.148)	76.2 ± 1.6 (73.4-79.1)	13.1 ± 1.0 (11.8-15.2)
Talon	M	13	0.111 ± 0.006 (0.098-0.117)	32.1 ± 0.5 (31.0-32.5)	18.4 ± 0.9 (16.2-19.3)
	F	18	0.110 ± 0.008 (0.096-0.123)	32.0 ± 0.8 (31.0-33.5)	18.7 ± 1.2 (17.0-20.3)
Culmen	M	13	0.082 ± 0.006 (0.075-0.093)	**32.3 ± 0.5 (32.0-33.5)	*10.8 ± 1.0 (9.3-12.1)
	F	18	0.083 ± 0.005 (0.076-0.095)	33.5 ± 1.0 (32.0-35.5)	11.5 ± 1.2 (9.8-13.6)
Cranium	M	13	0.078 ± 0.005 (0.067-0.083)	43.9 ± 0.9 (42.5-45.0)	5.5 ± 0.8 (4.1-6.0)
	F	18	0.080 ± 0.005 (0.071-0.086)	44.4 ± 0.6 (43.5-45.0)	5.7 ± 0.9 (4.1-6.2)
Wingchord	M	13	0.095 ± 0.005 (0.087-0.104)	495.9 ± 4.8 (490-500)	32.3 ± 1.1 (30.7-33.9)
	F	18	0.095 ± 0.005 (0.087-0.103)	507.1 ± 6.9 (495-515)	32.7 ± 1.6 (28.6-34.5)

* Males are significantly different from females, ANOVA $P < 0.05$.
** Males are significantly different from females, ANOVA $P < 0.01$.

TABLE 2. Growth parameters of Richards equation for nestling ospreys in Mexico by sex. Values are means ± S.D. (range).

variable	sex	n	Growth parameter *M*	 *W*	 *T*
Weight	M	13	1.01 ± 0.20 (0.74-1.35)	**1709.1 ± 87.7 (1575-1839)	41.4 ± 3.6 (35.6-46.7)
	F	18	1.05 ± 0.20 (0.80-1.38)	1938.1 ± 135.4 (1748-2129)	39.2 ± 3.4 (32.6-43.1)
Tarsus	M	13	1.66 ± 0.70 (0.81-2.84)	**73.3 ± 1.4 (71.0-75.1)	44.6 ± 2.1 (41.4-48.1)
	F	18	2.02 ± 0.45 (1.49-2.82)	76.4 ± 1.8 (73.2-79.0)	46.0 ± 1.9 (41.8-49.0)
Talon	M	13	1.50 ± 0.15 (1.29-1.68)	31.2 ± 0.7 (29.8-32.2)	50.6 ± 3.1 (46.7-55.9)
	F	18	1.59 ± 0.27 (1.25-2.05)	31.5 ± 1.1 (29.7-32.8)	52.6 ± 4.1 (47.2-58.7)
Culmen	M	13	1.81 ± 0.40 (1.13-2.29)	*32.0 ± 0.8 (30.7-33.2)	76.0 ± 5.5 (66.1-82.5)
	F	18	1.72 ± 0.43 (1.08-2.33)	34.0 ± 2.1 (31.3-37.7)	76.0 ±0.4 (65.6-84.8)
Wingchord	M	13	1.45 ± 0.35 (1.00-2.20)	481.6 ± 14.4 (461.2-510.5)	59.9 ± 5.7 (54.1-70.0)
	F	18	1.45 ± 0.21 (1.01-1.86)	485.2 ± 21.5 (454.9-531.1)	61.0 ± 6.5 (54.9-77.4)

*** Males are significantly different from females, ANOVA $P < 0.05$.**
**** Males are significantly different from females, ANOVA $P < 0.01$.**

TABLE 3. Comparisons by sex of growth parameters of the logistic equation of weight and tarsus length between sedentary and migratory osprey populations. Values are means ± S.E.

Variable	Sex	Nova Scotia [a]	Mexico	% [b]	P [c]
WEIGHT					
Asymptote [d] (A)	M	1499.5 ± 32.5	1638.9 ± 8.5	8.5	0.001
	F	1790.1 ± 12.7	1884.8 ± 29.1	13.1	0.017
Growth rate [d] constant (k)	M	0.1797 ± 0.001	0.1669 ± 0.001	7.1	0.000
	F	0.1804 ± 0.002	0.1691 ± 0.001	6.3	0.000
Inflection [d] point (t_i)	M	19.3 ± 0.25	21.5 ± 0.29	10.2	0.000
	F	20.4 ± 0.31	21.3 ± 0.26	4.3	0.042
Days to reach asymptote	M	41.6 ± 0.27	44.4 ± 0.47	6.3	0.000
	F	42.6 ± 0.20	46.2 ± 0.67	7.8	0.000
Days to reach fledging	M	54.4 ± 0.64	57.8 ± 0.71	5.4	0.002
	F	56.0 ± 0.87	59.1 ± 0.42	5.2	0.003
TARSUS					
Asymptote (A)	M	71.1 ± 0.35	73.1 ± 0.22	2.7	0.000
	F	73.9 ± 0.48	76.2 ± 0.40	3.0	0.001
Growth rate constant (k)	M	0.1432 ± 0.002	0.1420 ± 0.002	0.8	*0.592
	F	0.1420 ± 0.002	0.1410 ± 0.002	0.7	*0.631
Inflection point (t_i)	M	11.9 ± 0.26	12.7 ± 0.36	6.3	0.047
	F	12.9 ± 0.41	13.1 ± 0.29	1.5	*0.703
Days to reach asymptote	M	43.5 ± 0.29	43.7 ± 0.39	0.5	*0.531
	F	43.1 ± 0.45	46.5 ± 0.50	7.3	0.000

* N.S.

[a] migratory population

[b] % difference between populations

[c] probability of a greater t value, *a priori* multiple comparisons using modified t-test (see text)

[d] logistic equation according to Ricklefs (1967)

TABLE 4. Comparisons of growth parameters of weight and tarsus length between sedentary and migratory osprey populations. Values are means ± S.E.

Variable	Nova Scotia [a]	Mexico	% [b]	P [c]
WEIGHT				
Logistic growth rate constant (K) [d]	0.1800 ± 0.001	0.1681 ± 0.001	6.7	0.000
Richards curve shape parameter (m) [e]	1.27 ± 0.03	1.02 ± 0.04	19.7	0.000
TARSUS				
Logistic growth rate constant (K)	0.1429 ± 0.001	0.1419 ± 0.001	0.7	0.524
Richards curve shape parameter (m)	2.25 ± 0.09	1.84 ± 0.13	18.2	0.016
FLEDGING TIME	55.0 ± 0.09	58.7 ± 0.13	6.3	0.000

[a] migratory population
[b] % difference between populations
[c] probability of a greater t value, *a priori* multiple comparisons using modified t-tests (see text)
[d] logistic equation according to Ricklefs (1967)
[e] Richards equation rewritten by Brisbin et al. (1986)

Fig. 1. Map of the study area in Sonora, Mexico showing the 1985 (Desemboque) location and the 1987 (Punta Baja) location.

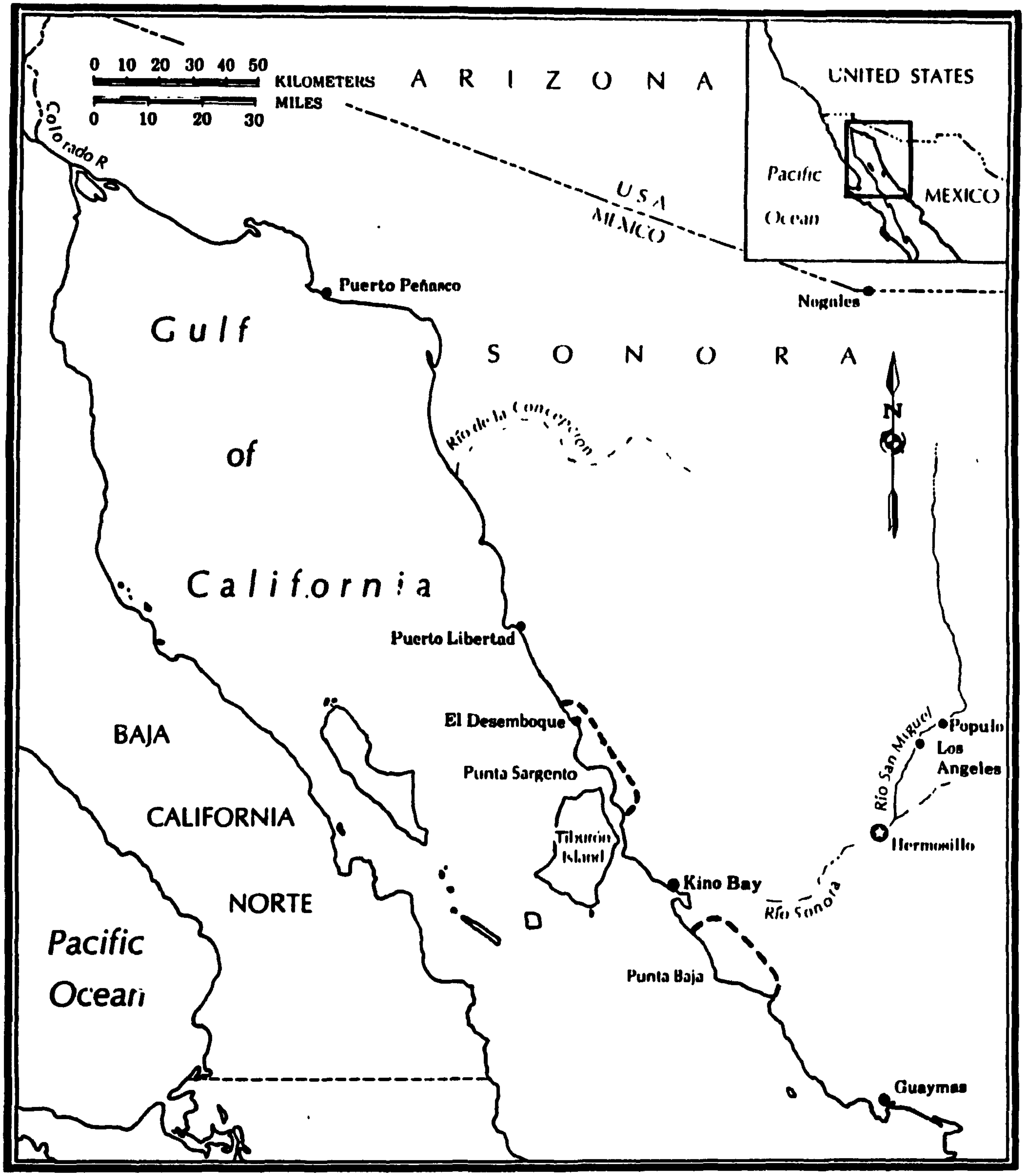

0 10 20 30 40 50
KILOMETERS
MILES
0 10 20 30
ARIZONA
UNITED STATES
Pacific Ocean
MEXICO
Colorado R
USA
MEXICO
Puerto Peñasco
Nogales
Gulf of California
SONORA
N
Río de la Concepción
Puerto Libertad
El Desemboque
Punta Sargento
Tiburón Island
BAJA CALIFORNIA NORTE
Pacific Ocean
Río San Miguel
Populo
Los Angeles
Hermosillo
Kino Bay
Río Sonora
Punta Baja
Guaymas

Fig. 2. Mean mass curves at 4 day intervals of male and female nestling ospreys plotted against day at which growth occurred.

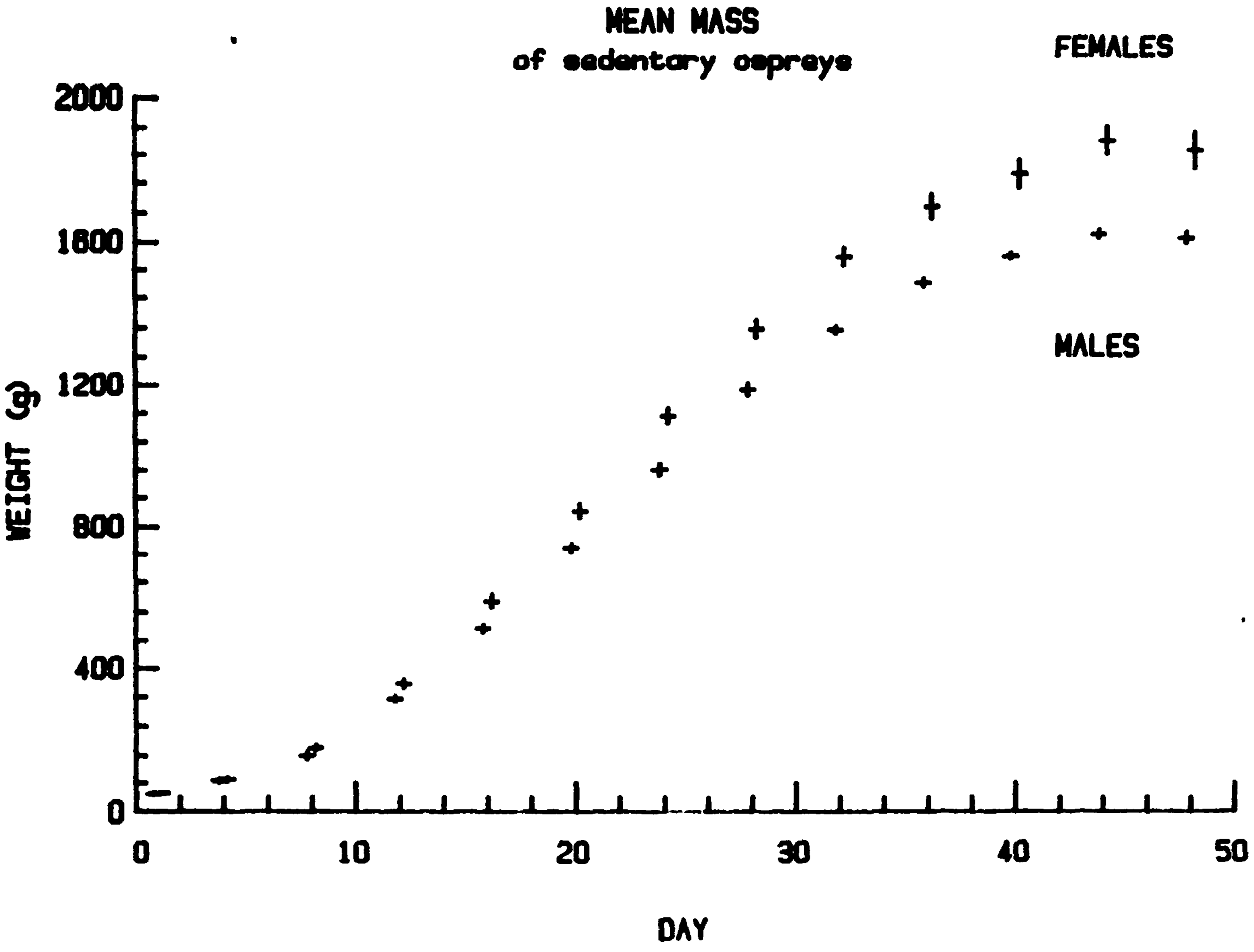

MEAN MASS
of sedentary ospreys
FEMALES
MALES
WEIGHT (g)
2000
1600
1200
800
400
0
0
10
20
30
40
50
DAY

Fig. 3. Mean tarsus length curves at 4 day intervals of male and female nestling ospreys plotted against day at which growth occurred.

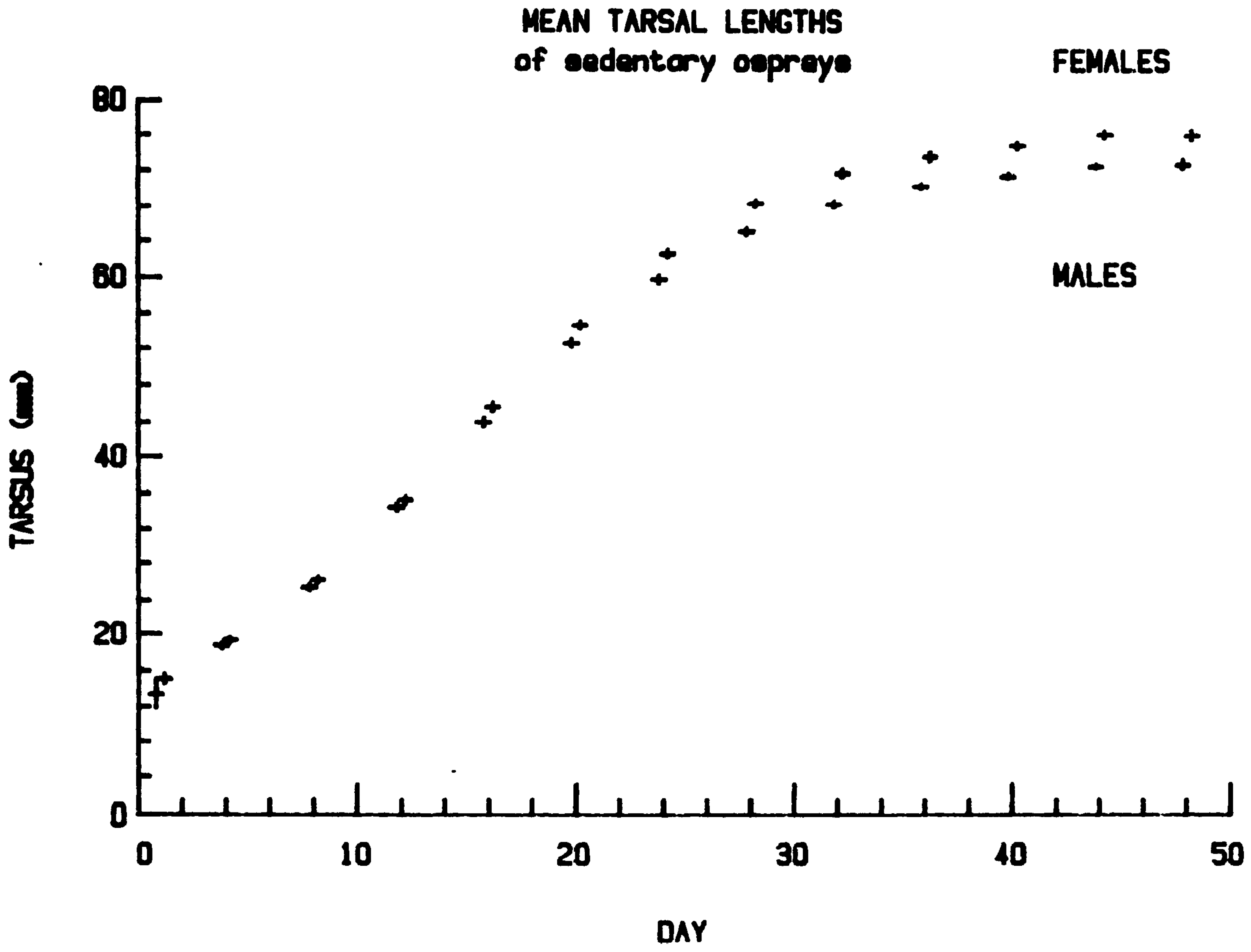

MEAN TARSAL LENGTHS
of sedentary ospreys
FEMALES
MALES
TARSUS (mm)
80
60
40
20
0
0
10
20
30
40
50
DAY

Fig. 4. Mean talon length curves at 4 day intervals of male (dashed line) and female (solid line) nestling ospreys plotted against day at which growth occurred.

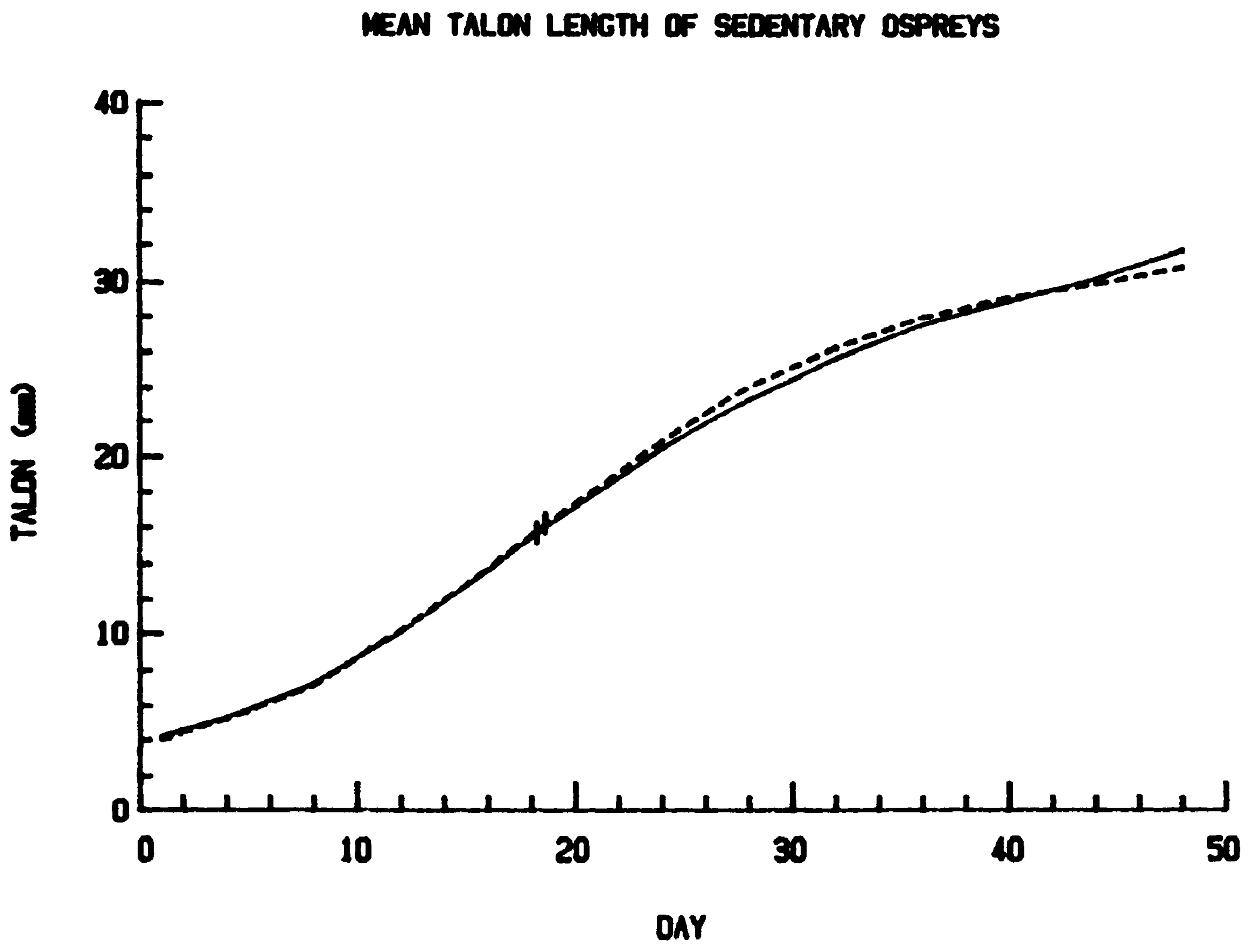

MEAN TALON LENGTH OF SEDENTARY OSPREYS
TALON (mm)
40
30
20
10
0
0
10
20
30
40
50
DAY

Fig. 5. Mean culmen length curves at 4 day intervals of male (dashed line) and female (solid line) nestling ospreys plotted against day at which growth occurred.

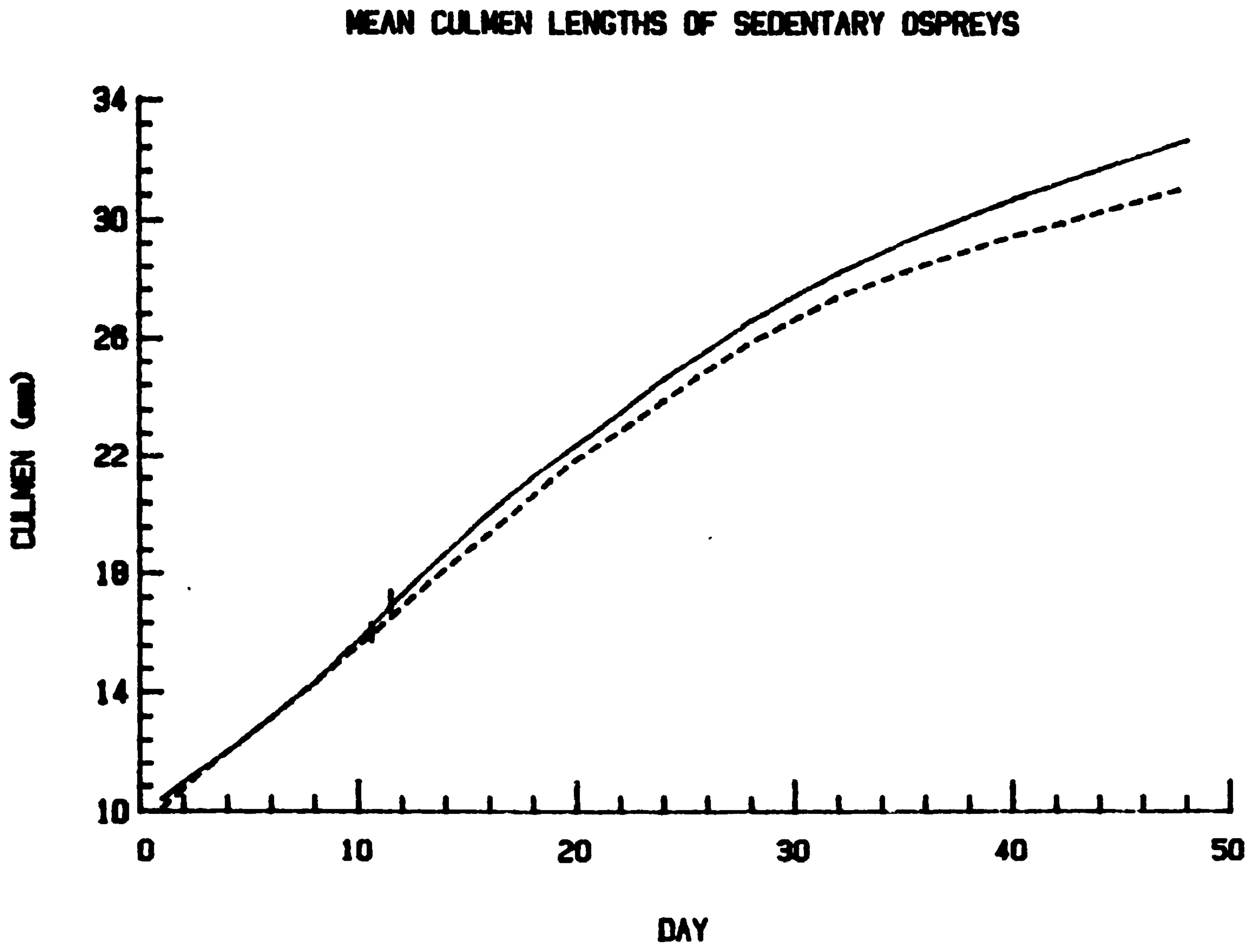

MEAN CULMEN LENGTHS OF SEDENTARY OSPREYS
CULMEN (mm)
34
30
26
22
18
14
10
0
10
20
30
40
50
DAY

Fig. 6. Mean cranium width curves at 4 day intervals of male (dashed line) and female (solid line) nestling ospreys plotted against day at which growth occurred.

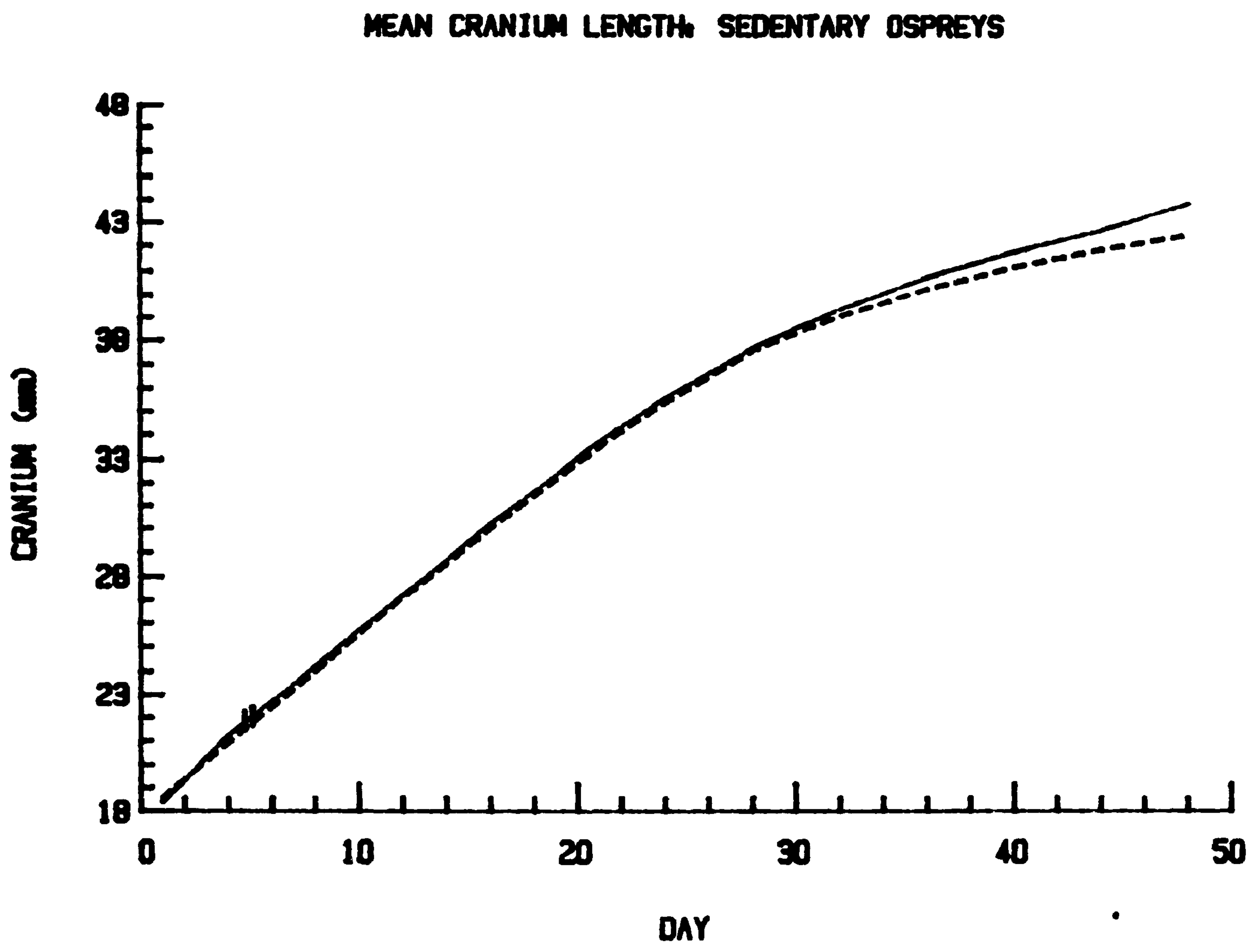
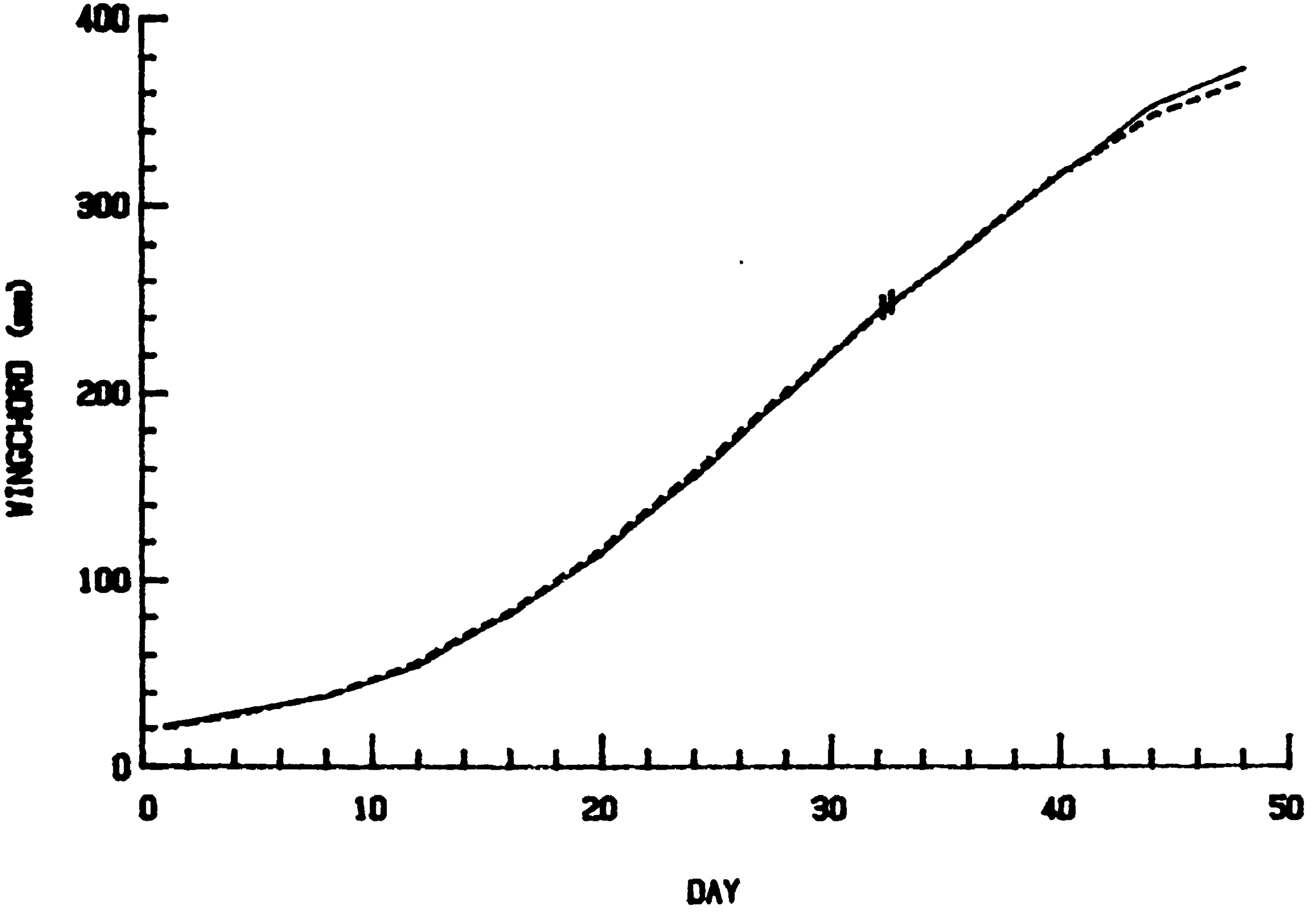
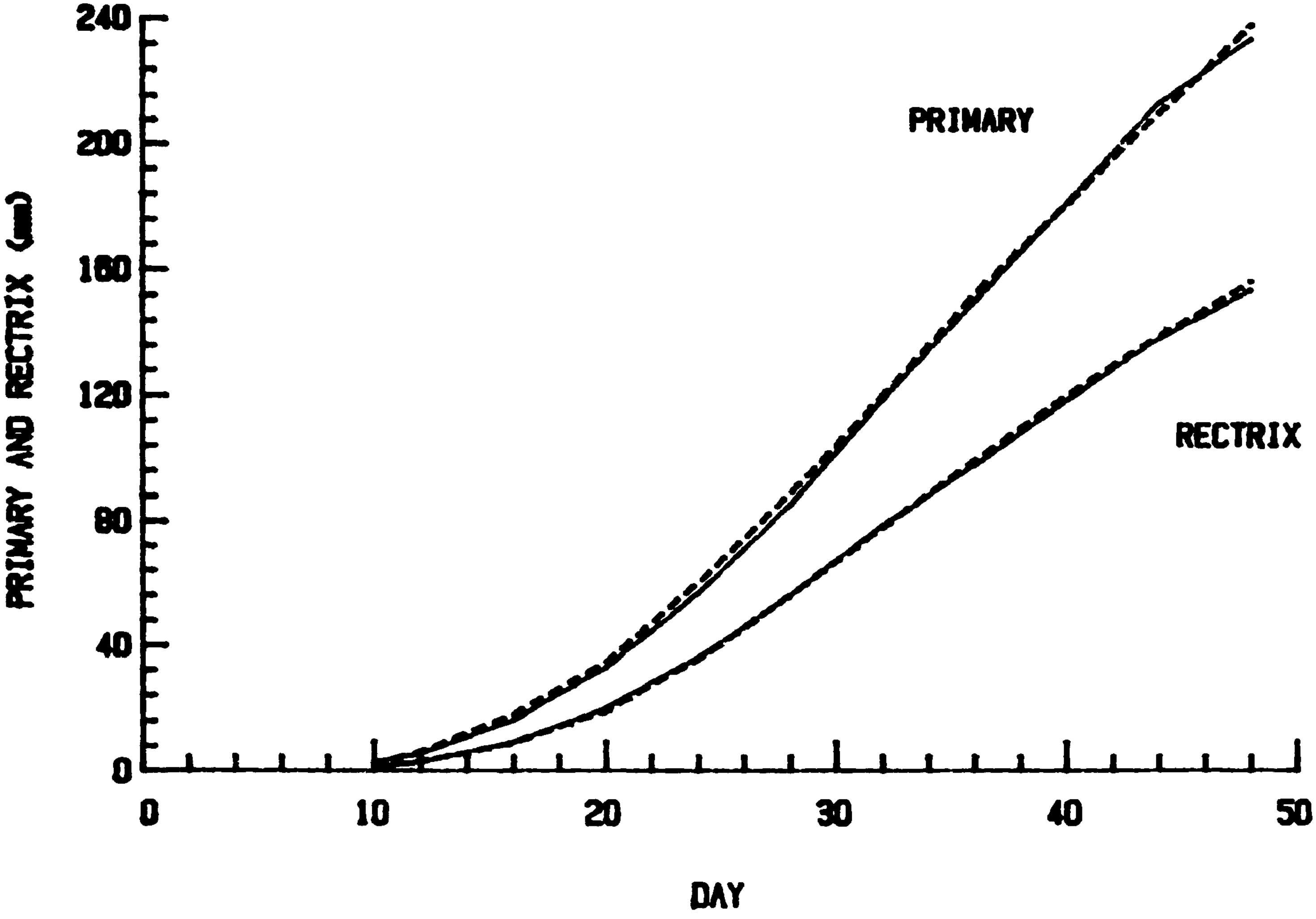

MEAN CRANIUM LENGTH: SEDENTARY OSPREYS
CRANIUM (mm)
48
43
38
33
28
23
18
0
10
20
30
40
50
DAY

Fig. 7. Mean wingchord length curves at 4 day intervals of male (dashed line) and female (solid line) nestling ospreys plotted against day at which growth occurred.



MEAN WINGCHORD LENGTH: SEDENTARY OSPREYS

Fig. 8. Mean primary and rectrix length curves at 4 day intervals of male (dashed line) and female (solid line) nestling ospreys plotted against day at which growth occurred.



MEAN PRIMARY AND RECRIX LENGTHS
SEDENTARY OSPREYS

CONNECTING STATEMENT

Chapters I and II were concerned with the growth of individual male and female nestling ospreys. However, osprey nestlings have no obvious external characteristics which can be used to determine their sex. Therefore, in Chapter III I present the results of an investigation of osprey karyotypes used to identify the sex of a sample of 31 nestlings in this study.

CHAPTER III: Chromosomes of the osprey *Pandion haliaetus*: Studies in solid Giemsa and GTG banding

ABSTRACT

A chromosome analysis of 31 ospreys was performed on fibroblast cells obtained from skin tissue. The chromosome number was found to be 2n=74. The division between macrochromosomes and microchromosomes was not always distinct, but the number of identifiable pairs was typically 26 with 22 microchromosomes (11 pair) remaining. Positive identification of the sex chromosomes was determined by solid Giemsa and GTG banding. The Z chromosome is similar in size and arm ratio to chromosome 1 while the W chromosome closely matches chromosome 7. The reliability and efficiency of this technique are discussed as well as karyological relationships within the Falconiformes.

INTRODUCTION

Although Class Aves is well studied, much of its karyology remains unexplored with fewer than 5% of avian species having been karyotyped (De Boer and Van Brink 1982; Shields 1982, 1983; Tegelstrom et al. 1983; Belterman and De Boer 1984; De Boer 1984). Furthermore, in the majority of studies, banding techniques have been conspicuously absent due to the difficulty of obtaining chromosomal material suitable for banding, as well as the time and extensive laboratory facilities these cultures require (Christidis 1985).

Many species of birds have no external characteristics which can be used to determine their sex. This is particularly true in species where nestlings hatch asynchronously, e.g. ospreys. The goals of the present study therefore, were twofold: 1) to sex nestling ospreys without sacrificing them and 2) to obtain basic data on osprey karyology. This paper describes the karyotype of the osprey using solid Giemsa stain and GTG banding techniques on fibroblast cells derived from skin tissue cultures.

METHODS

Fibroblast cells were obtained from the underwing patagium of 31 nestling ospreys collected in the field. A small area was cleared of feathers, swabbed with alcohol, and a 3 mm^3 sample of skin was excised using forceps and scissors. The tissue was placed in culture medium and shipped to the laboratory within 24 hours when possible, or refrigerated (4°C) until shipping could be accomplished. Upon receipt, cultures were established using minimal essential medium (MEM) + 15% fetal bovine serum (FBS) with antibiotics and incubated at 37°C in a CO_2 environment. When necessary, cultures were frozen and cells stored in liquid nitrogen for periods of 3 months to 1 year, then regrown for analysis.

At harvest, cells were treated with colcemid (0.2ug/ml culture medium) for 3 hours followed by hypotonic treatment with a warm 1:1 KCl/PO_4 solution. Cell preparations were fixed with cold Carnoy's solution and washed 3 times with the same fixative. The cell suspension was dropped onto frozen slides and the fixative evaporated over boiling water.

Slides for chromosome counts and morphological measurements were stained with 4% Giemsa. Length measurements and arm ratios (AR) were calculated for 10 metaphase cells (7 males, 3 females). Chromosomes were arranged into groups on the basis of relative length and centromeric position corresponding to the nomenclature of Levan et al. (1964), (metacentric: AR 1.0 to 1.7; submetacentric: AR 1.7 to 3.0; subtelocentric: AR 3.0 to 7.0; acrocentric: AR > 7.0). Relative length is defined as the percent of the total Z containing haploid chromosome length (%TCL) excluding the microchromosomes.

GTG banding using 0.05% trypsin in normal saline (0.9% NaCl) was used for chromosome identification. An idiogram of the banded karyotype was constructed for the macrochromosomes.

RESULTS

Chromosome number counts of 100 metaphase cells indicate a diploid number of 74. The karyotype is made up of a range of medium to small chromosomes as well as a large number of microchromosomes, but lacks any true large chromosomes (greater than 7.5 %TCL). The division between macrochromosomes and microchromosomes is not always distinct, but the number of identifiable pairs is typically 26 with 22 microchromosomes remaining (Fig. 1).

The majority (10/26) of the macrochromosomes are acrocentric, 7/26 are metacentric, 6/26 are submetacentric and 3/26 are subtelocentric. The actual number of pairs falling into submetacentric and subtelocentric categories in a given karyotype varied by 1 or 2 due to the clarity and degree of contraction of the metaphase spreads. Mean values for relative lengths, centromeric index and arm ratios are given in Table 1.

The macrochromosomes have been divided into 5 groups. The first group contains 3 relatively large metacentric to submetacentric pairs (1-3). Pair 2 is notable in that it contains a large non-staining region on the long arm and is frequently found in side to side association. The second group (pairs 4-7) contains 2 medium sized metacentrics and 2 small metacentrics of similar size and arm ratio. The third group contains 5 submetacentrics (pairs 8-12) of which pairs 11 and 12 are not always distinguishable. Group 4 contains 3 medium sized subtelocentrics (pairs 13-15). The remaining macrochromosomes (pairs 16-25) are acrocentric ranging in size from relatively large to small. The smaller pairs are difficult to identify without banding, although pair 25 often shows minute short arms. The Z chromosome is very similar to chromosome 1 in both size and arm ratio and is therefore not accurately identifiable, especially in the homomorphic male, using solid Giemsa stain. The W chromosome is a metacentric chromosome very similar to pairs 6 and 7. About half of the 22 microchromosomes can be seen to be acrocentric while the rest appear as dots.

Eight suitable GTG banded metaphase spreads were obtained representing 5 male and 3 female ospreys (Fig. 2). All the macrochromosomes have recognizable banding patterns except pairs 11 and 12. These two were indistinguishable in most of the karyotypes other than by a small size difference. The Z chromosome is easily identified by 4 equally small dark bands on the long arm while chromosome 1 is characterized by a median large dark band on the long arm and a prominent proximal dark band on the short arm. The banding pattern of the W chromosome closely matches the banding pattern of chromosome 6. These features are illustrated on an idiogram (Fig. 3).

DISCUSSION

Fibroblast cells derived from skin tissue proved to be a reliable technique of sexing osprey nestlings without risk of injury. A 100 percent success rate (n=26) was achieved with samples received in the lab within 48 hours, but viability dropped to 63% (n=27) when delivery was delayed by 1 week. The total of these figures is greater than 31 because 2 samples were obtained from some birds. Tissue cultures provided an additional advantage of continuous cell lines which remained viable after 1 year of storage in liquid nitrogen.

Solid Giemsa and GTG banding have provided the most obvious features of the osprey karyotype. Determining the sex of an individual bird (by the presence or absence of a heteromorphic pair) was possible using solid Giemsa stain, but positive identification of the sex chromosomes required GTG banding.

Finally, views differ as to the taxonomic position of the osprey within the order Falconiformes. Brown and Amadon (1968) placed the osprey, the sole member of the family Pandionidae, in the suborder Accipitres along with Accipitridae and Sagittariidae. Close relationship to Accipitridae is suggested by similarities in egg-white protein properties (Sibley and Ahlquist 1972) while arrangement of feather tracts resemble that of Cathartidae (Comptom 1938).

Although Accipitridae shows considerable variation between member species in both diploid number (2n=78-54) and the number of biarmed chromosomes, De Boer (1976) has identified 4 characteristics common to the family: 1) a low number of microchromosomes (6-12); 2) the absence of very large macrochromosomes; 3) a higher number of biarmed than acrocentric macrochromosomes; 4) the presence of a satellited chromosome pair.

Initial comparisons of karyotypes show no similarities to Cathartidae or Falconidae. The osprey does share some Accipitridae characteristics, i.e. a moderately high diploid number, a predominance of biarmed macrochromosomes and the absence of any truly large chromosomes, but differs by having a high number of microchromosomes and the lack of satellited pairs.

De Boer (1976) recommended treating Cathartidae, Falconidae, Sagittariidae and Accipitridae as distinct groups within Falconiformes. Since the osprey karyotype does not suggest any new relationships we conclude that Pandionidae should also be included as a separate group within the order.

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Table 1: Percent of total chromosomal lengths (%TCL), centromere indices (CI), and arm ratios (AR) of osprey macrochromosomes. Values are $\bar{X} \pm$ S.D. n=10.

No.	Group	%TCL	CI	AR
1	1	6.4±0.34	41.6±0.96	1.4±0.12
2	1	6.3±0.60	33.2±3.02	2.0±0.26
3	1	5.0±0.37	43.4±2.14	1.3±0.10
4	2	4.5±0.37	40.4±3.27	1.5±0.22
5	2	4.5±0.30	44.2±3.51	1.3±0.12
6	2	2.8±0.22	45.9±2.58	1.2±0.12
7	2	2.6±0.24	47.0±2.38	1.1±0.11
8	3	4.2±0.28	27.8±2.71	2.6±0.36
9	3	4.0±0.27	32.4±2.26	2.2±0.25
10	3	3.2±0.24	30.1±3.77	2.3±0.46
11	3	3.0±0.12	30.8±4.82	2.3±0.46
12	3	2.8±0.22	32.7±4.65	2.0±0.30
13	4	5.2±0.34	17.8±3.97	4.8±1.14
14	4	4.0±0.17	22.5±4.69	3.3±0.62
15	4	3.6±0.21	24.4±5.66	3.3±0.89
16	5	5.5±0.27		
17	5	4.7±0.33		
18	5	4.0±0.31		

Table 1: (continued)

No.	Group	%TCL	CI	AR
19	5	2.9±0.23		
20	5	2.7±0.19		
21	5	2.6±0.16		
22	5	2.5±0.11		
23	5	2.4±0.14		
24	5	2.1±0.24		
25	5	2.0±0.26		
Z		6.6±0.39	41.6±2.90	1.4±0.13
W		3.1±0.22	46.5±1.35	1.1±0.06

FIG. 1. Representative karyotype of a female osprey using solid Giemsa stain.

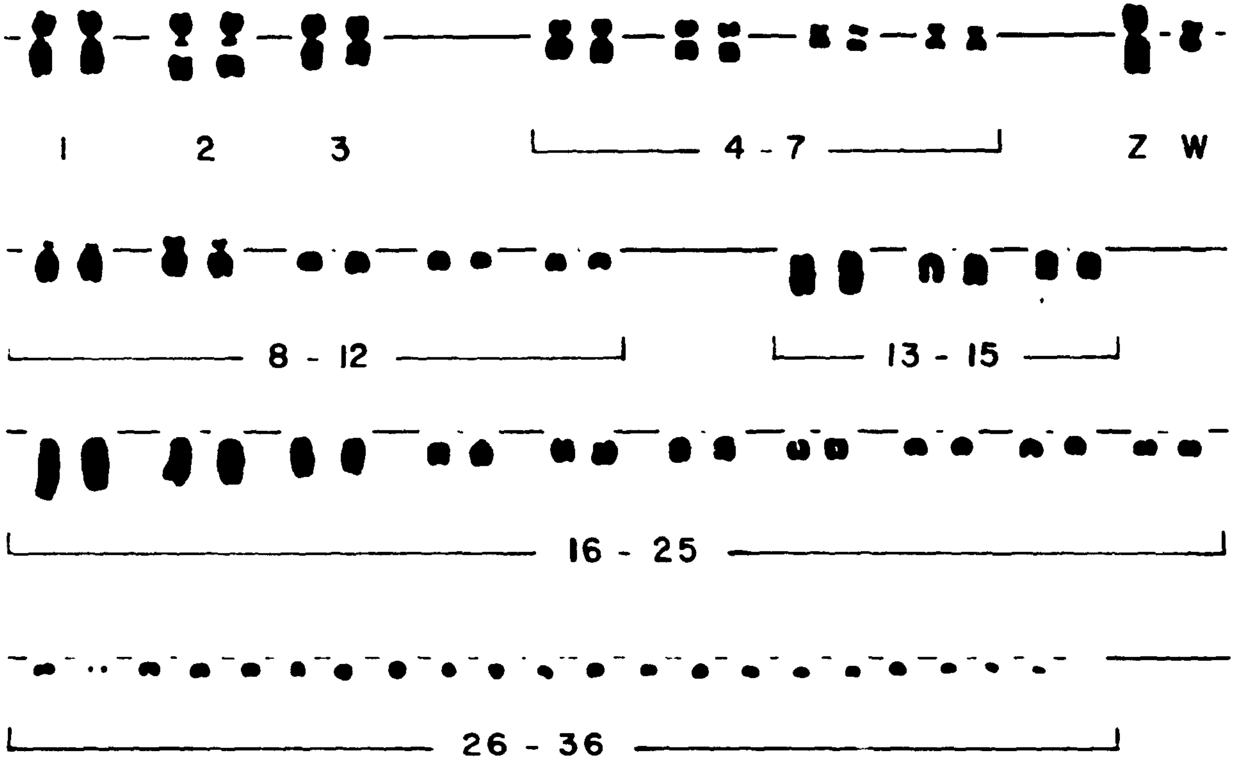

1
2
3
4 - 7
Z W
8 - 12
13 - 15
16 - 25
26 - 36

FIG. 2. GTG banded karyotype of a female osprey .

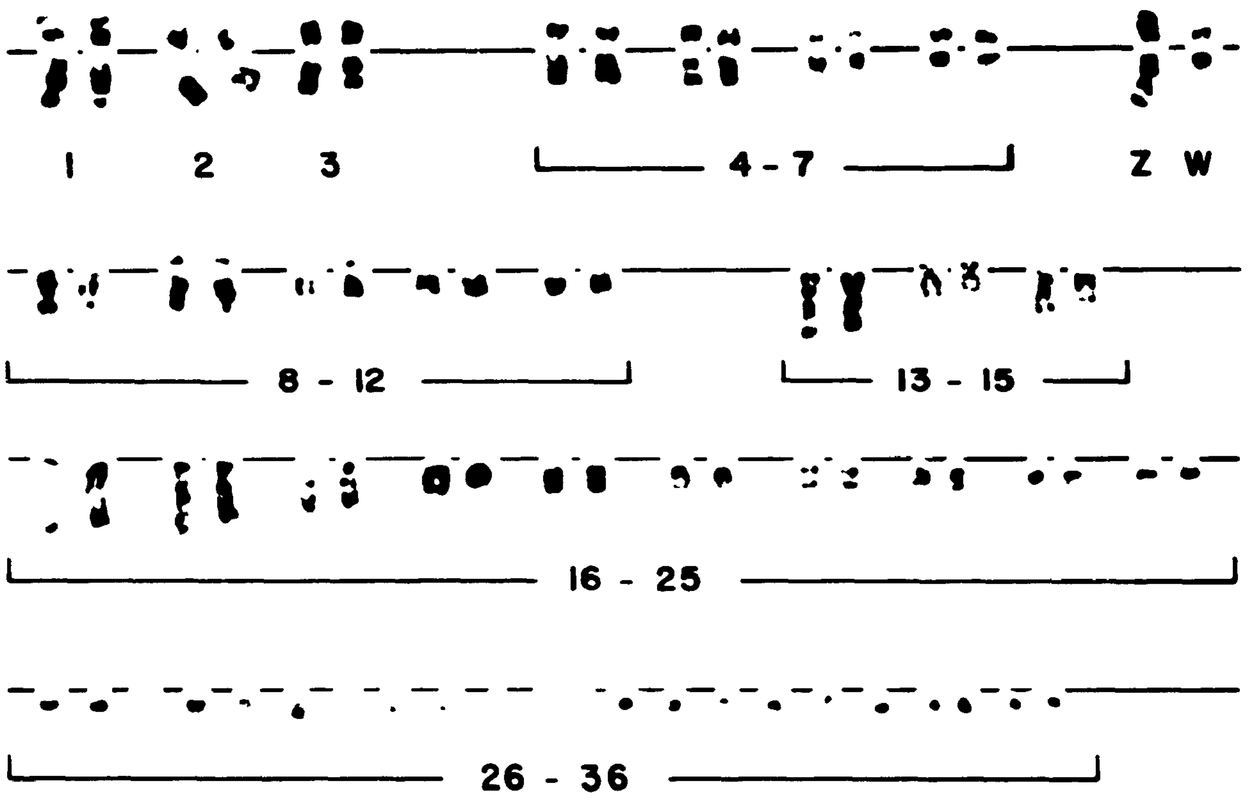
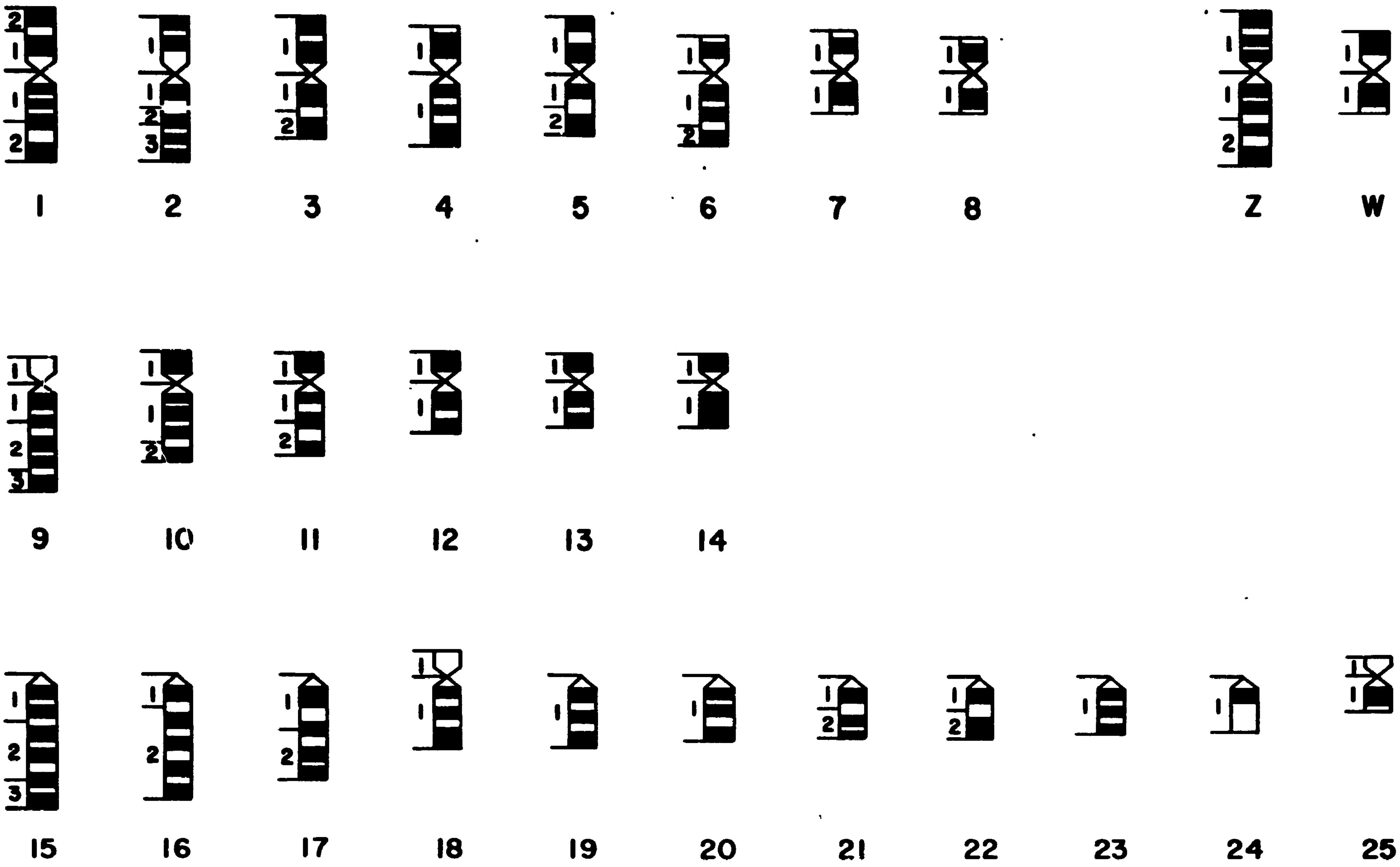

1
2
3
4 - 7
Z W
8 - 12
13 - 15
16 - 25
26 - 36

FIG. 3. Idiogram of GTG banded macrochromosomes.



1
2
3
4
5
6
7
8
Z
W
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25

STATEMENT OF ORIGINALITY

This thesis includes the following original contributions to the scientific literature:

- Quantification of sex-specific growth and asymptotic size of nestling osprey.
- Quantitative comparisons of differential growth of morphometric characteristics between male and female osprey nestlings.
- Documentation of timing and growth of plumage characteristics of osprey nestlings identified by sex.
- Quantification of geographic variation in growth parameters and body components of nestling ospreys in migratory and sedentary populations (perhaps the only such study for any raptorial species).
- Comparisons of observed and predicted asymptotes and growth parameters analyzed using the logistic model and the reparameterized Richards model.
- Quantification of the influence of brood size, hatch order and sex on the growth of osprey nestlings.
- Intraspecific evidence of larger body size and reduced growth rates, by sex, in a sedentary population nesting in desert conditions compared to a temperate migratory population.

- Comparisons of sex-specific growth of nestling ospreys in relation to published models of temperate zone passerines and raptors.

- Evidence contradicting published reports of predictions of sex-specific growth dynamics of dimorphic species, i.e. the smaller sex (males) should develop feathers earlier and leave the nest sooner than the larger sex (females) and the larger sex being more variable in weight accumulation

- The use of karyotypic analyses to identify the sex of nestling ospreys without sacrificing the bird.

- The first avian species to be karyotyped using cultures derived from skin tissue samples.

- First osprey karyotype to incorporate banding techniques.

CONCLUSION

This study did not support the prediction that males (the smaller sex) should develop feathers earlier and leave the nest sooner than females nor did it find the females to be more variable in growth. Therefore, the idea that males are at a competitive disadvantage and should grow faster than females seems maladaptive in ospreys in light of the much greater differences imposed by hatching asynchrony.

It was more difficult however, to assess the significance of the geographic variation in growth rate and asymptotic size observed in this study. It was evident that ospreys must adapt themselves in different parts of their range to the demands of the local environment but extensive studies on growth from sedentary and migratory populations (as well as food availability and adult body size) will be necessary before the observed patterns in growth rate can be directly attributed to natural selection acting on growth itself.