GROWTH RATES OF NESTLING EGYPTIAN VULTURES
Neophron percnopterus IN RELATION TO BROOD SIZE, HATCHING
ORDER AND ENVIRONMENTAL FACTORS

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ABSTRACT   Patterns of growth in weight, tarsus and feather (primary) are described for nestling Egyptian Vulture *Neophron percnopterus* in northern Spain. Maximum increase in weight and tarsus respectively occurred before 40 and 30 d. The primary growth rate was almost constant until fledging (75 d). Second-hatched nestlings either died before 14 d or grew in weight and tarsus at slower rates than first-hatched and single nestlings during the first development period (1-20 d). During the last period (40-60 d), however, this tendency reversed. Second-hatched nestling also suffered a relative delay in dates of primary emergence and achievement of feather fledging size. Hatching date and food habits were not related with growth patterns. A long period of rainy days seemed to affect to growth rates of second-hatched nestlings during the last development period favouring maintenance of feather growth in detriment of tarsus. The growth rates of the Egyptian Vulture seem to act as a fine-tuning mechanism of productivity.

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INTRODUCTION

Intraspecific variations in avian growth rates are determined by environmental factors such as diet quality, food availability, weather and other variables as brood size and hatching sequence (see Ricklefs 1983, O'Connor 1984 for reviews). Species with low biomass are known to regulate their reproductive effort by means of the clutch size, as a result of which growth rates are not subjected to great variation. In these species, regulation of parental investment may be attained after hatching through nestling starvation and brood reduction. This strategy is frequent among small and medium-sized raptors and owls (Newton 1979, Mikkola 1983) because the availability of food for nestlings may not be predictable at laying (O'Connor 1977). On the contrary, the growth rates of birds with reduced clutch size (1-2) can undergo great fluctuations, acting as a fine-tuning mechanism with regard to adverse environmental conditions (Ricklefs 1968, Drent & Daan 1980, O'Connor

1984). Brood reduction in these species seems to be almost independent of the physical conditions of the nestlings (Simmons 1988).

Old World vultures (Accipitridae) have low breeding rates (maximum of 1 young/pair/year) and very slow growth rates (Brown & Amadon 1968, Newton 1979, Drent & Daan 1980, Mundy 1982, Hiraldo 1983) probably caused by scarcity and unpredictability of food and/or dietary deficiencies (Houston 1978, Hiraldo *et al* 1979). The Egyptian Vulture is, with the Lammergeier *Gypaëtus barbatus*, the only vulture whose clutch usually has 2 eggs (Brown & Amadon 1968, Cramp & Simmons 1980). In Mediterranean Europe the clutch size of the Egyptian Vulture averages 1.86 ($n = 44$) and the mean brood size at fledging 1.42 ($n = 156$) (Bergier & Cheylan 1980, Donázar & Ceballos 1988). So, in most of the nests brood reduction occurs (see also Rodríguez-Jiménez & Balcells 1968, Mendelssohn & Leshem 1983). No other vulture reaches two nestlings with regularity. The Egyptian Vulture, therefore, seems to develop

an unique breeding strategy among the Accipitri-
dae vultures, but the relative roles of brood reduc-
tion and growth rates is unknown.

Our objectives are to determine (1) the growth
patterns in weight, tarsus length and feather length;
(2) the existence of growth pattern variations based
on brood size and hatching order; (3) the response
of these patterns under different trophic and clima-
tic conditions.

STUDY AREA AND METHODS

The research was conducted in Navarra (northern
Spain). This region covering 10,420 km², presents
a marked bioclimatic gradient (North-South) due
to the intergradation of the Atlantic and Mediter-
ranean climatic influences. The northern half of the
area has mountain ranges with a maximum eleva-
tion of 2,400 meters and a high yearly average rain-
fall (600-2,000 mm). The southern half is almost
plain, receiving scarce rainfall (350-600 mm). The
Egyptian Vulture breeding population within the
study area is estimated at 140 pairs (Donázar &
Ceballos 1988).

Data were obtained during 1986 and 1987. A to-
tal of 24 young of 18 broods were monitored.
Weekly nest visits began when nestlings were 8-14
days old and ended before fledging (70 days of
age). Normally, visits prior to and after this period
were not carried out in order to avoid dead due to
cold and to prevent premature fledging. During
each visit, the following data were recorded for
each young: weight (to the nearest 5 g, but no cor-
rection was made for state of crop); tarsus length
(to the nearest 0.1 mm) and fourth outermost pri-
mary length (sheath plus emerged vane, to the near-
est 1 mm). The values of the two last variables were
taken with vernier calipers.

The hatching dates of single and first-hatched
nestlings of double broods were estimated from a
linear regression relating fourth primary length to
age. For this purpose we used data from nestlings
of known age. This method has frequently been
used in other raptor growth studies (Juillard 1979,
Springer & Osborne 1983, Bechard *et al.* 1985,

Komen 1987) because primaries tend to show
growth rates independent of environmental and
trophic pressures (Peterson & Thompson 1977,
Olsen & Olsen 1987). Second-hatched nestlings
were considered to hatch 5 days after their elder
sibling (Parry-Jones 1985). Hatching intervals in
the Egyptian Vulture vary from 3 to 8 days. If the
interval between hatching is large, the second chick
generally dies (Mendelssohn & Leshem 1983).
Three climatic variables were considered: the num-
ber of rainy days, the total precipitation (litre m⁻²)
and the daily mean temperature (°C). The value of
these variables was determined for each young
from hatching to an age of 60 days. This informa-
tion was derived from the meteorological stations
of the Navarra Government located near the nest
sites studied.

For each nestling, the growth pattern was quan-
titatively defined by the following variables:
1) WEIG. ASYM. Weight asymptote, in g. Estima-
ted by fitting logistic, Gompertz and von Bertalanf-
fy equations to our growth data following the me-
thod proposed by Ricklefs (1967). We selected the
asymptote which achieved the best fit after having
omitted any value of final weight recession.
2) WEIG. TIME 10-90%. Time interval (in days)
for growth from 10% to 90% of the weight asymp-
tote. We estimated this parameter, which is inver-
sely proportional to the growth constant K, because
growth constants fitted to the different growth cur-
ves are not directly comparable (Ricklefs 1967).
3) WEIG. RATE 1-20 d. Weight gain rate (g/d) in
the first 20 days. Estimated considering 54 g for
single and first-hatched nestlings and 48 g for
second-hatched nestlings (Parry-Jones 1985) as the
value of day 1. The value of day 20 was calculated
from the value of the asymptote and the conversion
factors proposed by Ricklefs (1967).
4) WEIG. RATE 20-40 d. Weight gain rate (g/d)
from day 20 through day 40. Calculated in the same
manner as variable 3, using the values obtained for
the asymptote and the conversion factors proposed
by Ricklefs (1967).
5) WEIG. RATE 40-60 d. Weight gain rate (g/d)
from day 40 through day 60. Calculated in the same
manner as variable 3.

6) WEIG. MAX. Maximum weight (g) reached during the entire growth period.

7) WEIG. FLED. Fledging weight (g) at the last check prior to fledging.

8) WEIG. RECES. Weight recession rate (g/d). Calculated as the slope of the line fitted to the weight values from the day that maximum weight was recorded.

9) TARS. ASYM. Tarsus asymptote (mm). Calculated in the same manner as variable 1.

10) TARS. TIME 40-90%. Time interval (d) for growth from 40% to 90% of the tarsus asymptote. Calculated according to the method proposed by Ricklefs (1967).

11) TARS. RATE 1-20 d. Tarsus growth rate (mm/d) in the first 20 days. Calculated in the same manner as variable 3. The value of day 1 was considered to be 18.0 mm for all young (Morales *et al* 1986).

12) TARS. RATE 20-40 d. Tarsus growth rate (mm/d) from day 20 through day 40. Calculated by the same method as variable 4.

13) TARS. RATE 40-60 d. Tarsus growth rate (mm/d) from day 40 through day 60. Calculated by the same method as variable 5.

14) PRIM. RATE. Growth rate (mm/d) of the fourth primary. Though feather length growth tends to fit a curve, the measurements of the period prior to 60 days adjust perfectly to a line because the feather development is not yet completed when the fledgling leaves the nest. In consequence, the data were fitted to a line and its slope was calculated.

15) PRIM. EMERG. Age (d) at which fourth primary emerges. Calculated as the intersection of the regression line with the abscissa (age).

16) PRIM. FLIG. Age (d) at which fourth primary reaches the necessary length for fledging. Calculated from the regression line by interposition of the value of 310 mm. Some young start their first flights with this feather length (own obs.).

Values reached by the 24 nestlings studied were log-normalized and ordinated by means of a principal component analysis (PCA) with VARIMAX rotation (Pielou 1984). Similar multivariate procedures were previously used in other studies on avian growth (Bryant 1978, O'Connor 1978) becau-

se they reduce the dimensionality of data without losing a significant amount of information. Highly correlated variables are combined in axes (PCs) with may account for a high percentage of the original variance permitting the detection of the main data patterns and the projection of data swarm in a two-dimensional perspective defined by the components (Pielou 1984). After the PCA ordination, the factor scores of nestlings on the three first axes were tested by Mann-Whitney U-tests (Siegel 1956) to detect significant differences on the basis of brood size and hatching order. The effect of hatching date and climatic variables on the growth patterns defined by the PCA was tested by applying Spearman's rank correlation tests (Siegel 1956).
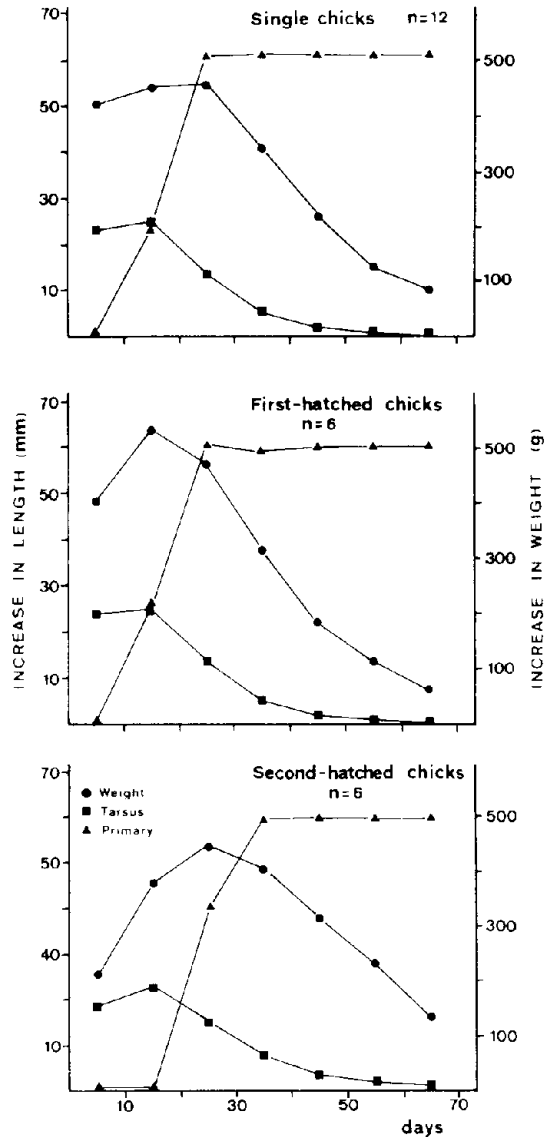
RESULTS

Growth patterns

For all the studied nestlings combined, maximum increase in weight and tarsus took place before the nestlings respectively were 40 and 30 days old (Figs. 1 and 2). The growth rates of these structures in the last part of the development period were highly variable (see coefficients of variation, c.v., in Table 1). Weight recession also had a high c.v. In spite of this variability in weight and tarsus development, the final size of the nestling (characterised by the variables maximum weight reached, weight at fledging and tarsus asymptote) was remarkably constant (see Fig. 1). The growth rate in feather length is fairly constant all through the nestling period.

The most frequent growth equation fitting with individual weight gain was the von Bertalanffy (13 nestlings). Three nestlings fitted into Gompertz and six into the logistic model. With respect to tarsus, 18 nestlings fitted into the logistic, 3 into Gompertz and 3 into von Bertalanffy. The hatching order and the brood size did not seem to be related with the growth equation (Table 2). The growth rates of second-hatched nestlings were, however, very different of single and first-hatched nestlings (Figs. 1 and 2). In all the three structures second-hatched nestlings suffered a notable delay in the initial parts
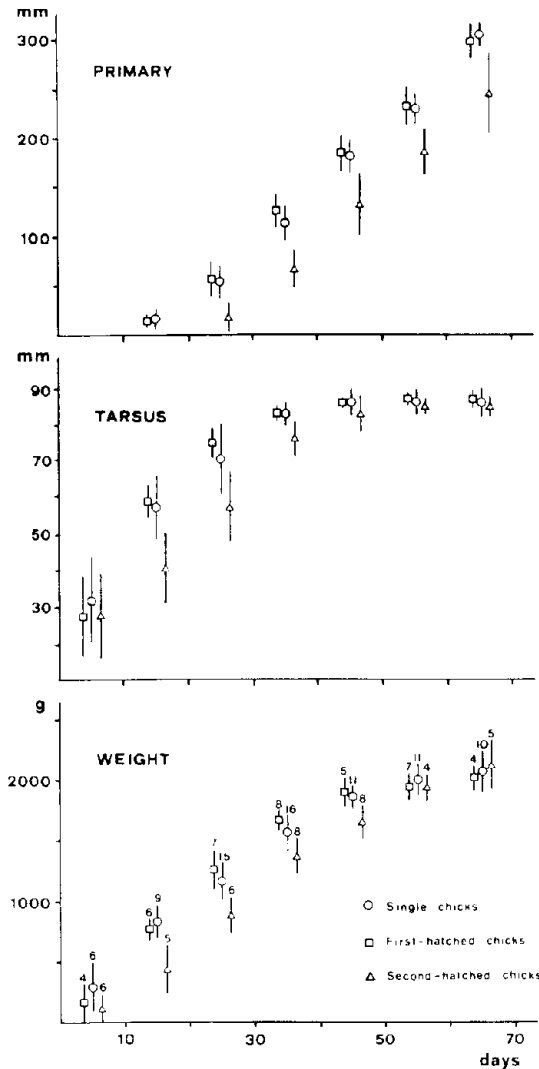
Figure 1. Weight, tarsus, and fourth outermost prima-ry growth curves for 24 Egyptian Vulture nestlings of 12 broods (12 singles and 6 doubles). For each 10-days period the mean value (point) and ± 1 standard deviate are shown. Sample size is indicated by numbers above bars.

Figure 2. Increases in weight and linear measurements of the nestlings Egyptian Vultures. Mean values for each 10-day period are shown.

of the nestling period. At the end of the growing period, however, there were no differences in tarsus size and weight. The delay in reaching the feather length necessary for the first flight results in a delay of 7-12 days for the first flight in second nestlings compared to the elder siblings (own obs.). In two

nest visited shortly after the birth of chicks, the dis-appearance of the youngest nestling was verified when these chicks were 5-10 days old. In the other nests, all the second-hatched nestlings surpassing the age of 14 days survived to fledging.

Table 1. Growth variables values: mean (m.), standard deviation (s.d.) and coefficient of variation (c.v.) for the 24 studied nestlings, and results of principal component analysis (only significant loadings are shown; $*$: $p < 0.05$; $**$: $p < 0.01$; $***$: $p < 0.001$). See methods for meaning of abbreviations.

	m.	s.d.	c.v.	Factor (PC) I	II	III
WEIG. ASYM.	2348.8	358.5	15.26	-	0.839***	-
WEIG. TIME 10-90%	58.6	19.5	33.34	-	0.831***	-
WEIG. RATE 1-20 d.	43.0	9.2	21.44	0.884***	-	-
WEIG. RATE 20-40 d.	40.5	6.1	15.06	-	-	-
WEIG. RATE 40-60 d.	19.0	7.4	38.72	-0.651***	0.640**	-
WEIG. MAX.	2064.2	147.2	7.13	-	0.923***	-
WEIG. FLED.	2036.3	166.6	8.18	-	0.861***	-
WEIG. RECES.	2.1	4.4	216.38	-	-	0.549*
TARS. ASYM.	87.4	3.2	3.65	-	-	-0.673**
TARS. TIME 40-90%	21.3	4.3	20.27	-0.703***	-	-0.432*
TARS. RATE 1-20 d.	2.5	0.3	11.57	0.880***	-	-
TARS. RATE 20-40 d.	1.0	0.2	18.44	-0.689***	-	-0.455*
TARS. RATE 40-60 d.	0.1	0.1	73.72	-0.708***	-0.412*	-0.426*
PRIM. RATE	6.0	0.3	6.90	-	-	0.627**
PRIM. EMERG.	18.0	3.5	19.45	-0.945***	-	-
PRIM. FLIG.	69.4	4.4	6.29	-0.810***	-	-
Proportion of variance (%)				34.86	26.20	12.58
Cumulative proportion (%)				34.86	61.06	73.64

The three first axes obtained from PCA application to the data matrix of 24 nestlings and 16 variables accounted for 73.64% of the variance (Table 1). The PC I accounted for 34.86% of the variance. Positive component scores were characterised by two variables: weight growth rate between days 1-20 and tarsus growth rate between days 1-20, and negative component scores by six variables: age at which the fourth primary emerges, age at which the fourth primary reaches fledging dimensions, tarsus growth rate between days 40-60, time to grow from 40-90% of tarsus asymptote, tarsus growth rate between days 40-60 and weight growth rate between days 40-60. This suggests that rapid increases in weight and tarsus length during the first days was related to slow growth rates in these variables during the final stages of development (more precocious in tarsus). This tendency also seemed to be related to an early primary feather development regarding both the

Table 2. Number of nestlings fitting into logistic (L), Gompertz (G) and von Bertalanffy (vB) growth equations. Sg: single nestlings, F-h: first-hatched nestlings, S-h: second-hatched nestlings.

|	Weight			Tarsus		
	L	G	vB	L	G	vB
Sg	4	2	6	9	2	1
F-h	1	1	4	4	1	1
S-h	1	2	3	5	0	1
Total	6	5	13	18	3	3

day of emergence as the day the necessary length for fledging is reached. The PC II accounted for 26.20% of the variance. Positive component scores were defined by five variables: maximum weight reached, weight at fledging, weight asymptote,

time to grow from 40-90% of the weight asymptote and weight rate between days 40-60%, and negative factor scores only by tarsus growth rate between days 40-60 (with a moderate correlation). This indicates that a low rate of weight gain during the whole nestling development but with relatively high increases during the third growth period (40-60 days), together with low rates of growth in tarsus during the same period, were associated with high weight at fledging. The PC III accounted for 12.58% of the variance. Positive component scores were defined by two variables: weight recession rate and growth rate of the primary, while negative component scores were characterised by four variables: tarsus asymptote, time to grow from 40-90% of tarsus asymptote, tarsus growth rate between days 20-40 and tarsus growth rate between days 40-60. Therefore, high tarsus growth rates, especially between 40-60 days were opposed to high feather growth rates and noticeable weight recession.

Given the independence between the axes, our results suggest that weight and tarsus growth rates evolved relatively in parallel during the first stages of the development and did not condition the final weight of the nestling which was related to high weight gain rates in the last part of the nestling period. On the other hand, the rate of feather development is independent of weight and tarsus growth rates; nevertheless, the early emergence of primaries and precocity in reaching the plumage development necessary for fledging seemed to be related to high rates of weight and tarsus increase in the first stages of development. Only in the final stage of the nestling period was a contraposition between feather and tarsus growth rates perceptible.

Effects of brood size and hatching order

The position of the 24 studied nestling on the planes defined by the three PCs are plotted (Fig. 3). It clearly shows a complete separation between second-hatched nestlings with respect to first-hatched and single nestlings. These second-hatched nestlings are clustered in the negative zone of the PC I. This shows that weight and tarsus
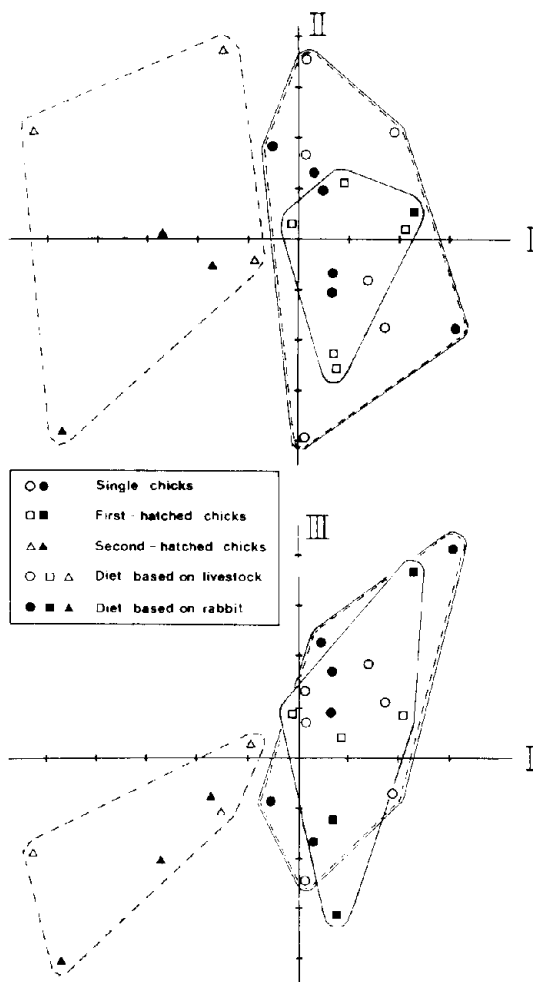
Figure 3. Ordination of the 24 studied nestlings on the three PCs.

growth rates in these nestlings were slower in the first stage of development whereas in the final stages the growth rates of these measurements increased (see also Figs. 1 and 2). The dates of primary feather emergence and achievement of fledging size, however, were delayed. No differences were found between single and first-hatched nestlings with respect to any axis (Mann-Whitney U-tests, $p > 0.05$).

Effects of hatching date, food habits and weather

No significant correlation was found between hatching date and the nestling scores along the three PCs, either when considering all the nestlings pooled nor within any one of the hatching order and brood size categories (single, first-hatched and second-hatched nestlings).

To determine the influence of food habits in the growth patterns we classified our studied nestlings into two different categories: nestlings whose diets were based on rabbits (*Oryctolagus cuniculus*), and nestlings whose diets were based on livestock carrion (see Donázar & Ceballos 1988 for details on diet analysis). Fig. 3 shows that growth patterns were independents from the composition of the diet. This has been verified (Mann-Whitney U-tests, $p > 0.05$) for all the nestlings pooled together and for each brood size and hatching order categories.

There were no overall significant correlations ($p > 0.05$) between the values of three meteorological variables and the distribution of all the nestlings along any of the PCs, considering both all the nestlings pooled together and each brood size and hatching order categories. The only exception was the high and very significant correlation between the number of rainy days and the position of the second-hatched nestlings along the PC III ($r_s = 1.000, p < 0.001$). This indicates that a high number of rainy days during the nestling period might determine a weight recession and the improvement of feather growth in such nestlings in detriment of tarsus growth during the last part of the development period.

DISCUSSION

The main result of our study is the difference of the growth patterns of second-hatched nestlings with respect to those of first-hatched ones and singles. In other Egyptian Vulture wild populations second-hatched nestlings show a similar tendency in weight and tarsus growth rates (see Morales *et al* 1986). Moreover, a second-hatched nestling reared in cap-

tivity by Parry-Jones (1985) weighed 500 g when 19 d old; this value agrees with that of our second-hatched nestlings (see Fig. 1). These similarities and the limited variability of the growth rates within brood size and hatching order categories shown by our results suggest that growth rates are independent of factors operating during the post-embryonic development and that sibling differences may be determined by pre-hatching constraints. Some factors as egg size, sex and chick size at hatching could influence the growth rates after hatching (see Ricklefs 1983 for review). Unfortunately, do not have enough information to evaluate the importance of these factors in the growth strategy of the Egyptian Vulture. Second-hatched nestlings seem to be usually smaller at hatching than their elder siblings (Parry-Jones 1985, Morales *et al* 1986); this inferiority might explain the low growth rates during the first development period (Bryant 1978, Stempniewicz 1980). A similar regularity among broods with respect to growth patterns of second-hatched Bald Eagles *Haliaeetus leucocephalus* was found by Bortolotti (1986) and ascribed to phenotypic disadvantages imposed by hatching asynchrony.

On the other hand, some parental investment constraints would reinforce the relative inferiority of second-hatched chicks at hatching. Younger Egyptian Vulture nestlings are known to be fed less frequently than their elder siblings in the first days of the development (Mendelssohn & Leshem 1983) similar to last hatched nestlings of other bird species (Brown 1983, Williams & Cooper 1983). This is probably due to the relative inferiority when begging for food (Mendelssohn & Leshem 1983). Moreover, the greater activity of the first-hatched sibling would result in frequent interruptions in brooding which would lead to hypothermia for the smallest sibling and, therefore, to reduce growth rates (Ricklefs 1983). In this context, the youngest sibling would die when the age-size differences between siblings are large (Mendelssohn & Leshem 1983). Our observations and those of other authors (Rodríguez-Jiménez & Balcells 1968, Mendelssohn & Leshem 1983, M. Morales & J.L. Perea pers. comm.) indicate that non surviving second-hatched siblings always die before 7-14 days of age. Those siblings capable

of surpassing this age can be expected to survive until fledging. Brood reduction and fratricide in eagles with clutches of two eggs seem also to be dependent on relative size difference between siblings and, consequently, on competitive ability for parental care (Edwards & Collopy 1983).

The selective forces determining this strategy may be linked with energetic constraints because big raptors spend an important amount of energy in growth of body components (see Collopy 1980). The daily energy requirements of a growing nestling may be reduced by growing at high rates during the first part of the development period for which reason the Gompertz and von Bertalanffy growth models would be selected (Ricklefs 1974). The weight of most of our chicks fitted into the von Bertalanffy curve with no differences with regard to brood size and hatching order categories. In addition the vulture could decrease the peak energy demand in broods with two nestlings by spacing the maximum requirements of siblings through hatching asynchrony and time differences in maximum growth rates (Bryant & Gardiner 1979, Hussel 1972). Therefore, the growth rates of the Egyptian Vulture act as a fine-tuning mechanism of productivity so that the two nestlings can be adjusted at the time of peak demand (Lack 1968, Ricklefs 1968, Drent & Daan 1980, O'Connor 1984). This strategy may be advantageous for the Egyptian Vulture since this species, as other vultures, exploits scarce and unpredictable food resources.

Our results suggest that, in the case of second-hatched nestlings, the plumage competes with weight and tarsus during the last part of the nestling period. This may be due to the relative delay for weight and tarsus growth in second-hatched nestlings which would cause the metabolic cost of the biosynthesis of the structures to overlap with feather growth during the last part of the development. The high energy consumption by feather biosynthesis (Houston 1973, O'Connor 1984) and the increase of flapping and other activities during this period (Summer 1933, Montevecchi *et al*. 1984) would cause an energetic deficit if the frequency of feedings decreases. In this context, if the energetic income is not enough to sustain the growth of all the body structures, it might by advantageous to invest preferably in some of them in detriment to others (see Calow & Townsed 1981). In other bird species it has been shown that, when a reduction of feedings occurs, the growth of the plumage is not affected whereas other body structures may suffer a decrease in growth rates (Houston 1976, Schreiber 1976, Collopy 1980, O'Connor 1984, Veiga 1985, Boag 1987). Our results agree with this tendency. The adoption of this strategy may be advantageous for the Egyptian Vulture since in this species a shortening of the nestling period would maximize the time for maturation of flight skills prior to migration, which frequently occurs in the days subsequent to the first flight (own obs.). Our results also suggest that this competition between structures occurs more frequently when the number of rainy days during the nestling period increases. This seems to be logical since it is known that adverse climatic conditions can diminish the rate of adult feeds (Kinaham 1975, Moss 1979, Newton 1979, Kuusela & Solonen 1984).

The independence of the final weights achieved with regard to other parameters and relatively low coefficient of variation of the variables characterising the final dimensions of the nestling are consistent with observations in other bird species (O'Connor 1978, Ross 1980, Ricklefs & Peters 1981, F. Hiraldo pers. comm.). On the other hand, all these variables seem to be almost entirely independent of the environmental influences.

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SAMENVATTING

Dit artikel beschrijft de gewichtstoeneming, de groei van tarsus en veren van de nestjongen van Aasgieren in Spanje. De maximale gewichtstoeneming en de tarsusgroei vindt respectievelijk plaats vóór de 40-ste en 30-ste dag. De groei van de slagpennen is vrijwel constant tot op het moment van uitvliegen (70-ste dag). Het tweede jong gaat òf binnen 14 dagen dood, òf ontwikkelt zich de eerste 20 dagen langzamer (gewicht en tarsus) dan het eerstgeboren jong (of jong uit 1 ei-legsel). Aan het eind van de nestperiode (40 - 60-ste dag) wordt het omgekeerde waargenomen.

De ontwikkeling van de slagpennen bij het tweede jong loopt achter bij die van het eerste. De geboortedatum en de voedselgewoonten van de ouders kunnen niet in verband gebracht worden met het waargenomen ontwikkelingspatroon van de jongen. Een langdurige regenperiode lijkt wel van invloed op de groei van het tweede jong (aan het eind van de nestperiode); de groei van de veren blijft constant, maar die van de tarsus neemt af. -JV