Growth and biometry of Mute Swan cygnets *Cygnus olor* in Groningen, The Netherlands

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Growth curves of 10 Mute Swan cygnets, weighed and measured from hatching until fledging, are presented. Biometrical data of 340 cygnets were collected during July, August and September in different years. The growth of cygnets is almost complete at that time, except for the flight feathers. The onset of primary growth was related to a sex specific level of weight development: females reached that stage at a lower weight than males did. Furthermore, an analysis of variance in the growth of primary feathers was made. There was no relation between the timing of primary growth and sex or colour morph. The number of cygnets in a brood proved to be the most important factor explaining deviations in the onset of primary growth. The effect of brood size on primary growth differed between years and is suggested to depend on food conditions, which might influence the rate of development of the cygnets.

Biometrical data are of great importance to assess the condition of individual birds and can therefore be used to predict survival chances. In growing animals the situation is rather complex, because biometrical values are strongly determined by age. For example, if one wants to know whether a growing cygnet is 'heavy' or 'light', the age of the cygnet must be known, in order to compare the weight with an average (or 'expected') weight at that age.

In this paper we describe the growth of 10 Mute Swan, *Cygnus olor,* cygnets between hatching and fledging. Growth curves of body weight, skull, wing, and the outer primary feather (p10) are presented.

Secondly, variation in a set of biometrical data obtained from 340 cygnets of known age has been analysed. These data include body weight, and length of skull, tarsus, wing, and p10. Several factors might have an effect on the relative size of those biometrical parameters. In our analysis we considered the individual cygnet's sex, colour phase ('grey' or 'white', Munro *et al.* 1968), as well as 'environmental' factors like number of cygnets in a brood, differences between years, and the timing of breeding (early or late in the breeding season).

Material and Methods

This study was carried out in the province of Groningen, the Netherlands (about 53°20′ N, and 6° 40′ E), as part of a long term study on the breeding biology and population dynamics of Mute Swans. The area is characterized by intensively used meadows and agricultural fields in mainly polder-like lowlands. Breeding habitats consist of ditches and small canals which are very numerous in the area.

In the 1986 breeding season growth curves were obtained from cygnets (9 males, 1 female) in four free living Mute Swan families. The cygnets were caught weekly between hatching and fledging (at an age of about 140 days). The cygnets were marked individually by small metal clips in the webs. As soon as the tarsus was full-grown the clips were removed and replaced by stainless steel leg rings.

Biometrical data were measured as follows: weight, using a digital household balance (accuracy of 1 gram), at a larger weight a Pesola spring balance (accuracy of 50 grams); skull, from bill tip to back of skull; tarsus, size of bone (*cf.* Cramp & Simmons 1977); wing, fore-arm up to wing tip (longest primary, usually p8); 10th primary (p10), from skin to tip. All lengths were measured to the nearest millimetre. Biometrical data were collected from 340 cygnets from 86 broods of known age, i.e. hatching dates of broods of ringed Mute Swan pairs were known, in 1986, 1987, and 1988. Measuring occurred in late summer (late July until September) while ringing cygnets aged 60-120 days.

For statistically testing for differences between

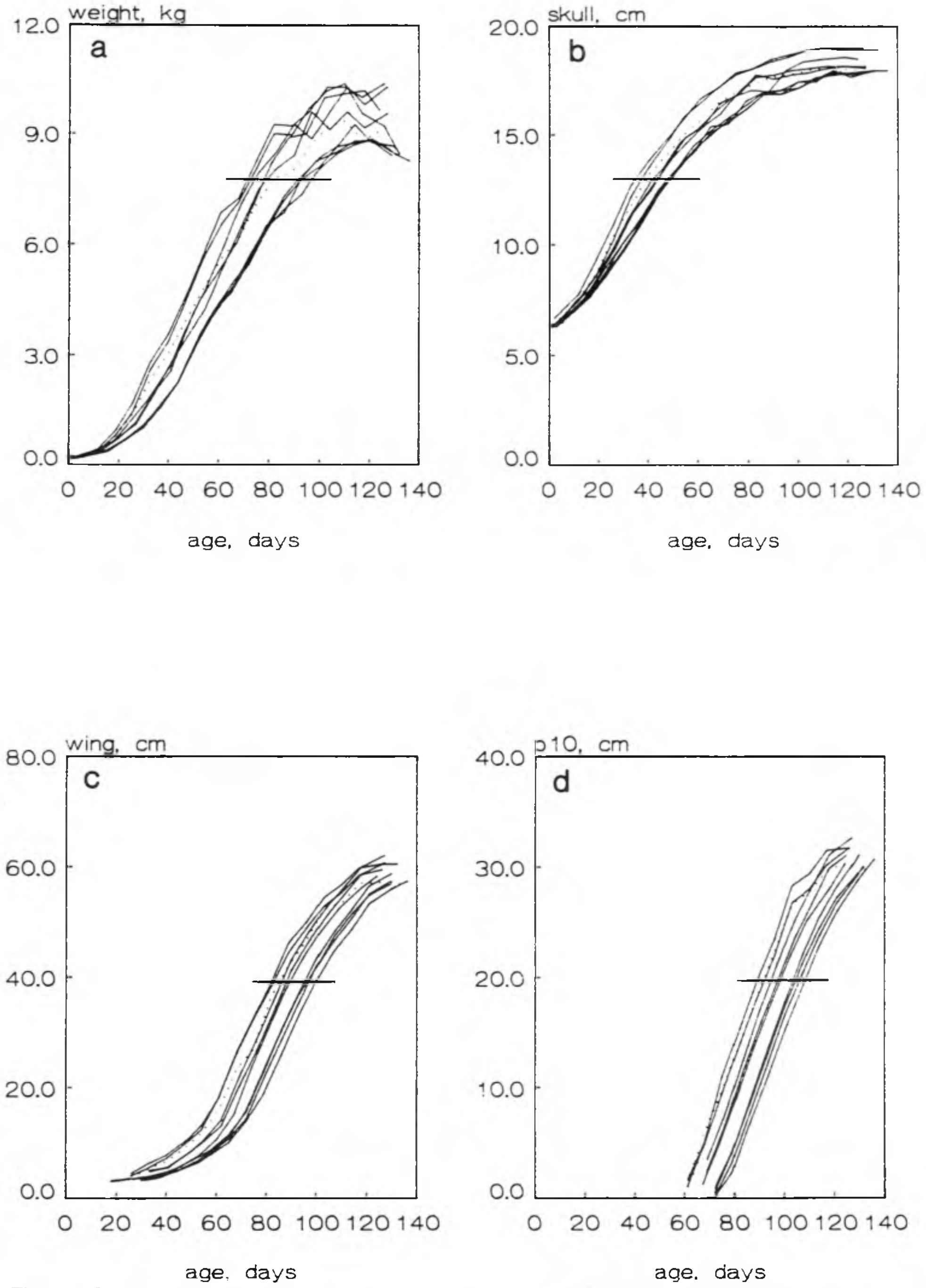

Figure 1. Growth curves of weight (A), skull (B), wing (C), and 10th primary (D) of 10 cygnets (— males, - - female) in free living Mute Swan families. The sequence of cygnets at the intersection lines in each figure are as follows (capitals refer to broods, female underlined): weight, AABBCADDDD; skull, AAABCDDDD; wing, AAABBCDDDD; p10, AAABBCDDDD.

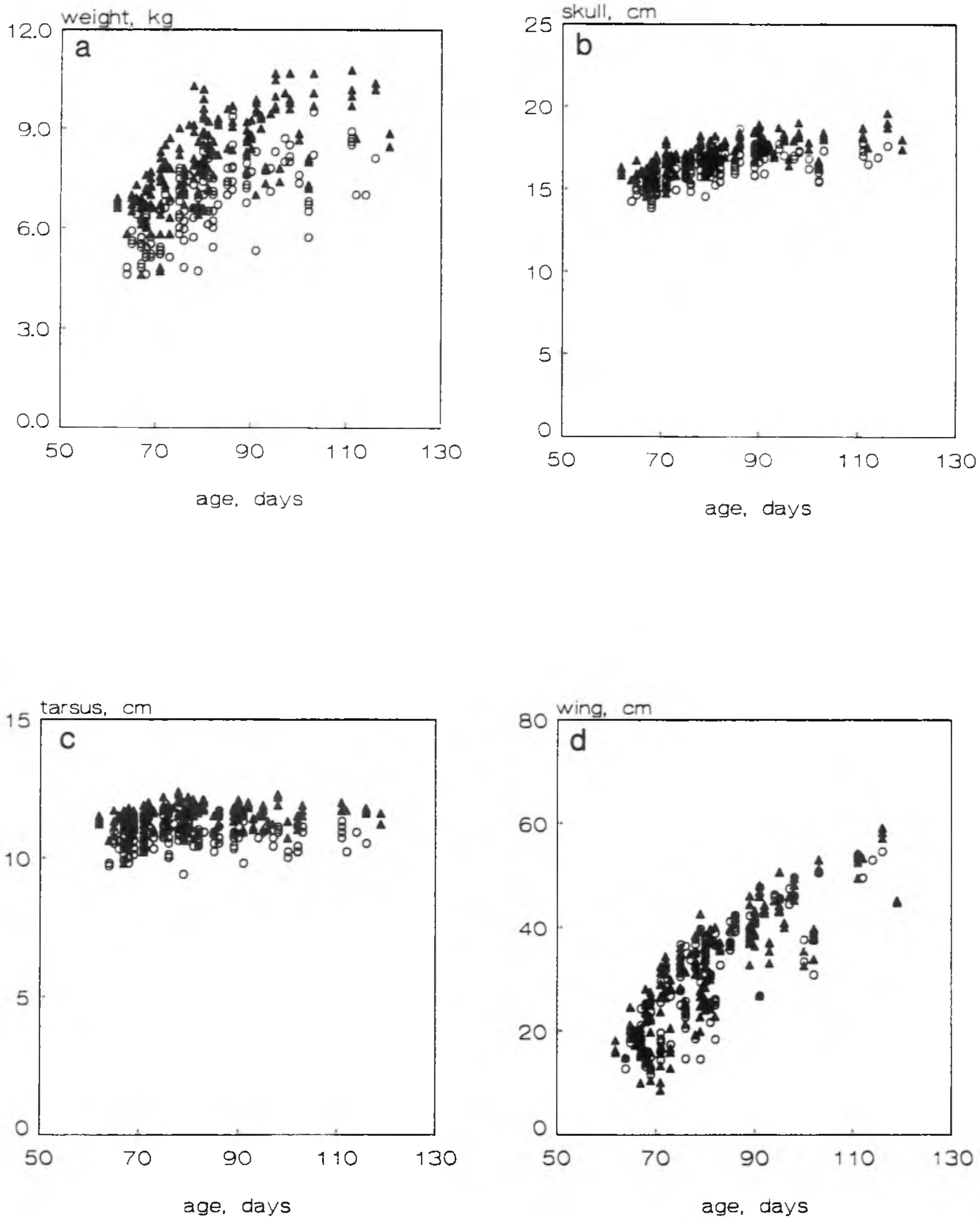

Figure 2. Weights (A) and lengths of skull (B), tarsus (C), and wing (D) in relation to cygnet age of 340 Mute Swan cygnets. Each dot represents one cygnet (▲ males, ○ females).

Table 1. Growth rates recorded in nine males and one female Mute Swan cygnets in the 1986 breeding season. Growth rates were obtained from linear regression of weight (2.5-7.5 kg), skull (10-15 cm), wing (20-45 cm), and p10 (5-25 cm), resp., on age. The range refers to lowest and highest recorded growth rates in the males.

	Mean growth rate ± 1 S.D. males	(range)	female
WEIGHT (g/day)	124.2 ± 20.4	(98.5-160.0)	112.7
SKULL (mm/day)	1.63 ± 0.17	(1.46-2.01)	1.62
WING (mm/day)	9.47 ± 0.53	(8.77-10.21)	9.47
P10 (mm/day)	6.03 ± 0.26	(5.73-6.49)	5.86

two regression lines (as in Fig. 3 and Fig. 4) we used the method of analysis of covariance as described by Johnston (1984). The two datasets of the regression lines are tested for different slopes as well as for different intercepts.

Results

The growth of the intensively studied cygnets is illustrated graphically in Fig. 1A-D, where the weight, and the length of the skull, wing and p10 are plotted against the age of the cygnets. All curves are quite well S-shaped, with the highest absolute growth rates at about halfway through development, except for the p10, which reaches its maximum growth rate during the first few days. Growth rates for the linear portions of the growth curves were obtained from linear regression analysis and are summarized in Table 1. Growth has been assumed linear at weights from 2.5 to 7.5 kg, skull lengths from 10 to 15 cm, wing lengths from 20 to 45 cm, and p10 lengths from 5 to 25 cm.

Differences in growth rate (variation in slopes of curves) may occur, for example in the weight (Fig. 1A and Table 1, range of growth rates), as well as differences in timing of the onset of growth (variation in position along the x-axis). The latter is best shown in the growth curves of p10 (Fig. 1D). Can the differences as suggested in Fig. 1 be ascribed to individual differences or to differences between broods? In order to indicate different broods a capital was assigned to each

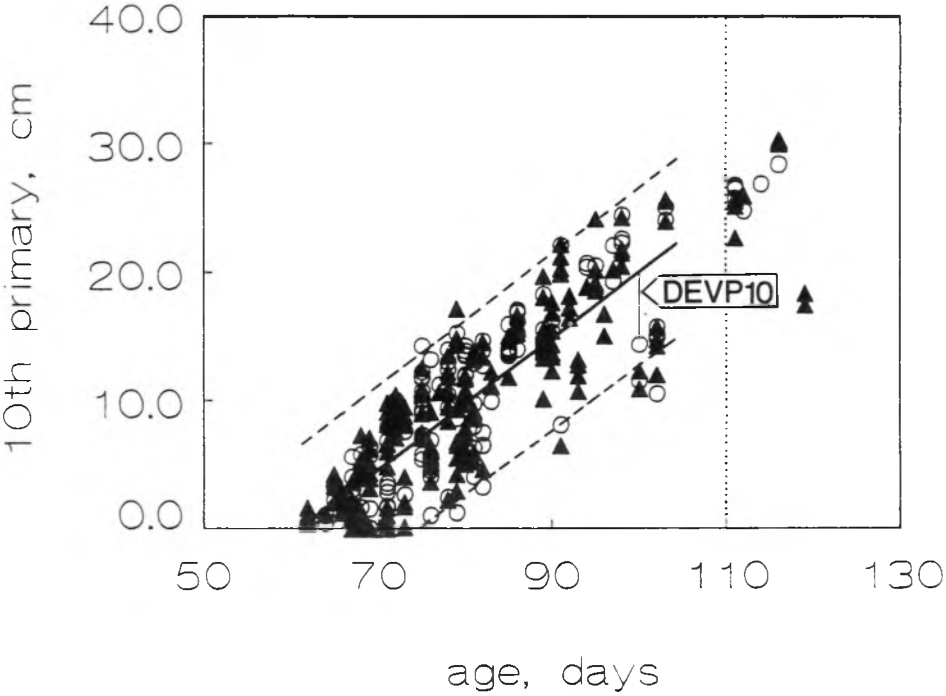

Figure 3. Length of 10th primary in relation to age. The linear regression line (bold) and 95% confidence limits (broken lines) are indicated for p10 lengths at ages between 60 and 110 days. DEVP10 was calculated from vertical distances between observed and predicted p10 lengths (▲ males, ○ females).

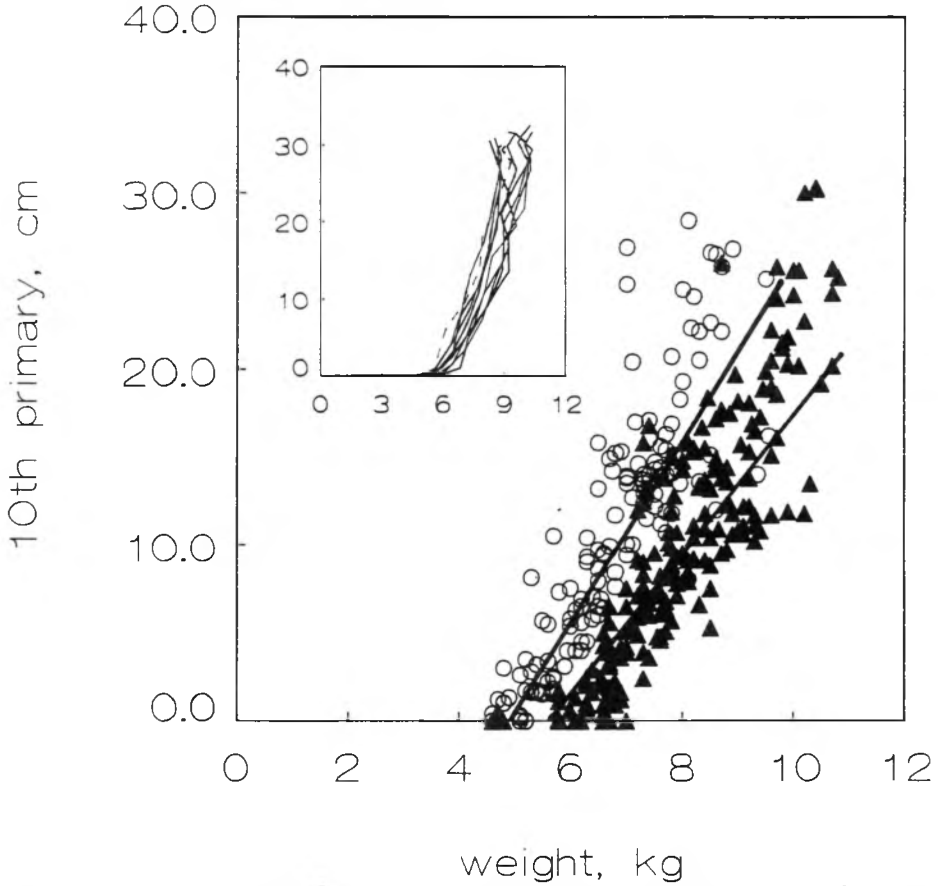

Figure 4. Length of 10th primary as a function of body weight in 340 cygnets in the prefledging period (▲ males, ○ females). Inset shows the relationship between p10 length and weight for the ten cygnets studied throughout their development (— males, - - female).

brood. Brood 'A' contained three cygnets (one female), brood 'B' two cygnets, brood 'C' one cygnet, and brood 'D' four cygnets. In Fig. 1A-D the cygnets are ordered according to their growth (from left to right) at the intersection shown in each figure. The sequence of curves at the intersection line is as follows (cygnets are indicated by the capital of the brood they belonged to, female underlined): weight AABBCADDDD, skull AAABCBDDDD, wing AAABBCDDDD, p10 AAABBCDDDD, clearly showing that individuals within a brood tend to grow at equal rates. However, sample sizes are too small to test this statistically.

Unfortunately, there was only one female among the 10 cygnets, so little can be said about differences related to sex. It is worth noting that the female belonged to the brood with the highest growth rates and that sexual differences might be larger than suggested in Fig. 1.

For the analysis of variation in growth we used

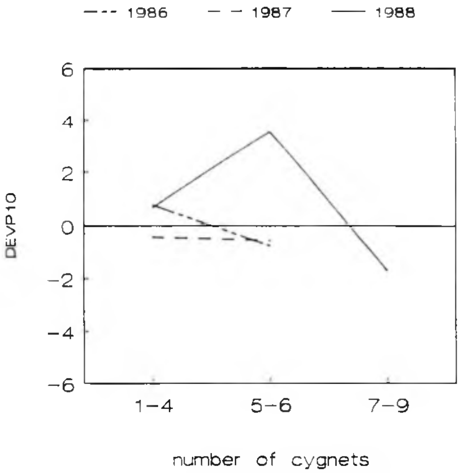

Figure 5. Deviations in p10 length (DEVP10) in relation to brood size in different years.

the biometric dataset of 340 cygnets caught in late summer. This period coincides with the growth of the flight feathers (see p10 in Fig. 3), whereas the growth of the skull and the tarsus is almost complete at that time (Fig. 2). At this age, sexual dimorphism in the Mute Swan has already become fairly pronounced: male cygnets are heavier and have larger skulls and tarsi than do females. We found a linear increase in the length of p10 between 60 and 120 days after hatching: p10 length (cm) = 0.51 (age) - 31.2 (R^2=0.69, P<0.0001). The slope of 5.1 mm/day is slightly lower than the growth rate of 6.0 mm/day recorded for the nine males (Table 1), because of statistical reasons (the slope in Fig. 3 is a result of both growth rate and different timing of onset of growth, see below). The 95% confidence limits of the regression of p10 length on age illustrate a large variation in p10 growth at a particular age (and, conversely, that p10 length is not a good predictor for age, despite its good linear relationship with age). Although males are heavier and larger than females (Fig. 2) the length of p10 at a particular age does not differ between the sexes (P>>0.05). This was tested by calculating the regression lines of p10 length on age for both sexes separately and compare the slopes and intercepts as explained before (Material & Methods).

Table 2. Mean values of DEVP10 and standard deviations per year in different brood size classes. Sample sizes are given in parentheses.

	Number of cygnets 1-4	5-6	7-9
Year 1986	0.76 ± 3.25 (30)	-0.78 ± 4.85 (22)	—
1987	-0.57 ± 3.47 (70)	-0.38 ± 3.27 (52)	—
1988	0.66 ± 3.29 (42)	3.55 ± 1.44 (37)*	-1.70 ± 3.31 (64)*

*significantly different from all other values (P<0.005)

In contrast, if p10 length is given as a function of each cygnet's weight, as illustrated in Fig. 4, a remarkable difference between the sexes appears. Linear regression of p10 length (between 0 and 25 cm) on weight gave for males p10 = 4.19 W-23.5 (R^2=0.69, P<0.0001) and females p10 = 4.96 W-23.4 (R^2=0.71, P<0.0001), where W is the weight in kg. The slopes and levels of both regression lines differed significantly (P<0.05 and P<0.0001, resp.). The regression lines intersect the weight-axis at 4.7 kg (females) and 5.6 kg (males), respectively.

Thus, Fig. 4 shows that the onset of primary growth is concentrated around a more or less fixed weight (about 5 kg for females and 6 kg for males), suggesting that a kind of threshold in the birds' development or condition should be reached before the flight feathers can start growing.

In order to analyse variations in growth in greater detail we calculated the deviations of p10 lengths from the linear regression line on age: DEVP10 = (observed length of p10) - (predicted length of p10 from linear regression), which is in fact the residual of the regression, *cf.* Bacon & Coleman (1986), see Fig. 3.

Values of DEVP10 were subjected to a 5-way analysis of variance, using the factors sex, colour phase, number of cygnets in a brood, year (1986/1987/1988), and hatching date divided in early broods (until daynumber 135), intermediate broods (daynumber 136 to 155), and late broods (after daynumber 156), so that the data were distributed more or less equally over the three hatching periods. It is important to note here, that a positive value of DEVP10 may refer to either a relatively high growth rate or an early onset of an individual's growth (or a combination of both growth rate and timing of onset). We can not discriminate between these, because we have just one value of each individual cygnet. However, from the cygnets that were studied throughout their development in Fig. 1D (p10) it seems reasonable to assume that the variation in DEVP10 is largely due to differences in timing of the onset of primary growth.

'Sex' and 'colour phase' (38% of the data set belonged to the 'Polish' or 'white' morph) had no significant effect on primary growth (P>>0.05). The 'number of cygnets in a brood' proved to be the most important factor in explaining deviations in p10 length (P<0.0005). 'Year' also had an effect (P<0.0005) and 'year' interacted significantly with the 'number of cygnets' (P<0.0005). The relationships between DEVP10 and brood size in different years are illustrated in Fig. 5. In 1988 intermediate numbers of cygnets in a brood (5-6) showed a remarkable positive DEVP10, suggesting good growing conditions for primary growth. Low numbers (1-4) or high numbers (7-9) of cygnets were not related to better growing conditions. In 1986 and 1987 the prosperous situation for intermediate numbers of cygnets in a brood was not found, and brood sizes

Table 3. Weather characteristics in spring and summer of 1986, 1987, and 1988.

	Year 1986	1987	1988
Σ TEMPERATURE (1 Jan - 1 Apr)	219.1	142.2	477.9
Σ TEMPERATURE (1 Jun - 31 Aug)	1508.8	1435.2	1453.6
Σ RAINFALL, MM (1 Jun - 31 Aug)	193	263	216

were smaller (large numbers of cygnets did not occur). T-tests for mean values of DEVP10 per brood size class per year revealed that all combinations were not statistically different ($P>0.05$) from each other, except for brood size 5-6 in 1988 and brood size 7-9 in 1988, being significantly higher and lower, respectively, than all other points (Table 2).

For 'hatching date' the same results were found as for 'year', because hatching dates correlated strongly with year. In 1986 mean hatching date was daynumber 148.8 with S.D. 7.4, in 1987 it was daynumber 155.3 ± 10.9 and in 1988 daynumber 133.9 ± 7.4. Both mean hatching dates and the variances per year differed significantly (Student's t-test, all combinations $P<0.0005$, variances in 1986 and 1988 were equal). Therefore we standardized hatching dates per year by expressing each hatching date as the deviation from its year mean divided by the year standard deviation. Then the effect of hatching date proved to be reduced to almost zero (regression of DEVP10 on standardized hatching dates revealed a slightly positive slope, $P=0.04$, $R^2=0.01$).

In conclusion, hatching date in itself does not influence the primary growth of cygnets, but differences between years and brood size do.

Discussion

The organization of cygnet growth

The growth of different parts of the body in Mute Swan cygnets is clearly separated in time, as in other nidifugous birds (O'Conner 1984). The early onset of tarsus growth is functional with respect to the long daily foraging trips that swan families make in most territories. In the same way an early development of the skull and bill, like early growth of the neck (Mathiasson 1981), may improve the intake of food.

The growth of primaries (and coincidentally the growth of the wing) starts when the rest of the body is almost full-grown. The same result was found by Mathiasson (1981). There is a remarkable high constant growth rate of primaries as soon as the feather emerges, in contrast to the usual slow start of skeletal growth (resulting in S-curves). It is possible that the initial development of the feather structure takes place inside the wing before the feather grows out of the skin. Together with the high growth rate this would shorten the period in which the vulnerable growing feathers are exposed.

We found that the onset of primary growth might be related to a fixed level of weight development. This finding supports the hypothesis, as proposed by Bacon & Coleman (1986), that the onset of primary growth requires a particular developmental stage. Cygnets growing at different rates will reach this stage at different ages and, therefore, will introduce variation of primary growth with age. In an ecological context, it implies that the moment the cygnets are able to fledge depends strongly on the weight development of the cygnets. This stresses the importance of growing up in a good quality territory (with respect to food availability). Apparently, males and females reach the stage of primary growth at different weights. There is, on the other hand, a distinct difference in weight development for the sexes, resulting in sexual dimorphism. Thus, a lower growth rate of weight in females is compensated by a lower threshold weight to allow primary growth. As a consequence, the onset of primary growth within broods occurs at about the same time for both sexes, which we consider to be functional in view of the simultaneous fledging of the sexes within a brood.

It must be stressed that our results on growth curves (Fig. 1) allow only for limited conclusions due to small sample sizes. As mentioned already, only one female was included in our sample. Furthermore, growth curves were obtained in one season from relatively small brood sizes. Studies in other areas show, for example, different weights at fledging (about 7 kg in Sweden (Mathiasson 1981) compared to 9 kg in our area), and much more variation between individuals or broods in Denmark (P.Andersen-Harild pers.comm.). Another point we want to raise is that, if primary growth rate would be invariable and deviations of p10 size were due to variation in timing of onset of growth, the analysis of DEVP10 could be slightly improved by calculating deviations in age from a 'standard' growth curve, instead of deviations in p10 size at a particular age. We need, however, accurate measurements of primary growth rates under different conditions (years, brood sizes, etc.) to prove that primary growth rate would not vary.

Environmental factors influencing primary growth

What can account for the effect of different years on the growth of primary feathers, as illustrated in Fig. 5? The weather conditions in the early spring of 1988 (the most prosperous year) were exceptionally good, in contrast to 1986 and 1987 (Table 3). Circumstances during primary growth in July and August, however, were equal in all years. So, weather conditions in early spring might influence the growth conditions of cygnets in summer. We would propose the food availability as a mechanism behind these relationships. Good weather in spring, as in 1988, may lead to better development of aquatic vegetation (*Lemna* spp., *Potamogeton* spp., etc.) in summer and consequently to better feeding conditions for the cygnets. However, this might only be the case for intermediate brood sizes of five to six cygnets. When the number of cygnets in a brood is large, as only found in the good year of 1988, the growth of those cygnets lagged behind (negative DEVP10), despite good growing conditions. Thus, there might have been competition for food between the cygnets within broods, resulting in far less favourable growing conditions. In terms of breeding strategies of Mute Swans, this might indicate a trade-off in good years between raising a lower number of cygnets which will grow well compared to raising a larger number of cygnets that will fledge later, and possibly in a weaker condition.

Future research could be focused on the weight development of cygnets, because weight development seems to determine the age at which the cygnets are able to fledge. Moreover, weight in itself could have an effect on the condition of the cygnets at the time of fledging and, therefore, might effect survival chances in the post-fledging period (Beekman 1991).

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