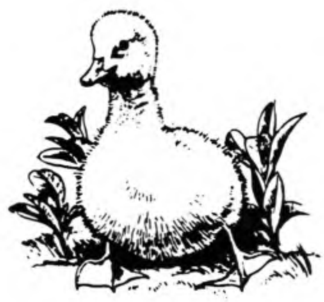
The growth and development of Whooper Swan cygnets *Cygnus cygnus*



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The growth and development of ten captive Whooper Swan cygnets hatched at the Wildfowl & Wetlands Trust Centre at Llanelli on 10-13 May 1990, were documented for the first 23 weeks of life. Weekly recording of biometrics, together with a photographic record, revealed: rapid growth with the first contour feathers appearing at 4.3 weeks and a 30-fold increase in weight relative to hatching weight within nine weeks. Fledging occurred at around 11.4 weeks, when the birds had achieved 79% of mean adult mass; and the tarsus reached 99.8% of its mean adult length by 18 weeks. Males were always heavier and usually larger on average than females of the same age. Data obtained were compared with other published studies. Development was more rapid than that for wild Whooper cygnets in Iceland indicating that captive rearing conditions were overcoming the presumed detrimental effect of shortened daylength, with lower latitude, upon time available for feeding.

The Whooper Swan *Cygnus cygnus* breeds mainly in the taiga and scrub zone of Northern Eurasia between latitudes 45° and 70°N in a range stretching from Iceland in the west to the Pacific coast of the USSR in the east, and migrates south each autumn to winter at lower latitudes (Ogilvie 1972). The time available for nesting and the rearing of juveniles before the families depart on autumn migration is short and consequently, in common with other northern swans, cygnets exhibit substantial weight gains and steep growth curves compared with other species (Kear 1972). The effect of latitude upon growth rates has been demonstrated in the closely-related Trumpeter Swan *Cygnus buccinator*, cygnets of which achieved first flight at 17.1 weeks on Jackson Lake, Wyoming at 44°N (Simon 1952) but reached the same stage after only 12 weeks at Kenai, Alaska at 60°N (Troyer in prep.). This view was also shared by Owen & Black (1990) who noted that the Trumpeter Swans in Alaska fledged in a shorter period than the similarly sized Mute Swans *Cygnus olor* in England, which they attributed both to differences in the quality and availability of food in the two regions and to the breeding latitude.

Growth rates of captive swans have been reported to be slower than those in the wild, for example Bewick's Swans *Cygnus columbianus bewickii* took more than twice as long to fledge at Slimbridge (52°N) than in the Arctic tundra at 70°N (Kear 1972). Such differences have been attributed partly to dietary factors but more importantly to the effect of shortened daylength at lower latitudes reducing time available for feeding. The Bewick's Swan cygnets bred in captivity were reared by their parents, however, and the effect of hand-rearing cygnets on a high-protein diet in confined and relatively disturbance-free pens was unclear. The aim of the study was to document the development and growth of hand-reared Whooper Swan cygnets, first to provide a comparison with available published data concerning swan growth rates and secondly to provide a scale of development for classifying cygnets of unknown history on the breeding grounds.

Methods

Ten cygnets were reared from two clutches laid by Whooper Swan pairs held by The Wildfowl & Wetlands Trust. The eggs were transferred to the incubation room of the Llanelli Centre and hatched over a period of 84 hours during the second week of May 1990. Upon hatching the cygnets were placed in the "Duckery" where they received a high-protein diet

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under conditions of constant temperature and red light (24 hours per day). Individually coded web-tags were placed on the cygnets to allow their subsequent identification and the birds were sexed by cloacal examination; three were male and seven female. After three days the birds were moved outdoors into a small grassy pen containing a cloche into which the birds could retreat during cold and wet conditions and into which they were moved at night. The cloche contained a white light source and the birds were therefore subject to 24 hour light conditions for the 25 days that they remained in the pen. During the fifth week after hatching the cygnets were placed in a larger pen containing a small pond with no artificial shelter, and where they received only natural daylight. During the ninth week they were finally moved into a large open pen containing a larger pond (1/3 ha). The high-protein pellet diet was provided for the birds throughout their development but in addition grass was available in the pens.

Weekly visits were made to Llanelli to monitor development of the ten cygnets. During the seventh week, three of the female cygnets, not required for the Llanelli breeding programme, were transferred to the Slimbridge centre. The monitoring of the development of these three cygnets continued on a near-weekly basis until the end of the study in week 23, which approximated to the stage at which wild cygnets migrate to the wintering grounds. In week 23 all the cygnets were again caught so that their final sizes and weights could be ascertained. On each sampling day a photographic record of the birds was taken including shots of the opened wing, together with the following biometric data:

1) Weight.	In weeks 1 to 7, birds were weighed with a spring balance. By week 8 the birds were large enough to be weighed with a 10kg Salter balance which was calibrated each week.
2) Skull.	Measured with 200 mm callipers: the distance between the bill tip and the back of the skull.
3) Cranium.	Measured with callipers: the maximum perpendicular distance between the underside of the lower mandible and the top of the cranium.
4) Tarsus.	Measured with callipers: the distance between the depression in the angle of the inter-tarsal joint and the distal tip of the tarsus bone.
5) Wing.	Measured with a ruler: the total length of the extended flattened wing, from the armpit to the tip of the longest primary.
6) Wing chord.	The distance between the carpal joint and the tip of the longest primary. Maximum chord i.e flattened primaries, was taken as opposed to standard chord as the former has been demonstrated to be a more easily repeatable method (BTO 1984, Owen & Montgomery 1978).
7) Primary.	Measured with a ruler between the first and second primary: the length of the second primary (ultimately the longest) from skin to tip.
8) Length.	The distance between the leading edge of the breast bulge and the tail tip of a sitting bird.
9) Height.	The distance between the top of the head and the ground of a sitting bird with a fully extended (but not stretched) neck.

The first seven of these measures are standard and easily repeatable, the last two are more subjective but were taken as a tool for ageing birds in the field by direct size comparison with parent birds. In addition

Table 1. Biometric data of captive Whooper Swans.

Week	n		Age (days)	Weight (kg)	Skull (cm)	Tarsus (cm)	Cranium (cm)	Wing (cm)	Length (cm)	Height (cm)
1	6	Mean	5.00	2.460	6.438	3.895	3.155	7.48	18.75	19.79
		sd	0.63	0.259	0.195	0.179	0.134	0.29	0.70	0.76
5	10	Mean	33.20	3.815	12.845	9.895	5.165	28.54	43.40	36.75
		sd	1.14	0.414	0.397	0.385	0.136	2.44	1.71	2.52
10	10	Mean	68.90	7.640	17.513	12.135	6.136	91.12	66.15	49.10
		sd	1.29	0.984	0.546	0.441	0.152	2.28	2.94	4.36
15	3	Mean	104.00	7.650	17.857	11.740	6.140	102.97	68.67	55.67
		sd	1.00	0.312	0.284	0.010	0.053	0.35	0.58	0.58
20	3	Mean	139.00	8.933	18.033	11.770	6.270	103.17	69.33	59.67
		sd	1.00	0.577	0.365	0.030	0.030	1.00	0.58	1.15
23	10	Mean	161.20	10.140	18.761	12.270	6.490	106.08	71.70	61.30
		sd	1.14	0.556	0.691	0.490	0.194	2.93	3.09	3.74

the moult stage of the flight feathers was recorded and coded according to Ginn & Melville (1983).

Results

The biometric data obtained from the weekly visits are given in Table 1 and illustrated in Figures 1 to 4. Data for each week have been amalgamated despite the variation in the hatch dates in order to increase the sample size (mean age of the cygnets is also given). Sample size in week 1 is small (n = 6) as cygnets from the second clutch were considered too young to handle.

Weight

Weight increase was linear initially with a mean weight gain of 127.3 g per day during the weeks 1 to 7 but then reached a plateau as adult weight was approached (Fig. 1). The precise levelling-off of the

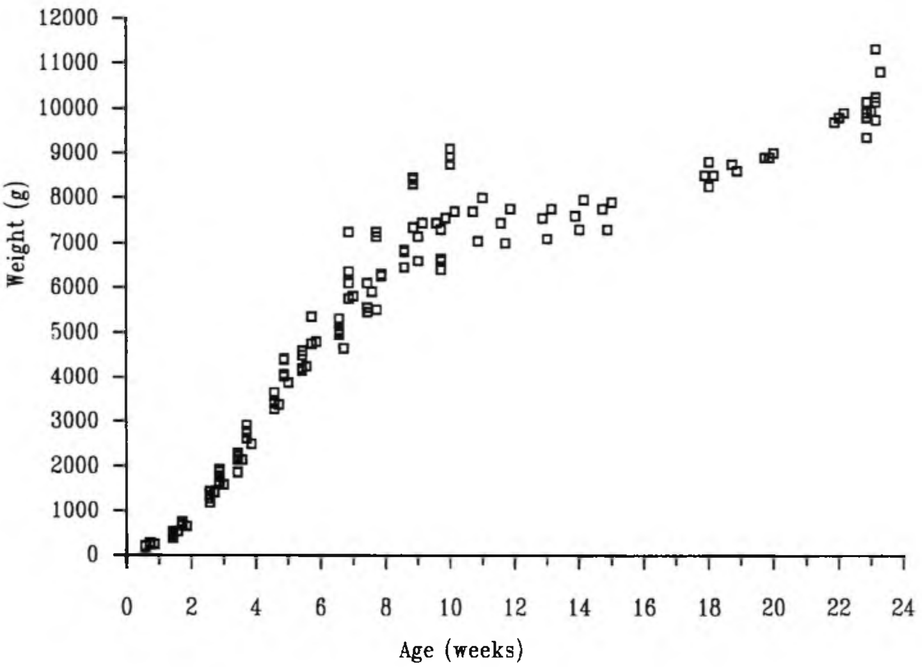

Figure 1. Weight of captive Whooper Swan cygnets from hatching date.

graph is masked by the small sample size after week 10 involving three of the smallest members of the cohort. Weight gain was broadly similar for all birds in any given week and the younger birds did not catch up with the older ones until adult weight was reached. A drop in weight was recorded between weeks 10 and 11 for all three cygnets at Slimbridge. This probably resulted from the very high temperatures recorded during this period (30°C+) which caused the birds to overheat and become listless, as well as reducing the amount of supplementary grazing available in the pen. These three birds began to increase in weight again in week 12 and weight gain continued at a steady rate until the end of the study period, with a mean weight gain of 31.2 g per day between weeks 12 and 23.

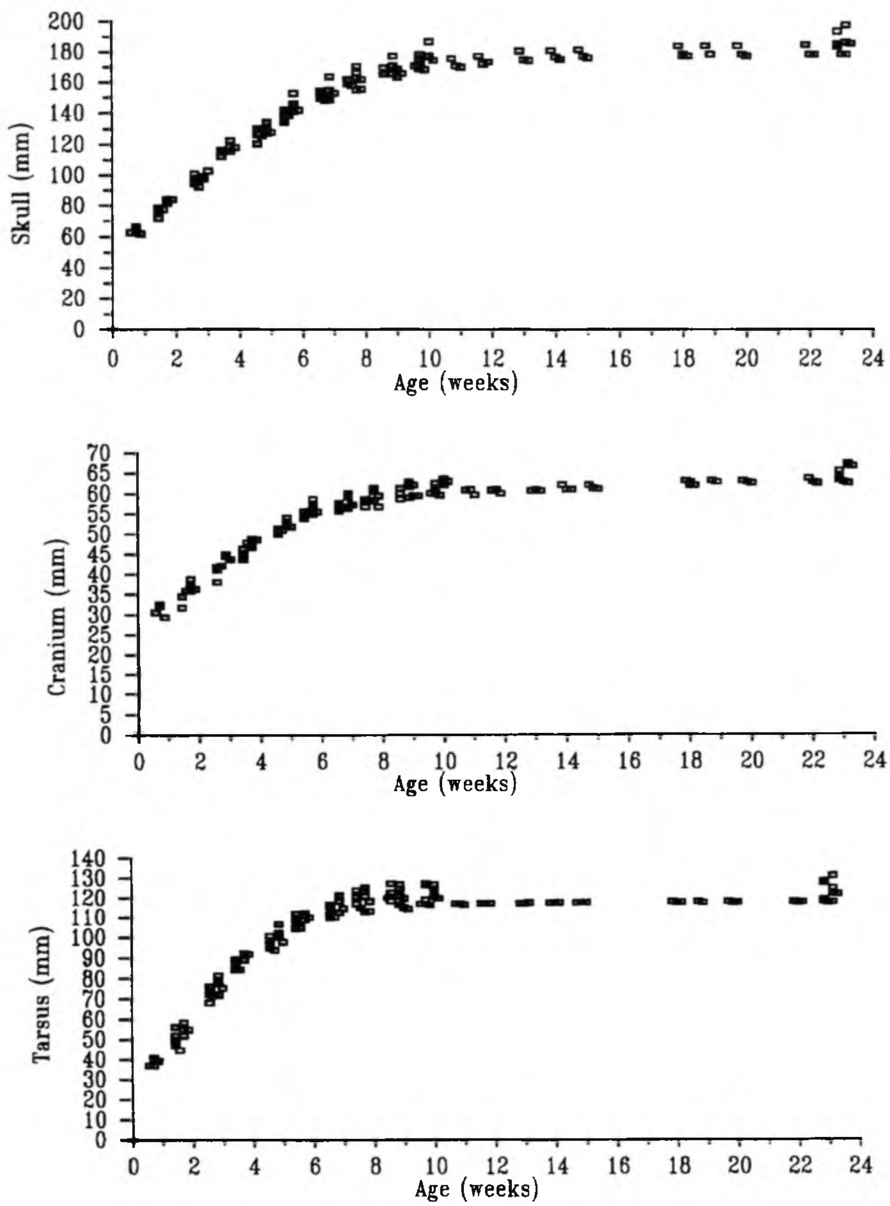

Figure 2. Skull length, cranial height and tarsal length of captive Whooper Swans from hatching date.

Skull, cranium and tarsus

The three bone measurements increased very rapidly in the early weeks with mean growth rates between weeks 1 and 7 of 2.09, 0.61 and 1.80 mm per day for skull, cranium and tarsus respectively, producing similarly steep growth curves (Fig. 2). The rate of increase in all measurements began to decline after week 7 for all measures, with the tarsus doing so most rapidly; there was little evidence of further tarsal growth by week 13. Skull growth continued at a very slow weekly rate until week 18; cranium measurements were still increasing slowly at the end of the study. Growth rates were again broadly similar for all birds in any given week and the younger birds did not catch up with the older ones until adult measurements were reached.

Wing and primary development

Total wing length produced a distinctly sigmoid growth curve when plotted against age (see Fig. 3). This curve reflects the tim-

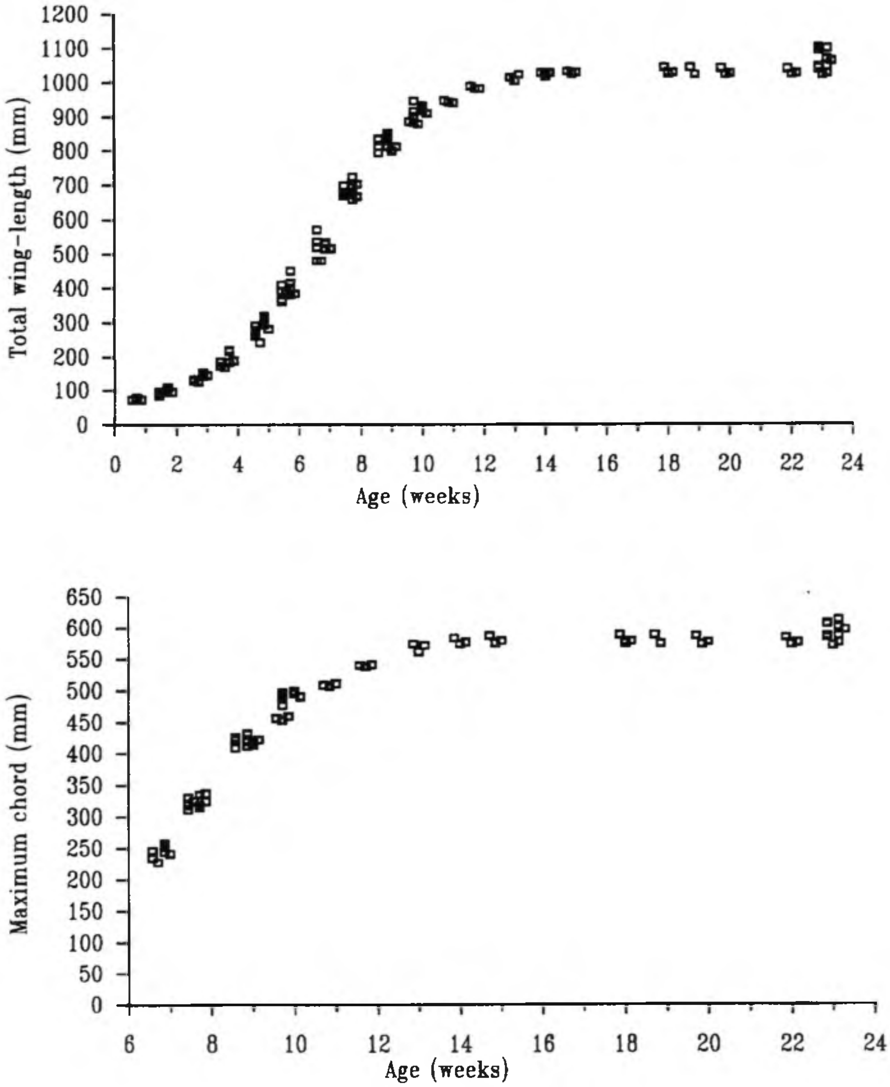

Figure 3. Total wing-length and maximum chord of captive Whooper Swan cygnets - age from hatching date.

Table 2. Primary moult scores of captive Whooper Swans (after Ginn & Melville 1983).

Week	*n*	P1	P2	P3	P4	P5	P6	P7	P8	P9	P10
1-5	10	-	-	-	-	-	-	-	-	-	-
6	10	1	1	1	1	1	1	1	1	1	1-2
7 & 8	10	2	2	2	2	2	2	2	2	2	2
9 & 10	10	3	3	3	3	3	3	3	3	3	3
11-15	3	4	4	4	4	4	4	4	4	4	4
17 & 18	3	5	5	5	5	5	5	5	5	5	5

ing of the stages in the development of the wing. Relative growth is small initially until the appearance of the flight feathers in week 6. Growth is then rapid with the combined development of both the fore-wing and the primaries. The curve begins to tail off after week 10 but the primaries continued to develop reaching their maximum length by week 18. Wing length began to decrease gradually after week 18 at a mean rate of 0.10 mm per day as a result of abrasion of the tips of the primary feathers.

Primaries (and secondaries) were found to develop rather evenly on each bird with

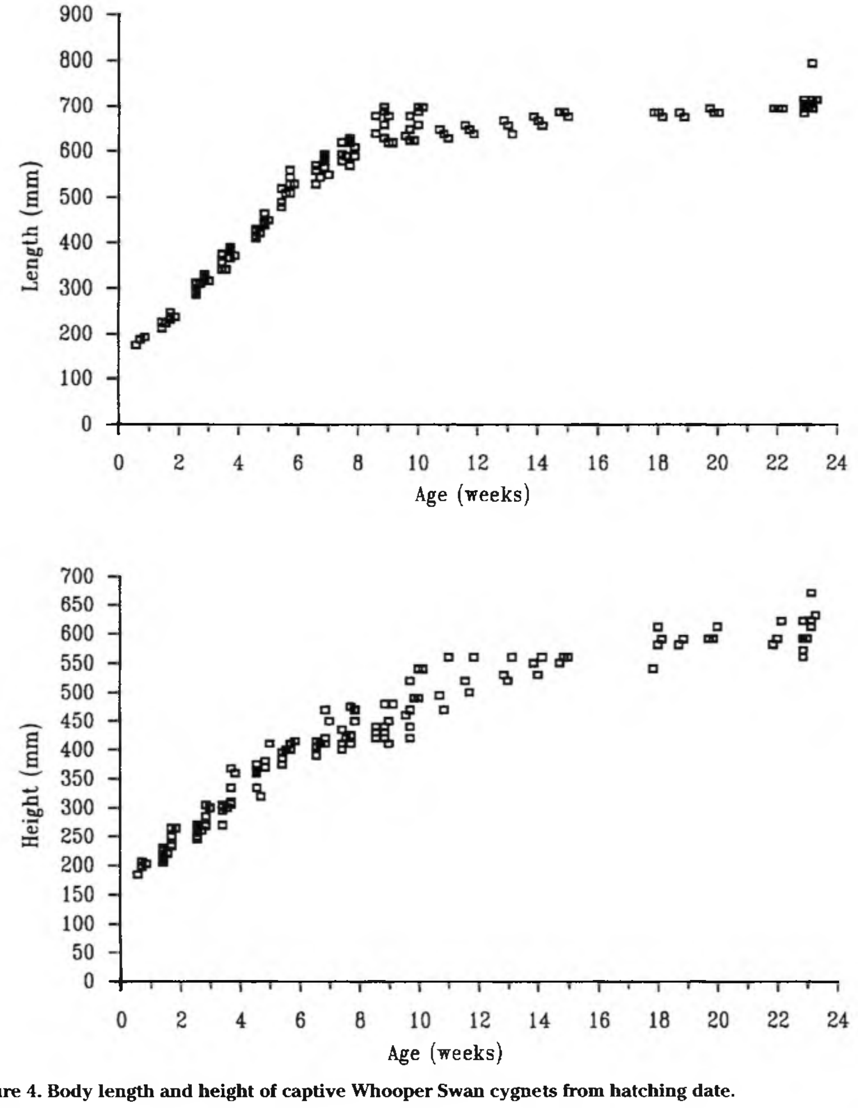

Figure 4. Body length and height of captive Whooper Swan cygnets from hatching date.

little variation in development between individuals (Coefficient of Variation, C = 0.072%). Moult scores of the primaries were uniform for the group in all weeks except week 6 when the outermost primary (P10) of three birds achieved a score one higher than the remainder of the wing (see Table 2). Fledging has been demonstrated to occur in geese when the feathers are about 85% of their final length (Owen 1980). In this study this point fell between weeks 11 and 12 i.e. around day 80 when the birds had achieved an average weight of 7500 g. Date of first flight was not recorded as the birds were pinioned in one wing.

Length and height

Length was found to produce a similar growth curve to the bone measurements with an initial rapid increase tailing off at around 9 weeks but with growth continuing at a very slow rate until the end of the study (see Fig. 4). Height produced a generally similar growth curve (Fig. 4). Increase in height was again rapid in the first weeks and began to tail off around week 8. However the tail off was less marked than with the length measurement and growth continued at a moderate rate until the end of the study.

Plumage development

The first contour feathers, defined as those forming the outlines or contour of the adult bird (Ginn & Melville 1983), to appear were the scapulars and underwing coverts which appeared on all birds at 4.3 weeks. These were soon followed by head

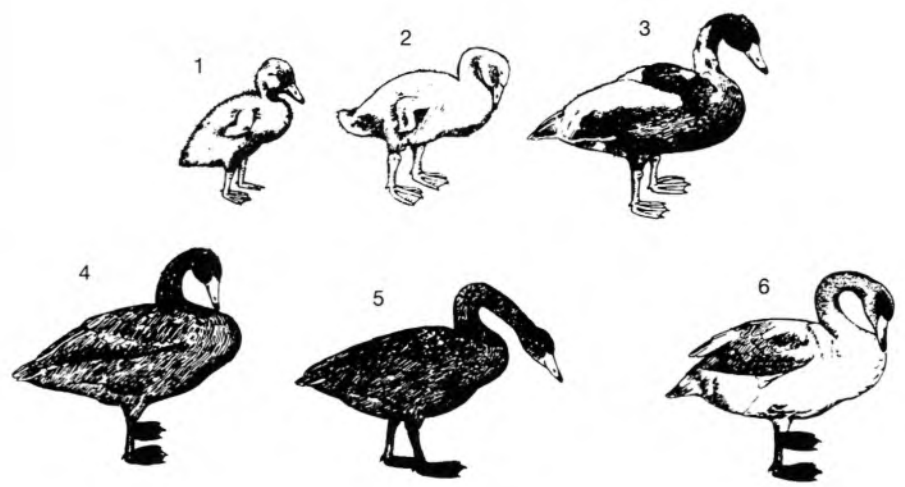

Figure 5. Stages in the development of Whooper Swans

Stage	Age in captivity (weeks)	Description
1	0-2	Downy. Body rounded, neck and legs short.
2	3-4	Downy. Body shape long, neck and legs look long.
3	5-7	Contour feathers appear contrasting with remaining down giving untidy look. Neck and tail become obvious. Legs still pinkish.
4	8-11	Contour feathering increasingly uniform but some down remaining. Primaries well developed but still flightless. Body shape approaching that of adult swan. Legs become blackish.
5	12-14	Fledging has occurred – birds capable of flight. No down remaining. Contour feathers uniformly grey.
6	15+	White patches of contour feathers appear and increase in extent. Bill patterns well defined.

Table 3. Comparison of biometrics of captive Whooper Swan cygnets within two sex categories (Mann-Whitney U paired comparisons). Note: M = male, F = female.

Week		*n*	Weight (kg) mean	Weight (kg) sd	Skull (cm) mean	Skull (cm) sd	Cranium (cm) mean	Cranium (cm) sd	Tarsus (cm) mean	Tarsus (cm) sd	Length (cm) mean	Length (cm) sd
2	M	3	0.598	0.15	7.840	0.56	3.503	0.20	5.260	0.38	18.575	0.76
	F	7	0.569	0.13	7.690	0.39	3.574	0.16	5.211	0.49	22.857	1.32
	U		13		13		12		8		11	
	P		0.569		0.569		0.732		1.000		0.909	
4	M	3	2.607	0.41	11.900	0.36	4.630	0.26	9.037	0.25	38.100	0.85
	F	7	2.336	0.30	11.530	0.23	4.694	0.17	8.770	0.28	36.143	1.73
	U		16		16		9		16		18	
	P		0.253		0.210		0.732		0.209		0.086	
6	M	3	5.100	0.43	14.440	0.92	5.673	0.21	11.153	0.47	54.167	0.20
	F	7	4.571	0.43	14.044	0.27	5.507	0.09	10.803	0.26	50.429	2.15
	U		17		14		16		21		19	
	P		0.134		0.425		0.252		0.017		0.051	
8	M	3	6.833	0.64	16.620	0.47	6.010	0.14	12.393	0.10	62.500	0.50
	F	7	6.029	0.64	15.920	0.33	5.834	0.15	11.659	0.32	59.357	1.70
	U		17		18		18		21		21	
	P		0.170		0.087		0.085		0.017		0.022	
10	M	3	8.433	0.99	18.087	0.54	6.293	0.06	12.610	0.13	69.000	1.00
	F	7	7.300	0.82	17.267	0.34	6.069	0.13	11.931	0.35	64.929	2.61
	U		17		20		19		20		19	
	P		0.138		0.030		0.053		0.030		0.066	
23	M	3	10.567	0.64	19.667	0.23	6.660	0.10	12.797	0.31	73.667	5.51
	F	7	9.957	0.45	18.373	0.34	6.413	0.18	12.040	0.36	70.857	1.22
	U		19		21		19		20		13	
	P		0.067		0.016		0.053		0.030		0.639	

feathers and greater wing coverts giving the birds a distinctly ruffled appearance. By week 6 contour feathers had also begun developing on the neck, breast, flanks , wings and tail leaving distinctive clumps of down feathers on the fore-wing protecting the developing flight feathers, which were all in pin at this stage. Contour feather development was rapid giving the birds an almost uniform coverage by week 8 with down remaining only on the wings, lower back, and head. No down was immediately visible by week 10 although some remained on the underwing until week 11. The cygnets remained a uniform grey colour during this period but there was an obvious whitening of feathers by week 15. White areas of feathers developed on the mantle, flanks and belly giving the birds a mottled appearance, and these areas increased in extent during the remainder of the study. Figure 5 details changes in the appearance of the cygnets during their development.

Coloration of the soft parts of the cygnets changed during the course of the study. There was a slow increase in the definition of the black tip of the bill in contrast with the pink base. Leg colour, however, changed markedly from a greyish-pink in the first 7 weeks to a greyish-black by week 8.

Comparison between sexes

Mann-Whitney U paired comparisons were conducted between the sexes on all variables considered for each week of data in which all ten birds were processed (i.e. weeks 2 to 10 and week 23). Such comparisons are valid as there was no significant difference in age between the sexes at any sampling point (U = 12, P = 0.81 for weeks 2-7 and week 23), despite differences in sampling dates at the two sites.

Male cygnets were consistently, but not always significantly larger on average than females in terms of weight, skull, cranium, tarsus, and length during the study and these differences increased in magnitude and significance with age (see Table 3). By week 10 significant differences existed between the sexes in terms of skull and tarsus, with near-significant differences in cranium and body length. Differences between the sexes were more marked in some variables than others. Tarsus differed most consistently with significant differences between the sexes from week 6 to week 23. Weight however, although differing consistently between sexes with males on average 10.4% heavier than females during the period week 1 to 10, did not achieve a significant difference in any one week. Similarly at week 23 the difference in weights between the two sexes did not reach statistical significance.

Table 4. Comparison of biometrics of captive and wild Whooper Swan cygnets (Mann-Whitney U paired comparisons).

Week		*n*	Weight mean	(kg) sd	Skull mean	(cm) sd	Tarsus mean	(cm) sd
8	Captive	10	6.270	0.719	16.130	0.485	11.879	0.442
	Wild	23	5.078	0.804	14.072	0.723	10.947	0.628
	U		200		230		205	
	P		0.001		0.000		0.000	
9	Captive	10	7.380	0.759	16.850	0.410	12.040	0.468
	Wild	6	5.800	0.518	15.038	0.287	12.000	0.573
	U		60		60		32	
	P		0.001		0.001		0.828	
10	Captive	10	7.640	0.984	17.510	0.546	12.140	0.441
	Wild	4	5.650	0.252	14.748	0.369	12.033	0.363
	U		40		40		23	
	P		0.005		0.005		0.671	

Table 5. Comparison of biometrics of captive and wild Whooper Swan cygnets - females from week 8 only (Mann-Whitney U paired comparisons).

Week		*n*	Weight mean	(kg) sd	Skull mean	(cm) sd	Tarsus mean	(cm) sd
8	Captive	7	6.029	0.624	15.920	0.331	11.659	0.318
	Wild	11	5.164	0.802	14.470	0.806	11.368	1.019
	U		87		105		64	
	P		0.063		0.001		0.821	

Comparison with wild birds

Biometric data from this study were compared with data collected during 1988 of 21 cygnets of known age from wild broods hatched at a latitude of 65°40'N at Skagafjordur, Northern Iceland (Rees *et al.* 1991) together with 12 cygnets ringed and measured from the same area in 1990 (Rees & Einarsson unpubl.). The minimum age for each brood was calculated for the 1988 cygnets by estimating the date on which the last egg was laid (eggs are laid at an average rate of one per 36 hours and final clutch size was known) for those nests at which fresh eggs were discovered, and by adding to this the 31 day incubation period (Kear 1972). In 1990 visits to the nests were less frequent during the egg-laying period and the minimum age of the 1990 broods was calculated, less precisely, from the date at which incubation was first recorded during near-daily observations of swans in the study area and by adding the 31 days incubation period.

Of the total of 33 known-age cygnets ringed and measured in Iceland, 23 (including all 21 cygnets from 1989) were calculated to be in their eighth week of growth upon capture, six in week 9 and four in week 10. Data from the cygnets aged ten weeks appeared anomalous since the weight and skull measurements had lower means than from cygnets aged nine weeks although the tarsus mean was higher. This may have resulted from the fact that all four cygnets at ten weeks came from the same brood. It has been demonstrated amongst Icelandic Whoopers that variance in egg size within a clutch is significantly smaller than that between clutches (Rees *et al.* 1991), and this may hold true for cygnets. With this reservation these data were compared with the corresponding weekly data from captivity.

Data for each week were lumped despite differences in the sex ratios between the wild and captive birds in order to increase sample size. Such a treatment is conservative as in all cases the sex ratio amongst the captive birds was more strongly biased towards females than amongst the wild birds. As male cygnets in captivity were demonstrated to be consistently larger than females throughout their development, the observed sex bias would tend to reduce any apparent difference in the growth rates between wild and captive, given the assumption that captive birds would be larger.

Mann-Whitney U paired comparisons revealed that the wild cygnets in their eighth week of growth were significantly smaller than captive birds of the same age for all corresponding measurements considered, including weight, skull and tarsus (see Table 4). For cygnets in their ninth and tenth weeks of growth, captive birds were again significantly larger than those in the wild in terms of weight and skull but not in terms of tarsus. When females alone were compared for week 8 the same relationships were detected although the smaller sample size prevented the difference in weight from achieving significance (see Table 5).

Development of the flight feathers was also slower in the 1989 Icelandic birds with five cygnets showing no primary growth at eight weeks, whereas all ten captive cygnets had developed primaries by week 6.

Discussion

The growth curves documented for the captive Whooper cygnets indicate very rapid increases in all measurements. Increase in weight relative to hatching weight (taken to be 210 g as quoted by Kear 1972) was very rapid with a thirty-fold increase within nine weeks. This is higher than figures quoted by Kear 1972 for other species of swan with the closest comparable increase being 34.1 times hatching weight at 10.7 weeks for captive Trumpeter Swans, a closely related species (after Banko 1960).

Similarly growth in tarsus length was very rapid and by week 18 had reached 99.8% of the average adult tarsus length of 118 mm (Cramp & Simmons 1977). This agrees well with the findings of studies of other northern swans. In Bewick's Swans and Tundra Swans *Cygnus columbianus columbianus* tarsus length had reached the average adult measurement by the first winter (Evans & Kear 1978, Limpert, Allen & Sladen 1987).

Relative tarsus growth was more rapid than that of the skull and cranium, a situation also recorded in similar work on geese. Owen (1980) for example reported that the legs of goslings grew more quickly than other parts of the body, suggesting that this would enable them to run faster, with consequent advantages in escaping from ground predators during their flightless period. This would also appear to be true of Whooper cygnets which can run at similar speeds to their parents and push their way through thick aquatic vegetation (E.C. Rees pers. comm.). Development of the tarsus in relation to other parts of the body was more rapid in the wild than in captivity. This may have certain adaptive advantages for the wild birds which would be more likely to face the threat of ground predators, and indicates that control of the relative growth of different parts of the body may not simply be genetic; exercise and food availability may also be important. The fledging time (the point at which growth reached 85% of adult wing length) of around 11.4 weeks recorded in this study is later than the 8.6 weeks recorded by Hantzsch (1905) for wild Whoopers from the continental population, but earlier than the 14.1 weeks quoted by Owen (1977). It agrees most closely with the 12 weeks recorded for wild Trumpeters in Kenai, Alaska at 60°N quoted by Kear (1972) and is less than other quoted figures for Trumpeter Swans including 13-21.4 weeks in Alaska (Bellrose 1978) 17.1 weeks at Jackson Lake, Wyoming at 44°N (Simon 1952) and 13 weeks for captive birds in Manitoba at 50°N (Kear 1972). It is also less than the 13-15 weeks recorded for Mute Swans *Cygnus olor* in England (Birkhead & Perrins 1986). Precise fledging dates in the wild are difficult to obtain and are often unreliable (Owen 1980), but it would appear that the fledging time recorded in this study was shorter than most comparable values quoted by other authors for wild swans.

Abrasion of the primaries after reaching maximum length in week 18 was rapid with a mean daily reduction in primary length amongst three cygnets of 0.10 mm per day (0.022% of mean maximum chord). This is considerably faster than the 0.02 mm per day (0.009% of mean maximum chord) recorded for wild juvenile Coots *Fulica atra* (Visser 1976) despite the obvious difference in wing use between captive and wild birds.

Weight achieved at fledging (7500 g) was 79% of the mean adult body weight of 9.45 kg quoted by Boyd (1972) a very similar figure to the 70-75% of breeding adult weight achieved by fledging Mute Swans in Sweden (Mathiasson 1980).

The measurements of length and height were taken in order to provide a rough and ready tool for ageing cygnets in the wild by comparison with their parents. However, both measurements are difficult to obtain accurately and are useful mainly for comparative studies (Owen & Montgomery 1978). Length will vary with the way a bird is positioned while height depends greatly on the degree to which the neck is extended. Conditions of measurement were therefore made as similar as possible each time and the procedure now needs to be repeated for a sample of adult birds in order to provide a scale for use in the field. To this scale needs to be added critical visible changes in plumage. The first appearance of contour feathers is one such indicator. In the captive birds these were the scapulars and underwing coverts which appeared at around 4.3 weeks, agreeing very closely with the 4.0 weeks quoted by Sheperd (1962) for wild Trumpeters in Alaska to reach the same stage. Another indicator is the first appearance of white feathers in the plumage. In the study this occurred during week 15, roughly half of the four and a half to five months recorded for Mute Swans to reach the same stage in Denmark (Andersen-Harild 1981). Figure 5 illustrates a six-point scale for cygnet development in order to approximate age in relation to size and plumage characters. Data from this study indicates an approximate correction factor for wild cygnets of: wild = captive x 0.75. However environmental factors affecting cygnet development will vary both between localities and between territories within a locality, and therefore will need to be taken into account when using this scale.

The documented size difference between male and female cygnets is consistent with the findings of other authors. The significantly larger male tarsus measurements for example agree with the findings of Limpert *et al.* (1987) who reported significant differences between the sexes in terms of tarsus length in Tundra Swans, with males being larger in all age groups considered. Differences in weight between sexes however, although consistent, with males on average 10.4% heavier than females during the period week 1 to 10, did not achieve significance.

In contrast Mathiasson (1980) working on Mute Swans reported a clear difference in body weight between male and female cygnets with males on average 28% heavier than females at fledging. The larger sex-difference in terms of weight in Mute Swans compared to the Whoopers in this study agrees with Kear (1972) who stated that the difference between the sexes is smaller in the northern swans than in the low-latitude species.

The significantly faster growth rates of captive birds over wild birds, although well known in geese (Wurdinger 1975) were unexpected as the opposite has been reported for closely-related species such as the Bewick's Swan (Kear 1972). The slower growth rates of Bewick's Swans parent-reared in captivity, were attributed largely to reduced daylength at lower latitude which in turn reduced time available for feeding. The enhancing effect of increased latitude upon growth rate was also stressed by Owen & Black (1990), but they added that variation in the fledging period of different species of geese all raised under identical conditions of continuous daylight in captivity also conformed to the general hypothesis of increasing growth rate with latitude. This would indicate that growth rates are genetically determined rather than resulting as a direct response to daylight length. Feeding rate will be limited in any case by the capacity of the oesophagus to store and the gizzard to process ingested food. Whooper cygnets in Iceland feed in bouts interrupted by other activities and spend much of the "night" asleep despite the availability of 24 hours of daylight during the period May-July (O.Einarsson pers. comm.).

Clearly in this study captive conditions were overcoming any effect of reduced daylength from week 5 onwards, allowing the cygnets to achieve growth rates in excess of those in the wild in Iceland. Since the 24 hour light conditions provided during the first four weeks of growth, which allowed maximum time for feeding, would have mirrored daylight conditions in Iceland, this factor alone cannot account for the more rapid growth rates observed in captivity. The provision of a high-protein pellet diet in conjunction with available grazing may have contributed to more rapid growth, although this is not always the case. For example, it has been shown in the North American Ruddy Duck *Oxyura jamaicensis jamaicensis* that individuals hand-reared in a hatchery grew at a slower rate and developed plumage later than those in the wild at the same latitude (Hays 1959). This might indicate an inadequacy in the diet provided, or that some other variable, such as disturbance or stress, was inhibiting duckling growth in captivity. Mayhew (1985) suggested that stress amongst captive Wigeon *Anas penelope* had a marked effect upon feeding behaviour, but added that captive birds not subjected to stressful conditions would exhibit largely unaffected feeding behaviours. As the Llanelli centre was not open to the public during the study period and the birds also became remarkably tame, disturbance and stress levels were low and presumably had a minimal effect upon growth rates.

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