

Biometrics and timing of primary moult of non-breeding Mute Swans *Cygnus olor* at Lake IJsselmeer, the Netherlands

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This paper examines the influence of weight and size upon the timing of wing moult of 488 non-breeding Mute Swans caught during the flightless period at Lake IJsselmeer (the Netherlands) in 1983. Primaries grew at a rate of 6.3 mm/day, but the growth rate slowed down later on. Start of wing moult showed a peak in the first ten days of July. Adult males began on average six days earlier than adult females. Weights are low, compared to other studies. Weight was strongly correlated with size. There was a slight tendency for larger sized swans to start moult earlier. The correlation between body weight and start of wing moult is highly significant, the heaviest swans started earliest. The swans lost weight over time. The low weights and weight-losses might indicate that food is limiting.

Several studies have been carried out on moulting Mute Swans *Cygnus olor* in Western Europe (Andersen-Harild 1981a,b, Mathiasson 1973, 1981a,b). Hitherto little attention has been paid to the timing of primary moult. This paper reports on the timing of primary moult of the Dutch population of non-breeding Mute Swans at Lake IJsselmeer. The aim of this study is to analyse the possible influence of weight and measurements on the timing of primary moult.

The Mute Swan is a common breeding bird in the lower parts of the Netherlands with 3,000-4,000 breeding pairs (SOVON 1987). Breeding birds stay in their territory with the growing cygnets during wing moult. Non-breeders migrate to special locations which provide sufficient food and safety from predators. Lake IJsselmeer and Lake Grevelingen are the most important sites in the Netherlands. Lake Grevelingen is a salt-water lake with eelgrass *Zostera marina* as the main food source. Maximum numbers vary between 1,000 and 2,000 (Meininger *et al.* 1984, 1985).

Lake IJsselmeer is a shallow fresh-water lake of 2,000 km² surrounded by man-made dikes (Fig. 1). A submerged vegetation of green algae *Cladophora* sp. grows along these dikes on boulders. The algae are only present during summer and form the only food source for the swans. Mute Swans are absent in winter, but in summer flocks of moulting non-breeders assemble along the dikes (Fig. 2). The average

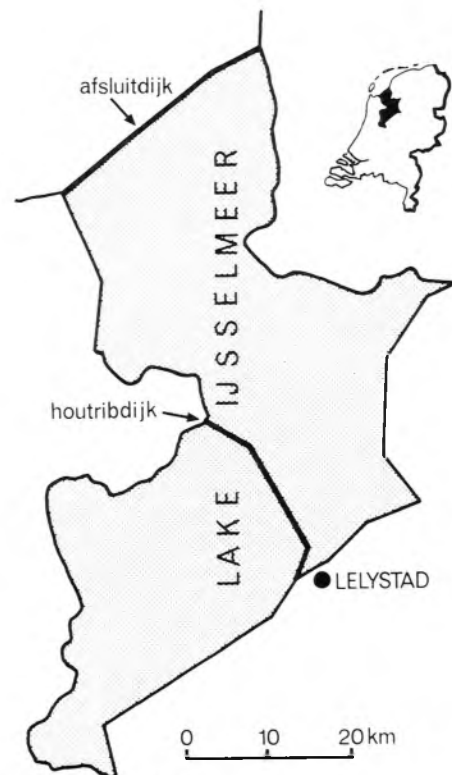


Figure 1. Map of Lake IJsselmeer.

maximum in July is 3,960 individuals (Table 1). The Houtribdijk (52°37'N, 5°25'E), length 30



Figure 2. Flock of moulting Mute Swans along the Houtribdijk, 28 June 1983. Photo © Klaas van Dijk

km, holds the largest numbers with up to 3,000 individuals. Numerous recoveries reveal that the Mute Swans of Lake IJsselmeer are almost exclusively of Dutch origin (Renssen 1981, Van Dijk 1991). Exchange with birds from the large moulting sites in Denmark does not apparently occur (Andersen-Harild 1981a).

Methods

In 1983 small boats with out-board engines were used to capture flightless swans along the Houtribdijk on 21 June (12), 5/6 July (155), 18/19 July (89), 25 July (76), 8/9 August (107) and 26 August (49). There was at least a delay of one hour between catching and processing the swans ashore. After being sexed (cloacal examination) and ringed, leg colour was used to determine colour morph (grey or leucistic/Polish', Andersen-Harild 1978). Swans were classified as first summer (born in 1982) by the presence of small grey/brown (grey morph) or light beige (leucistic morph) feathers on the lower back, supplemented by information about bill-colour and knob-size. The other swans were aged as adults (born before 1982), although some could not be divided properly and were put in the category 'unaged' (born in or before 1982).

Length (to the nearest mm) of the flattened p10 (outermost primary) from the tip to its origin from the skin was used to describe primary moult. The start of primary moult is defined as the day when the new primaries appear. We have taken a delay of three days for the few flightless swans which still had their old primaries and a delay of 1.5 day for swans lacking all primaries. For all other individuals growth rates of p10 (derived from recaptures) were used to work back to the start-date of primary moult.

Five structural measurements (all to the nearest mm) were taken. The width of the foot-web (between outermost toe-webs, fully stretched), the wing length (maximum chord with a stopped ruler) with subsequently the length of p10 subtracted to obtain a moult-independent wing-size, the length of the fore-arm (radius and ulna, measured with slide callipers) and the length of the tip of bill to the nearest end of the nostril and the nearest end of the eye. These last two measurements were taken from projected colourslides, taken of each swan following a standard procedure. Weight was measured with Pesola spring balances to the nearest 0.1 kg. All measurements were carried out by the first author.

The analysis is based on 488 birds (263 males, 220 females and 5 of unknown sex) of which 29 were caught twice. The swans were divided into 157 first summer (1S), 320 adult and 11 unaged birds. The leucistic morph was recorded in 41.4% of the birds ($n = 486$), divided into 33.3% of males ($n = 261$) and 50.5% of females ($n = 218$). Statistical analyses were carried out with SPSS. Significance was determined at the 0.05 level.

Results

Timing of wing moult

Growth rates of p10 are presented in Figure 3. These data show a constant rate for quite a long period, but suggest a probable slowing down in the latter stages. To clarify that growth rate decreases as moult progresses, we have divided the recaptured swans into three different groups. The first group of 15 birds with p10 < 200 mm at recapture had an average growth rate of 6.3 mm/day (SD = 0.28). There were no significant differences (t-tests) between ages (sexes combined) and between sexes (ages combined). The second group of six swans caught with p10 < 100 mm and recaptured with p10 > 200 mm had an average growth of 5.7 mm/day (SD = 0.59). The third group consisted of seven swans caught with p10 > 100 mm ($\bar{x} = 165$) and recaptured with p10 > 200 mm ($\bar{x} = 244$). These birds had a growth rate of 5.0 mm/day (SD = 0.63), which is significantly lower than the growth rate of the first group (t-test, $P < 0.005$). For reasons of simplicity we state that p10 grows with a constant rate of 6.3 mm/day from the start up to a length of 200

Table 1. Numbers of Mute Swans at Lake IJsselmeer, based on aerial counts. * Afsluitdijk not counted.

	1980	1981	1982	1983	1984	1985	1986	1987	1988	1989
June	3,484	3,432	3,613	4,103	3,071	1,489*	2,177	2,415	3,040	4,030
July	3,510	4,542	4,284	4,748	4,134	3,600	3,709	2,870	3,560	4,686
August	3,458	4,052	4,232	4,129	3,949	3,302	2,867	2,521	3,056	3,220

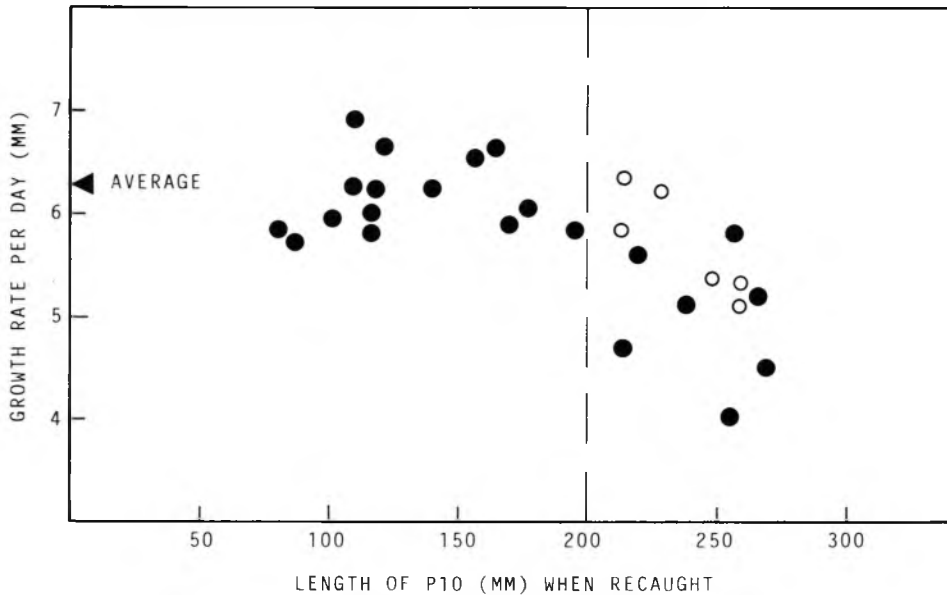


Figure 3. Growth rates of p10 of 28 flightless Mute Swans caught twice in 1983. Average growth rate is indicated for p10 < 200 mm. Open dots refer to birds caught with p10 < 100 mm and recaptured with p10 > 200 mm.

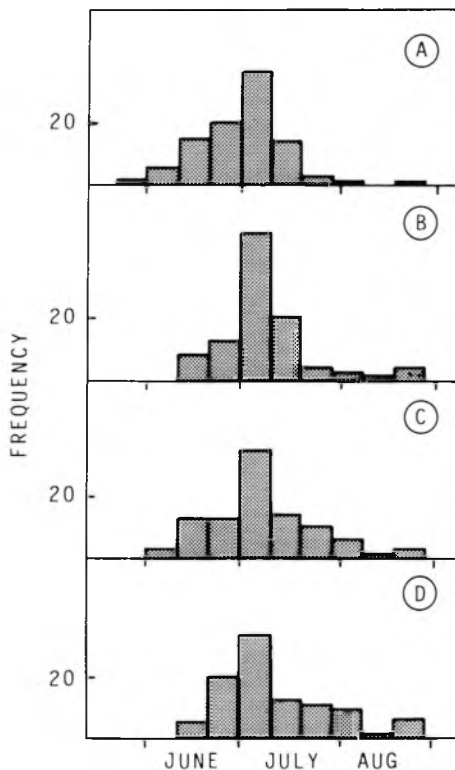


Figure 4. Timing of start of primary moult of flightless Mute Swans caught at Lake IJsselmeer in 1983. A = adult male ($n = 180$), B = first summer male ($n = 80$), C = adult female ($n = 137$), D = first summer female ($n = 77$).

mm and afterwards with a rate of 5.0 mm. We could not correct for a likely further decrease in growth rate as p10 approaches its final length (320-340 mm). This is a minor problem as only five swans were caught with p10 longer than 250 mm (maximum 268 mm).

The timing of the onset of wing moult is variable (Fig. 4). The first swan must have started at the end of May and some probably still had to start by the end of August. All groups exhibit a peak in the onset of primary moult in the first ten days of July. Adult males began on average on 3 July (SD = 15 days) and adult females began on average at 9 July (SD = 18). First summer males began on 11 July (SD = 15) and first summer females on 14 July (SD = 18). Adult males started significantly earlier than adult females (t-test, $P < 0.001$) and adult males started significantly earlier than first summer males ($P < 0.0001$). Other differences were not significant.

Structural size

The structural measurements are shown in Table 2. Males were significantly larger than females for all five measurements (t-tests, $P < 0.005$). There were no significant differences between first summer and adult males, except for the tip of bill to nostril ($0.025 < P < 0.05$). Adult females were significantly larger sized than first summer females, except for the tip of bill to nostril. These differences were greatest in foot-web ($P < 0.005$) and less pronounced in wing,

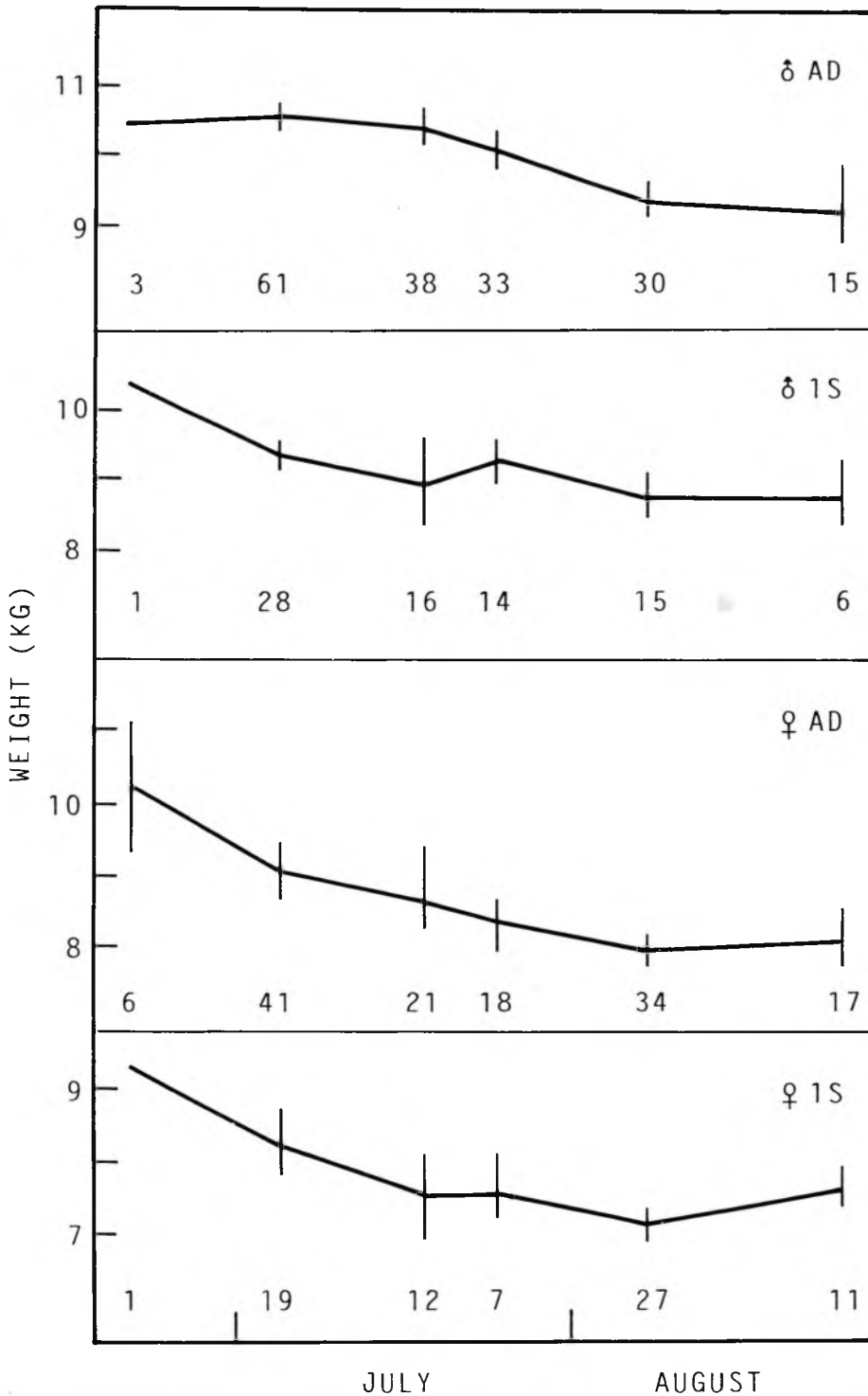


Figure 5. Weights of moulting Mute Swans in 1983. The data represent actual weights at processing. Bars indicate 95% C.I., sample sizes (broken down by sex and age) are indicated under each graph.

Table 2. Structural measurements (mm) of flightless Mute Swans caught in 1983. Values are mean \pm SE, number of individuals (n) and range.

	Wing	Fore-arm	Foot web	Nostril to bill tip	Eye to bill tip
Adult male	264.8 \pm 0.06 (176) 242-287	303.8 \pm 0.06 (178) 280-321	186.3 \pm 0.06 (179) 161-206	61.4 \pm 0.03 (179) 54-74	152.0 \pm 0.06 (179) 134-176
Adult female	250.3 \pm 0.08 (133) 227-279	285.5 \pm 0.09 (136) 251-317	174.9 \pm 0.07 (137) 152-194	57.0 \pm 0.03 (137) 49-67	142.5 \pm 0.07 (137) 126-165
First summer male	264.1 \pm 0.10 (79) 243-281	305.2 \pm 0.08 (80) 282-320	185.4 \pm 0.09 (79) 162-201	60.4 \pm 0.04 (79) 53-76	151.3 \pm 0.08 (79) 138-179
First summer female	247.1 \pm 0.13 (76) 214-274	282.3 \pm 0.12 (77) 247-309	170.8 \pm 0.09 (76) 152-190	56.0 \pm 0.04 (77) 49-64	141.1 \pm 0.08 (77) 127-160

fore-arm and tip of bill to nostril ($0.025 < P < 0.05$).

Weight changes

Mean weights and ranges for each age and sex class are shown in Table 3. The heaviest male (12.8 kg) weighed more than twice as much as the lightest female (5.4 kg). Differences between sexes (broken down by age) and between ages (broken down by sex) were very significant (t-tests, $P < 0.0005$). The average weights decreased in the course of time (Fig. 5). This downward trend is noticeable from the beginning of July

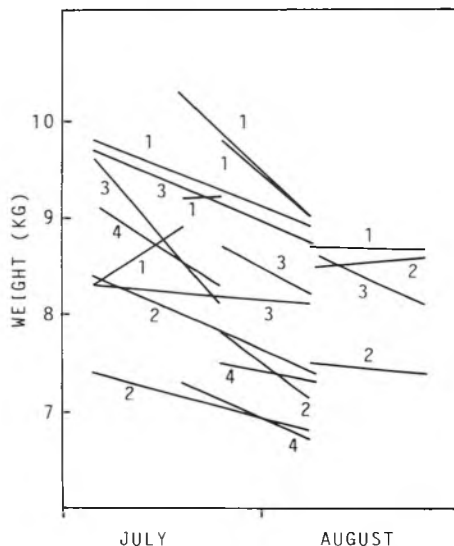


Figure 6. Changes in body weight of 19 flightless Mute Swans caught twice in 1983. Numbers indicate different sex and age classes: (1) adult male, (2) adult female (3) first summer male and (4) first summer female.

Table 3. Average body weights (kg) of flightless Mute Swans caught in 1983. Data represent actual weights at processing.

	N	Mean \pm SE	Range
Adult			
Males	179	10.08 \pm 0.07	7.2-12.8
Females	137	8.50 \pm 0.09	6.1-12.2
First summer			
Males	80	9.05 \pm 0.08	6.1-10.4
Females	77	7.58 \pm 0.09	5.4-10.4

until the beginning of August. The average weights remained constant during August. The data from recaptured swans confirm this pattern of weight losses (Fig. 6). These recaptured birds lost on average 25 g (SD = 27.0) per day. There were no significant differences between ages (sexes combined) and between sexes (ages combined) in the median weight decreases of the recaptured swans (Mann-Whitney U-tests).

Relationship between timing of moult, weight and size

We have used converted weights for the analysis of the influence of weight on the other parameters. We assume that each swan loses 25 g/day at a constant rate during wing moult. The converted weights were determined by increasing the actual weights by 25 g for each day between catching and the calculated day of start of primary moult. The relationship between weight and size is obvious (Table 4). Structurally larger swans are heavier. Both wing measurements give the best correlations. Models of three-dimensional combinations of measurements of wing, foot-web and bill do not improve the correlations with weight.

Table 4. Correlations between body weight and structural sizes of Mute Swans caught in 1983. Presented are Pearson's correlation coefficients (r). Significance is indicated by: NS $P > 0.05$, * $0.025 < P < 0.05$, ** $0.005 < P < 0.025$, *** $P < 0.005$.

	Wing		Fore-arm		Foot web		Nostril/bill		Eye/bill	
	r	P	r	P	r	P	r	P	r	P
Adult										
Male	0.23	***	0.32	***	0.21	***	0.15	**	0.17	**
Female	0.60	***	0.61	***	0.48	***	0.38	***	0.43	***
First summer										
Male	0.48	***	0.41	***	0.38	***	0.12	NS	0.05	NS
Female	0.49	***	0.49	***	0.33	***	0.27	**	0.35	***

Table 5. Correlations between size and start of primary moult of Mute Swans caught in 1983. For explanation see Table 4.

	Wing		Fore-arm		Foot web		Nostril/bill		Eye/bill	
	r	P	r	P	r	P	r	P	r	P
Adult										
Male	0.09	NS	-0.07	NS	0.12	NS	-0.05	NS	-0.17	**
Female	-0.14	NS	-0.06	NS	-0.02	NS	-0.11	NS	-0.17	*
First summer										
Male	-0.26	**	-0.28	**	-0.03	NS	-0.14	NS	-0.17	NS
Female	-0.14	NS	-0.26	**	-0.14	NS	-0.25	**	-0.30	***

Table 6. Correlations between body weight and start of primary moult of Mute Swans caught in 1983. For explanation see Table 4.

	r	P
Adult		
Male	-0.46	***
Female	-0.38	***
First summer		
Male	-0.48	***
Female	-0.42	***

There is only a slight tendency that larger sized swans start earlier with primary moult than smaller sized individuals (Table 5). The correlations between body weight and the start of wing moult are much better (Table 6). Heavier swans begin to moult earlier than lighter ones, so a bird's condition influences the timing of primary moult. Results of multiple regression analyses (Table 7) confirm that weight is the most important variable in all age and sex classes to explain differences in the timing of the start of wing moult. The contribution of size measurements is negligible.

Discussion

It should be remembered that there are several sources of potential bias. For instance, the

catching method results in a sample of swans which are unable to fly. Birds not yet in moult, or already able to fly again could not be caught. Considering the accuracy of weights, swans often defaecate one to three times between capture and processing. Fresh droppings weigh around 0.1 kg (Bacon & Coleman 1986). Assumptions about the time-lag between shedding the old feathers and appearance of the new, about constant weight loss and about the independence of growth rate and weight loss upon each other and upon size and the start of moult may also cause bias. More detailed research is necessary to make clear if these assumptions are reliable. Finally, the data are based on a study of just one year. As many waterfowl species show considerable annual fluctuations in the timing of breeding, migration and moult, one should be careful in comparing these data with other findings.

The growth rate of p10 in the constant stage (6.3 mm/day) is comparable with the scarce data from literature. Mathiasson (1973) recorded a rate of 6.5 mm ($n = 7$) for p5 and Andersen-Harild (1978) mentions a rate of 6-7 mm. Bauer & Glutz von Blotzheim (1968) quote a rate of 7 mm. There have been relatively few studies which have measured feather growth rates and most relate to captive birds (Ginn & Melville 1983). Owen & Ogilvie (1979) showed that wild Barnacle Geese *Branta leucopsis* have equal growth rates of primaries irrespective of age or sex. They suppose a probable slowing down of

Table 7. Relative importance of weight and size for prediction of start of primary moult of Mute Swans caught in 1983. Presented are stepwise multiple regression analyses with start of primary moult as dependent variable and weight and size measurements as independent variables with $P = 0.05$ as the limit for inclusion and deletion. r^2 is the squared multiple correlation coefficient.

	Step	Variable	r^2	P
Adult male	1	weight	0.21	<0.001
	2	foot-web	0.26	<0.001
	3	fore-arm	0.28	0.03
	4	eye/bill	0.29	0.04
	5	nostril/bill	0.32	0.02
Adult female	1	weight	0.14	<0.001
	2	wing	0.19	0.01
First summer male	1	weight	0.23	<0.001
First summer female	1	weight	0.17	<0.001

growth in the latter stages. Owen & King (1979) clearly demonstrate with several recaptures of wild Mallard *Anas platyrhynchos* that the growth rate of the longest primary is equal for males and females and significantly declines as moult progresses. Our findings agree with these studies.

The swans of Lake IJsselmeer range in start of primary moult from the end of May to the end of August with a peak in the first ten days of July (Fig. 4). Non-breeders along the Swedish west coast started between mid-June and the beginning of September with a peak around the end of July and the beginning of August (Mathiasson 1973). The Swedish swans showed a clear tendency for males to start moult somewhat earlier than females, corresponding with our findings that adult males begin six days earlier than adult females. Unpublished data (Zwanenwerkgroep Avifauna Groningen) confirm that paired birds with no offspring which stay in their territory during wing moult show a similar difference between the sexes. Adult males have a longer flightless period due to a similar growth rate of the primaries compared to that of the females, combined with a longer wing. The adaptation that males start wing moult earlier is useful for both members of the pair in order to regain flight ability at the same time. Visual observations suggest that a high proportion of the moulters at Lake IJsselmeer are paired. This agrees with the age distribution of ringed swans which shows that 41% are older than three years (Van Dijk 1990).

The weights of the Dutch non-breeding swans

(Table 3) are low in comparison to other data. Andersen-Harild (1981b) mentions averages of adult males from different moulting areas in Denmark varying from 10.3 to 11.6 kg. Differences were mainly caused by differences in food quality. Mathiasson (1981b) found in Sweden that first summer males weighed on average 10.0 kg and first summer females 7.8 kg. Reynolds (1972) presents data for first summer swans from England, where males weighed on average 11.0 kg and females 8.2 kg. The low Dutch weights might indicate that the availability and/or quality of the food at Lake IJsselmeer is not sufficient to support all the swans adequately. Although the average weights of the Dutch swans are low, they still decrease in the course of time (Figs. 5, 6). The loss of weight is in agreement with data from Denmark, where the swans lost up to 20% of their body mass during moult (Andersen-Harild 1981b). An English analysis, however, could not find a distinct decrease in weight during moult (Bacon & Coleman 1986). The weight losses of the Dutch swans may be another indication that food is rather scarce at Lake IJsselmeer.

Body mass is the most important parameter in explaining the variation in start of wing moult (Tables 6, 7). Our findings that moult starts first in the heaviest individuals agrees with Danish investigations (Andersen-Harild 1981b). Further studies at Lake IJsselmeer are necessary to test the hypothesis that food availability might influence timing of wing moult through body condition.

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