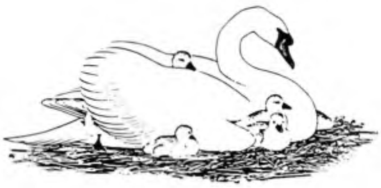
SECTION 6: BIOMETRICS, PHYSIOLOGY AND GENETICS

Laying date and clutch size in relation to body weight in the Mute Swan *Cygnus olor*



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Mute Swan laying dates and clutch sizes vary with average temperature of the preceding winter, indicating more severe losses of body reserves, or unfavourable feeding conditions, and consequent delayed clutch initiation after cold winters. Weights of females, prior to laying, were lower after a cold winter than after a mild winter, but weights at hatching were similar in both years of study. Individual weights of females allow for prediction of laying date and clutch size. Whereas males hardly change in weight during the breeding season, females put on large body reserves prior to laying, and deplete their reserves almost until the level of starvation during laying and incubation. Some females were unable to fly prior to laying, because of too heavy a wing load; others could not fly at hatching, due to emaciated breast muscles. Female weight loss during egg laying varied with clutch size, and was closely related to total clutch weight. Weight loss during incubation was considerable and fairly constant. It is argued that females may use a threshold weight as a proximate factor to control clutch size. Finally, the differential tasks of the sexes in breeding are discussed against the risks of jeopardizing future reproductive success.

Mute Swans, *Cygnus olor*, show large individual variation in clutch size (3-12 eggs with typical clutches of 5-8 eggs) and laying dates (early March to late May, with 90% of clutches initiated between 20th March and 1st May, Reynolds 1972, and pers. obs.). On a population level, differences in laying dates and clutch sizes are found in relation to winter temperature: after cold winters, birds start egg-laying later in spring, and produce smaller clutches than after mild winters (Birkhead *et al.* 1983 Walter *et al.* 1991). The first relation is also found in other waterfowl, e.g. the Coot *Fulica atra* (Perdeck & Cavé 1989).

Clutch size in waterfowl is thought to have evolved in relation to food availability for females during egg-laying (Lack 1968). The timing of egg laying is thought to be limited by the ability of females to find sufficient food supplies before egg formation commences (Perrins 1970). Reynolds (1972) showed that, in Mute Swans, clutch size decreased with laying date, and found that females increased approximately 2 kg in body weight before laying. He developed a model in which he hypothesized that, through food intake, the rate of weight increase of an individual bird would determine whether it could produce large clutches early in the season or smaller clutches later on. This model operates within circa-annual limits set by the environment, e.g. temperature and growth seasons of food plants (Drent & Daan 1980). In other words, timing of egg laying and number of eggs would largely depend on the rate at which females can accumulate body reserves before clutch initiation. Clutch size in the Mute Swan is indeed positively correlated with body weight of the female before laying (Mathiasson 1981).

Carcass analyses in several other bird species showed that body reserves, and especially protein reserves, are related to the number of developing follicles in the ovary (e.g. Jones & Ward 1976 Houston *et al.* 1983, Krapu 1981, Raveling 1979). Ankney & MacInnes (1978) found that fat- and protein reserves in arctic breeding Lesser Snow Geese *Chen c. caerulescens*, at the moment of arrival at the breeding grounds, determined clutch size. Moreover, body reserves were depleted during incubation, and some females died on the nest due to starvation. These studies relied on birds that were killed for analysis, and weight changes of individual birds could hence not be assessed.

The large variation in clutch sizes and laying dates has important repercussions for individual birds, not only in terms of number of offspring, but also for the chance of survival of young and their probability to reproduce.

Consequently, it is important for an individual maximizing its yearly reproductive output, to lay down body reserves as early as possible in the season, aiming to produce early and large clutches.

This paper provides evidence that body weight is closely correlated with both laying date and clutch size in individual Mute Swans. Comparison of laying dates and clutch sizes in relation to body weights is made between an extremely late year and an extremely early year. The data are based on free living birds, which could be recaptured several times during the breeding season. Hence, the costs (expressed as weight loss) of several stages in the reproductive cycle could be assessed for both sexes. Proximate clutch size control by females is discussed against the weight constraints they are facing. Moreover, the contribution of male and female in reproduction is discussed in relation to physical abilities and limitations of the sexes.

Study area

The study area is situated in the province of Groningen, in the northern part of the Netherlands. The Mute Swan population in Groningen increased rapidly between 1960 and 1985; before this swans were scarcely observed. At present, approximately 200 pairs of Mute Swans breed, and another 50 non-breeding, territorial pairs can be found in the study area. Densities reach approximately 0.4 pairs *km^{-2} in grassland areas (polders), and 0.07 pairs *km^{-2} in areas with arable land (see Van Dijk *et al.* 1986). For this study, pairs breeding in grassland areas within 10 km from the city of Groningen (lat. 53°13'N, long. 06°34'E) were investigated. The habitat in which they breed, consists of wet to moderately wet grasslands on clayey or peaty soils, with numerous drainage ditches 1-5 m wide. Furthermore, the area is characterized by intensive agricultural use, with heavy grazing by cattle and extremely high levels of fertilization. The swans benefit from this intensive land use through high quality food stocks consisting of various grasses *Gramineae* with high protein contents, and submerged or floating macrophytes (e.g. *Ceratophyllum* spp., *Elodea* spp., *Lemna* spp., *Myriophyllum* spp. and *Potamogeton* spp.) that grow in the ditches. Algae also form a part of the diet, especially in early spring. Conflicts with farmers, claiming damage to their grasslands by swans, result in high clutch losses, due to illegal egg-removal and nest destruction.

Methods

Breeding pairs were located in early spring and focal-pairs were selected, on the basis of their territorial behaviour. If birds defended their territory fiercely enough to allow for regular captures, they were observed almost daily in the pre-laying period. As soon as the nest was built, the birds were captured using a swan hook, weighed and measured. Hence, weights of birds just before laying (one or two days) could be collected. In 1986, these captures were repeated on about a weekly basis for successful pairs until cygnets fledged, or until failure of the breeding attempt. No captures were made during egg-laying. In this period, females were considered too vulnerable to damage of their developing eggs. Moreover, care was taken not to disturb the birds from their nests at an early stage. In 1989, weights of females were collected before laying, and when birds had completed their clutches, and at hatching. Metal ring numbers (allowing identification of individual birds), dates of laying

Table 1 Laying dates, clutch sizes and weights of female Mute Swans in 1986 and 1989. Averages and standard deviations, sample sizes in brackets. Differences tested using Student's t-test. Laying dates as day number, day 60 = 1st March.

	1986 ($T_{av.}$=1.5°C)	1989 ($T_{av.}$=5.7°C)	Level of significance
Laying date	112 ± 15 (*n*=7)	80 ± 7 (*n*=21)	$P<0.0005$
Clutch size	5.3 ± 1.3 (*n*=7)	6.9 ± 1.3 (*n*=15)	$P<0.01$
Female weight prior to laying	10.8 ± 1.0 (*n*=7)	12.1 ± 0.7 (*n*=21)	$P<0.005$
Female weight at hatching	6.9 ± 0.5 (*n*=6)	7.2 ± 0.6 (*n*=9)	N.S.

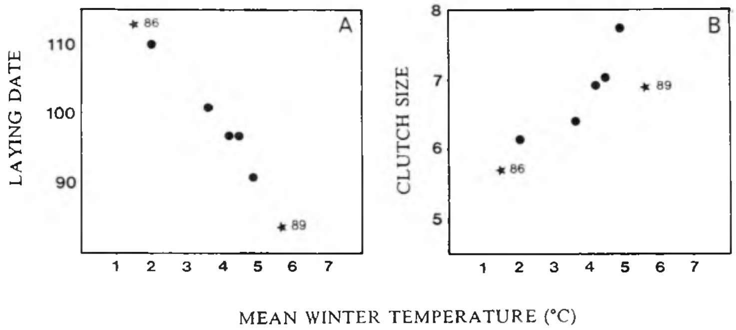

Figure 1 Mute Swan laying dates (A) and clutch sizes (B) in relation to average winter temperatures (December-February, in °C). After Birkhead *et al.* (1983), stars denote data from this study.

the first egg, clutch size and total weights of freshly laid clutches were recorded. Weights were taken to the nearest 50 grams, using a spring balance. Weather data originate from Eelde Airport (at 15 km distance).

Results

Between year variation: effects of winter temperature

Average laying dates and clutch sizes, as observed in the Groningen Mute Swan population, were plotted against temperatures of the preceding winter (average daily temperatures from December-February incl., = $T_{av.}$), and compared with data as given by Birkhead *et al.* (1983). The winter of 1985-86 was severe ($T_{av.}$ = 1.5°C) and the winter of 1988-89 was very mild ($T_{av.}$ = 5.7°C). With decreasing winter temperatures, birds started laying later (Fig. 1A) and produced smaller clutches (Fig. 1B) in the following spring. With data from Groningen, the regression as given by Birkhead *et al.* (1983) can be extended over a larger range of winter temperatures and, apparently, remains linear. However, clutch size in Groningen in 1989 appears somewhat lower than would be expected.

Birkhead *et al.* (1983) suggested that body reserves in females were more severely depleted after cold winters, and that it thus would take longer to replenish these reserves before reaching breeding condition. Moreover, the growing season of the swans' potential food plants starts later after cold winters. Table 1 compares laying dates, clutch sizes, and weights of females prior to laying and at hatching in 1986 and 1989. Laying dates of the weighed females were one month in advance in spring 1989, and clutches were significantly larger. Weights of females caught prior to laying show that they were significantly heavier in 1989. At hatching, no significant differences in weights were found between years. Unfortunately, only one individual female was caught in both years. She laid 6 eggs, starting on 8th April in 1986, and 9 eggs, starting on 21st March in 1989, with respective weights of 11.4 kg and 12.4 kg prior to laying. In both years she weighed 6.5 kg at hatching, which confirms the general pattern outlined above.

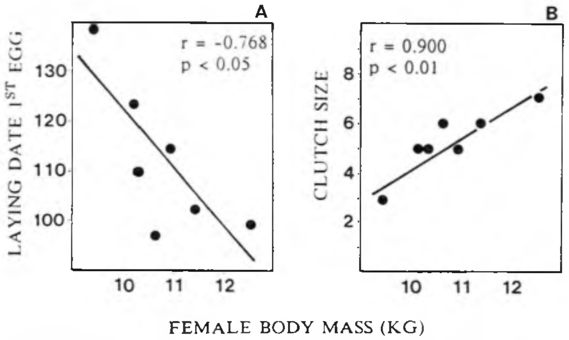

Figure 2 Mute Swan laying dates (A) and clutch sizes (B) in relation to female body weights.

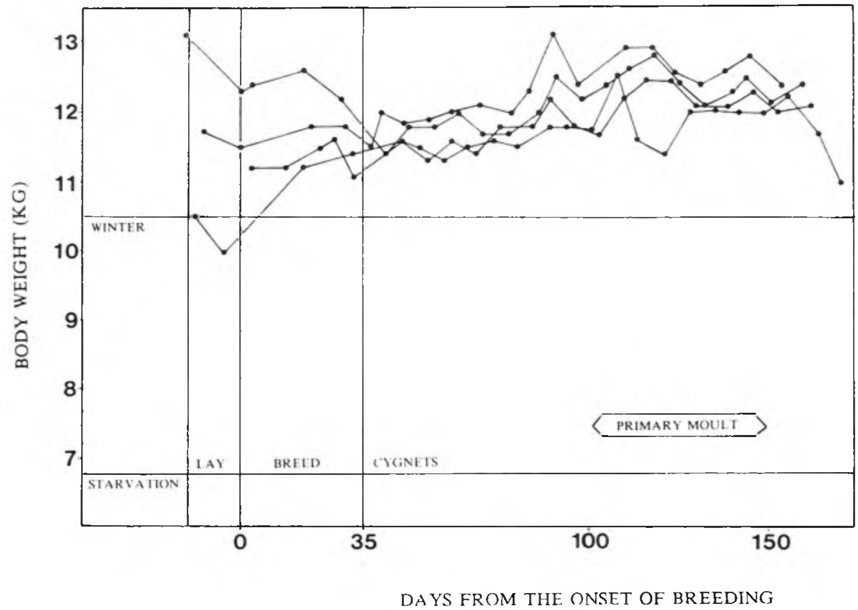

Figure 3 Weight changes in Mute Swan males, in relation to the stage in the reproductive cycle. Average winter weight and starvation weight are indicated.

Within year variation: effects of body weight

To determine the effect of individual body weights on clutch initiation, data from 1986 are presented in detail. Spring was extremely late in that year, and the thaw did not commence until 5th March, after a continuous frost period of about five weeks. The ditches remained ice covered for at least 10 more days, all vegetation in the grasslands had turned brown. Hence,

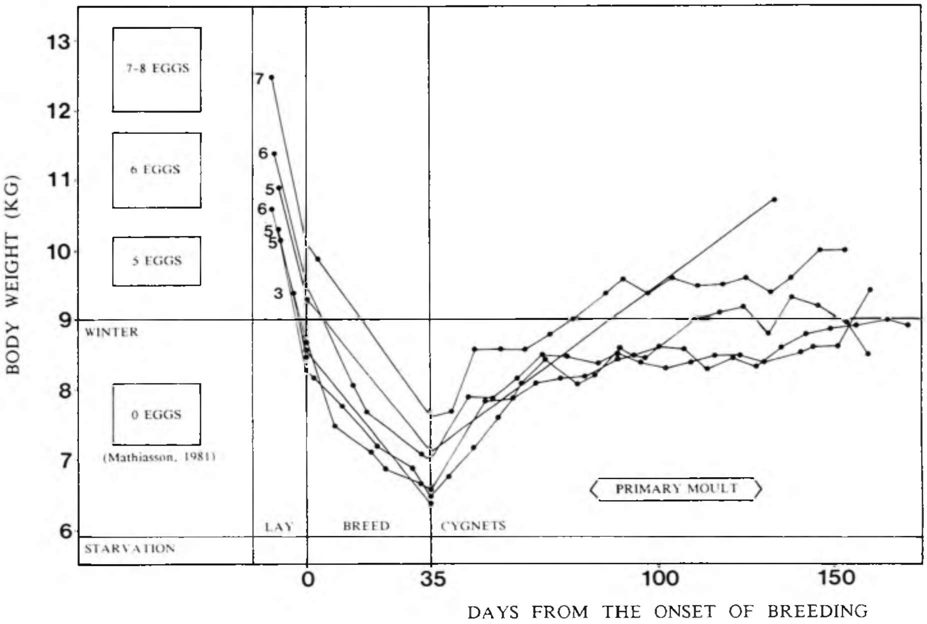

Figure 4 Weight changes in Mute Swan females, in relation to the stage in the reproductive cycle. Clutch sizes laid by individual females are indicated, and compared to weights and clutches as given by Mathiasson (1981). Average winter weight and starvation weight are indicated.

feeding conditions were considered very unfavourable and must have had a limiting effect on the rate at which birds could accumulate body reserves needed for breeding. Seven breeding pairs were caught on a regular basis. Of these seven pairs, laying dates ranged from 7th April to 19th May, and clutch sizes ranged from 3-7, decreasing with date. Females caught at the onset of laying varied in weight from 9.4-12.5 kg. The heaviest females were the first to lay eggs and produced the largest clutches, whereas lighter females were later and laid smaller clutches. The relation between female body weight and laying date, and female body weight and clutch size is shown in Figures 2A and 2B respectively. Laying date significantly decreased with increasing weight ($y=-1.14x + 234.8$, $r^2=0.590$, $P<0.05$) and clutch size significantly increased with higher weight ($y=1.14x - 6.99$, $r^2=0.810$, $P<0.01$), despite small sample sizes ($n=7$ in both cases).

Weight changes related to sex

Since birds could be captured and weighed several times during the breeding season, weight changes can be plotted against the stage in the breeding season for both sexes. Figure 3 shows weights of male Mute Swans throughout the season of 1986. Although some variation in weight occurs, there is no clear trend. Males tend to maintain stable weights between 11 and 13 kg throughout the season. Only during egg-laying, while the female is off foraging and the male spends a large proportion of his time guarding the nest, males may lose some weight. Males have ample opportunity to feed while guarding territory borders and the nest when females are incubating. Their weights are well above average winter weight for adult males, as measured in severe winters in Groningen, and 4-6 kg above starvation weight, which was determined by Andersen-Harild (1981a).

In the same year, the pattern of weight changes for females is in sharp contrast to that of males (Fig. 4). Prior to egg-laying, females are 0.5-3.5 kg heavier than average adult females in winter. During egg-laying, females lose weight to a level of about winter weight (9 kg). The clutches produced by the individual females are indicated in the figure and compared to weights and clutch sizes as given by Mathiasson (1981). The data obtained in Groningen are in quite good agreement with those from Sweden. During incubation, the decline in weight continues until hatching. This decline is due to the fact that the female incubates the eggs almost continuously for a period of 35 days, without feeding. Males do not share in incubation. Some females may reach weights close to starvation weight, which is 5.9 kg (Andersen-Harild 1981a). After hatching of the eggs, the parents and the cygnets usually leave the nest within a day. After this, females rapidly regain weight, in about 5 weeks, until approximately 8.5-9 kg. In both sexes, weights during primary moult remain relatively stable.

Female weight changes during egg-laying and incubation

Whereas weights of breeding Mute Swan males remain stable throughout the breeding season, weight losses in females during egg-laying and incubation may amount 3-5 kg (approximately 30-45% of body weight prior to laying). Female weight loss during egg-laying is in very close accordance with the total weight of the clutch that she laid ($r=0.993$, $P<0.001$, Figure 5), and amounts to approximately 150-200 g*day^{-1} (laying intervals of 1.5-2 days, average egg weight 330 g). Virtually the entire mass of eggs originates directly from the female body itself. This would mean that the female uses her body reserves for egg formation, and that she does not acquire essential nutrients for egg formation through feeding in the laying period. However, this does not explain the considerable time allocation for feeding by females during laying. The efficiency of transferring body reserves into eggs is estimated at 70-80% (King 1973, Aliskauskas & Ankney 1985). Considering that turn-over efficiency from food plants into eggs is even lower, and using 2.5 kg for average

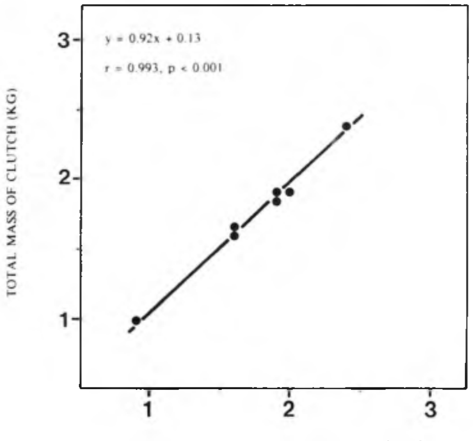

Figure 5 Relation between weight loss of individual Mute Swan females and total weight of the fresh clutch actually laid.

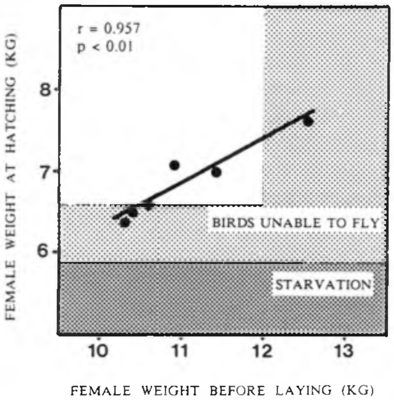

Figure 6 Relation between Mute Swan weight prior to laying and weight at hatching. Limits between which birds must operate to avoid flightlessness or starvation are indicated by light and heavy shading respectively.

clutch weight, females would have to consume 0.5-1 kg in excess of their daily energy requirements during the egg-laying period.

Weight losses of females during incubation are fairly constant (2.17 ± 0.23 kg, *n*=6, range 1.9-2.5 kg). Over 35 days of incubation, the rate of weight loss can be calculated as 62 g*day^{-1}. By the end of the incubation period, females are seen more and more off the nest to feed. This probably reflects the depletion of body reserves, since female weights are close to starvation weights by the time of hatching. After hatching, the rate of weight increase in females is approximately 80 g*day^{-1}, and body reserves are replenished until a weight of 8.5-9 kg is reached.

The importance of sufficient body reserves for breeding is not only reflected by the fact that heavier females lay more eggs. Heavier females also maintain higher weights at hatching than light females do (Figure 6). Lighter females take more risks than heavy females, since they end-up closer to starvation weight. Moreover, females that deplete their reserves down to a body weight of 6.5 kg or less, take the risk of being unable to fly at hatching, and hence increase predation risk by, for example, foxes *Vulpes vulpes*. Some of these females, which proved to be rather shy, tried to escape at catching but could only run for their lives, instead of simply flying away. One female (Fig. 4), weighing only 9.4 kg before laying, eventually produced a clutch of three eggs (totalling one kg), but the eggs were predated after two weeks of incubation. Apparently the female anticipated her lack of reserves (8.4 minus 2.2 kg would be 6.2 kg at hatching) by leaving the nest for feeding trips, and lost her clutch. On the other hand, laying down large body reserves for breeding may also result in flightless-ness, before laying, due to too heavy a wing-load. Females of over 12 kg proved to be too heavy to take off and prevent us catching them.

Discussion

The role of body reserves in reproduction of swans

Whether or not individual Mute Swans can breed, depends on the ability of females to put on body reserves, needed for egg-formation and incubation. Andersen-Harild (1981b) showed that the proportion of potential breeders that did actually nest, decreased with lower winter temperatures. Presumably, food intake rate after cold winters was insufficient for females to accumulate body reserves needed for breeding. Birds that do not breed, have indeed substantially lower body weights in spring than breeders (Mathiasson 1981). So, even though Mute Swan pairs may occupy territories, their ability to breed depends on accumulated body reserves prior to laying. It is likely that this applies to other swan species as well.

This paper provides evidence that female body weights after a cold winter were lower than after a mild winter, resulting in delayed onset of breeding and smaller clutches. Moreover, it is shown that differences in body weight, within a given year, dictate clutch size and laying date to a large extent. Heavy birds were able to lay early and produce large clutches, and less heavy birds started later and laid smaller clutches. So, to reach a high reproductive output, a female Mute Swan needs to attain a high food intake rate in early spring. An additional advantage of being early may be that there is still time available to regain body condition for a replacement clutch, in case the first clutch is lost (Bacon & Beekman 1991).

The decline of Mute Swan clutch sizes with progressing date (Reynolds 1972) can not be explained yet. Food, as the only regulating factor for clutch size in relation to date is difficult to understand. Since nutritional conditions presumably improve with date, birds should be able to produce larger clutches later in the season, but this is in contradiction with the pattern observed by Reynolds (1972). Feeding experiments, in which birds obtain supplementary food prior to laying, could elucidate how clutch size and laying date are controlled through food availability. Differential food intake rates and the existence of a variable threshold level, triggering clutch initiation, have to be assessed before the model put forward by Reynolds (1972) can be validated. Moreover, the specific role of different body components used for egg formation and incubation, e.g. protein and fat (cf. Ankney & MacInnes 1981, Krapu 1981), would be interesting to investigate in detail, for understanding the causal factors underlying body condition and clutch formation. Considering the difficulties of (re-)capturing free living Mute Swans as long as they do not defend a nest, this problem should perhaps be tackled experimentally, with birds in (semi-)captivity.

We are far from understanding the ultimate factors regulating clutch size control in Mute Swans. However, an individual female may use her weight at hatching of the cygnets, or her starvation weight, as a level for proximate control of clutch size at a certain date. Since this weight level is rather fixed and the costs of incubation, in terms of weight loss, are fairly constant, a female may avoid starvation by controlling the number of eggs she actually lays. If she terminates laying at about 9 kg, she will have sufficient reserves for incubation. If, at that moment, additional eggs are developing in the ovary, it is expected that these will be resorbed. How this mechanism operates in relation to date, leading to reduced clutch sizes later in the season, remains to be solved.

Genetic differences between individuals also contribute to differences in laying date and clutch size in the Mute Swan (Bacon & Perrins 1991). Moreover, physiological limitations or hormone levels in relation to daylength may be of importance. Meijer *et al.* (1988) showed that in the Kestrel *Falco tinnunculus*, neither food intake in itself, nor the condition of the laying female determined clutch size (independently of date): clutch size was determined through an endogenous program in which hormones dictated the onset of incubation.

Finally, the hypothesis that late birds might terminate laying at an earlier moment, to enhance survival of young that would consequently hatch earlier (Drent & Daan 1980), may also explain the trend of reduced clutches with progressing date, operating through natural selection pressures. In the Mute Swan, the reproductive cycle is extremely long. Cygnets do not fledge within half a year from the laying of the first egg, and this may have important consequences for the survival of late cygnets. A late female, laying only half the number of eggs that an early female lays, advances the date of hatching of her cygnets by about one week. So, the adaptive significance of different reproductive tactics can only be fully understood in relation to the reproductive value of the offspring produced (*cf.* Dijkstra *et al.* 1988).

Weight limits and task sharing in reproduction

Mute Swans are typically sedentary birds in the Netherlands, where a temperate, maritime climate prevails, and hence they do not need to spend energy on a long migration between geographically segregated wintering grounds and breeding grounds. Unexpectedly, and similarly to arctic breeding geese (*cf.* Ankney & MacInnes 1978), breeding female Mute Swans operate between closely defined weight limits, (that determine their ability to fly and escape predation, Fig. 6). At the high end of the weight scale, too heavy a wingload (defined as weight per cm^2 wingsurface) results in flightlessness. In Groningen, the chance of predation is minimal and the cost of being flightless seems to be relatively small as compared to the benefits of producing one or two extra eggs. Maximizing clutch size in this way would be impossible for migratory bird species.

At the low end of the weight scale, having almost depleted their body reserves just before hatching, females are faced with three options. Clutch predation, due to leaving the nest unattended while on feeding trips, results in total failure for that year since females cannot regain condition for a repeat clutch at such a late stage. Secondly, emaciation of the breast muscles and consequent flightlessness could result in predation of the female herself: again that chance is small, although it may be easier for a predator to kill an emaciated bird than a female in breeding condition. Finally, total depletion of reserves may result in starvation, hence jeopardising future reproduction. The females appear well able to prevent severe condition loss, to minimize risks and to maximize hatching success. In Groningen, predation of clutches and emaciated swans is rare, and starvation on the nest has not been proved so far. It is not yet known whether the Groningen situation has existed long enough (in evolutionary terms) to relax the genetic programme as shaped by natural selection. It is quite likely that the lower and higher weight limits, as discussed above, still operate in dictating the behaviour of the swans, even in the present-day low-risk situation in Groningen.

The fact that female Mute Swans are apparently often close to the limits where risks of flightlessness or starvation start operating, cannot but raise the question why males do not share in incubation. In this species tasks are clearly separated: the female lays eggs (obligatory) and incubates, whereas the male defends the territory against intruders and neighbouring pairs. Occupying a territory is the first requirement for reproduction, and with the densities found in Groningen, competition for territories is likely to be rather severe. Territories in this polder landscape are typically 0.5-1.5 km² in size and are fiercely defended. Physical combat is common, and in some cases one of the males involved is killed by its opponent. Hence, for males it is important to maintain a good condition, and sharing in incubation means loss of weight, thus jeopardizing territorial defence. Moreover, females are much smaller than males, and if a female would meet the neighbouring male at the territory border her chances of losing the fight and being beaten to death are considerable, although data are lacking. From the point of view of a female, losing the male due to lack of his physical condition would almost certainly result in losing the territory and chances for present and future reproduction. For a male, losing the territory implies high risks in obtaining a new one; losing the female due to starvation probably only means that he has to find a new mate; the territory remains. Differential tasks in breeding Mute Swans appear to be functional, and are maintained by the physical abilities and limits of the sexes.

The members of the Mute Swan Study Group, Avifauna Groningen, are too numerous to mention for their invaluable help in collecting data on breeding pairs and their nesting success, and in catching birds. I am especially grateful to Ben Koks and Hans Zwaagstra, together with whom I learned to discover the many interesting features of the swans' breeding biology in the field. Ben Koks also collected many weights of breeding females. Land-owners kindly gave permission for access to their properties. It is with great appreciation that I recall the many fruitful discussions with Theo Meijer and Bart Nolet on the subject. Herbert Prins and Frieda van Essen kindly made valuable comments to improve the paper. Finally, I want to thank Prof. Dr. R.H. Drent for supervision in 1986, as well as for never fading and stimulating attention and valuable suggestions. Presentation of this paper at the Swan Symposium was made possible by financial support from the Prins Bernhard Fund and the World Wide Fund for Nature-the Netherlands.

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