EFFECTS OF BODY CONDITION ON MOLTING IN MALLARDS[1]

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Abstract. The effects of high and low protein food on molting in penned, wild-strain Mallards (*Anas platyrhynchos*) from southwestern Sweden were studied in 1979, 1980, and 1985. Body condition, as indicated primarily by lipid deposits, declined during the flightless period. This decline was probably more the result of a strategy to recover flight capability rapidly than the result of stress. By metabolizing stored lipids, birds may be able to seek refuge in habitats offering protection from predators, even if food in such habitats is scarce. During the flightless period, food quality did not affect the growth rate of the primary feathers. But when exposed to low protein food, even after recovering flight capability, birds, especially males, developed shorter wing feathers; this feather shortening may reduce their condition capacity, i.e., their capacity to increase body condition without reducing their flight capacity in late autumn. A lowered condition capacity could lead to decreased survival of the ducks when exposed to severe winter conditions. Female Mallards demonstrated a higher condition capacity than males, which may contribute to the more rapid recovery of female primaries. Since the final length of the primaries is affected by food quality during molting, wing length is probably not a variable suitable for use in a condition index.

Key words: Mallards; molting; food quality; body condition; primary growth; wing length; flight capacity.

INTRODUCTION

Reproduction, molting, and migration constitute the major energy-demanding functions in migratory birds (King 1974:7). In Anseriformes, as in several other aquatic and marsh-dwelling birds with high wing-loading (Stresemann and Stresemann 1966:20), all flight feathers are molted simultaneously. Thus Mallards (*Anas platyrhynchos*) molting in a restricted wetland area must rely on the food resources available there while they are flightless, i.e., for three to four weeks (Boyd 1961, Balat 1970). Declining weight in Canada Geese, *Branta canadensis* (Hanson 1962, Hanson and Jones 1976) and Mallards (Folk et al. 1966) during growth of the remiges has earlier been attributed to nutritional stress caused by limited food availability. In contrast, Ankney (1979, 1984) did not find any evidence that molting caused nutritional stress in either the Lesser Snow Goose (*Chen caerulescens caerulescens*) or the Brant (*Branta bernicla*). Still, Boyd and Maltby (1980) noted that Brant with well developed new primaries weighed less than those with undeveloped ones. Furthermore, Owen and Ogilvie (1981) found that most Barnacle Geese (*Branta leucopsis*) lost weight gradually during molting; these authors suggested that weight loss may be

of selective advantage because lighter birds generally have shorter flightless periods. The same conclusion was drawn by Douthwaite (1976), who found that both male and female Red-billed Teal (*Anas erythrorhyncha*) lost weight during molting. However, he did not believe that the weight loss was stress-related. South African Shelduck (*Tadorna cana*) males lost about 25% of their premolt weight, but no detrimental effects on the survival of the molting birds were noted (Geldenhuys 1983). Young and Boag (1982) did not find any significant weight decrease in male Mallards during the flightless period, contrasting with the studies of Folk et al. (1966).

The contradictory results obtained, both within and among species, necessitated further investigations of the importance of body weight and body condition in molting ducks. In wetland management it is also important to know how qualitative differences in various habitat characters can affect molting ducks. High protein food is required by egg-laying Mallard hens and newly hatched ducklings, whereas other energy-demanding phases during the annual cycle depend on food of plant origin to increase lipid reserves (Chura 1961; Sugden 1973; Swanson and Meyer 1973; Krapu and Swanson 1975; Pehrsson 1982a, 1984). In the present study the importance of protein-rich food to molting Mallards has been evaluated experimentally on penned birds.

METHODS

Wild-strain Mallards taken from a population on the Swedish west coast were held in captivity in outdoor pens described earlier by Pehrsson (1982a, 1984). In 1979 and 1980, males and females were kept in two separate pens on rocky ground covered with a thin layer of earth with grass, herbs, and bushes. A shallow concrete pond was divided by a fence so that two groups of ducks sharing the pond were isolated from each other. One of the two bird groups obtained high protein food, i.e., rolled oats and turkey pellets (22% crude protein), both ad libitum, while the other group received only oats ad libitum. Still, ducks in both groups could forage for earthworms (Lumbricidae) and other invertebrates on the ground. However, production of eggs of significantly different sizes between the two foraging groups (O. Pehrsson, unpubl.) proves that the two experimental groups form two different nutritional levels denoting high- and low-protein food groups. Most of the ducks used both years spent one year in each of the different food-quality groups.

The ducks were weighed (WEIG) on a Mettler balance to the nearest g about once a week from June to September in 1979 and from April to October in 1980. At each weighing after dropping of the old remiges, the wing was straightened and flattened to measure wing length (WIL). In 1980, the length of the 9th primary was measured by gently pushing a thin ruler between the 9th and 10th primaries.

To obtain a size index (SIZIND), three body measures were taken in late autumn. The lengths (mm) of the forearm (ULRA), tarsus (TARS), and sternal ridge (STER) were measured with a caliper-square, and the size index was obtained by multiplying the three body measures:

$$SIZIND = ULRA/100 \cdot TARS/100 \\ * STER/10. \qquad (1)$$

Wing and bill measures were avoided because they may vary irrespectively of body size. Wing length may depend on food quality, as is found in the present study, and bill length may be shorter in bred strains of game-farm ducks (Greenwood 1975, Figley and VanDruff 1982, Pehrsson 1982b). Furthermore, the wing length of captive birds, which are wing-clipped on one side as in this study, may deviate from flight-capable wild birds.

A condition index was obtained by dividing the weight (WEIG, g) by the size index (Eq. 1):

$$CONIND = WEIG/SIZIND. \qquad (2)$$

To analyze the growth patterns of the new primaries from ducks representing different sex and diet groups, growth curves were fitted thus:

$$WIL = (C - B) \cdot (1 - e^{(-R \cdot NDATE)}) + B, \qquad (3)$$

where C = asymptotic length of the wing, B = y-intercept, R = a growth rate parameter, and NDATE = no. days after DROPDATE (the date with the first observation without primaries).

Early periods of primary growth (the first 18 and first 27 days) were compared among the groups in the linear regression model:

$$WIL = M \cdot NDATE + B, \qquad (4)$$

where M = slope or growth in mm day^{-1}.

The flight capability of a duck can be related to both wing length and body weight. With increasing wing loading the capacity of the wing is decreasing, and thus the length of the flightless period must depend on the wing capacity,

$$WICAP = WIL^2/WEIG \cdot 100, \qquad (5)$$

the inverse value of wing loading.

Wing lengths and weights of wild Mallards caught in Lake Kvismaren (59°10′N, 15°23′E), of hand-reared ducks from eggs from Lake Mälaren (59°30′N, 16°45′E), of wild ducks shot at Öster-Malma (59°05′N, 17°10′E), and of hand-reared ducks from game-farm eggs have been used to identify a lower wing capacity necessary for flight in Mallards. For comparison, some measurements were also made on domestic ducks.

In 1985, a small group of adult Mallards was held in captivity without being wing-clipped after the flightless period. Wing length and weight were measured each day during molting in July, and their flying capability was monitored periodically to obtain a more exact value of the WICAP necessary for flight. Later in autumn, wing length, and weight were measured on 25 August and 15 November.

In males the percentage of brown basic feathers (BROWN) in the gray alternate or nuptial plumage was estimated on every measurement occasion. In those males where the whole eclipse could be followed (Fig. 1a), this male molting parameter was compared between diet groups by curve fitting as follows:
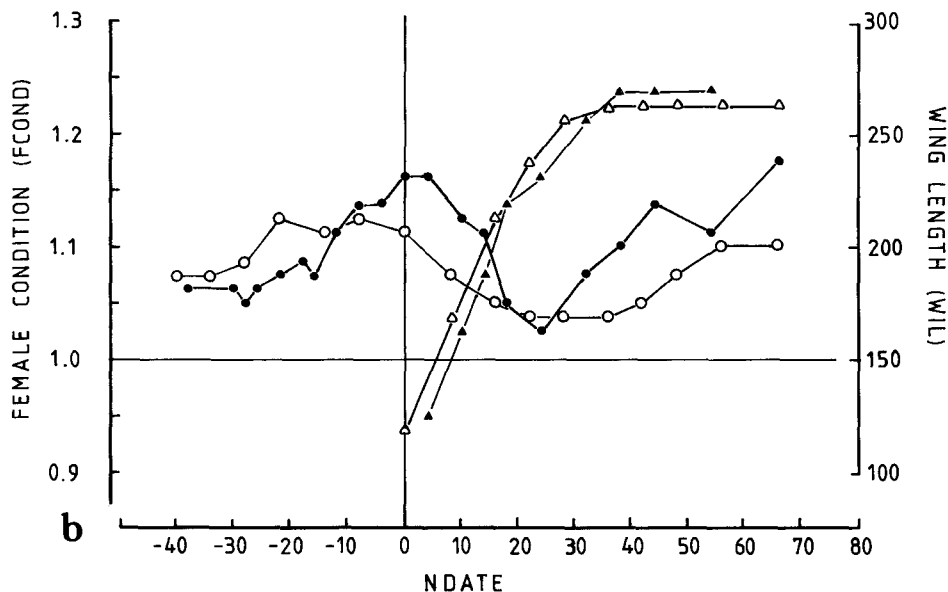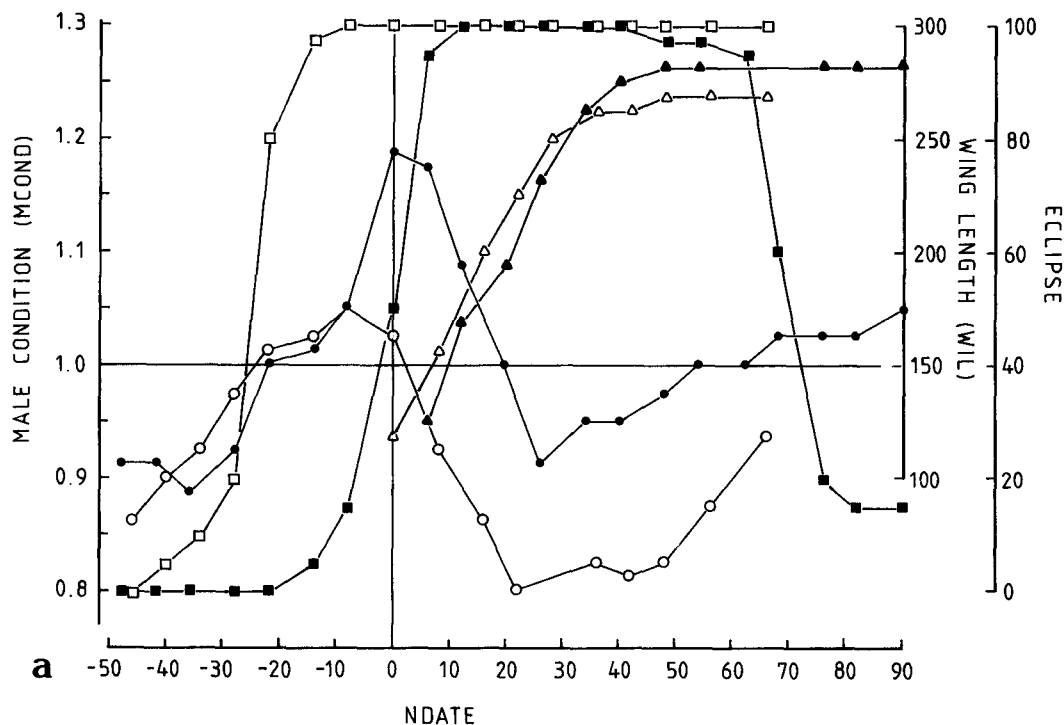
FIGURE 1.   Male (Fig. 1a) and female (Fig. 1b) body condition (MCOND and FCOND respectively, circles), wing length (WIL, mm, triangles), and percentage basic or eclipse plumage (ECLIPSE, squares) for one male (a) and one female (b) Mallard during two seasons. Ducks were provided with either high (filled symbols) or low protein food (empty symbols) during molting. The time scale starts on the date of the first observation without primaries (NDATE = 0).

TABLE 1. Condition index (CONIND, Eq. 2) of captive wild-strain Mallards weighed from April to October in 1979 and 1980.

Sex	N^a	n^b	Mean	Range	CV
Males	30	568	234.6	185.7–310.3	9.7
P^c			<0.001		
Females	27	604	245.3	169.4–333.2	11.1

[a] N = No. birds.
[b] n = No. measurements.
[c] P = Probability (from t-test) that sexes differ by chance.

$$BROWN = A(NDATE - MECLDATE)^2 + ECLLENG, \qquad (6)$$

where MECLDATE = mean eclipse date or the time in days from DROPDATE until the eclipse length is half over, and ECLLENG = approximate eclipse-length parameter in days.

RESULTS

BODY CONDITION

A total of 1,172 weighings were performed on 34 specimens of which 23 were measured both years. Each weighing provided a condition index (CONIND, Eq. 2). The variations in condition index were similar in both sexes (Table 1): the minimum condition index being 60.0% of the maximum condition index in males and 57.8%

in females. The mean condition index, however, was significantly higher in females; consequently, the condition of each sex has been calculated separately: male condition (MCOND = CONIND/234.6) and female condition (FCOND = CONIND/245.3). By calculating in this way the mean condition of each sex equals 1.00 (cf. Fig. 1).

The maximum weight (MAXWEIG, Table 2) at about dropping of the primaries (Fig. 1) was significantly higher in the high protein group than in the low protein group for both males and females. Even the minimum weight towards the end of the flightless period (MINWEIG, Table 2) was significantly higher in high protein males, but not in high protein females. The period between maximum weight (MAXWEIG) and min-

TABLE 2. Molting variables in relation to food quality. For explanation of variables see Results: body condition and eclipse plumage.

Variable	Sex	High-protein food			P^b	Low-protein food		
		n^a	Mean	SE		n	Mean	SE
MAXWEIG	Male	18	1,155.2	26.4	**	11	1,029.2	29.2
P^b			*				ns	
	Female	16	1,055.7	26.1	*	11	967.8	33.6
MINWEIG	Male	18	979.0	22.2	*	11	896.9	27.9
P^b			*				ns	
	Female	16	902.4	20.3	ns	10	880.4	28.4
MAXDATE	Total	34	2.6	1.3	*	22	−2.1	1.1
MINDATE	Total	34	32.3	1.7	ns	21	31.1	2.5
DATEDIFF	Total	34	29.6	1.7	ns	21	33.0	2.8
DROPDATE	Male	19	21 Jun	2.2	ns	11	26 Jun	3.5
P			***				***	
	Female	16	18 Jul	5.5	ns	11	22 Jul	4.7
MMAXCOND	Male	16	1.12	0.03	*	8	1.01	0.03
FMAXCOND	Female	15	1.11	0.02	*	11	1.01	0.03
MMINCOND	Male	16	0.95	0.02	*	8	0.88	0.02
FMINCOND	Female	15	0.95	0.02	ns	10	0.91	0.03
MCONDEKL	Male	16	0.0065	0.0009	*	8	0.0036	0.0004
FCONDEKL	Female	15	0.0056	0.0006	*	10	0.0037	0.0004
MECLDATE	Male	19	29.9	1.4	*	11	36.1	2.5
ECLLENG	Male	19	91.0	3.4	ns	11	97.8	4.8

[a] n = No. Mallards.
[b] P = Probability from Pitman's nonparametric, two-tailed permutation test (Bradley 1968:68–86; program at Gothenburg University Computing Centre) that food quality groups and sexes differ by chance; * = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$, ns = $P > 0.05$.

imum weight (MINWEIG) comprised the flight-less molting period. During this period there was a general reduction in both weight and condition which was most pronounced in the high protein group (15.3% in males and 14.5% in females).

The loss of condition during the flightless period was higher in males (15.2% in high and 12.9% in low protein birds) than in females (14.4 and 9.9% respectively). Both male maximum (MMAXCOND) and male minimum condition (MMINCOND) were significantly higher in the high protein group than in the low protein group (Table 2). In females however, the corresponding difference was significant only in maximum condition (FMAXCOND) but not in minimum condition (FMINCOND). The rate of condition decline per day was significantly higher in the high protein group for both males (MCONDEKL) and females (FCONDEKL). In most females the condition difference was larger than that shown in Figure 1b, but the minimum condition typically was about the same, i.e., it was independent of food quality. The female in Figure 1b was thus less affected by food quality than most others. Both maximum and minimum male condition were significantly lower in the low protein group (Fig. 1a).

No significant differences were found between the sexes in the timing of maximum and minimum weights, and the sexes are pooled in Table 2. On average, maximum weight (at MAXDATE) in the high protein group was attained 4.7 days later than in the low protein group in relation to DROPDATE. Thus in the low protein group, primary drop occurred after weight reduction had already started, while in the high protein group, weight was still increasing after DROPDATE (Fig. 1). Minimum weight was reached about 32 days after primary drop (MINDATE), and there was no significant difference between protein groups, nor was there any significant difference in time elapsed between the date of maximum and minimum weight (DATEDIFF); the common mean equaled 31 days. Both males and females dropped their primaries, on average, a few days later in the low protein group, but the differences were not significant. Molting of the primaries started about 27 days later in females than in males.

PRIMARY GROWTH

The growth curves, fitted to Eq. 3, of the primaries (WIL) in the high and low protein groups in both males and females are drawn in Figure
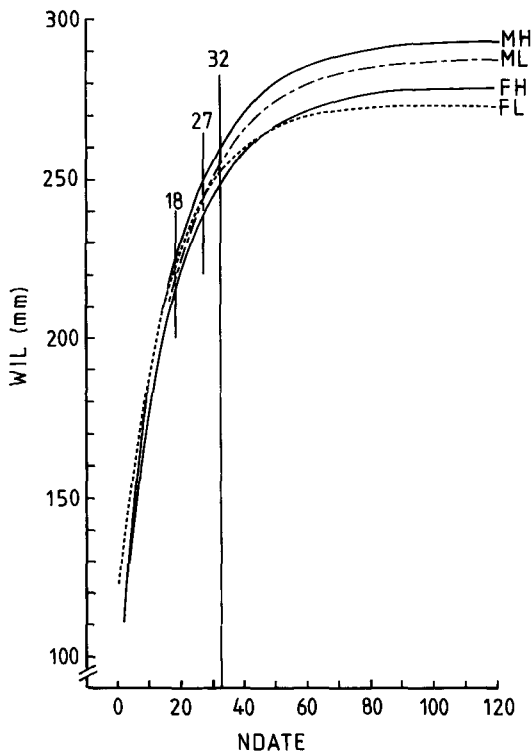

FIGURE 2.   Primary growth (WIL) in male (M) and female (F) Mallards fed high (H) and low protein (L) food during molting (from Eq. 3).

2. The curves can be separated into two parts: (1) before and (2) after MINDATE (NDATE = 32). During the first period, when condition was still declining, there was no significant difference in primary growth rate (M in Eq. 4) either between diet groups or between sexes. The pooled mean growth rate was 5.71 (SE = 0.11, $n = 55$) mm day^{-1} during the first 18-day period and 5.21 (SE = 0.068, $n = 55$) mm day^{-1} during the first 27-day period. In Eq. 4 the growth rate (M) has been related only to date, NDATE, but in Eq. 3 the growth rate parameter (R) has been related to both date and asymptotic or final length of the primaries (C). In this latter comparison, growth rate was significantly higher in females than in males (Table 3). Thus the primary growth patterns differ between the sexes. In males the linear growth rate M_{0-18} was correlated to the exponential growth rate R ($r = 0.63$, $P < 0.001$), but there was no such correlation in females ($r = 0.19$, $P > 0.05$). Similarly, in males, both M_{0-18} and M_{0-27} were negatively correlated to the rate of condition decline, MCONDECL ($r_{0-18} = -0.63$, $P <$

TABLE 3. Mean growth rate (R) and length (C and MAXWIL) of primaries in relation to food quality from wing length (WIL) measurements. R and C from Eq. 3. MAXWIL = maximum measurement of WIL.

Variable	Sex	n[a]	High[b]	P[c]	n	Low[d]
R	Male	19	0.0561	ns	11	0.0546
P[c]			*			**
	Female	11	0.0633	ns	10	0.0639
C	Male	19	294.0	*	11	287.5
P			***			***
	Female	11	276.9	ns	10	274.2
MAXWIL	Male	19	291.3	**	11	282.8
P			***			***
	Female	13	273.2	ns	10	268.9

[a] n = No. Mallards.
[b] High-protein food ad libitum.
[c] P = Probability according to Table 2.
[d] Only oats ad libitum.

0.01; $r_{0-27} = -0.51$, $P < 0.05$), but this was not true in females, FCONDEKL ($r_{0-18} = 0.00$; $r_{0-27} = 0.01$). Between the diet groups, however, there was no significant difference in R. After the average MINDATE (NDATE = 32, Fig. 2), dif-

TABLE 4. Wing capacity, WICAP (Eq. 5), indicating the average flight capability of molting Mallards at maximum weight (MAXWEIG) before the flightless period and at minimum weight (MINWEIG) 32 days after dropping the primaries. The final wing length, MAXWIL, is from Eq. 3. Comparisons are made with domestic ducks and with Mallards that are either wild, captive wild-strain, or from captive game-farm populations.

	n	Mean	SE	Range
High-protein diet				
MAXWIL at MAXWEIG,				
Males	18	0.742	0.019	0.629–0.987
Females	13	0.709	0.019	0.596–0.841
MINWIL at MINWEIG,				
Males	18	0.709	0.017	0.610–0.957
Females	11	0.718	0.016	0.659–0.860
Low-protein diet				
MAXWIL at MAXWEIG,				
Males	11	0.784	0.027	0.684–0.911
Females	10	0.745	0.021	0.655–0.832
MINWIL at MINWEIG,				
Males	11	0.728	0.019	0.637–0.846
Females	10	0.743	0.026	0.612–0.862
Kvismaren,				
wild	38	0.721	0.011	0.582–0.861
Mälaren,				
wild-strain	42	0.705	0.009	0.612–0.883
Öster-Malma,				
Wild	35	0.701	0.017	0.557–0.973
Game-farm	58	0.531	0.011	0.410–0.797
Domestic duck	4	0.393	0.023	0.356–0.455

ferences appear in the growth curves. As expected, wings were longer in males than in females (Table 3, Fig. 2), but the maximum and asymptotic wing lengths were significantly shorter in males from the low protein group than in males from the high protein group. In females the difference between the diet groups was significant only to the 10% level.

From Eq. 3 the wing length (MINWIL) has been calculated at minimum weight (MINWEIG). That is 32 days after DROPDATE. In males the mean MINWIL ($262.0 \pm SE\ 1.8$, range 246.2–277.6, and $254.8 \pm SE\ 2.8$, range 233.1–266.0 in high and low-protein groups respectively) was 90% of the final wing length (MAXWIL, Table 3) in both diet groups. In females the corresponding percentage was 92 in the high (MINWIL = $252.0 \pm SE\ 2.0$, range 240.8–263.0) and 94 in the low protein group (MINWIL = $253.4 \pm SE\ 2.1$, range 242.5–265.7), reflecting the more rapid growth in females. In males the length of the 9th primary averaged 105 mm shorter than the final wing length (SE = 1.4, n = 11). Thus primary length after 32 days was only 84% of the final length.

WING CAPACITY

A measure of the flight capability has been obtained from the wing capacity (WICAP, Eq. 5) by relating squared wing length to body mass. The lower wing capacity necessary for flight was calculated to be about 0.58 (Table 4). Domestic ducks, most of the extreme game-farm ducks, and probably some released game-farm-strain Mallards never reached this level, whereas wild-strain ducks generally exceeded it. High and low protein ducks of both sexes also exceeded the

TABLE 5. Wing length (WIL, mm) and wing capacity (WICAP) after molting in 1985.

	n	WIL			WICAP			%[a]
		Mean	SE	Min.	Mean	SE	Range	
(1) At 1st flight								
Males	6	241	5.0	228	0.61	0.0091	0.59–0.64	85.2
Females	4	221	1.1	219	0.59	0.0166	0.54–0.61	82.7
Total	10				0.60	0.0091		84.2
(2) On 25 August								
Males	7	283	2.5	276	0.77	0.026	0.70–0.89	
Females	8	270	2.2	262	0.76	0.022	0.70–0.87	
Total	15				0.77	0.016		
(3) On 15 November								
Males	7	283	2.4	276	0.62	0.029	0.53–0.74	
Females	8	270	2.0	260	0.61	0.025	0.53–0.75	
Total	15				0.61	0.027		

[a] WIL in % of MAXWIL.

0.58 WICAP-level. No significant differences in WICAP levels were found between sexes or protein groups. The first day on which WICAP exceeded 0.58 occurred on average 24.4 (SE = 0.56, $n = 55$) days after primary drop, which was one week before the average minimum weight (MINWEIG) was reached.

In 1985, the mean wing capacity (WICAP) for six male and five female birds at first flight was 0.60 (Table 5). However, the flight capability of the birds at this stage of molting was limited: they could only jump up and fly horizontally a few meters. When average wing lengths in % of MAXWIL (Table 5) on the date of this first flight were used in Equation 3 (cf. Fig. 2), they yielded NDATEs of 26.0 days in males and 21.2 days in females for the high protein group and 25.5 days in males and 18.9 days in females for the low protein group. On 25 August, by which time the autumn migration of wild birds has usually started, the final wing length (MAXWIL) was attained. Values were still similar about two months later in mid-November (Table 5). In late August, wing capacity (WICAP) was high but had decreased to low levels again by mid-November, and most birds with a WICAP below 0.60 were reluctant to fly or had difficulties doing so.

ECLIPSE PLUMAGE

In males from the high protein group the mean eclipse date (MECLDATE, Eq. 6) occurred significantly earlier compared with the low protein group (Table 2). The shorter eclipse length (ECLLENG, Eq. 6) in the high protein group, how-ever, was not significantly different from that in the low protein group.

DISCUSSION

BODY CONDITION

Body condition i.e., the state of lipid reserves and muscle protein, varied considerably between various molting phases in both male and female Mallards. The conditional state attained, however, was dependent on food quality. The sexes differed somewhat in their sensitivity to food quality and in their rate of molting progress. Generally, body condition was higher in females than in males, and condition loss was lower in females than in males. This may reflect a higher capacity of females to endure nutritional stress, as during egg laying and incubation. In females the nutritional stores required for molting are probably lower than those required for reproduction. In this respect Mallards are similar to penguins which lose 37 to 45% of their body weight during their molting fasts (Richdale 1957: 195); however, the penguin weight losses during molting are not any greater than their losses during the breeding fasts (Williams et al. 1977). Some of the experimental low protein female mallards failed to lay eggs but managed to molt. During molting, energy reserves were significantly less depleted in females than in males, and this relationship was independent of food quality. There was no significant difference in minimum condition between high protein and low protein females after the flightless period as there was in males. This suggests that molting is a more stress-

inducing process in males than in females and agrees with the findings of Nichols et al. (1982) i.e., that survival rates were lower in males than in females during extremely dry years, and of Whyte and Bolen (1984) that males lost more weight than females as a result of winter stress.

The more rapid weight and condition reduction in high than in low protein birds supports the hypothesis that the weight decline is an adaptive strategy for reducing weight and shortening the flightless period (Douthwaite 1976, Owen and Ogilvie 1981). This weight reduction may minimize the delay necessary before flying to a better feeding habitat from a sheltered but poor molting site. By continuously accumulating lipids until the old primaries are dropped, even the amount of muscle protein necessary for flight of the heavier bird might be maximized, "corrected for body size" (Owen and Cook 1977). However, during the period of low flight muscle activity in molting ducks (Milne 1976, Korschgen 1977, Reinecke et al. 1982) and geese (Ankney 1979, Raveling 1979), pectoral muscle weight is reduced. With an ample supply of energy and protein the flightless duck may retire to a sheltered molting site where protective cover may be more important than high food-quality. Hartman (1985) noted that invertebrate consumption by males hiding in a sedge belt was lower during the flightless period in July than during the preflightless period in June. By remaining immobile and primarily utilizing body nutrient reserves, vulnerability to predation is minimized as is the length of the flightless period.

THE FLIGHTLESS PERIOD

Assuming that the purpose of the weight-reduction period is primarily to facilitate an early flight capacity, and since surplus nutrients are used for maintenance during this time, then ideally, this period should equal the flightless period in length. Since the captive birds were wing-clipped, their flight capacity could not be evaluated. Still, the 32-day mean period between dropping of the primaries and minimum condition is comparable to the duration of "the whole flightless period" (29 to 33 days) of penned, hand-reared Mallards in Czechoslovakia (Balat 1970) and to the calculated length of "the flightless period" (33 to 36 days) of wild Mallards caught in Essex, England (Owen and King 1979). Shorter (2.5 week) flightless periods have been reported, as "completely renewed" wings in some captive

Mallards in Manitoba (cf. the 18-day line in Fig. 2) after dropping of the old primaries (Hochbaum 1944). These remarkable figures may have been obtained from small, light females whose higher primary growth rate capacity might have rendered them ready for flight at an earlier date. Intermediate flightless periods e.g., 23 to 24 days in Dutch park Mallards (Timmermann and Lebret 1951), 24 to 26 days in captive English Mallards (Boyd 1961), 21 to 28 days in most Manitoban captive ducks (Hochbaum 1944), suggest that domesticated and urbanized populations have shorter flightless periods than wild-strain birds. At Öster-Malma and the adjacent Tovetorp, where game-farm ducks may have contaminated the gene pool of the Mallard population, Klint (1982) reported that, on average, males and females were capable of flight after 27.5 and 29.2 days, respectively.

However, after 32 days, the high mean wing capacity of the experimental Mallards, especially the high maximum values, indicate that some ducks may begin flying after a considerably shorter period. Theoretically, if the wing capacity value 0.58 is valid, the majority of ducks should be able to fly one week before minimum weight is attained, and my estimates of the flightless period would correspond well with the intermediate periods reported by several authors. Still, if only short, immature primaries are present, flight may be difficult and inefficient.

This hypothesis was verified in 1985: when forced, molting Mallards were able to fly short distances at an average wing capacity of 0.60, corresponding to a flightless period of 19 to 26 days. However, the birds tired swiftly and became reluctant to fly. An additional week would have been necessary for effective migration to more distant wetlands. Still, this ability to make short flights could save them from a predator attack at the molting site. The shorter flightless periods in females and in light birds can partly explain the contradictory nature of literature statements, where sexes were rarely separated and compared.

WING LENGTH

The maximum wing length of the Swedish high protein, experimental birds was longer (18 mm in males and 16 mm in females) than that of adults caught in Britain (Owen and Cook 1977, Owen and Montgomery 1978). In December, after attaining their highest autumn weights, both

male and female British birds were heavier than the Swedish, experimental, high protein birds at the time when the Swedish birds weighed most before molting. Consequently, the wing capacities of the English birds (0.62 in males and 0.63 in females, Eq. 5) were lower than both hand-reared and wild birds in Sweden.

Normally, flight-ready ducks can, with little risk from predators, search for suitable feeding habitats in which to complete their molt. In contrast, the penned, low protein ducks were unable to fly to a better feeding habitat. Possibly, the lower average wing length in these birds resulted from their inability to obtain high protein food after flight capability had been achieved. Similarly, at maturity, late-hatched and presumably nutrient-stressed Redheads (*Aythya americana*) had 4 to 5% shorter wing feathers at maturity than early-hatched ducks (Smart 1965). Since the 9th male primary in Mallards is about 105 mm shorter than the length of the wing, the average reduction in the length of the primary in males from the low protein group (4.6%) was proportionately similar to that in late-hatched Redheads. Poor feeding conditions lasting through the entire molting period can occur and may explain the between-year variation in adult wing length found by Owen and Montgomery (1978). They concluded that wing growth can be affected by conditions occurring during previous breeding or molting seasons.

During migration, a high wing capacity, favored by long wings and reduced weight, may be advantageous. After arriving at the wintering area, an increase in body condition, with maintained flight-capability, necessary for enduring the winter is limited by wing length which cannot be increased after migration. The average squared wing length in low protein males was only 94% of that in the high protein birds, implying a corresponding reduction in wing capacity in the low protein birds. These birds may have had a reduced upper condition level, which could become a handicap under severe winter conditions. It follows that poor summer conditions could reduce their winter fitness, thereby hampering reproduction during the following spring.

WING LENGTH AS A SIZE INDEX

Wing length can be affected by the abundance of food resources during the reproductive and molting periods as well as by abrasion of the wing feathers between molts (cf. Owen and Cook 1977).

Thus there are good reasons for not using wing length as an index of structural body size, especially with the purpose to determine body condition. Visser (1976) found that wing length in the Eurasian Coot (*Fulica atra*) showed annual fluctuations; consequently, he also believed this measure to be an unreliable indicator of body size. Harris (1970) used sternum and culmen lengths. Owen and Cook (1977) found a close correlation ($r = 0.74$, $P = 0.001$) between wing length and body weight, suggesting that this character can be used as a good estimator of body size. In late autumn, however, when the wing capacity necessary for flight is heavily utilized, a high correlation between body weight and wing length may be expected. Bailey (1979) found a somewhat stronger correlation between total length and fat-free carcass weight ($r = 0.76$, $P < 0.0001$) in the Redhead. By multiplying bill and sternum lengths, both of which showed weaker correlations ($r = 0.74$ and 0.79 respectively, $P < 0.01$) with skeletal weights in American Wigeon (*Anas americana*) than did wing length ($r = 0.81$, $P < 0.01$), Wishart (1979) obtained a slightly higher correlation ($r = 0.82$, $P < 0.01$) with skeletal weight. Consequently, there are other measures besides wing length that may correlate well to structural body size. In the present study a three-dimensional size or volume index is obtained by multiplying three body measures.

TIMING OF THE MOLT

The time available for molting is usually longer in males than in females, since females do not start molting until the brood is fledged. Among the experimental females, the latest molt (first observation without primaries) began on 30 August. With winter approaching, a rapid wing-feather molt, which depends less on food quality, may be of selective advantage. Captive male Mallards displayed a prolonged basic molt or an eclipse period (Palmer 1972:94), which can be even longer in a low protein environment. In addition to molting their wing feathers, males must also molt into and out of basic plumage to obtain a level of protection against predators similar to that of females. Thus wing molting is more complicated in males; moreover, they have a lower capacity for accumulating nutrient stores.

CONCLUSIONS

In this study, investigations were performed which would have been very difficult to carry out

on wild birds in natural wetlands. Penned birds may deviate somewhat from wild ones, but their general traits should be similar as long as the penned birds originated from wild stock that had been kept in captivity for only a few generations. On the other hand, the literature indicates that certain aspects of molting strategy may vary between populations. Nevertheless, I have established here that molting of the wing feathers in Mallards from the Swedish west coast is preceded by an increase in the level of stored nutrients that are utilized during the flightless period to supply energy and protein; moreover, the weight reduction resulting from utilization of these reserves helps to shorten the flightless period. The weight reduction in molting Mallards is similar to that occurring in wintering American Black Ducks (*Anas rubripes*) and may be explained in the same way (Reinecke et al. 1982): stored fat provides an energy reserve that can last longer in ducks with low lean tissue weight than in those with higher weights because of the lower energy requirements of the former, and this process is internally programmed. Body weight reduction represents an adaptation rather than a response to stress. Still, the molting process may be more of a strain for males than for females, which have a higher condition capacity and have to molt only once before autumn migration; in contrast males must molt into and then out of their eclipse plumage. Low food availability during the whole molting period may reduce wing length, especially in males.

ACKNOWLEDGMENTS

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