

REMAX GROWTH AND BODY MASS OF MALLARDS DURING WING MOLT

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ABSTRACT.—We captured, banded ($n = 4,129$), and weighed ($n = 809$) Mallards (*Anas platyrhynchos*) during wing molt in western Poland. The condition of remex development was assessed ($n = 3,421$). We recaptured and remeasured 248 birds. The rate of remex growth in males (calculated by two methods) was 6.7 and 5.5 mm/day ($P < 0.02$). Males regained flight capability in 22–29 days, when remiges had reached 75–83% of final length. During the flightless period, males and females lost 12% of body mass. Birds whose flightless period was extended to replace only a few damaged quills continued to decline in body mass, which indicates that rate of mass loss was unrelated to costs of feather synthesis. We conclude that decrease of body mass is related to constraints on foraging time. We think this is a response to high exposure to predation during foraging. Reduction of flightlessness seems to be realized by a high growth rate of remiges, which was almost constant and independent of body mass. Received 24 August 1988, accepted 25 September 1989.

LIKE other waterfowl, Mallards shed all their primaries and secondaries simultaneously, and are flightless during the period of wing molt. Flightless birds are more susceptible to predation, and movements are constrained. This situation influences habitat selection, antipredator behavior, foraging, and energy budget. Body mass decreases and body composition changes during flightlessness. Several hypotheses attempt to account for the changes in body mass. Hanson (1962) concluded that remex molt is a period of great nutritional stress for Canada Geese, and birds must catabolize body tissues to build feathers. Ankney (1979) argued that flightless geese can meet their nutrient requirements from the diet, and that maintenance of a superfluous reserve would be a waste of energy. Decreased body mass during molt may be adaptive, because it enabled birds to fly before completing growth of remiges, and this reduced the flightless period (Douthwaite 1976, Dean and Skead 1979, Owen and Ogilvie 1979, Bailey 1985, Austin and Fredrickson 1987, Sjöberg 1988). Young and Boag (1982) suggested that ducks may lose feeding opportunities as a result of secretive behavior. Douthwaite (1976) suggested that reserves accumulated before the molt make birds less vulnerable to food shortages where they would be exposed to predators. These hypotheses are not mutually exclusive, and Pehrsson (1987) suggested that limitation of foraging and use of body reserves minimize exposure to predation and simultaneously shorten flightlessness.

STUDY AREA AND METHODS

This study was conducted in the floodplain of the River Warta at its confluence with the Odra River, western Poland (Majewski 1986). Flightless ducks concentrate in willow bushes (*Salix* spp.) surrounded by shallow water. The number of male Mallards that molt here reaches 25,000, many times greater than the number of local breeders.

In 1981–1982 flightless Mallards were surrounded and driven into a net enclosure (Majewski 1981). Birds were banded (3,788 males and 341 females), weighed to the nearest 20 g (640 males and 169 females), and the ninth primary was measured to the nearest 1.0 mm (3,143 males and 278 females). The birds were then released. We recaptured 337 males and 13 females, typically after 3–9 days. Each was remeasured. Because most females were trapped late in the season, there were relatively few recaptures.

We calculated the rate of remex growth from differences between lengths of the remiges divided by number of days between capture and recapture of each individual ($n = 237$). Birds with broken or pulled remiges were excluded, but some damage to remiges might have been overlooked. When caught for the first time, some birds shed their remiges, but regrowth was not yet visible. Recapture of these birds ($n = 12$) provided remex growth rates from the beginning of feather replacement.

The remex length required to resume flight was established from the longest primaries among captured birds. We assumed that birds capable of flying could not be captured. We measured final length of the ninth primary in 18 males and 50 females caught or shot in other seasons. We estimated duration of flightlessness from the growth rate of remiges.

Changes in body mass during molt were calculated

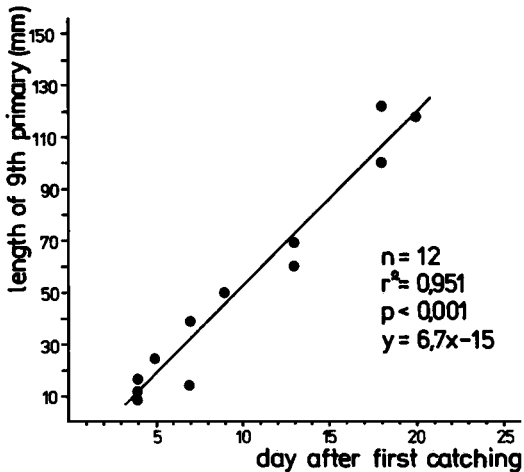


Fig. 1. Length of the ninth primary in recaptured, flightless male Mallards, trapped initially with no emerging primary feathers.

using regression of body mass to remex length. This value was assumed to represent a molt-stage index. Only birds captured the first time were used. This method excluded possible influence of capture on body mass. We also measured change of body mass in 26 retrapped birds. Date of molt initiation in captured birds was estimated by backdating, using the average rate of remex growth.

RESULTS

Course of remex molt.—Remiges in males caught the first time with no emerging primaries grew 6.7 (SE = 0.5) mm per day (Fig. 1). In males captured twice with growing remiges, the rate averaged 5.5 mm/day ($n = 237$, SD = 0.94, SE = 0.06, Fig. 2). Exceptionally low values might have been caused by undetected damage to growing remiges that inhibited their growth. This may partly explain differences in remex growth rates estimated by the two methods ($t = 2.475$, $P < 0.02$). Average growth rate of female primaries calculated from remeasuring was also 5.5 mm/day ($n = 11$, SD = 0.56, SE = 0.17). Remex growth rate in males decreased over the flightless period (Fig. 2).

No males with ninth primary longer than 150 mm were caught, and the number of males captured decreased markedly above 135-mm primary length. Presumably most males could fly at this stage (135–150 mm) of remex length. This was 75–83% of the final length of 181 mm ($n = 18$, SD = 6, range: 172–193). The longest ninth

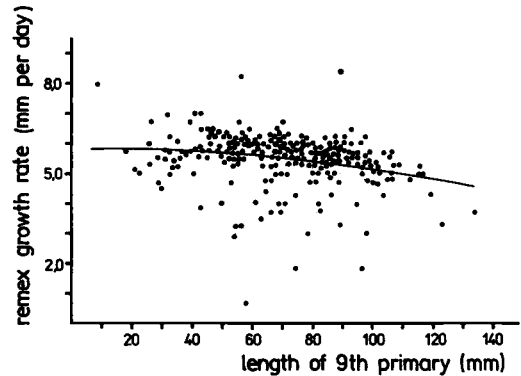


Fig. 2. Remex growth rates of male Mallards at various stages of primary growth based on measurements of the ninth primary averaged for two captures ($n = 237$, $y = 5.8 + 0.0018x - 0.000085x^2$, $R^2 = 0.0624$, $P < 0.001$).

primary in females was 123 mm. Small samples of captured females ($n = 278$) did not permit us to detect any gradual decrease of remex length. Apparently a majority of females could fly when the primary reached 125 mm (73% of final length of 171 mm [$n = 50$, SD = 6, range: 157–185]).

We estimated *initial stage of molt* (time elapsed between onset of flightlessness and emergence of small blood quills) from recapture of birds caught before regrowing remiges were visible ($n = 12$). Time of quill appearance was calculated by backdating using average growth rate of 5.5 mm/day. Regrowth began, on average, one day after the first capture. This is only part of the initial stage of molting, because all captured birds were flightless already. Assuming that birds can be caught with equal probability on any date between onset of flightlessness and the emergence of remiges, we estimated this initial stage of molting lasted two days.

Based on estimated remex growth rate of individuals caught the first time without emerging feathers (6.7 mm/day), remex length above which males can fly (135–150 mm) is reached in 20–22 days. We predicted 25–27 days of flightlessness from the growth rate in birds with twice-measured remiges. Assuming two days from the loss of flight ability to the appearance of blood quills, we calculated that male Mallards in this population were flightless for 22–29 days.

Changes in body mass.—Body mass of molting male Mallards ranged from 870 to 1,420 g ($\bar{x} = 1,120$ g, $n = 640$, SD = 90). Body mass of females

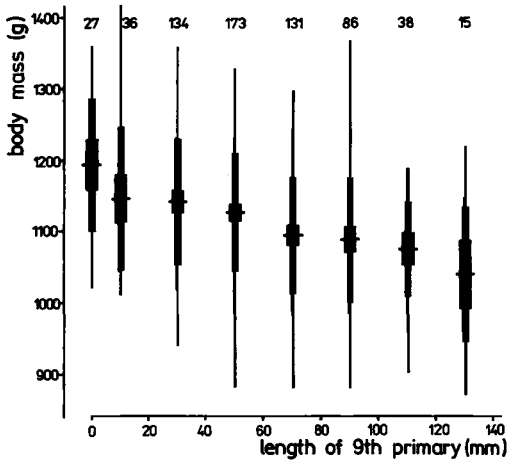


Fig. 3. Body mass of male Mallards at various stages of remex growth. Means, ± 2 SE, ± 2 SD, and ranges are shown; $df = 6$, $r = -0.9697$, $r^2 = 0.9403$, $P < 0.001$, $y = 1170 - 0.997x$. Sample sizes are given for each period.

ranged from 760 to 1,180 g ($\bar{x} = 990$ g, $n = 169$, $SD = 85$). Body mass of both males and females declined during molt (Figs. 3 and 4). Regression equations for this trend indicate a 12% decrease in mass for both sexes during the molting period.

Changes of body mass of males found by weighing the same individuals recaptured after

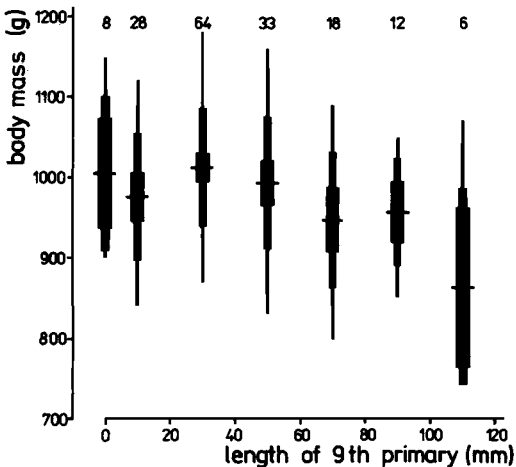


Fig. 4. Body mass of female Mallards at various stages of remex growth. Means, ± 2 SE, ± 2 SD, and ranges are shown; $df = 5$, $r = -0.8137$, $r^2 = 0.6621$, $P < 0.05$, $y = 1020 - 1.01x$. Sample sizes are given for each period.

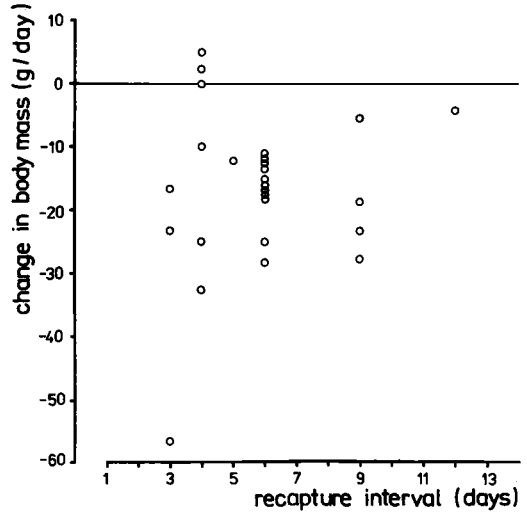


Fig. 5. Body mass changes in Mallard males captured twice ($n = 26$).

3-12 days varied from +20 g to -250 g. The average decrease was 17 g/day ($n = 26$, $SD = 12$, Fig. 5), and was significantly greater than 5 g/day calculated for birds captured only once ($t = 4.895$, $P < 0.001$, Figs. 3 and 4). Loss of body mass was noted until the ninth day after capture (Fig. 5). Average rate of decrease of body mass in individuals recaptured < 300 m from first capture was 13.7 g/day ($n = 21$) and was lower than in individuals recaptured at 1,300-1,800 m (28.7 g/day, $n = 5$, $t = 2.696$, $P < 0.05$). Body mass changed rapidly among some individuals and others maintained their mass (Fig. 5).

Males that remolted individual damaged remiges were flightless longer, and individuals recaptured in day 37-50 of flightlessness weighed 21% less than those beginning to molt (Fig. 6). No correlation was found between body mass and remex growth rate in males (Fig. 7), although both values decreased during molt.

DISCUSSION

Decreased body mass appears to be characteristic of dabbling ducks during molt. In nine other species or populations, body mass decreased by 10-24% during flightlessness (Shewell 1959, Rowan 1963, Folk et al. 1966, Oring 1969, Douthwaite 1976, Dean and Skead 1979, DuBowy 1985, Pehrsson 1987, Sjöberg 1988; some of the data recalculated). No significant decreases in body mass were reported in two

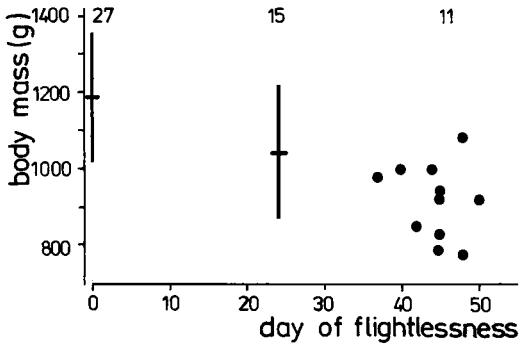


Fig. 6. Body mass of male Mallards during the normal period of flightlessness (means and ranges for the beginning and end of flightlessness), and masses of individuals remaining flightless longer due to remolt of remiges damaged during capture.

cases (Young and Boag 1982, DuBowy 1985), but samples were small.

The costs of feather replacement probably do not cause nutritional stress as suggested by Hanson (1962) and are not the chief reason for the decrease in body mass in Mallards. We found that individuals that remained flightless longer because of damaged remiges continued to lose mass, although only a few remiges were being replaced. The remex molt is preceded by molt of body plumage whose mass is 2.5 times that of the feathers replaced during the flightless period (Young and Boag 1981, 1982). However, increased body mass before the remex molt occurs in dabbling ducks (Folk et al. 1966, Oring 1969, Douthwaite 1976, Young and Boag 1982, DuBowy 1985, Pehrsson 1987). This may be related to the use of resources during flightlessness. The areas where dabbling ducks molt appear to have abundant food resources (Gavrin 1970, Lebret 1971, Kortegaard 1974, Sjöberg 1988). By implication, the decrease of body mass is not a result of limited food supply. Pehrsson (1987) found that captive Mallards fed *ad libitum* increased body mass before remiges were shed and lost body mass during flightlessness, regardless of food quality. We think that loss of body mass during wing molt results not from high nutrient requirements or limited food supplies, but from constraints on foraging time.

We found increased loss of body mass after capture until at least the ninth day. This cannot be related to only handling or movements after release, although loss of body mass was higher in individuals that moved longer distances.

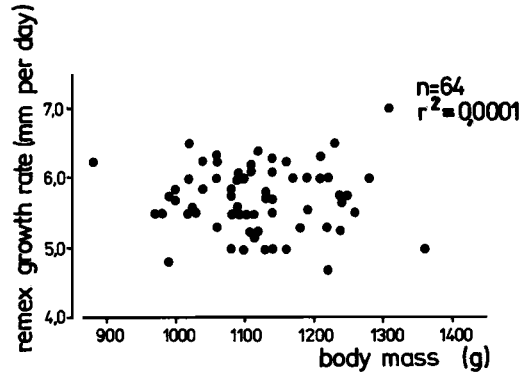


Fig. 7. Remex growth rate and body mass in male Mallards. Body mass of individuals at first capture was compared with remex growth rate between the first and second capture.

We think that prolonged body-mass loss may be caused by an increase in secretive behavior after capture, and by the move to new sites where foraging was less effective.

The Ankney (1979) hypothesis (to explain decrease of body mass as loss of superfluous reserves) cannot be applied to our case. We found that individuals that remained flightless longer continued to lose mass, and their mass was much lower than ducks during normal molt (Fig. 6). They did not feed more intensively to maintain body mass when they depleted reserves. In our opinion, limited foraging and the use of body reserves during flightlessness are responses to high predation on dabbling ducks that forage in shallow waters. Secretive behavior and short forays out of shelter minimize exposure to predation.

Greater predation and limited movements should promote a shorter flightless period. This is supported by the observations that ducks begin to fly before completing remiges growth. Low body mass may favor earlier flight. Pehrsson (1987) calculated that two groups of Mallard males that differed in body mass on average 80 g started to fly within 0.5 day of each other. This does not support strongly the hypothesis that limited foraging during molt is related to a decrease of body mass which would allow birds to fly sooner. We believe that hiding during the day is a more important response to predation than reduction of the flightless period by losing body mass.

Owen and King (1979) found a significant, positive correlation between the early growth

rate of remiges and body mass of male Mallards during the wing molt, but not in female Mallards. We found no such correlation for males (Fig. 7). Remiges apparently grow independently of concurrent reserves. Pehrsson (1987) found no difference in remex growth ratio in Mallards fed on high and low protein food. Low protein diet influenced remex growth only after the flightless period and produced shorter primaries. He also showed that remex growth rate decreased slightly during flightlessness, and that a distinct decrease began 30 days after the remiges were shed and when birds regained their flying capability. In our opinion, flightlessness is shortened by an apparently high growth rate of remiges which is almost constant and independent of body mass.

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