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CHARACTERISTICS OF THE MOULTS IN THE MALE MALLARD
(*Anas platyrhynchos*)

by

© DONALD A. YOUNG

A THESIS
SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH
IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE
OF MASTER OF SCIENCE

DEPARTMENT OF ZOOLOGY

EDMONTON, ALBERTA
FALL, 1977

THE UNIVERSITY OF ALBERTA

FACULTY OF GRADUATE STUDIES AND RESEARCH

The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research, for acceptance, a thesis entitled "Characteristics of the moults of the male mallard (<u>Anas platyrhynchos</u>)" submitted by Donald A. Young in partial fulfilment of the requirements for the degree of Master of Science.

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Supervisor

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Date....June 1, 1977....................

ABSTRACT

In this study, I collected 130 adult male mallards from populations in southern Manitoba, Saskatchewan and Alberta to document their moults and to determine the relationship between these moults and changes in various physical parameters.

A description of the moults was based on feather replacement in various pterylae. Using colour characteristics of contour feathers and follicle appearance, viewed from the dermis, it was possible to describe seven discrete moult classes and to trace the sequence of feather replacement.

Body weight remained constant during the moults. Nonetheless, pectoral muscle weights declined significantly while leg weights increased significantly during the flightless period, a phenomenon likely related to the changing locomotory role of the two muscle complexes.

Testis regression was closely correlated with the onset of the prebasic moult, suggesting that the cessation of breeding activity was at least indirectly related to the initiation of the prebasic moult.

Heart weight declined significantly in flightless birds, probably because of decreased exercise.

Liver weights increased in post-breeding mallards, as did other components of the digestive system. The weight-length characteristics of the gastro-intestinal tract increased during the moults, a trend likely related to changes in quantity and/or quality of the diet to one containing a greater proportion of high fiber foods.

Subcutaneous lipid depots were lowest in breeding birds, increased significantly during the prebasic body moult, with a temporary but significant decrease in flightless birds. Carcass lipid depots decreased in flightless birds but not significantly, suggesting that subcutaneous lipids were metabolized before carcass reserves. The decrease in lipid reserves during the flightless period also indicates that total energy intake was insufficient to sustain the depot levels. The buildup of lipid reserves prior to remiges moult is probably an adaptation to provide flightless mallards with an energy reserve to supplement food intake during a period when their mobility is inhibited.

Total protein reserves did not change significantly through the study. This suggests that the protein demands during the moults were adequately met by the diet.

ACKNOWLEDGEMENTS

I would like to express my gratitude to Dr. D.A. Boag for his advice and encouragement throughout the program and for aid in preparation of this manuscript. Mr. E. M. Wright and Mr. Justice M. A. MacPherson provided critical reviews.

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Drs. W.C. Mackay and J.K. Lauber, Department of Zoology and Dr. F. Wolfe, Department of Food Science graciously provided lipid extraction and other laboratory equipment. Ms. N. Hargraves and Ms. C. Bartlett gave valuable assistance with various aspects of laboratory work.

Messrs. L. Harder and P. Pearlstone advised on statistical treatment of the data.

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INTRODUCTION

Members of subfamily Anatinae moult twice annually: a prebasic (post-breeding) moult that replaces alternate (breeding) plumage with basic (eclipse) plumage and a prealternate moult that is the converse (Humphrey and Parkes 1959). Most species of dabbling ducks moult on or near the breeding grounds; some undertake "moult migrations" to traditionally used moulting areas, for example, the Delta Marsh in south-central Manitoba (Hochbaum 1955, 1959, Salomonsen 1968). Such marshes provide the necessary requirements for these ducks during various stages of the moults: food, permanent water and protective habitat (Hochbaum 1955, Oring 1964, Salomonsen 1968, Kortegaard 1974, Tamisier 1974).

Several authors have provided generalized descriptions of anatid plumages (Millais 1902, 1913, Dwight 1914, Phillips 1922-1926, Sutton 1932, Stresemann 1948, Salomonsen 1949, Kortright 1953, Weller 1957, Delacour 1964, Bellrose 1976, Palmer 1976), but their sequence and duration have not been well documented.

Among the Anatinae, genus Anas, the best description of plumages and moults has been provided by Oring (1968) for gadwalls (Anas strepera). For mallards (Anas platyrhynchos), plumage sequence has been alluded to only briefly (Jackson 1915a, b, Hochbaum 1959, Johnson 1961) and descriptions of moults have dealt primarly with the remiges

(Millais 1902, Heinroth 1911, Timmermann and Lebret 1951, Veselovsky 1954, Boyd 1961, Balat 1970).

The two moults in mallards occur within a 5 to 6 month period. As with all birds, these moults increase the bird's energy requirements (Kendeigh 1949, Blackmore 1969, Payne 1972, Thompson and Boag 1976) and may impose nutritional stresses that result in depleted body reserves as suggested by Hanson (1962) for Canada geese (*Branta canadensis*).

With few exceptions (Hanson 1962, Harris 1970), body weight alone has been used to describe body condition in waterfowl (Hohn 1947, Folk *et al*. 1966, Hay 1974). Hanson (1962) used body and muscle weights, as well as subjectively measured fat deposits to describe body condition in Canada geese. Harris (1970) attempted to relate blood components to body weight as a measure of condition in breeding blue-winged teal (*Anas discors*). More recently, Evans and Smith (1975) suggested that lipid and protein reserves be considered as separate indices of body condition since they are not necessarily depleted simultaneously. Although logical, neither the indices, nor the techniques for deriving them have been used to evaluate condition in moulting waterfowl.

In light of the volume of literature describing the mallard, it is surprising that its plumages, moults, and related physiological characteristics have not been investigated in more detail. In an attempt to fill this information gap, I quantified some characteristics of the moults of adult male mallards.

The mallard was chosen because of its wide distribution and local abundance in the study area (the Delta Marsh, Manitoba). Adult males were chosen because, 1) their plumages were distinct and changes were easily quantified, 2) reproduction likely would have less impact on their moult and body condition than on females (Calverley and Boag 1977), and 3) adult males could be distinguished from juveniles into the late autumn thus eliminating inherent differences between age groups.

My study addressed the following: 1) characteristics of alternate-to-basic-to-alternate sequence of plumages, 2) timing and duration of the moults and 3) plumage characteristics as related to the following anatomical parameters:

a) weight and composition of the whole carcass,
b) weight and composition of major pectoral and leg muscles,
c) status of the reproductive system,
d) weight and length of various organs, particularly of the digestive system,
e) lipid and protein reserves as indices of condition.

METHODS

This study was based on the physical characteristics of 130 adult male mallards collected between 5 May and 28 October, 1976 from the Delta Marsh in south-central Manitoba as well as Saskatchewan and Alberta. The marsh, encompassing approximately 4,800 hectares of shallow bays separated by stands of giant reed (Phragmites australis), has been described in detail by Hochbaum (1955) and Anderson and Jones (1975).

During the reproductive period (May through early June) male mallards frequented the open water and edges of ponds and bays where they were collected with a shotgun and decoy traps (Delta Waterfowl Research Station Unpubl. data). However, when they approached the flightless period they moved into the interior of the marsh and once flightless, frequented dense stands of giant reed, hardstem bulrush (Scirpus acutus), and cattail (Typha latifolia). During this period, they were secretive by day, necessitating collection at night using modifications of techniques described by (Cummings and Hewitt 1964, Bishop and Barratt 1969).

Their techniques were modified to increase the efficiency of capture in the following ways: two floodlamps with 500 watt quartz iodide bulbs (General Electric) were permanently mounted on the bow of an airboat and supplied with power from a 1500 watt gas-powered Honda ~~gen~~erator. A hand-held spot-lamp with a 110,000 candle power aircraft landing lighting (AC Sparkplug Co.) was operated by the driver and connected to the 12 volt electrical system of the boat.

Male mallards were located by manoeuvering through bays and channels on dark, calm nights. When a bird was sighted, the driver positioned the boat parallel to the bird while concentrating the spot-lamp directly on the bird. An assistant, located in the bow, then scooped the bird out of the water with a long-handled landing net. Once in the boat, birds were killed immediately by injecting 10 ml of 95% ethanol into the brain. To prevent decomposition of food items in the esophagus and proventriculus, 20 ml of 70% ethanol were injected into the esophagus which was then tied off anteriorly.

Collections continued this way, and with a shotgun, until early September; thereafter, personnel at the Station shot male mallards from the Delta Marsh until they migrated in late October. The autumn sample was supplemented by birds collected in southern Saskatchewan and Alberta.

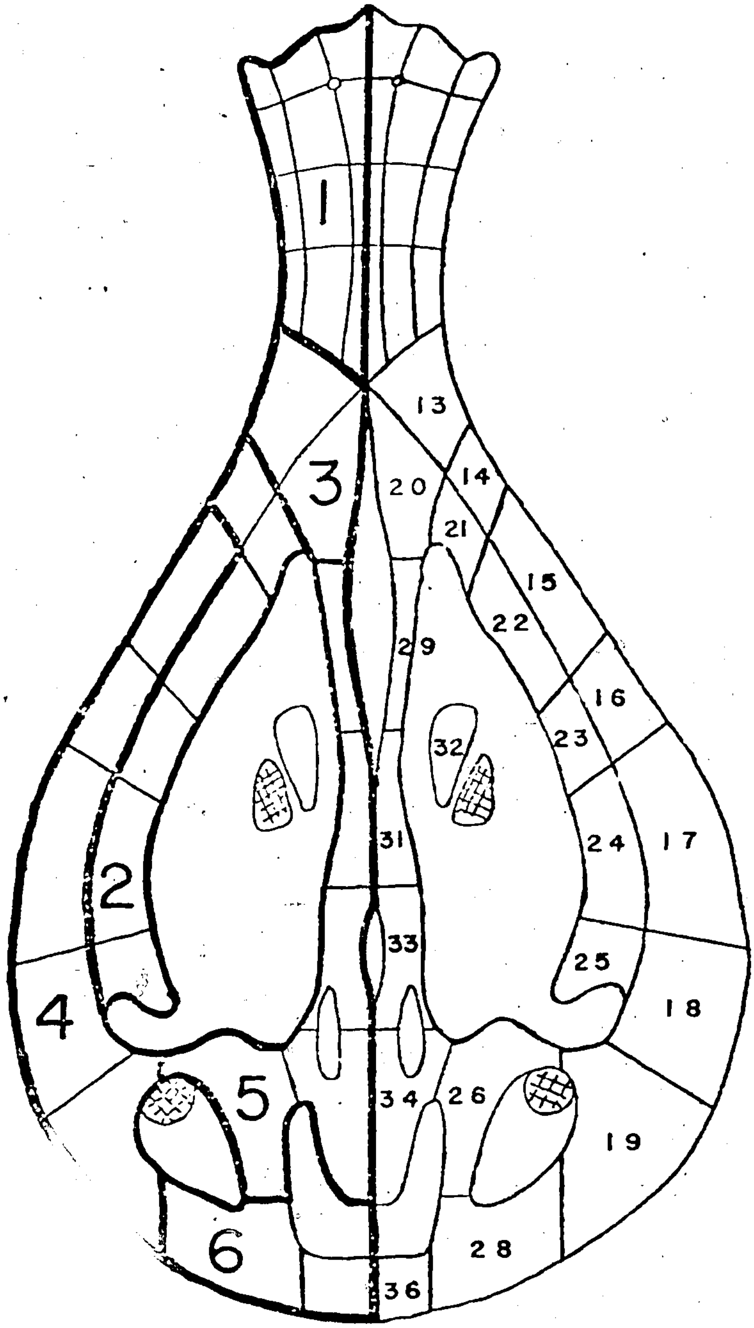
The following information was recorded from each bird: date, time of day, location and social status (unpaired, paired or flocked). Autopsies were performed in almost all cases within 12 hours of collection; during this interval, birds were stored in a refrigerator.

Each bird was skinned (Billard and Humphrey 1972). The skin was weighed, scraped of excess fat, dried flat and saved for future reference.

A description of the moult was based on a record of feather replacement on the flat skins. An outline of a mallard skin (Fig. 1) was traced onto a glass plate and subdivided onto the sections conforming to 6 feather tracts described by Humphrey and Clark (1961) and Billard and Humphrey (1972). Each section was then further subdivided to aid in following the moult within each feather tract (Fig. 1). This transparent outline enabled me to count the number of blood quills of developing contour (pennae) and down feathers in all but the capital tract where these two types of teleoptiles could not be distinquished. The actual number of developing feathers was expressed as a percentage of the maximum number of blood quills ever recorded in that area. Values were then coded in the following fashion:

Percent of maximum number of blood quills	Code
0	0
1 - 20	1
21 - 40	2
41 - 60	3
61 - 80	4
81 - 100	5

gure 1. Outline of mallard skin displaying the six feather tracts on left and subdivisions within each tract on right. Subdivision 32 is part of tract 5. Cross-hatched regions represent position of wings and legs. Feather tracts:1 - capital (head and neck); 2 - ventral (sides and flanks); 3 - anterior ventral and spinal (upper breast and back); 4 - mid ventral (breast and belly); 5 - spinal-scapular (back and mid rump); 6 - posterior spinal-caudal (abdominal and caudal).


1
13
3
20
14
21
15
22
29
16
32
23
2
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5
34
26
19
6
28
36

The score for each tract (tract score) was derived by summing the coded scores for each area within that tract. Because of feather density in the capital tract, actual counts were not feasible. Therefore, I assigned a code that ranged from 0 to 3 based on general observations of moulting intensity in this tract. A total moult score was obtained through addition of all six feather tract scores.

All flat skins were then examined for external plumage characteristics which would facilitate separation of the sample into discrete groups or moult classes (m. c.) - (Table 1). Using this technique, it was difficult to distinquish between only two of the seven moult classes. Externally, body plumage was similar in m. c. 4 and 5, however, birds with wing lengths shorter than 20 cm invariably belonged to m. c. 4.

Skins were then examined internally to note the relative distribution of developing feathers (blood quills). Based on these observations, it was possible to confirm the establishment of seven separate moult classes (Table 2).

Characteristics of the carcass and its component parts reflecting the physiological state of the bird, were investigated by weighing, measuring, and analyzing for lipid, water and protein content. The pectoral muscles (_M_. _pectoralis_, _M_. _supracoracoideus_, _M_. _coracobrachialis_) were removed, freed of adhering fat and weighed. The leg (including femur, fibula and tibiotarsus) and associated musculature were dissected free and weighed. Since bone

Table 1. External plumage characteristics of adult male mallards in the seven moult classes

Moult Class	External Characteristics
1	Metallic green head with white neck-collar. Chestnut brown chest and pearly grey sides. Brownish back and black rump. White outer and black central rectrices.
2	Same as 1 except feather wear is prominent in rectrices and tertiaries. Some feathers of basic plumage on sides and flanks.
3	Head and neck with a mixture of green and brown. Less distinct neck-collar. Numerous brown feathers of the basic plumage present on all regions of the body. Much feather wear.
4	Mottled brown body plumage gives bird a female-like appearance except for darker head. Some rectrices and all remiges in early stage of renewal.
5	Body plumage same as 4 but remiges nearing completion.
6	Head and neck and upper breast in basic plumage but sides and belly nearly in alternate plumage.
7	Essentially the same as 1 except for a few isolated areas of basic plumage on head, neck and upper breast. Most alternate rectrices completed.

Table 2. Internal plumage characteristics of adult male mallards of the seven moult classes

Moult Class	Internal Characteristics
1	No new contour feathers (blood quills) in any feather tract.
2	Follicles in lateral regions of ventral tract possess developing contour feathers of basic plumage.
3	Growing contour and down feathers of the basic plumage apparent in follicles of all tracts.
4	Growing contour feathers of the basic plumage, if present, confined to the posterior spinal tract. No growing down feathers present.
5	Growing contour feathers of the alternate plumage apparent in follicles of the posterior spinal and ventral tracts. Large concentrations of down feathers in follicles of ventral tract.
6	Numerous growing contour and down feathers of alternate plumage in medial region of ventral tract.
7	Growing contour follicles of the alternate plumage confined to capital, ventral and caudal tracts. No or few growing down feathers present.

weights remained static throughout the year, the initially weighed samples adequately reflected muscle weights.

Four sketetal measurements were taken to calculate the area of pectoral muscle attachment (Evans and Smith 1975): a-length of sternum, b-depth of the carina , c-distance from the base of the carina to the distal end of the coracoid, d-maximum width of the sternum. The standard volume for the muscles was then described by the formula: $V=b(ad+0.433c^2)$ (Evans and Smith 1975). Lean dry weight of the pectoral muscles was expressed as a percentage of the standard area of muscle attachment. A second muscle index, also proposed by Evans and Smith (1975), was calculated by expressing the lean dry weight of the pectoral muscles as a percentage of the lean carcass weight. This index should not change if changes in muscle weight reflect fluctuating water content.

The sternum was removed to facilitate dissection of the following organs: heart, liver, gizzard, intestines, caeca and testes. The weight-length characteristics of these organs were recorded , the testes also being fixed in Bouin's solution. The remainder of the carcass was frozen for future analysis.

The lipid content of the carcass and one set of pectoral muscles was determined separately through a lipid extraction technique. A sample (20 grams) of pectoral muscle was sliced while frozen and evaporated to dryness in a vacuum oven at 70°C for 18 hours. This procedure gave dry weight from which moisture content of this muscle mass also could be calculated. This tissue was powdered with a mortar and pestel and refluxed with petroleum ether (B.P.=30° - 60°C) for 6 hours in a soxlett extractor. The ether extractable lipids were collected in pre-weighed flasks, the ether evaporated over a steam bath with the quantity of lipid residue determined gravimetrically. Prior to weighing, flasks were dried at 70° - 80°C for 5 minutes and cooled to room temperature in a dessicator (Medford 1976).

Carcass analyses for lipid content were also conducted. The carcass minus skin, feet, liver, testes, small and large intestines, and one set of leg and pectoral musculature was ground in a commercial meat grinder and then weighed to obtain a wet carcass weight. The resulting mass was then homogenized in a commercial Waring blender; a subsample (25 grams) was evaporated to dryness in a vacuum oven for 24 hours at 70°C to obtain dry weight and moisture content of the sample. The dried tissue was then analyzed for lipid content in the same fashion as described for the pectoral musculature. Carcass lipid content was expressed as a percentage of dry weight(total carcass lipids) and wet weight (lipid index). Protein content was calculated from tissue weight minus water and lipids. With each extraction, a standard and a blank was run through the refluxing procedure to determine variation between extractions. Variations between extractions were not significant ($P > 0.05$).

A one-way analysis of variance using Duncan's Multiple Range Test at the 0.01 probability level was used to establish whether moult classes were significantly different from each other (Nie *et al*. 1975).

RESULTS AND DISCUSSION

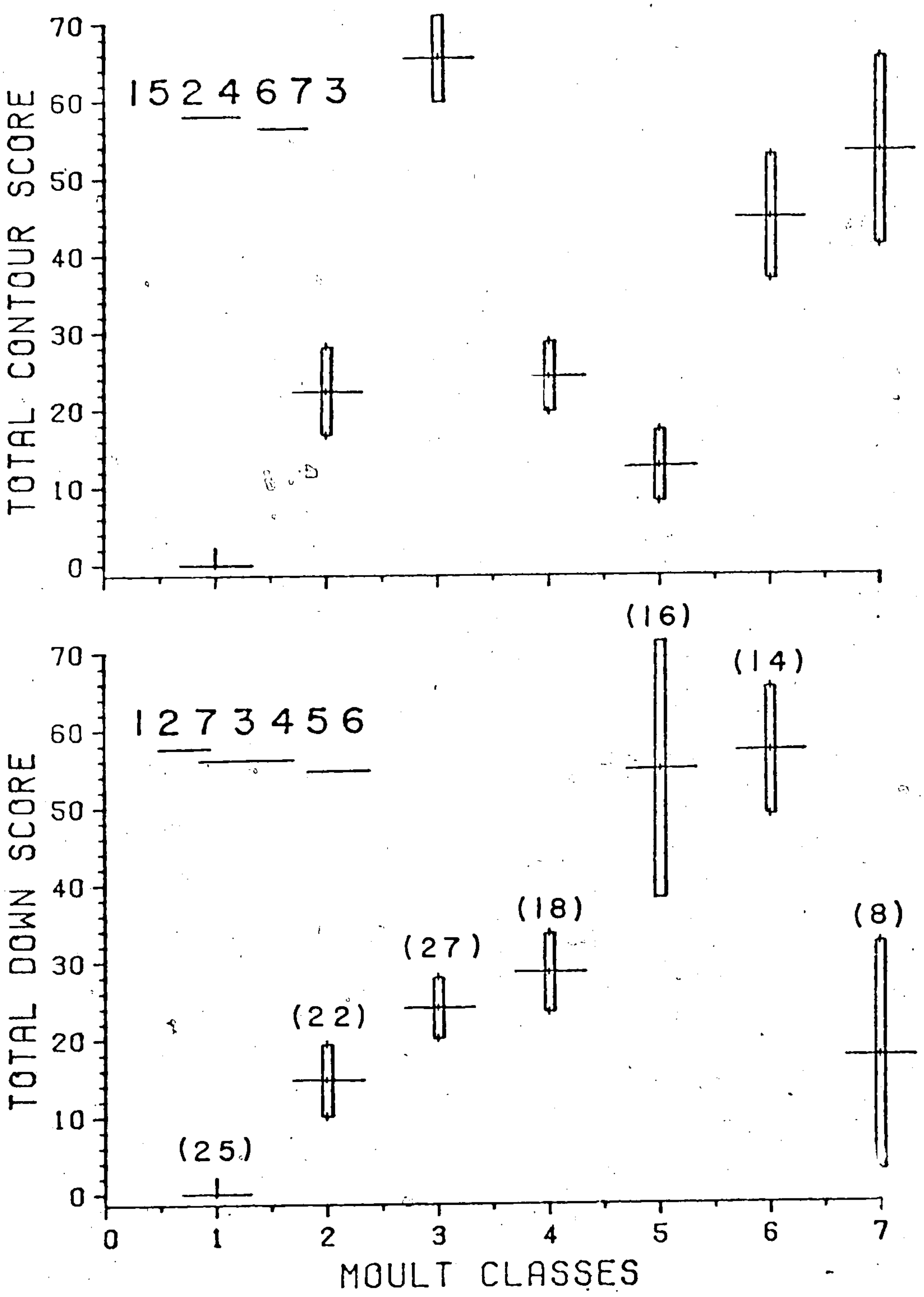
Plumage Replacement in Adult Male Mallards

Until recently, most authors have subscribed to Dwight's (1902) system for naming plumages and moults. Humphrey and Parkes (1959, 1963) proposed a new system that named moults on the basis of incoming plumages, a system which is now widely used partly because of the supportive evidence presented by Watson (1963). This method for naming plumages and moults will be used throughout the following discussion of mallard moults: a prebasic (post-nuptial) moult replaces alternate (nuptial) plumage with basic (eclipse) plumage and a prealternate moult that is the converse.

Moult of Body Feathers

Total moult scores for both contour and down feathers were plotted against moult class (Fig. 2). For the contour feathers, the moult scores were significantly different ($P < 0.01$) among moult classes except for 2 and 4 and 6 and 7; these internally similar moult classes were separated readily by external examination (Table 1) and collection date. Male mallards in m. c. 2 differed from those in m. c. 4 in almost all external features: birds in m. c. 2 were essentially in full alternate plumage, while m. c. 4

Figure 2. Total moult scores for each moult class of adult male mallards. Total contour scores (upper). Total down scores (lower). Figure illustrates mean and 95 percent confidence interval. Duncan's Multiple Range Test at the 0.01 probability level was used to establish whether moult classes were significantly different from each other. Numbers sharing a line beneath them were not significantly different. Numbers in parentheses indicate sample size for each moult class.


TOTAL CONTOUR SCORE
1 5 2 4 6 7 3
TOTAL DOWN SCORE
1 2 7 3 4 5 6
(25)
(22)
(27)
(18)
(16)
(14)
(8)
0
10
20
30
40
50
60
70
0
1
2
3
4
5
6
7
MOULT CLASSES

birds were flightless and in basic plumage. Birds in m. c. 6 were distinguished from those in m. c. 7 in possessing extensive areas of basic plumage in the upper chest, neck and head regions in contrast to a few isolated regions in an almost complete alternate plumage.

The periods of heaviest contour feather replacement corresponded with m. c. 3 and 6 (Fig. 2), the prebasic and prealternate body moults. Furthermore, among flightless birds (m. c. 4 and 5), new pennae were minimal and largely confined to the alar and caudal tracts.

The replacement of the down feathers appeared to be a more gradual process than contour feather replacement (Fig. 2). Nonetheless, it was possible to distinguish between the moult classes in question by considering a combination of external characteristics (Table 1) and collection dates. Birds in m. c. 2 could be differentiated from those in m. c. 7 on the basis of worn feathers: the primaries, tertiaries and rectrices were extremely frayed in m. c. 2 whereas they were in good condition in m. c. 7. Birds in m. c. 3 were still flying and were characterized by a combination of alternate and basic plumages whereas birds in m. c. 4 were in the initial stages of the flightless period and possessed complete basic plumage. Most birds in m. c. 5 were still flightless but some were flying if their wing lengths exceeded 25-26 cm. By contrast, all birds in m. c. 6 were flying and displayed areas of new alternate plumage on the sides and belly.

Down replacement was concentrated mainly in m. c. 5 and 6. This suggested that whereas contour feathers were replaced twice in rapid succession, most down feathers appeared to be replaced only once, primarly during the prealternate moult.

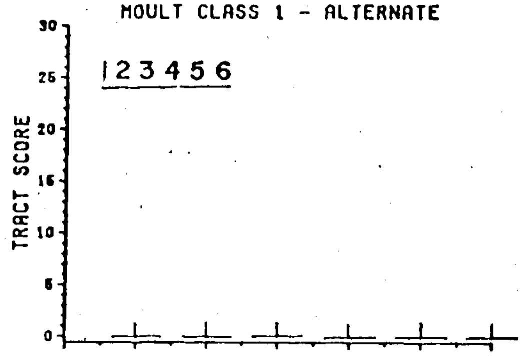
While total moult scores were useful in separating moult classes, they did not provide information on feather growth in individual feather tracts. Contour and down tract scores for each moult class were therefore plotted against individual feather tracts (Figs. 3 and 4). The general pattern and intensity of contour feather moult were similar ($P > 0.05$) for m. c. 3 and 6 as well as m. c. 6 and 7 (Fig. 3). Until m. c. 3 and 6 , down replacement was minimal in all feather tracts (Fig. 4), once again suggesting that most down was replaced early in the prealternate moult.

These ata show that, for a given moult class, new feathers were replaced with different intensity in each feather tract. Thus it was possible to characterize the intensity and distribution of the moult for each moult class.

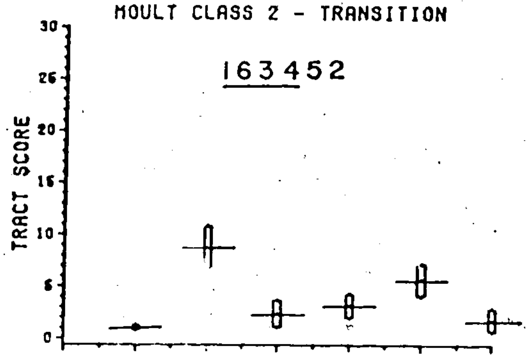
Differences existed between feather tract scores not only within given moult classes (Figs. 3 and 4) but between moult classes as well (Figs. 5 and 6). These differences ($P \leq 0.01$) were most obvious in contour tracts 2 and 4 (Figs. 5 and 6). This fact, coupled with the differences in total moult scores (Fig. 2) provided quantifiable evidence

Figure 3. Tract scores for contour feathers in each feather tract of adult male mallards. Transition refers to a transitional stage when birds are moulting from one plumage to another.Basic and alternate refer to plumages.

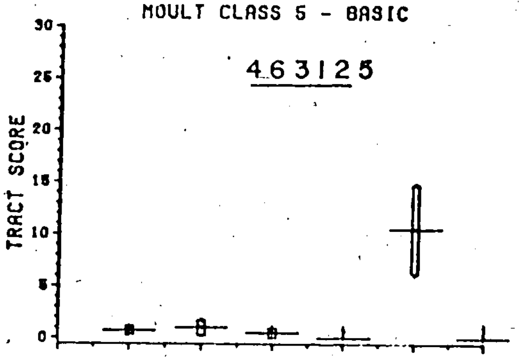
MOULT CLASS 1 - ALTERNATE



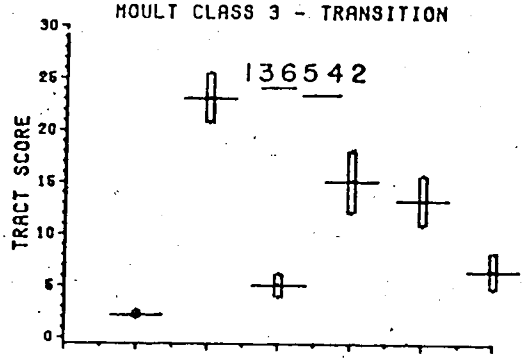
MOULT CLASS 2 - TRANSITION



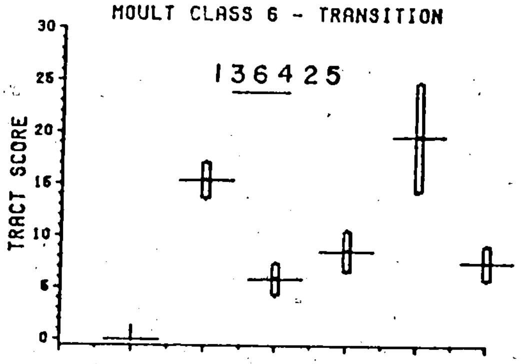
MOULT CLASS 5 - BASIC



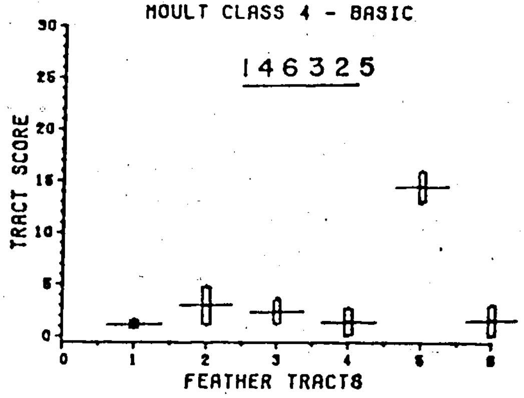
MOULT CLASS 3 - TRANSITION



MOULT CLASS 6 - TRANSITION



MOULT CLASS 4 - BASIC



MOULT CLASS 7 - TRANSITION

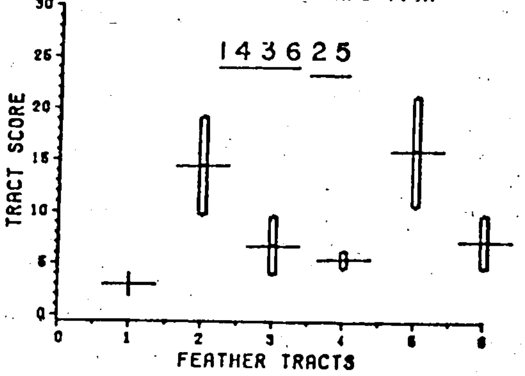


Figure 4. Tract scores for down feathers in each feather tract of adult male mallards.

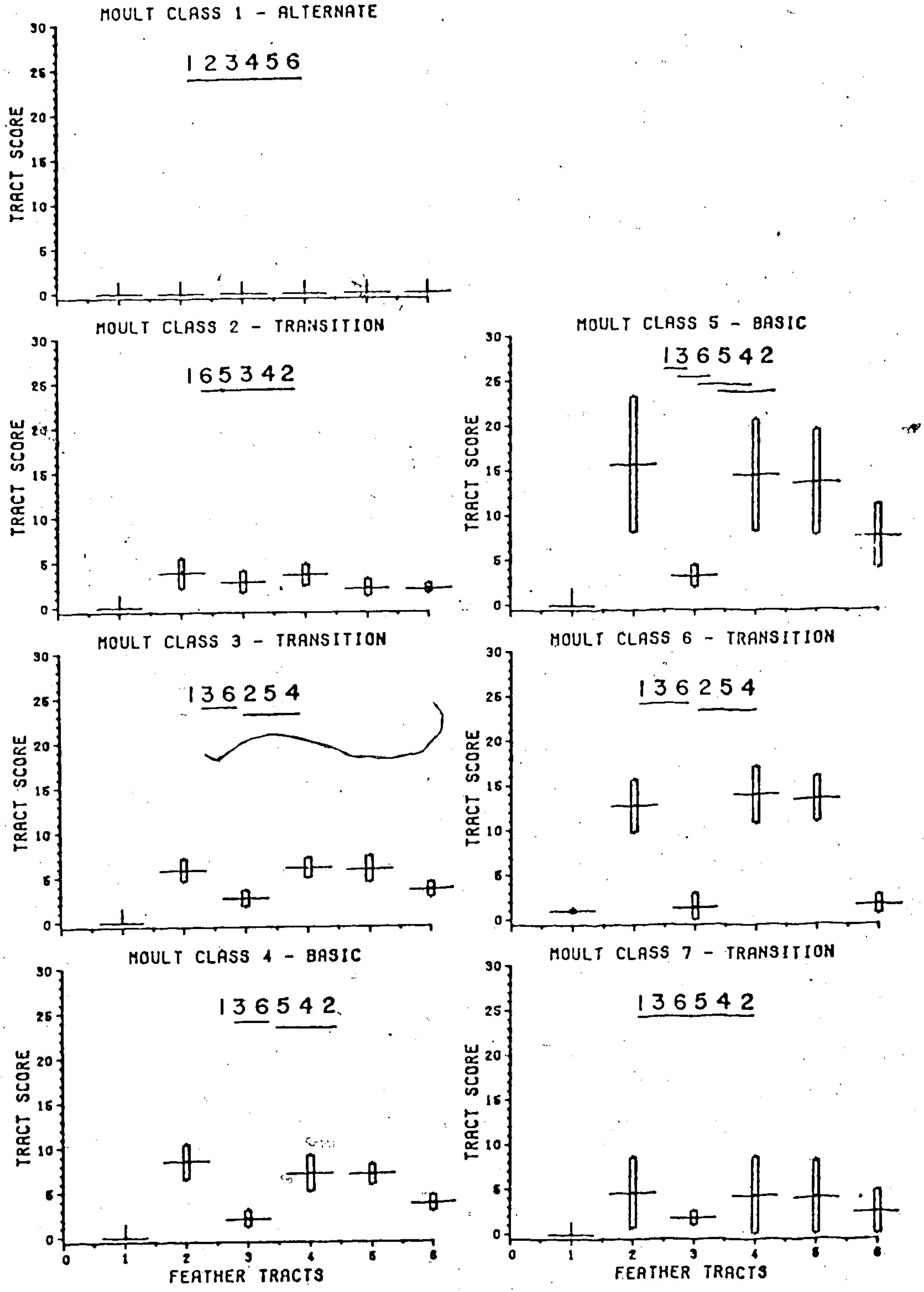

MOULT CLASS 1 - ALTERNATE
123456
MOULT CLASS 2 - TRANSITION
165342
MOULT CLASS 5 - BASIC
136542
MOULT CLASS 3 - TRANSITION
136254
MOULT CLASS 6 - TRANSITION
136254
MOULT CLASS 4 - BASIC
136542
MOULT CLASS 7 - TRANSITION
136542
TRACT SCORE
0
5
10
15
20
25
30
FEATHER TRACTS
0
1
2
3
4
5
6

Figure 5. Individual tract scores for contour feathers in each moult class of adult male mallards.

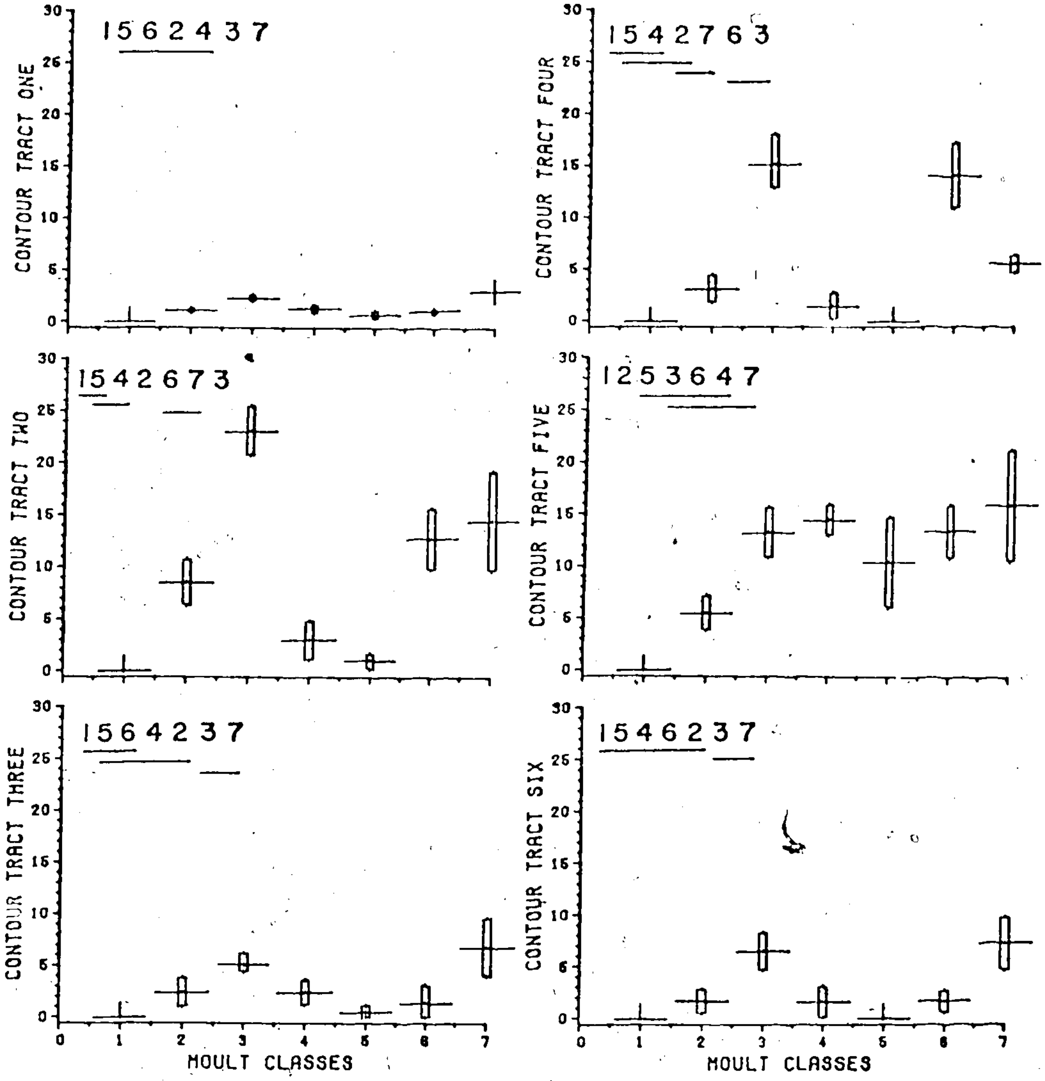
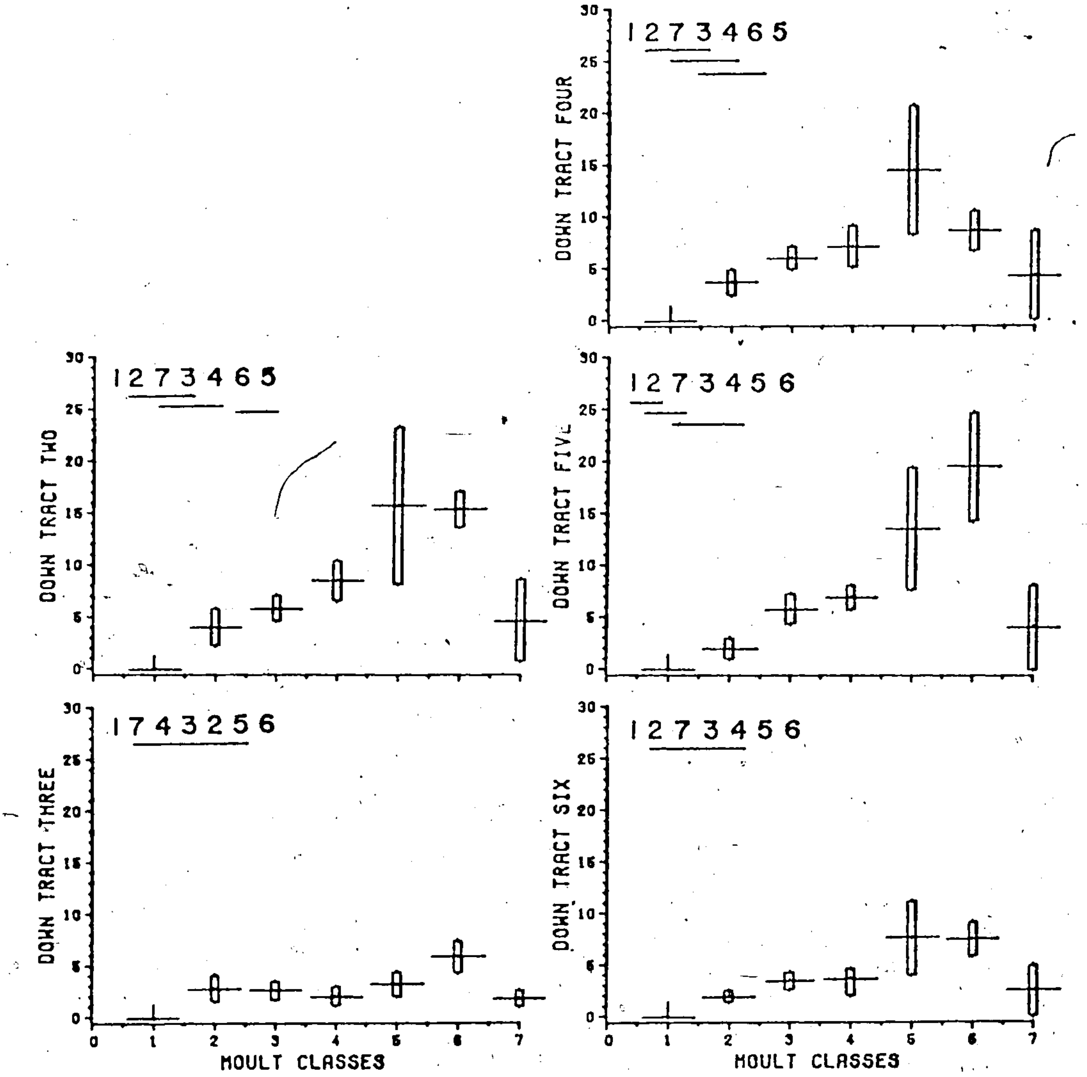

1562437
CONTOUR TRACT ONE
1542763
CONTOUR TRACT FOUR
1542673
CONTOUR TRACT TWO
1253647
CONTOUR TRACT FIVE
1564237
CONTOUR TRACT THREE
1546237
CONTOUR TRACT SIX
0
5
10
15
20
25
30
0
1
2
3
4
5
6
7
MOULT CLASSES
MOULT CLASSES

Figure 6. Individual tract scores for down feathers in each moult class of adult male mallards.


DOWN TRACT FOUR
1 2 7 3 4 6 5
DOWN TRACT TWO
1 2 7 3 4 6 5
DOWN TRACT FIVE
1 2 7 3 4 5 6
DOWN TRACT THREE
1 7 4 3 2 5 6
DOWN TRACT SIX
1 2 7 3 4 5 6
0
5
10
15
20
25
30
0
1
2
3
4
5
6
7
MOULT CLASSES
MOULT CLASSES

supporting the establishment of the seven moult classes.

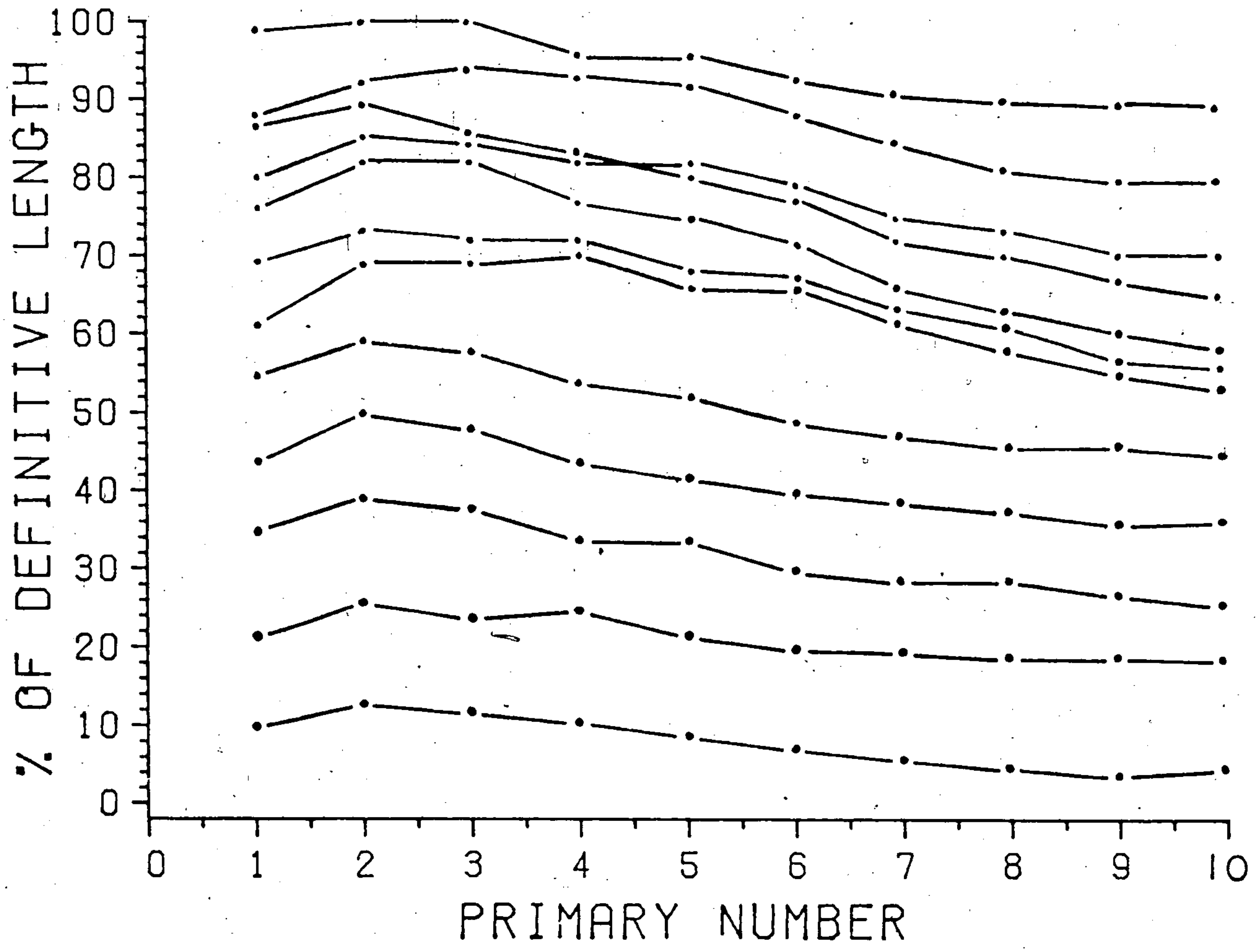
Moult of the Alar Tract

The remiges were not lost in any particular order; in several situations I captured adult drakes which were shedding remiges as they flapped across the water. This was similar to reports by Hochbaum (1959), Weller (1957), Oring (1968) and Balat (1970). All remiges were lost within a few days, and the sequence of replacement varied only slightly. I observed that the proximal primaries were renewed slightly earlier than the distal primaries, similar to the sequence in redheads (Weller 1957). In most cases, the primaries erupted simultaneously but there was evidence of differential growth rate among them. Based on measurements of length, the proximal primaries, with the exception of number 1, grew more rapidly than the distal ones (Fig. 7).

Primary (greater) coverts, both upper and lower, were retained until after the remiges were lost, their replacement being quite variable. Median and lesser coverts were replaced last and often over an extensive period of time, a phenomenon also reported for redheads and gadwalls (Weller 1957, Oring 1968).

Mallard drakes are flightless for 3 to 4 weeks (Hochbaum 1959 Boyd 1961, Balat 1970) and are capable of flight before the primaries are fully grown (Balat 1970, Palmer 1976, B.D.J. Batt pers. comm.). Batt reported that

Figure 7. Length of adult male mallard primaries as a percent of definitive length in 12 individuals at different stages of primary growth.


% OF DEFINITIVE LENGTH
100
90
80
70
60
50
40
30
20
10
0
0
1
2
3
4
5
6
7
8
9
10
PRIMARY NUMBER

captive drakes were capable of flight at wing chord lengths of 25 to 26 cm. This corresponds to a ninth primary (longest) length of 13.5 to 14.5 cm or when it has completed 70 to 75% of its growth. At this stage, the proximal primaries have grown to at least 80 to 85% of their definitive length (Fig. 7).

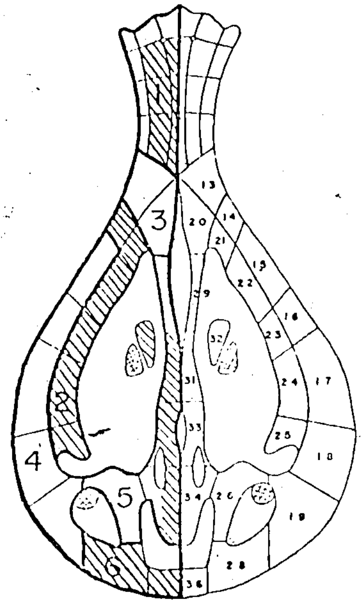
Pattern and Sequence of Moults

Based on both external and internal evidence, it was possible to describe seven moult classes and trace the sequence of feather replacement from May to November (Figs. 8 and 9). No blood quills of the basic plumage were observed until the third week of May when pennae were found in the head, sides, flanks and mid-rump. This situation, typical of m. c. 2, was observed into mid-June in paired birds. Heavy prebasic moult of pennae in all tracts (m. c. 3) was noticed as early as late May in some males but not until mid-July in others. The prebasic moult was essentially complete by the time males were flightless (m. c. 4).

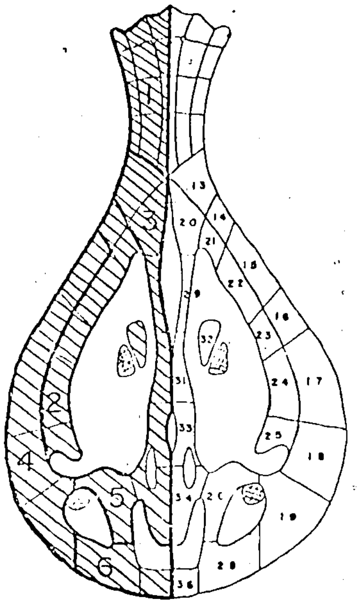
While the rectrices were not lost simultaneously, at least some were lost before the remiges were dropped. This sequence was similar to the observations of Weller (1957) for redheads and Oring (1968) for gadwalls. I observed that the remiges were not lost in any particular order but generally followed loss of tertials and a few rectrices.

Figure 8. Distribution of blood quills on internal surface of male mallard skins of the various moult classes. Lined regions represent areas containing developing contour and down feathers. Dotted regions represent concentrations of developing down feathers. Cross-hatched regions represent position of wings and legs. Open, unnumbered areas represent apteria. Moult class 1 is not illustrated since no developing feathers were present. Transition refers to a transitional stage when birds are moulting from one plumage to another. Skins representative of the moult classes are located at the University of Alberta, Department of Zoology museum.

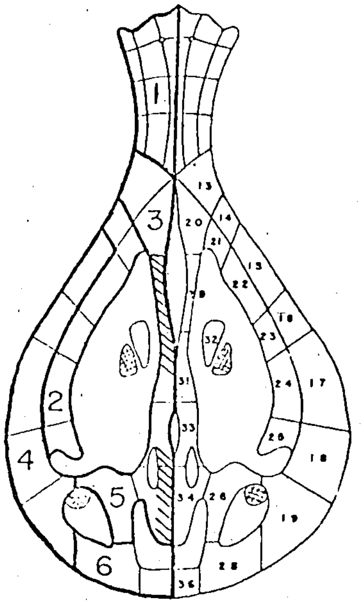
2 -TRANSITION



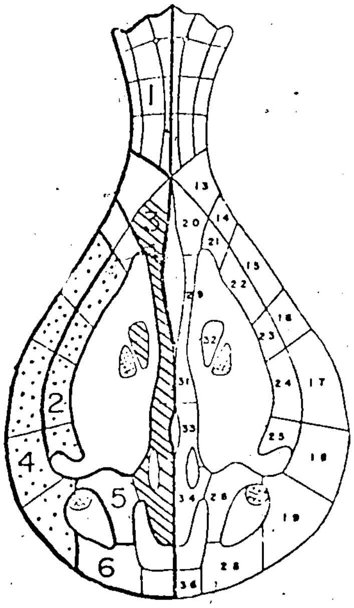
3-TRANSITION



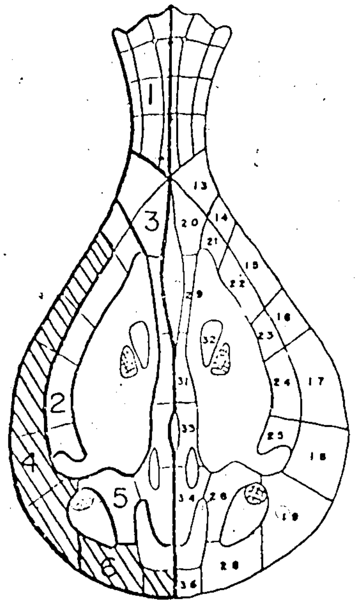
4-BASIC



5 -BASIC



6-TRANSITION



7 -TRANSITION

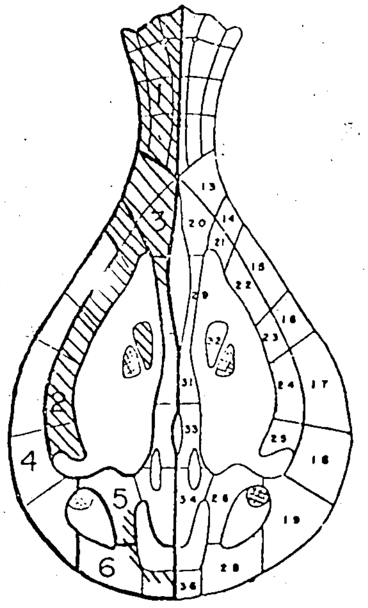
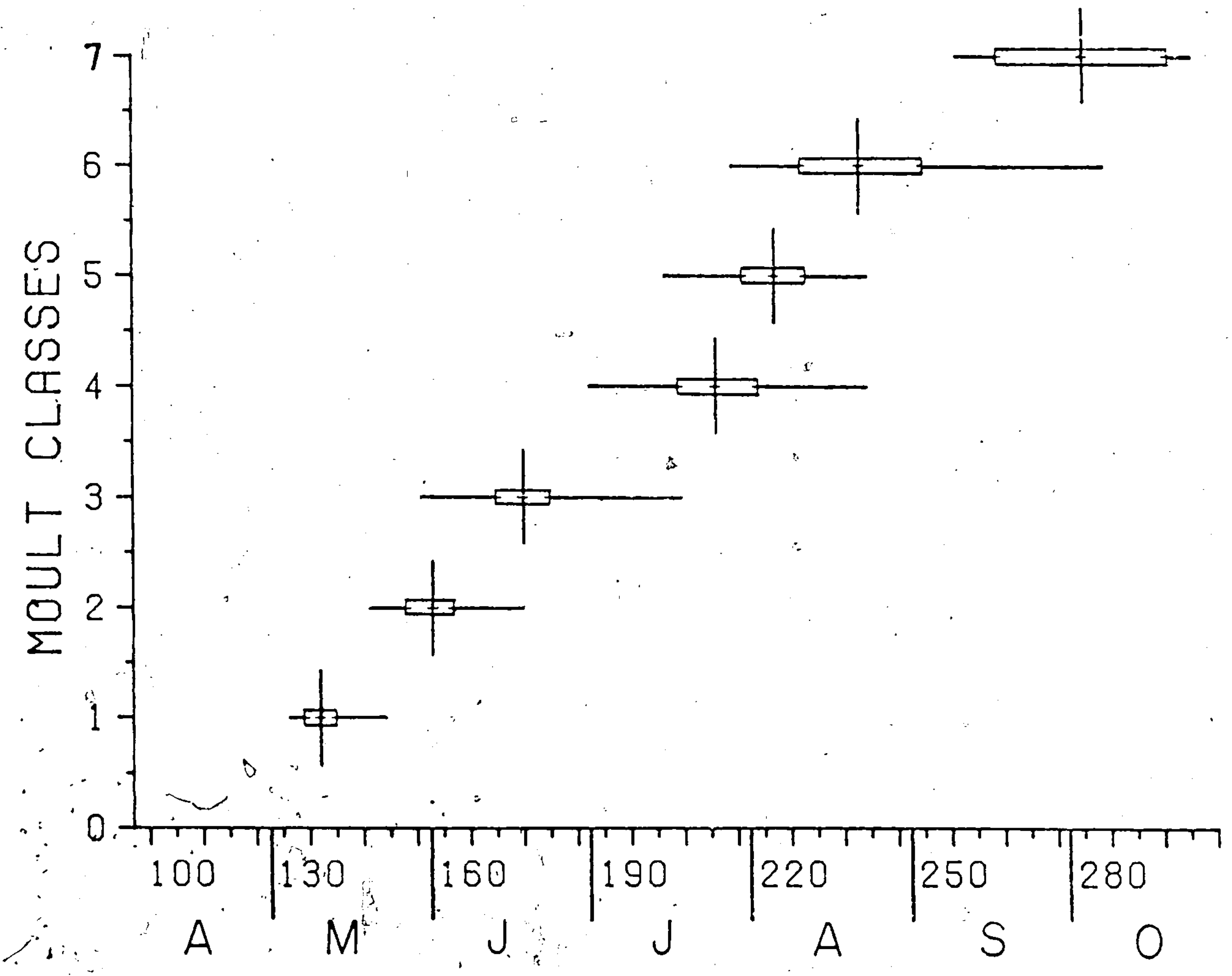


Figure 9. Distribution of moult classes over time in adult male mallards. Figure illustrates mean, 95% confidence limits and range. Month and day of the year are shown on the x axis.


MOULT CLASSES
0
1
2
3
4
5
6
7
100
130
160
190
220
250
280
A
M
J
J
A
S
O

During the early flightless stage, the last of the prebasic body moult was completed, giving the drake a female-like appearance typical of the male basic plumage. The first flightless male was captured in early July but flightless drakes were observed in mid-June and have been reported even earlier (Hochbaum 1959). The peak of the flightless period was in July but flightless adult males were captured into the last week of August.

As remiges neared lengths where flight was possible (wing chord of 25 to 26 cm), the prealternate moult of contour and down feathers commenced. Moult class 5 was characterized by large numbers of developing down follicles in the sides and flanks, lower breast and belly but only small concentrations of alternate pennae in the mid-rump and back (Fig. 8). Extensive down replacement in August in mallards concurred with observations by Oring (1968) on down replacement in gadwalls. While down was usually closely associated with contour feather moult, such was not the case in m. c. 5.

Most birds were capable of flight by mid-August, a time when the prealternate moult of pennae and down was prominent ventrally and posteriorally (Fig. 8). This stage, referred to as m. c. 6, was encountered in late July but drakes with newly grown remiges were observed earlier in the month. By this stage, rectrices of the basic plumage were generally complete and portions of the ventral tract (chest, belly and sides) had assumed alternate plumage. Birds in m. c. 6 were observed on the prairies as late as October but the majority were at this stage in early September.

The prealternate moult moved laterally and anteriorally (Fig. 8). Birds in m. c. 7 had concentrations of pennae only in lateral and anterior parts of the ventral tract and capital tracts (upper sides and flanks, scapulohumerals, upperback and neck and head regions). Externally, with the exception of a few isolated regions, these birds appeared to be in complete alternate plumage. Replacement of rectrices of the basic plumage occurred in this class, some being retained in late October.

From this moult class, mallard drake's assumed complete alternate plumage (m. c. 1). However, Oring (1968) and Ward (pers. comm.) have suggested that the tertiaries in many dabbling ducks may be replaced before the following spring.

In summary, the prebasic moult is initiated anteriomedially in tracts 1, 2 and 5 in m. c. 2, radiates into all tracts in moult class 3 and finishes dorso-medially in tract 5 in moult class 4 (Fig. 8). The prealternate moult follows the same pattern in reverse: the first alternate pennae were observed medially in tract 5 in m. c. 5, the next, posterio-medially in tracts 4 and 6 of m. c. 6 and the last anterio-medially in tracts and 3 of m. c. 7 (Fig. 8).

This moult sequence ensures that the areas exposed to the greatest amount of conductive heat loss, the breast and belly, moult their contour feathers while the water temperatures are warmest. Furthermore, while the birds are flightless, virtually all feather replacement is confined to the alar tract. Down replacement is also concentrated during the warmest part of the season and at times when some of the contour feathers have already been replaced, thereby minimizing thermoregulatory costs.

Changes in Body Parameters

Measurements of Body Components

Body weight increased significantly ($P < 0.01$) with time, from spring to autumn (Fig. 10). Nevertheless, it was evident that at any one time there was considerable variation around the mean weight. This reflected a variation in physical condition at the time of collection more than inherent variation in the size of the birds. For example, by separating the sample into the seven moult classes, the variation around the mean was reduced (Fig. 11). The weight of adult male mallards was lowest in spring. It increased an average of 150 grams before they moulted their remiges in m. c. 4. This 12 % increase in weight was similar to a 10.6 % increase reported by Folk *et al.* (1966) in mallards and a 15% increase reported by Hay (1974) in gadwalls. This weight gain prior to moult of the alar tract is not peculiar to waterfowl as Morton and Welton (1973) and Penney (1967) reported a similar occurrence in white-crowned sparrows (*Zonotrichia leucophrys*) and Adelie penguins (*Pygoscelis adeliae*) respectively. The surprising fact is that these mallards were gaining weight while undergoing the prebasic body moult.

Like Hohn (1947) and Weller (1957), I found no significant decrease in weight ($P > 0.05$) during the flightless period (Fig. 11) which contrasts with what most

Figure 10. Distribution of body weights over time in adult male mallards.

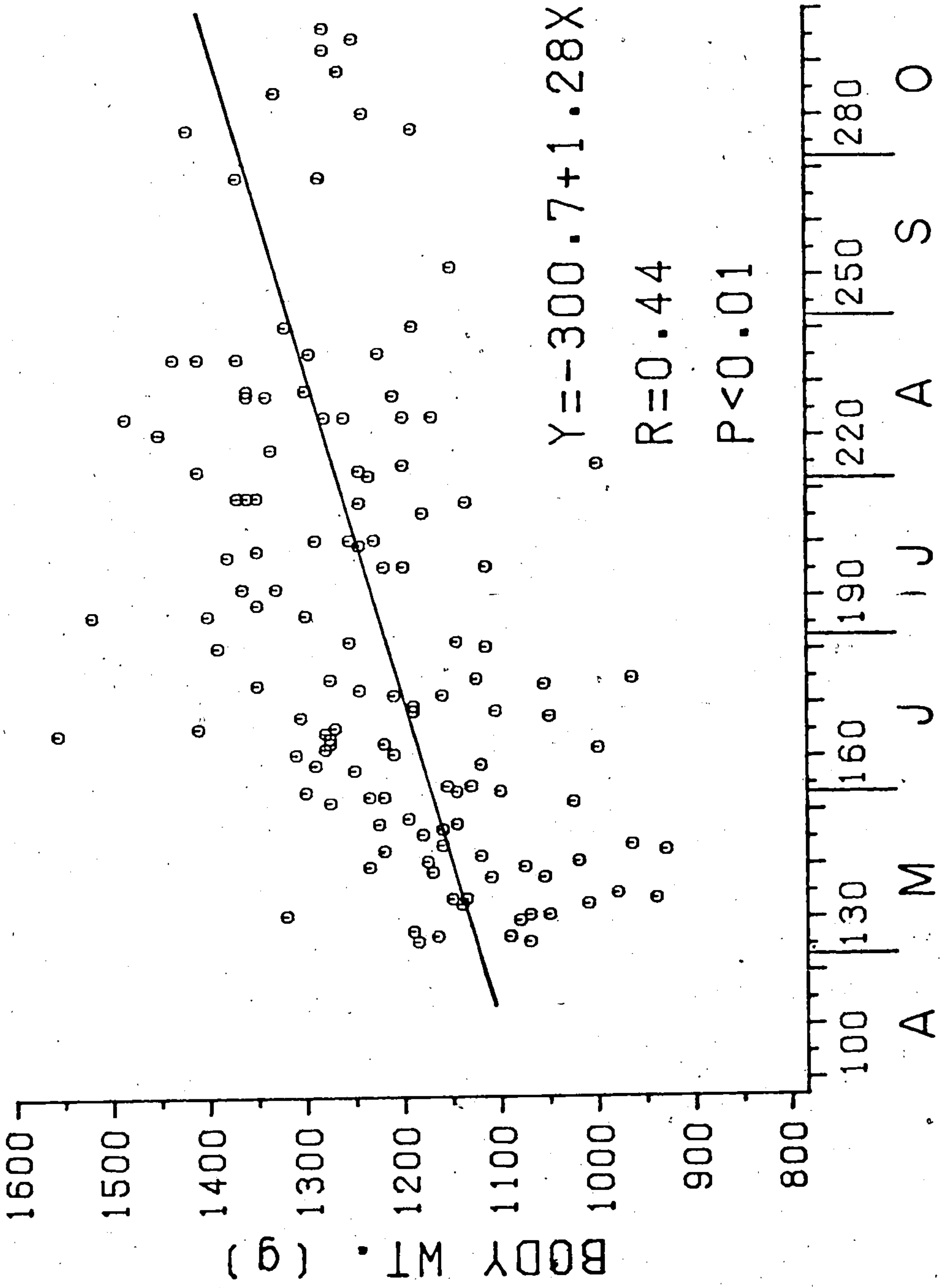
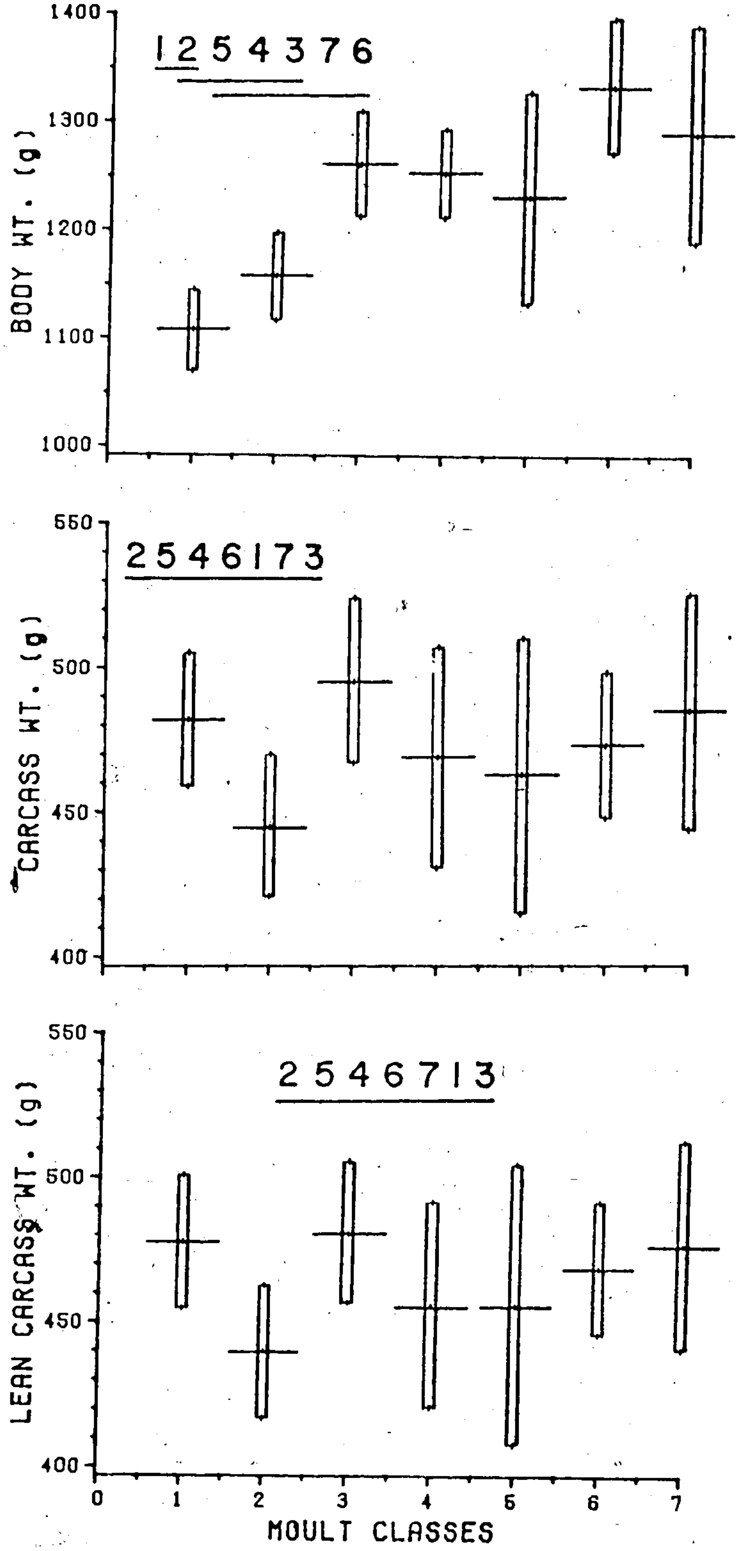

BODY WT. (g)
1600
1500
1400
1300
1200
1100
1000
900
800
100
130
160
190
220
250
280
A
M
J
J
A
S
O
Y=-300.7+1.28X
R=0.44
P<0.01

Figure 11. Body weights for seven moult classes of adult male mallards (upper). Carcass weights for seven moult classes (middle). Lean carcass weights for seven moult classes (bottom).


1400
1300
1200
1100
1000
BODY WT. (g)
1 2 5 4 3 7 6
550
500
450
400
CARCASS WT. (g)
2 5 4 6 1 7 3
550
500
450
400
LEAN CARCASS WT. (g)
2 5 4 6 7 1 3
0
1
2
3
4
5
6
7
MOULT CLASSES

of the waterfowl literature has reported (Hanson 1962, Folk *et al*. 1966, Oring 1969, Hay 1974). This suggests that flightless male mallards on the Delta Marsh did not encounter serious difficulties in meeting the energy requirements of the wing moult. Although weight loss during the moult o[illegible] remiges is common in redpolls (*Carduelis flammea*), [illegible]nguins and woodcock (*Philohela minor*) (Evans 196[illegible]y 1967, Owen and Krohn 1973), the bullfinch (*[illegible]hula pyrrhula*) and various sparrows do not lose weight during this period (Newton 1968, Odum and Perkinson 1951, Myrcha and Pinowski 1970, Morton *et al*. 1973, Morton and Welton 1973)

The weight increase in mallards (8%) following the wing moult is common in migrant birds and is generally associated with hyperphagia prior to fall migration. Weller (1957) reported that redheads also were heaviest at this time of year.

With the exception of a non-significant decrease ($P > 0.05$) in m. c. 2, carcass weights followed the same pattern as total body weights (Fig. 11): carcass weights were lowest in moult class 2, highest in moult class 3, but overall were not significantly different ($P > 0.05$) throughout the study The 30 gram decrease in body weight during the flightless period was also observed in carcass weights, indicating that skin weights did not change during the wing moult.

The pattern of change exibited by lean carcass weights (Fig. 11) was almost identical to carcass weights , indicating that changes in carcass lipids constituted only a small percentage of total carcass weight (0.9 to 1.8% - Fig. 12). Odum (1960) and Connell et al. (1960), recorded constant lean weights during the wing moult of several passerines and Evans and Smith (1975) recorded similar results in the bar-tailed godwit (Limosa lapponica). Other authors have recorded slight increases in lean body weights in passerines during this period (King and Farner 1959, King et al. 1965, McNeil and de Itriago 1968, Newton 1968, Blackmore 1969, Myrcha and Pinowski 1970, Morton and Welton 1973).

Although carcass and lean carcass weights decreased during the wing moult, the change was not significant ($P > 0.05$). The implications of this will be discussed in sections dealing with fat and protein reserves.

Combined pectoral muscle weights of birds in m. c. 4 were significantly lighter (40 grams, $P < 0.01$) than of birds of m. c. 3 (Fig. 13). This weight change has also been recorded in Canada geese (Hanson 1962) and gadwalls (Hay 1974) but the water, fat and protein components of these muscles have not been described for waterfowl.

Water content of the pectoral muscles did not change as the moult proceeded ($P > 0.05$ - Fig. 12). Lipid and protein content will be discussed in later sections. Overall, these three constituents were static through the seven moult classes (Fig. 12); the 40 gram decrease in weight could not be attributed to any one component.

Figure 12. Wet pectoral muscle weights and their components for moult classes of adult male mallards. Wet pectoral muscle weights (top). Lipids (second from top). Protein (second from bottom). Water (bottom).

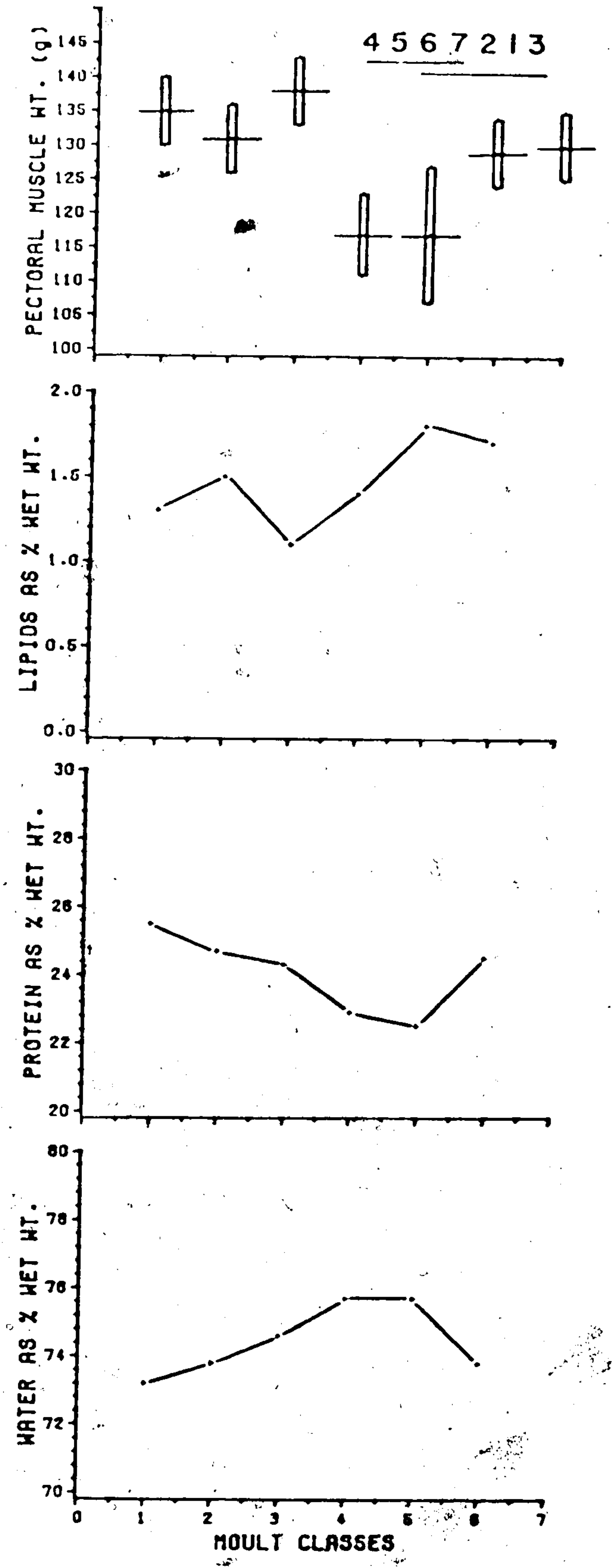
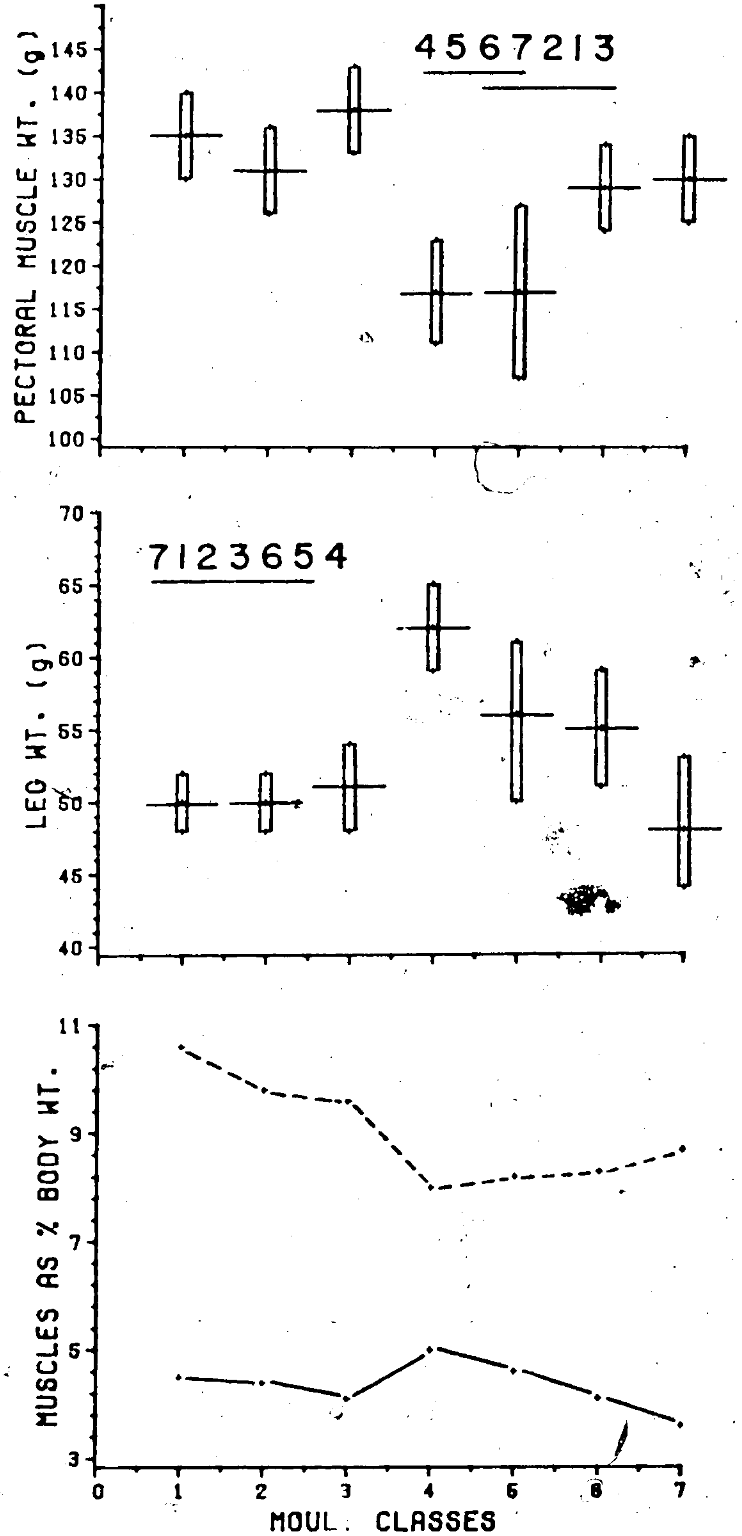

4 5 6 7 2 1 3
PECTORAL MUSCLE WT. (g)
145
140
135
130
125
120
115
110
105
100
LIPIDS AS % WET WT.
2.0
1.5
1.0
0.5
0.0
PROTEIN AS % WET WT.
30
28
26
24
22
20
WATER AS % WET WT.
80
78
76
74
72
70
0
1
2
3
4
5
6
7
MOULT CLASSES

Figure 13. Wet pectoral muscle weights for seven moult classes of adult male mallards (upper). Wet leg weights for seven moult classes (middle). Muscle weights as a percentage of total body weight (bottom). Dotted line represents pectoral muscles and solid line represents legs.


4567213
PECTORAL MUSCLE WT. (g)
145
140
135
130
125
120
115
110
105
100
7123654
LEG WT. (g)
70
65
60
55
50
45
40
MUSCLES AS % BODY WT.
11
9
7
5
3
0
1
2
3
4
5
6
7
MOULT CLASSES

Leg and pectoral muscle weights changed in opposite directions, relative to body weight, over the sequence of moults (Fig. 13). Leg weights were stable through m. c. 1, 2 and 3 but increased significantly (20 grams, $P < 0.01$) in m. c. 4, the initial stage of the flightless period. During m. c. 5 and 6, leg weights declined slightly and by m. c. 7 had reached the levels recorded for m. c. 1, 2 and 3. Although this phenomenon has been previously described, the percentage increase noted (16), was less than the (41) recorded by Hanson (1962) in Canada geese or by Hay (1974) for gadwalls (28 to 29).

Another body component, the gonads, were examined to study the relationship between testis regression and onset of the prebasic moult. Testis weight regressed rapidly after 15 May (Fig. 14) and no paired males with a testis weight less than 6 grams were collected. This value agrees with Johnson's (1961) estimate of the testis weight below which spermatozoa cease to be produced and was used as a reference point to separate breeding from post- breeding males. Using this value, I estimated the length of the breeding season. Mallards arrived paired on the Delta Marsh in early April and a segment of the population was apparently still capable of insemination in late June (Fig. 14).

When testis weight was compared with moult class (Fig. 15), it was apparent that breeding was confined to birds in m. c. 1 and a few individuals in m. c. 2. Testis

Figure 14. Distribution of left testis weight over time in adult male mallards.

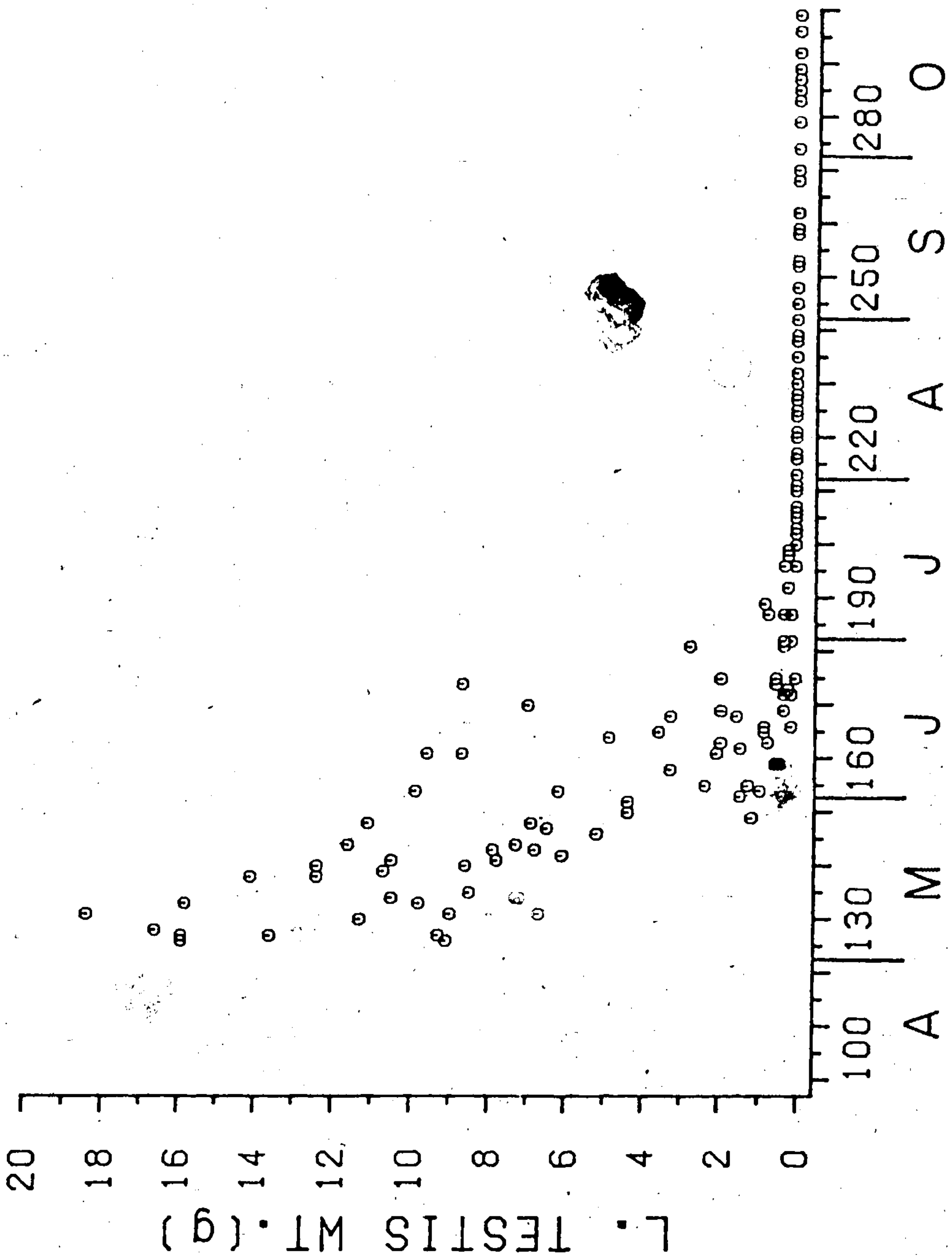
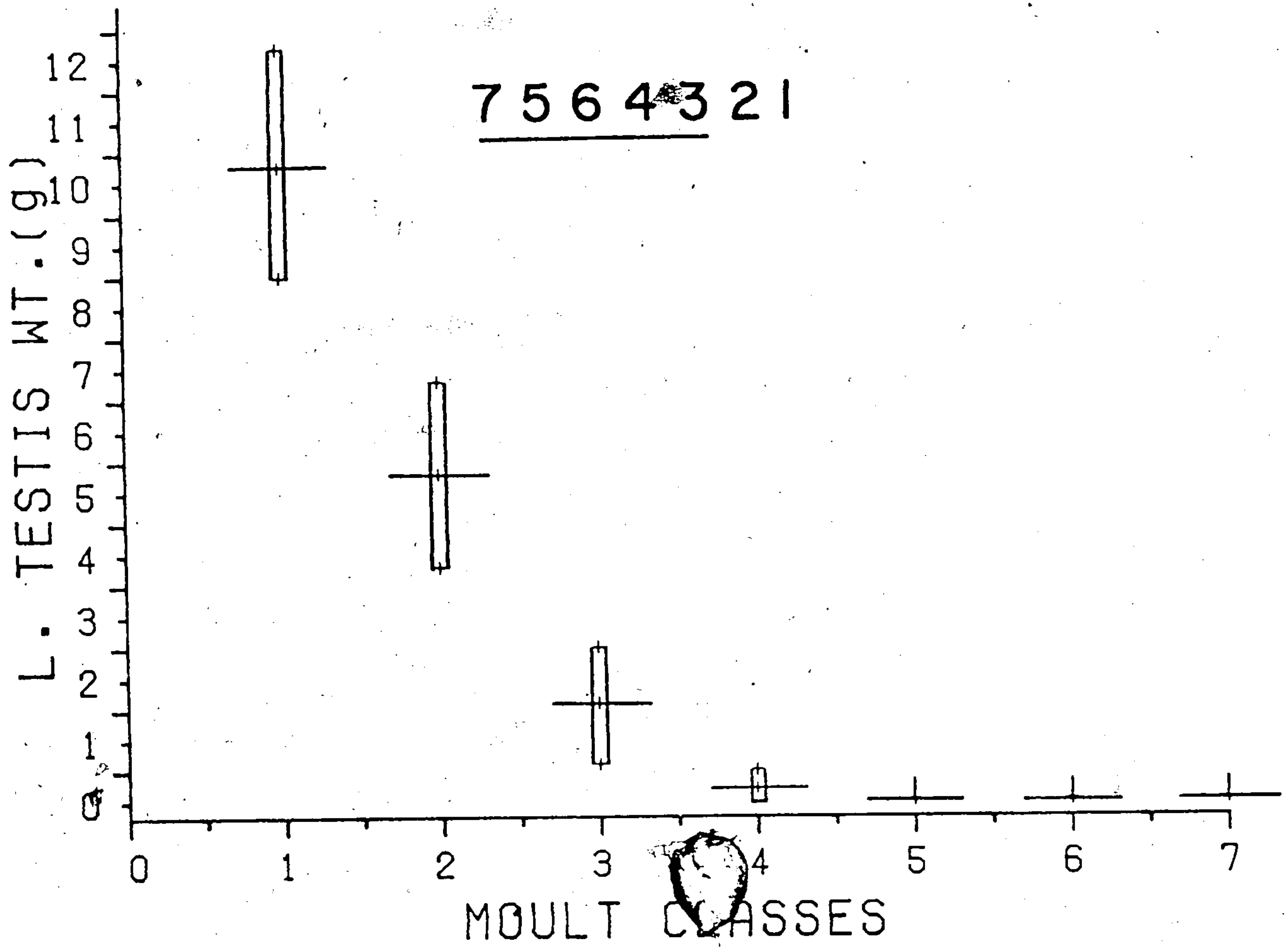

L. TESTIS WT.(g)
0
2
4
6
8
10
12
14
16
18
20
100
130
160
190
220
250
280
A
M
J
J
A
S
O

Figure 15. Left testis weights for seven moult classes of adult male mallards.


7 5 6 4 3 2 1
L. TESTIS WT.(g)
12
11
10
9
8
7
6
5
4
3
2
1
0
0
1
2
3
4
5
6
7
MOULT CLASSES

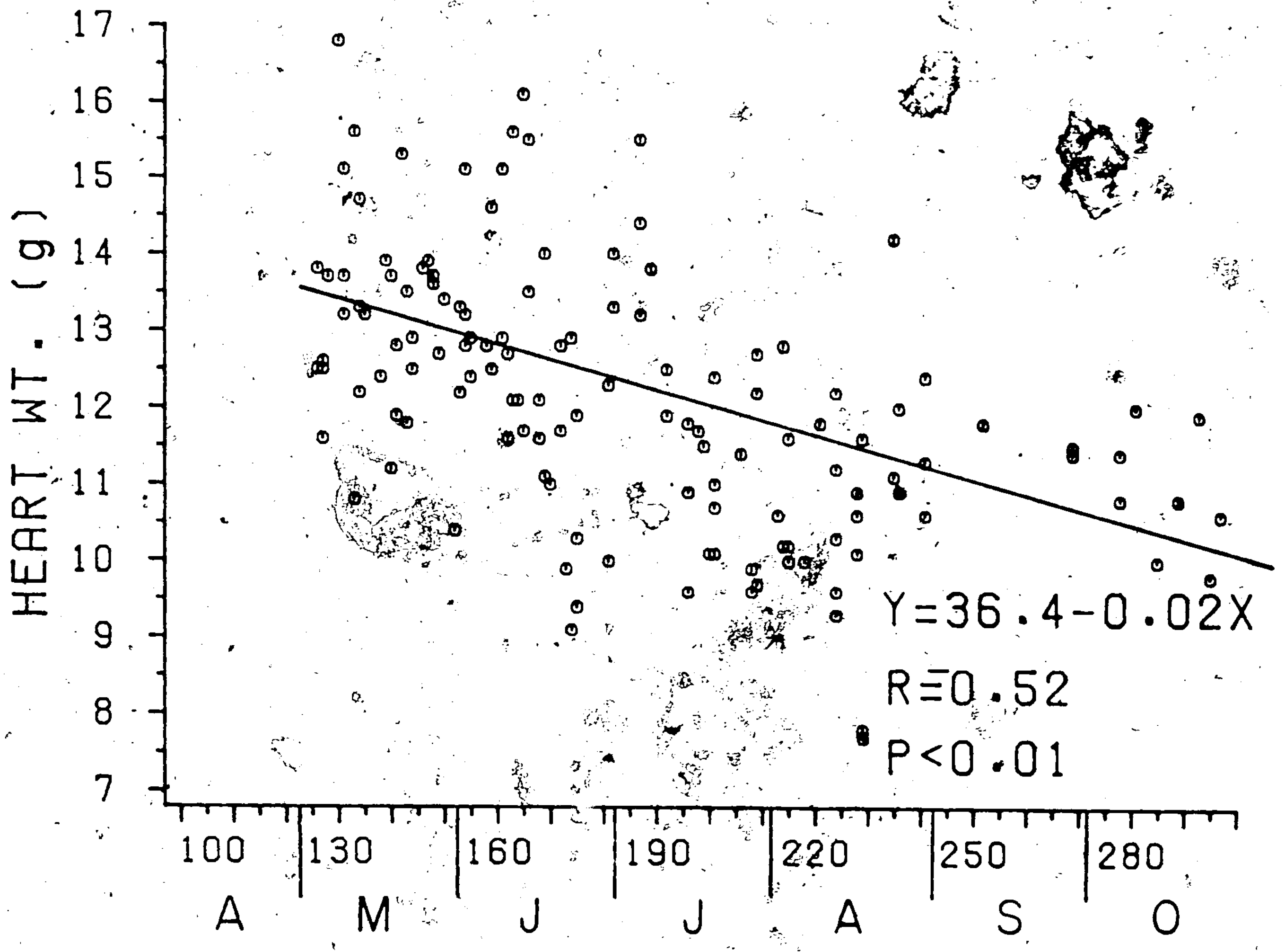
regression was evident among males in m. c. 2 and was essentially complete by the flightless period (m. c. 4), after which weights decreased only slightly. This pattern conforms to the 2-stage process of regression described by Johnson (1961): an initial rapid phase during the first weeks of the prebasic moult followed by a gradual phase lasting up to 2 months.

Whether cellular activity in the testes is related to the onset of prebasic moult and the assumption of basic plumage is subject to debate. Seligmann and Shattock (1914), Walton (1937) and Emmens and Parkes (1940) observed that castration did not promote the assumption of basic plumage in male mallards. Hohn (1947) supported this view, noting no relationship between seasonal plumage change and activity of the seminiferous epithelium. On the other hand, Johnson (1961) reported a close correlation between testis regression and initiation of the prebasic moult. I too observed this relationship but this does not imply that testicular activity is causally related to plumage change. For example, no dramatic change in histological appearance ot the testes accompanies the assumption of alternate plumage (Hohn 1947, Johnson 1961). It therefore appears that while testis regression is not primarly responsible for the prebasic moult in mallards, the cessation of breeding activity is in some way linked to the initiation of this moult.

Heart weight was recorded as an index of activity. Heart weight decreased with season during the study (Fig. 16). As with all other organs measured, variability in heart weight was reduced when birds were placed into the various moult classes (Fig. 17). Heart weights of birds in m. c. 4 declined significantly (P < 0.01) from those of m. c. 3. Size of the heart is related to the degree it is exercised (Goss 1964, Akester 1971, Rakusan _et al_. 1971, Burton 1972). Heart weights in spring are heavier probably because of the demands of migration and reproductive activity (Sowls 1955, Hochbaum 1959). These weights were maintained throughout the breeding season. Once reproductive activities ceased, males spent much of their time loafing and feeding (Hochbaum 1959, Oring 1969, pers. obs.). Flightless birds were extremely secretive (Hochbaum 1959, Oring 1969, pers. obs.), spending most of their time in stands of emergent vegetation and venturing into open water mainly at night. A significant decrease in activity such as that seen in flightless mallards could result in atrophy of heart muscle (Beznak 1954, Beznak _et al_ . 1969). With the regaining of flight and its associated activity, hearts of these birds also showed a tendecy to increase in size, albeit only slightly.

Another reason for peak heart weights in spring could be increased metabolic rates associated with thermoregulation during cold, spring weather (Sturkie _et al_ . 1970). Bump _et al_. (1947) and Delane (1968) reported

Figure 16. Distribution of heart weights [illegible] time in adult male mallards.


HEART WT. (g)
17
16
15
14
13
12
11
10
9
8
7
100
130
160
190
220
250
280
A
M
J
J
A
S
O
Y=36.4-0.02X
R=0.52
P<0.01

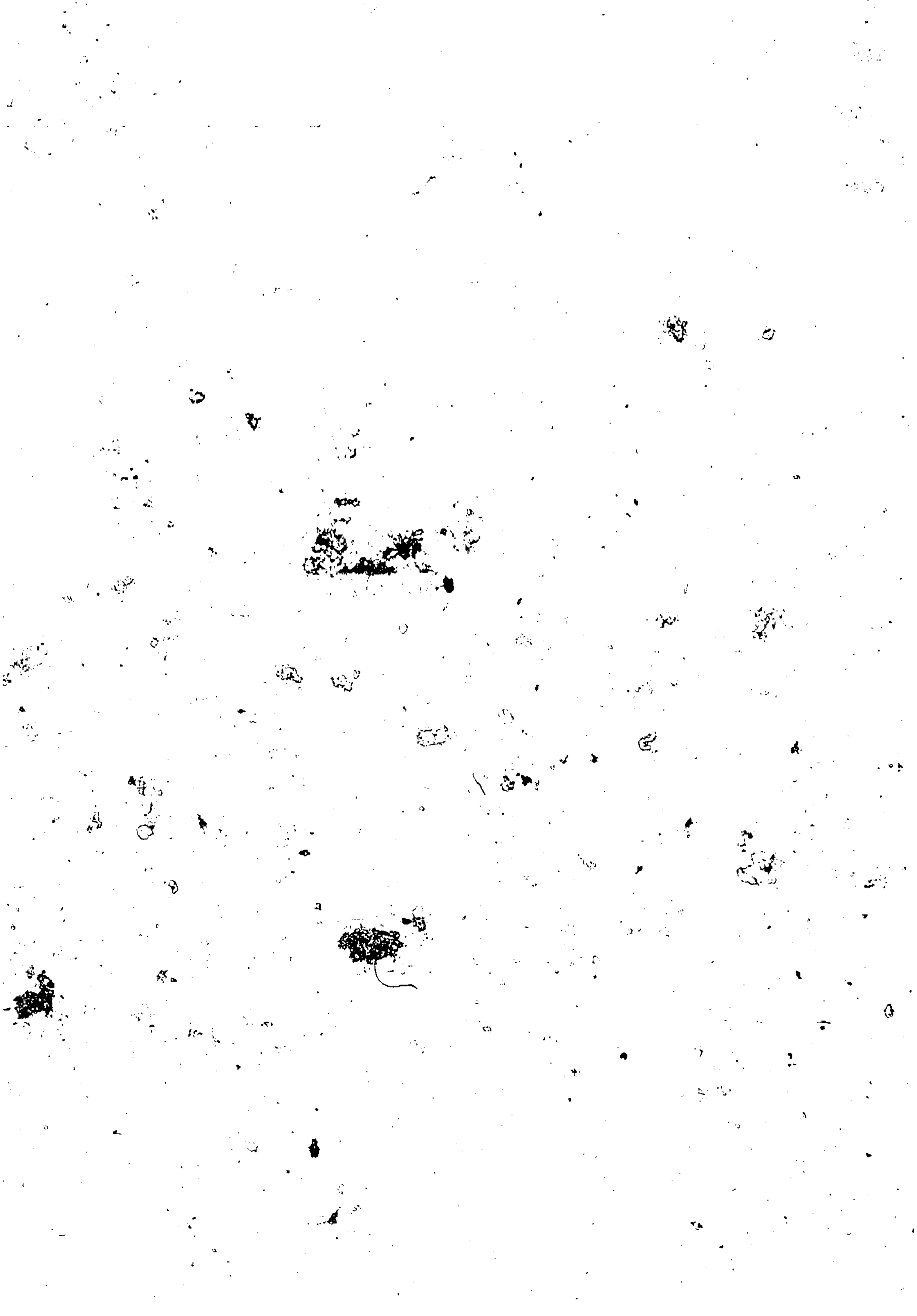
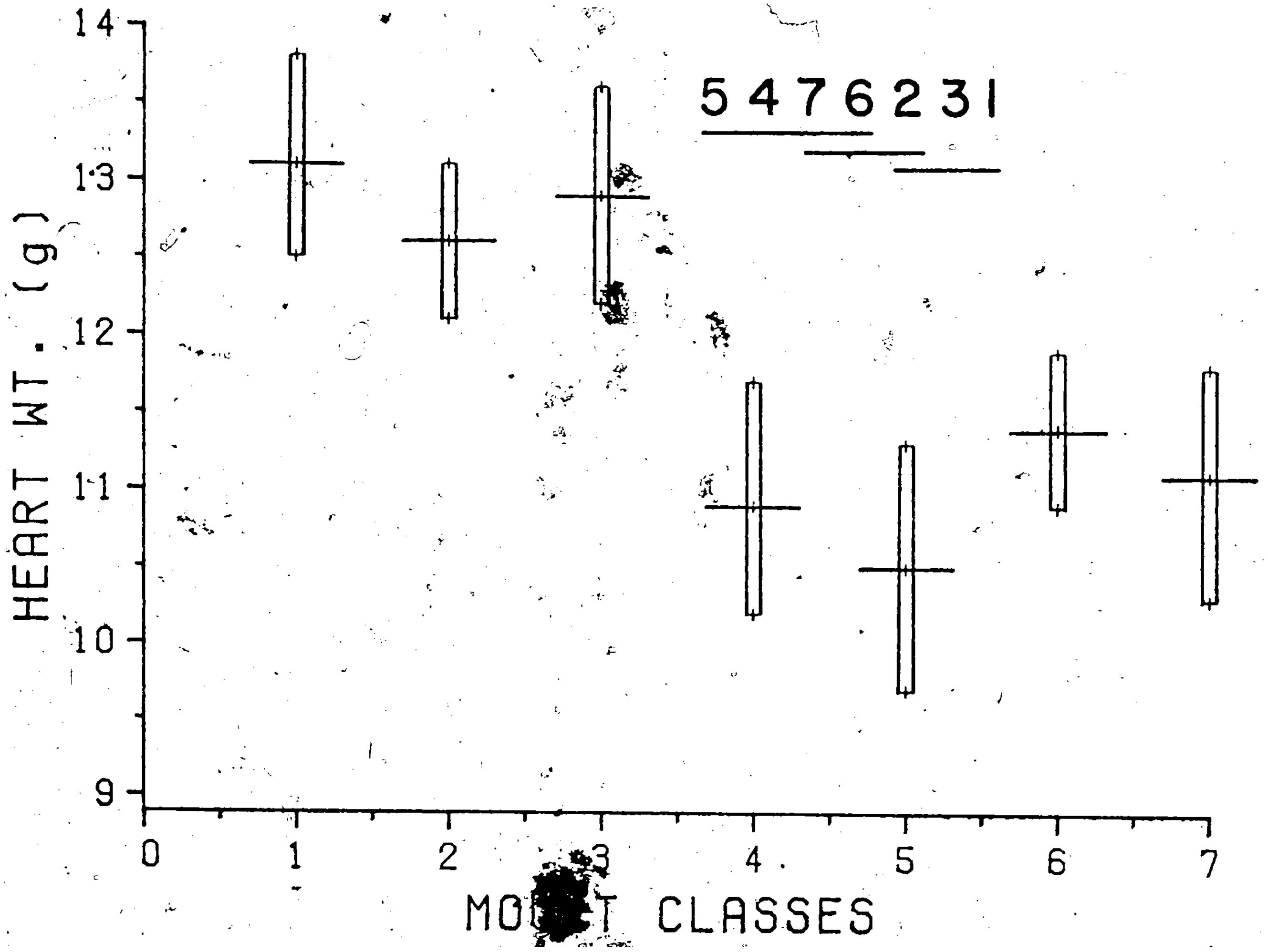


Figure 17. Heart weights for seven moult classes of adult male mallards.


14
13
12
11
10
9
HEART WT. (g)
0
1
2
3
4
5
6
7
MO[illegible]T CLASSES
5 4 7 6 2 3 1

increased metabolic rates in upland game birds exposed to cold conditions.

The weight of mallard livers was lightest in spring, increasing steadily into October (Fig. 18). When birds were placed in moult classes, the same trend was observed (Fig. 19). Liver weights of birds in m. c. 4 and 6 were significantly greater ($P < 0.01$) than those of birds in m. c. 1 and 2.

Hanson (1962) observed that livers of flightless geese were not significantly different from those of wintering geese. Once the wing moult was completed, liver weights increased by 61%. Hanson concluded that normal liver weights during the flightless period indicated that liver activity did not increase in response to an assumed transamination of muscle protein into feather keratin. Hanson also suggested, without quantification, that increased liver weights following the flightless period were related to hyperphagia, as birds replenished depleted pectoral muscles and lipid reserves prior to migration.

In response to increased protein requirements for feather production, birds must increase protein intake or degrade protein reserves within their bodies (Spearman 1971). Since protein reserves did not decrease significantly ($P < 0.01$) during the moults, it appeared that the diet provided adequate protein. If total energy intake was sufficient to meet the metabolic requirements then the liver would convert any excess into lipid stores (m. c. 2,

Figure 18. Distribution of liver weights over time in adult male mallards.

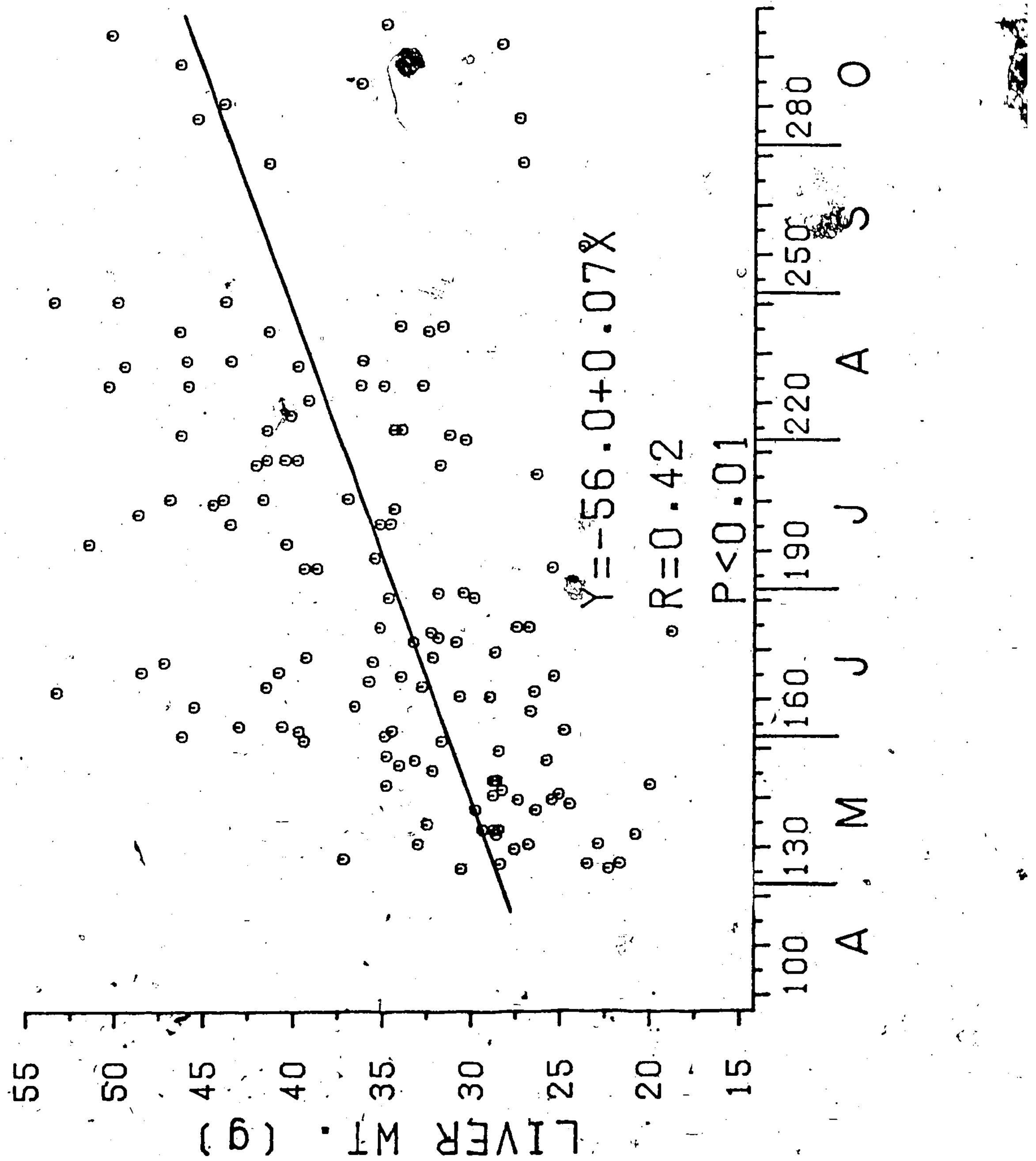
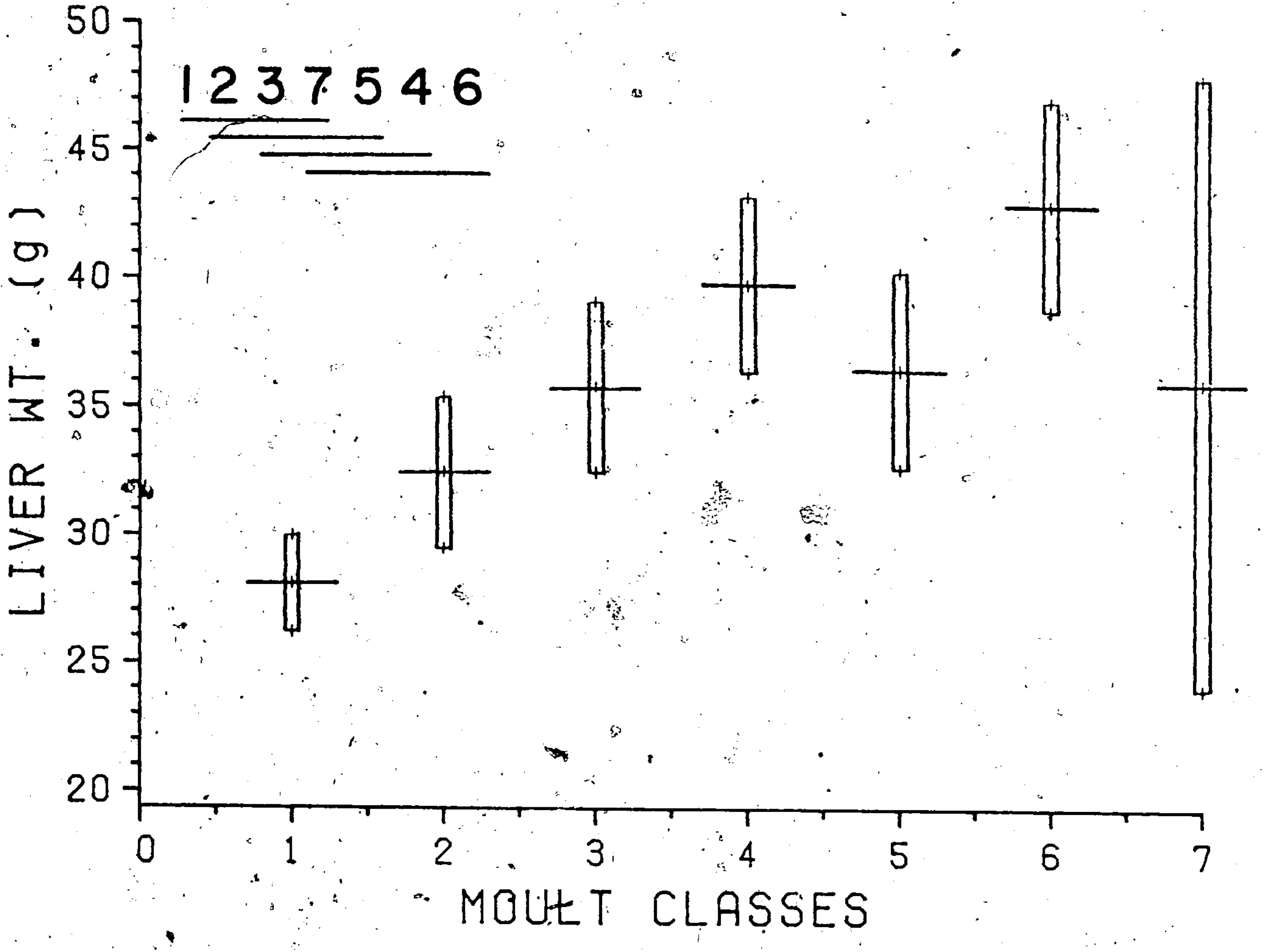

LIVER WT. (g)
15
20
25
30
35
40
45
50
55
100
130
160
190
220
250
280
A
M
J
J
A
S
O
Y=-56.0+0.07X
R=0.42
P<0.01

Figure 19. Liver weights for seven moult classes of adult male mallards.


1 2 3 7 5 4 6
LIVER WT. (g)
50
45
40
35
30
25
20
0
1
2
3
4
5
6
7
MOULT CLASSES

3, 6 and 7 - Fig. 19). If total energy intake was insufficient (m. c. 4 and 5 - Fig. 19), the liver would convert stored glycogen into glucose to meet metabolic demands (Keeton 1972). Presumably, the increased liver weight in post breeding birds was a functional response to its increased activity in lipogenesis and lipolysis. Pendergast and Boag (1973) suggested that increased liver weights in spruce grouse were related to changes in the nutritional composition of the diet, and reflected differing rates of lipid storage.

Components of the digestive tract were examined to study the impact of diet on their size. The gizzard (ventriculus) increased in weight from spring to autumn (Fig. 20). In general, the sample of birds could be divided into two groups: pre-flightless birds (m. c. 1 to 3) and flightless and post-flightless birds (m. c. 4 to 7 - Fig. 21). Gizzards, lightest in m. c. 1, increased significantly (17%, $P < 0.01$) by m. c. 3. Once birds moulted their remiges, gizzard weights again increased significantly (25%, $P < 0.01$), remaining at this weight until autumn (Fig. 21).

The length of the small intestine increased with season but this trend was even more apparent when moult classes were compared (Fig. 21). Small intestine lengths were significantly longer ($P < 0.01$) in m. c. 3 to 7 than in m. c. 1.

Figure 20. Distribution of gizzard weights over time in adult male mallards.

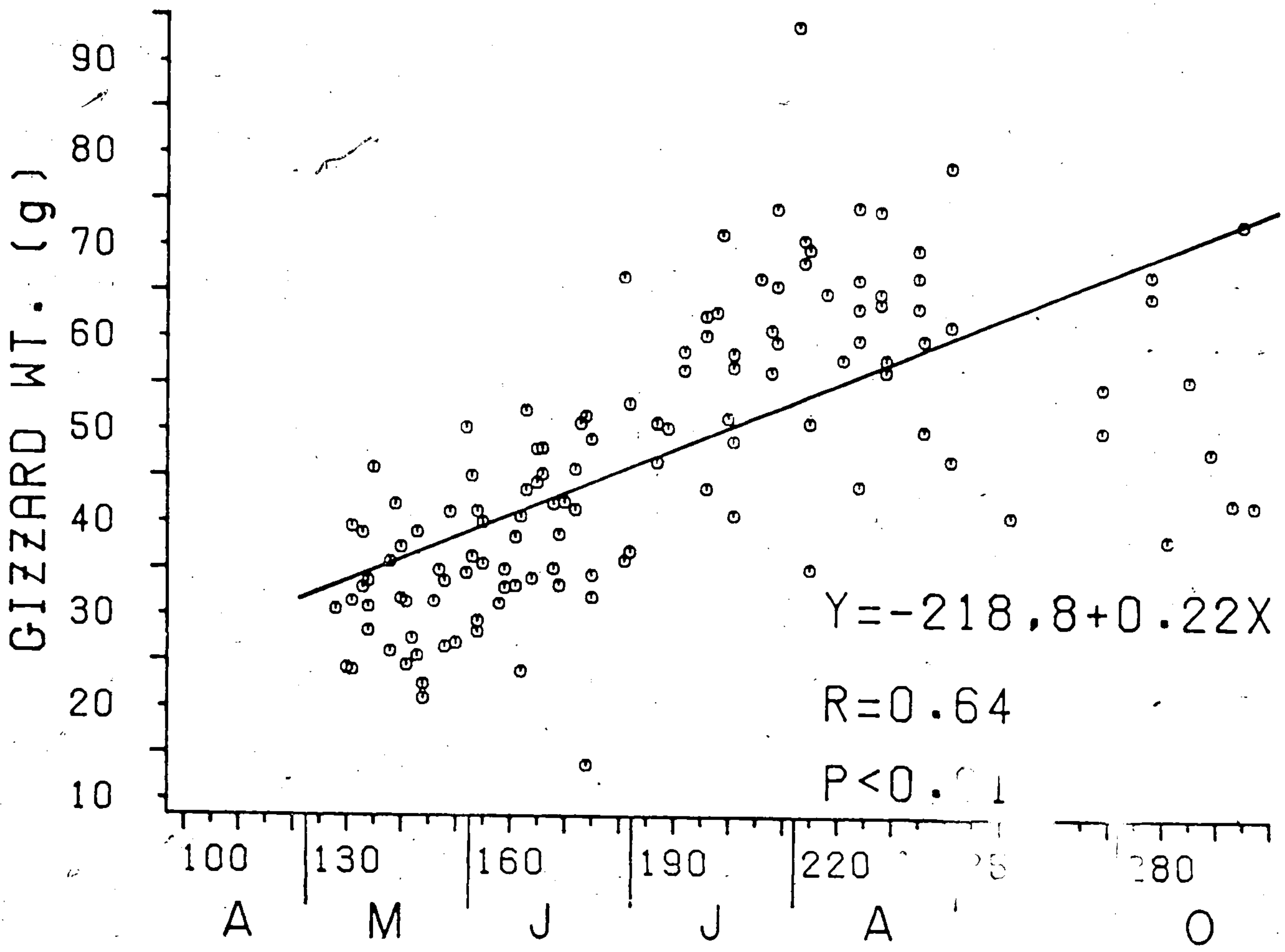
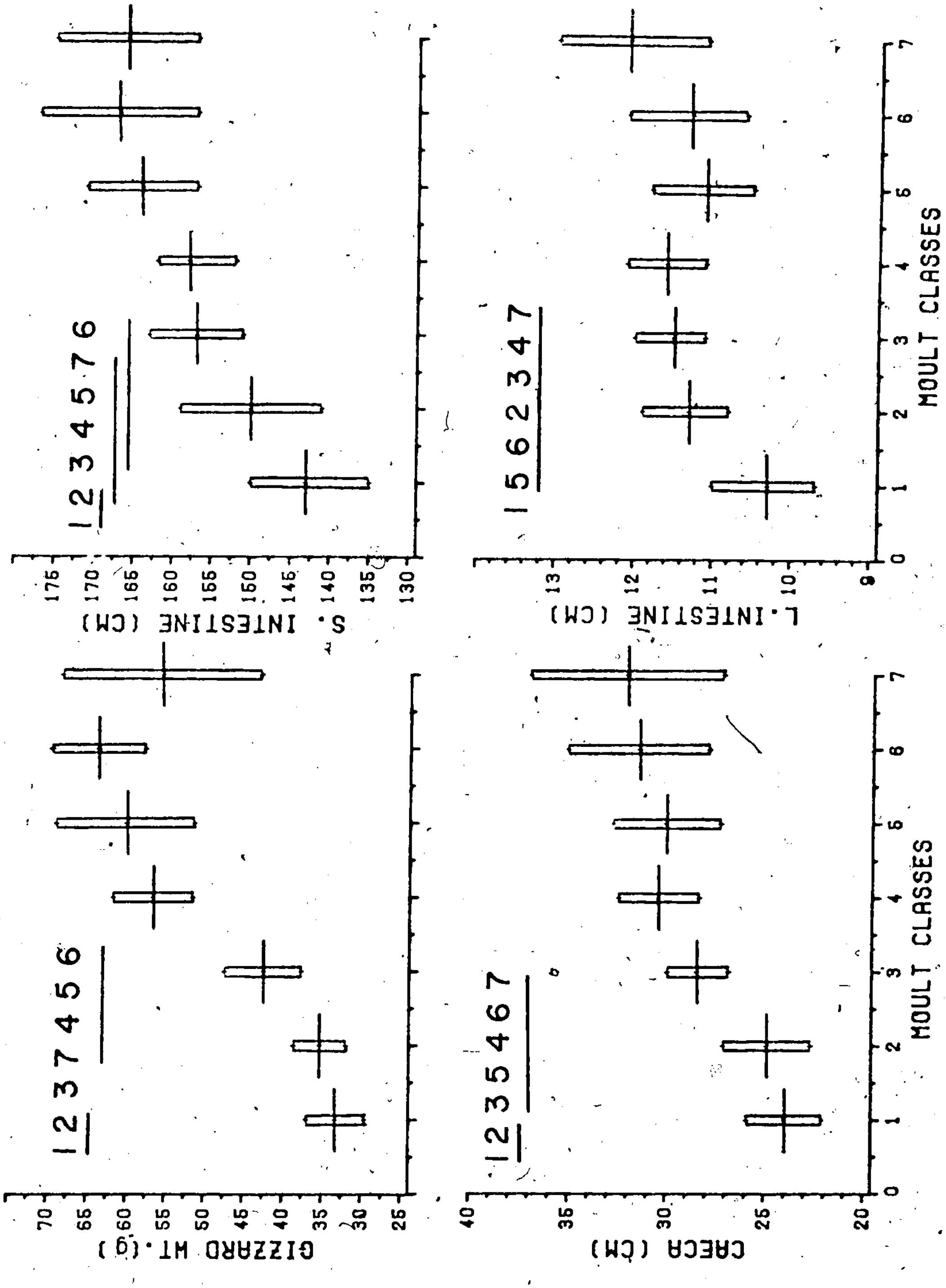

GIZZARD WT. (g)
90
80
70
60
50
40
30
20
10
100
130
160
190
220
250
280
A
M
J
J
A
O
Y=-218,8+0.22X
R=0.64
P<0.01

Figure 21. Gizzard weights for seven moult classes of adult male mallards (upper left). Small intestine length for seven moult classes (upper right). Caeca length for seven moult classes (lower left). Large intestine length for seven moult classes (lower right).


GIZZARD WT.(g)
70
65
60
55
50
45
40
35
30
25
1 2 3 7 4 5 6
S. INTESTINE (CM)
175
170
165
160
155
150
145
140
135
130
1 2 3 4 5 7 6
CAECA (CM)
40
35
30
25
20
1 2 3 5 4 6 7
L.INTESTINE (CM)
13
12
11
10
9
1 5 6 2 3 4 7
0
1
2
3
4
5
6
7
MOULT CLASSES
MOULT CLASSES

The tendency for gut components to increase in weight-length characteristics was repeated when caeca lengths (total) were examined (Fig. 21). Birds in m. c. 3 to 7 possessed significantly longer caeca ($P < 0.01$) than those in m. c. 1 and 2.

Although the trend toward increased length was not as dramatic, large intestine lengths were significantly longer ($P < 0.01$) in m. c. 2 to 7 than in m. c. 1 (Fig. 21).

In general, the weight-length values of the gastro-intestinal tract were greater in post-breeding birds (m. c. 3 to 7) than in breeding birds (m. c. 1 and some individuals in m. c. 2). The observed changes in the digestive tract probably reflected dietary change and/or increased food intake during the moults. Leopold (1953) and Lewin (1963) reported that the intestines and caeca of various gallinaceous birds increased in length in response to a diet of low quality fibrous foods. Moss (1972), in a study of captive red grouse (Lagopus lagopus scoticus) concluded that grouse adapted to changes in diet by varying their gut lengths. Pendergast and Boag (1973) reported that wintering spruce grouse had longer intestines and caeca because of a dietary change to large quantities of high fiber conifer needles. Presumably, gizzard musculature increases with greater activity due to greater food intake and/or to facilitate mechanical breakdown of harder food items. Increased intestinal length enhances absorptive processes and increased caecal length ensures more efficient use of food (Pendergast and Boag 1971, 1973, Fenna and Boag 1974, Thompson and Boag 1975).

Male mallards had greater weight-length gut characteristics and stable body weights during the moults. This suggests that their diets changed both in quantity and/or quality (high fiber foods) during the moults and birds were not in poor "condition" when evaluated on body weight.

Moults and Energetics

Moulting requires an expenditure of energy (Kendeigh 1949) as the result of increased metabolic rates (Perek and Sulman 1945, King and Farner 1961, West 1960, Blackmore 1969, Lustick 1970, Thompson and Boag 1976). The actual increase in metabolized energy during the moult varies from 5 to 30% (Payne 1972). This increased energy demand can be attributed to two major sources: cost of feather production and heat loss from exposed vascularized papillae (Irving 1964, Payne 1972, Thompson and Boag 1976). The energy cost of feather growth represents 7.6 to 8.6% of daily energy requirements of white-crownned and house sparrows (<u>Passer domesticus</u>) (King and Farner 1961, Blackmore 1969) and 13% in brown-headed cowbirds (<u>Molothrus ater obscurus</u>) (Lustick 1970). If one assumes that the energetic cost of producing a unit biomass of feathers is constant for a given bird, increases above this value must be related to thermogenesis.

Since many birds moult at temperatures below their thermoneutral zone (35 - 40°C), some energy must be devoted to thermoregulation, particularly when heat is lost across vascularized surfaces. Blackmore (1969) suggested that at lower temperatures (22°C), this heat loss was negligible since the house sparrow moult increased in duration and decreased in intensity. In contrast, Lustick (1970) reported that at temperatures below 25°C, oxygen consumption increased from 13 to 24% in moulting cowbirds.

If one assumes that moulting results in accelerated metabolic rates and energy demands, increased food consumption should occur or body reserves will be depleted (Spearman 1971). This depletion may occur in either fat or protein stores, depending on the nature of the diet. As Evans and Smith (1975) concluded, fat reserves will decrease when total energy intake is insufficient, but protein reserves will not be degraded providing protein consumption is adequate; the reverse situation also applies. Since lipid and protein metabolism are not as intimately linked as Hanson (1962) suggested (Evans and Smith 1975, W. C. Mackay pers. comm.), it is more accurate to examine lipid and protein reserves as separate indices of body condition.

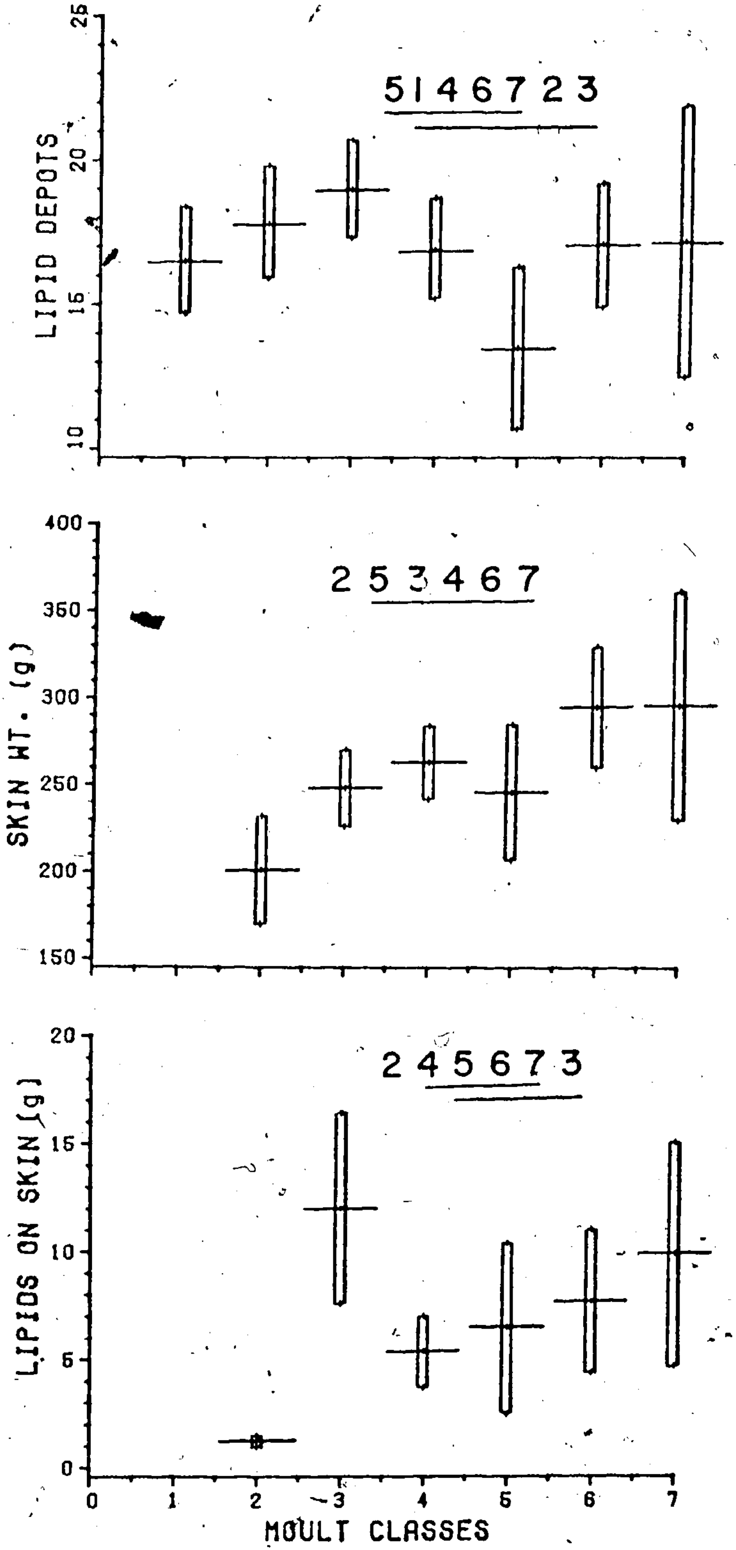
Lipid Reserves Associated With Skin

Since skins were required for plumage studies, it was not feasible to include them in lipid extractions. As a result, established and new techniques were employed to obtain a measure of subcutaneous lipids and those associated with the skin itself.

Owen and Krohn (1973) measured lipid deposition by assigning scores of 0 (no fat) to 3 (very fat) to seven areas of the carcass. They averaged these scores to obtain a "fat index". Because an average value allows for little differentiation between birds, I summed the seven values to obtain a lipid depot value which could range from 0 to 21 (Fig. 22). Following breeding, male mallards began to store significant amounts of lipids. While some of this subcutaneous lipid store was lost during the flightless period, it was recouped once the birds began to fly again. Apart from moult class 5, lipid indices were not significantly different between moult classes ($P > 0.05$). Because of the subjectivity inherent in this method, it could be considered only a relative index of amounts of stored lipids.

Another index of skin and subcutaneous lipids in mallards was fresh skin weight (Fig. 22). Moult class 2 birds had significantly lighter skin weights ($P < 0.01$) than any other class analyzed. Skin weights did not change significantly after m. c. 3.

Figure 22. Lipid depot values for seven moult classes of adult male mallards (upper). Skin weights for six moult classes (middle). Weights of lipids adhering to skin for six moult classes (bottom).


LIPID DEPOTS
25
20
15
10
5 1 4 6 7 2 3
SKIN WT. (g)
400
350
300
250
200
150
2 5 3 4 6 7
LIPIDS ON SKIN (g)
20
15
10
5
0
2 4 5 6 7 3
0
1
2
3
4
5
6
7
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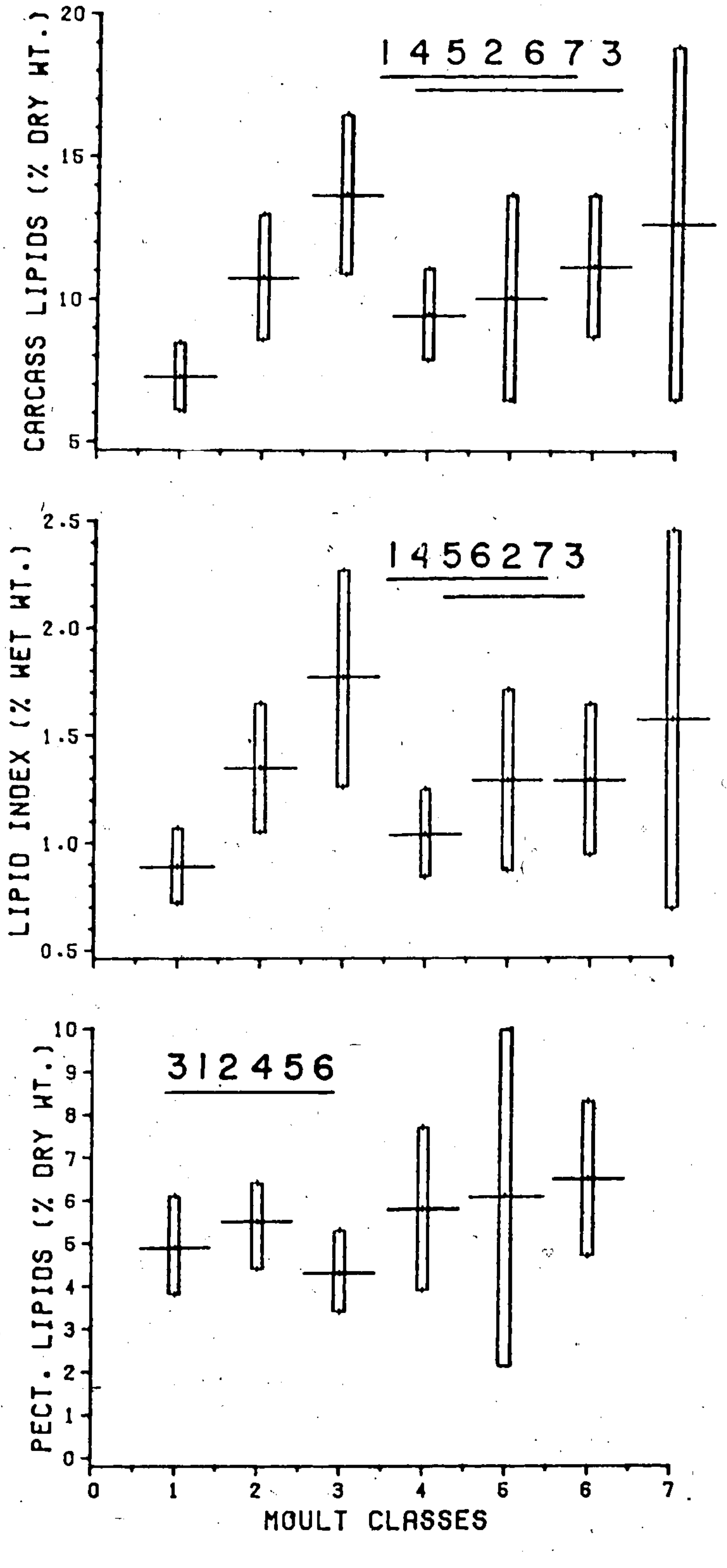
To ensure that blood quills were visible for counting, lipids adhering to the skin were removed and weighed. Although birds had small quantities of lipid adhering to the skin following breeding (m. c. 2), lipid stores incresed 80% by m. c. 3 (Fig. 22). Much of this reserve was lost in the early flightless period (moult class 4) but restoration of these lipids was evident once birds were flying again. The implications of this dynamic process will be discussed in terms of total lipid reserves.

Because of sampling error inherent in lipids measured from scraped skins, weights presented in Figure 22 are indicative only of relative amounts of stored lipids.

Muscle and Carcass Lipids

The existence of substantial lipid stores in avian pectoral musculature is well documented (George and Jyoti 1955, George and Naik 1958, 1960, Hartman and Brownell 1961). Figures 23 and 12 illustrate that mallard pectoral muscle lipids were relatively constant regardless of moult condition. If the energetic demands of the moult could not be met by food intake, one might expect a depletion of these lipids similar to that observed in carcass and subcutaneous fat stores (Figs. 22 and 23). The fact that pectoral muscle lipids were not consumed suggests that these reserves are mobilized only as a last resort. George and Jyoti (1955) concluded that these lipids were used primarily as an energy source during flight and only for other bodily functions

Figure 23. Carcass lipid values for seven moult classes of adult male mallards (upper). Lipid index values for seven moult classes (middle). Pectoral muscle lipid values for six moult classes (bottom).


CARCASS LIPIDS (% DRY WT.)
20
15
10
5
1 4 5 2 6 7 3
LIPID INDEX (% WET WT.)
2.5
2.0
1.5
1.0
0.5
1 4 5 6 2 7 3
PECT. LIPIDS (% DRY WT.)
10
9
8
7
6
5
4
3
2
1
0
3 1 2 4 5 6
0
1
2
3
4
5
6
7
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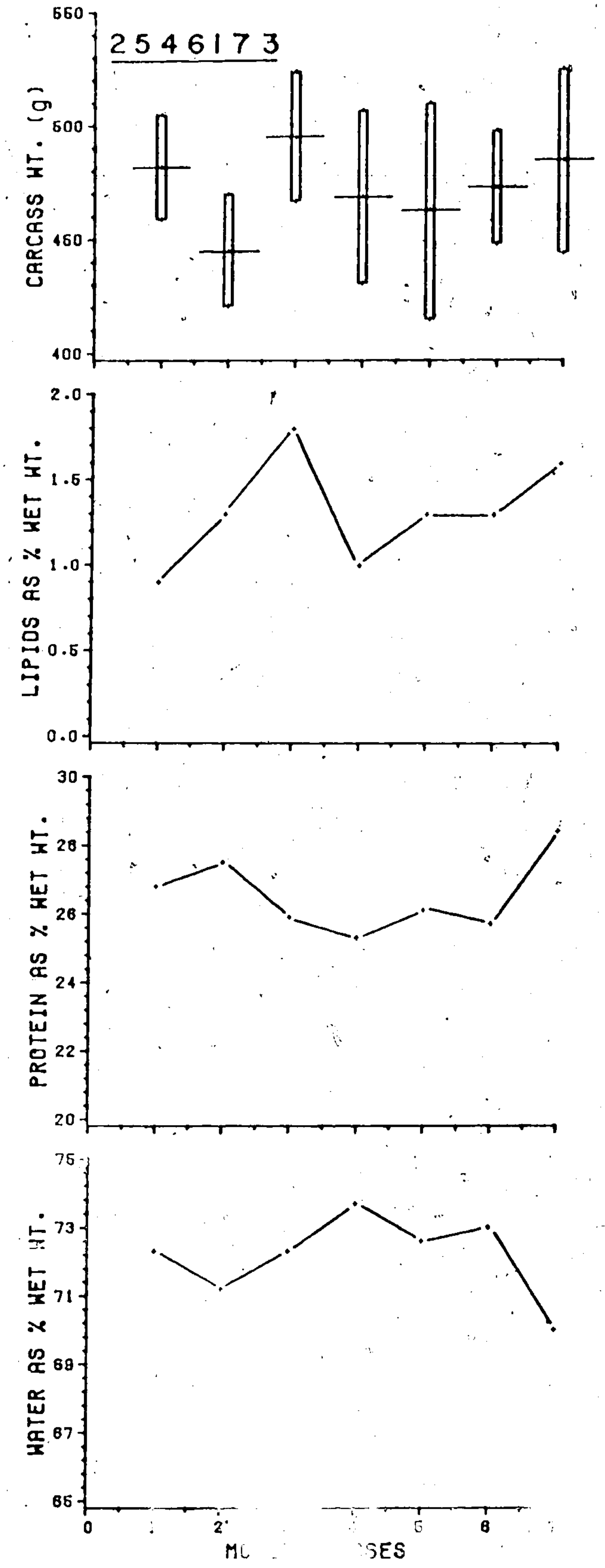
during starvation.

Carcass lipids were lowest in m. c. 1 but increased significantly (47%, $P < 0.01$) by m. c. 3 (Fig. 23). Although carcass lipids declined slightly during the flightless period, with the exception of minimum levels in m. c. 1, they did not differ significantly between moult classes (Fig. 23).

The lipid index was a measure of ether extractable lipids expressed as a percentage of wet carcass weight (Evans and Smith 1975). These data exhibited the same trends described for carcass lipids (% dry weight) except that lipid levels in m. c. 1 and 4 were significantly less ($P < 0.01$) than m. c. 3 (Fig. 23). Water and lipid content were negatively correlated (Fig. 24), however, the correlation was not statistically significant ($P > 0.05$). McNeil and de Itriago (1968) reported a significant negative correlation between water and lipids which they claimed enabled migratory birds to increase lipid reserves without increasing wing loading.

Lipid reserves, both subcutaneous and carcass, generally declined following arrival of mallards on the breeding grounds because of increased metabolic demands associated with cold weather, reproductive behavior (spacing and chasing) and poor feeding conditions (Zimmerman 1965, Yarbrough 1970, Ryder 1975). These reserves were minimal in breeding males at Delta. The cessation of breeding activity, coupled with warmer weather and greater food

Figure 24. Wet carcass weights and their components for moult classes of adult male mallards. Wet carcass weight (top). Lipids (second from top). Protein (second from bottom). Water (bottom).


2546173
550
500
450
400
CARCASS WT. (g)
2.0
1.5
1.0
0.5
0.0
LIPIDS AS % WET WT.
30
28
26
24
22
20
PROTEIN AS % WET WT.
75
73
71
69
67
65
WATER AS % WET WT.
0
2
6
8
MO SES

availability provided the opportunity to replenish lipid reserves. Although carcass and subcutaneous lipids declined during the moult of remiges, they were not at an annual minimum as other authors have reported for passerines (Odum and Perkinson 1951, King and Farner 1959, Helms 1968, Myrcha and Pinowski 1970). Hanson (1962) reported maximum lipid reserves in migrating Canada geese and minimum reserves during the wing moult. Owen and Krohn (1973) noted that woodcock were not able to store fat until the moult was completed.

In contrast to these results, Newton (1968), Yarbrough (1970) and Morton and Welton (1973) recorded lipid increses throughout the moult of remiges and subsequent body moult in various passerines. Based on these data, they suggested that the energy requirements of the moults were more than compensated by food consumption. The prealternate moult in mallards was apparently compatible with lipid gains in m. c. 6 and 7 (Figs. 22 and 23), at least in the year studied.

Of what adaptive significance is this dynamic process? Subcutaneous lipids provide an efficient insulative layer, a potentially valuable asset since mallards in prebasic body moult may loss heat across exposed papillae while in relatively cold water. Once flightless, mallard diets probably change radically (Perret 1962). For example, many birds in m. c. 3 were observed and collected while feeding on waste grain in stubble fields near the marsh. Access to this high energy food (Watt and Merrill 1963) was denied once birds confined themselves to the marsh. The large lipid reserves prior to the moult of the remiges were probably associated in part with hyperphagia. This could be an adaptation to provide birds with an energy reserve during the flightless period when food intake may decrease due to behavioral characteristics (secretive and inactive nature) or because of a needed period of adjustment in the morphology of the digestive tract (Fig. 21). Once flying again, lipid reserves are replenished (Figs. 22 and 23); this probably reflects premigratory fattening but once again could serve as insulation during heavy prealternate body moult.

Protein Reserve

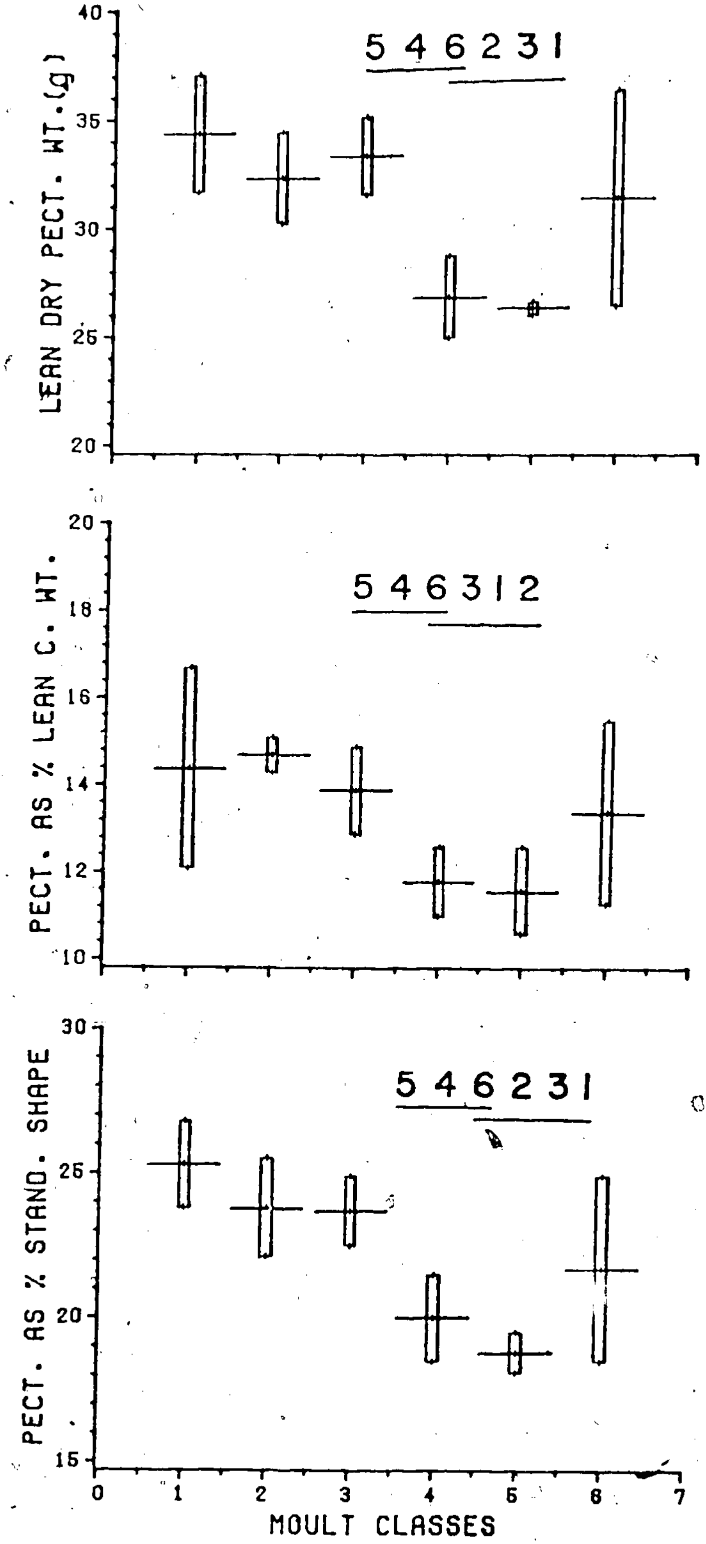
Body weight in male mallards increased an average of 150 grams during the prebasic body moult (m. c. 2 and 3, Fig. 13). This increment was attributable to increases in lipids associated with the skin as well as carcass weight increases (Figs. 13 and 23). Body weight decreased 30 grams during the flightless period. Since skin weight did not change significantly and lipids adhering to the skin decreased only 7 grams, most of the decrease in body weight was due to weight loss in some component(s) of the carcass. As Figure 13 demonstrates, there was in fact a 25 to 30 gram decrease in wet carcass weight during this period.

Water constituted the greatest percentage of carcass weight and did not change significantly ($P > 0.05$) over the moult classes (Fig. 24). Zimmerman (1965), Newton (1968) and Myrcha and Pinowski (1970) reported similar results in several passerines. Lipid content as previously mentioned, fluctuated more dramatically (Fig. 24) and accounted for most of the significant decrease in carcass weight. The balance of the carcass , primarily protein, did not change significantly ($P > 0.05$) through the moult classes although it did increase slightly, apparently at the expense of water content, in m. c. 7 (Fig. 24). This may function in the same manner as lipid storage with extra protein providing a reserve during migration when protein intake may be insufficient (Kendall <u>et</u> <u>al</u>. 1973, Evans and Smith 1975).

The pectoral musculature is the largest single carcass constituent. Pectoral muscles were heaviest in breeding birds (m. c. 1) as well as birds in heavy prebasic body moult (m. c. 3). Once the remiges were lost, the pectoral musculature decreased significantly (17%, $P < 0.01$). Both muscle indices proposed by Evans and Smith (1975) also declined significantly ($P < 0.01$) during the flightless period (Fig. 25). This weight was not regained until birds were flying again (Fig. 25). Since components of these muscles did not change significantly ($P > 0.05$) through the moult classes, weight loss was a result of a concommitant decrease in water, lipids and protein.

The fate of the lost tissue in flightless birds has been the subject of much debate. The fact that pectoral muscles are not required for strenuous activity during the flightless period could result in disuse atrophy (Hanson 1962). Hanson (1962) and Hay (1974) also speculated that this muscle mass might act as a protein reserve to supply amino acids for feather growth and leg muscle hypertrophy. Kendall _et al_. (1973) demonstrated that the sarcoplasm in the pectoral muscles could act as a protein reserve when the diet of birds lacked sulfur amino acids necessary for activities such as laying and moulting (Holman _et al_. 1945). These results lent more credibility to Hanson's (1962) hypothesis, especially in light of the drastic decrease in pectoral muscle weights (36%) in geese. Hay (1974) also observed a significant decline in these muscles but also

Figure 25. Lean dry pectoral muscle and pectoral muscle indices for six moult classes of adult male mallards. Lean dry pectoral muscle weights (top). Pectoral muscles as a percent of lean carcass weight (middle). Pectoral muscles as a percent of standard shape (bottom).


LEAN DRY PECT. WT.(g)
40
35
30
25
20
5 4 6 2 3 1
PECT. AS % LEAN C. WT.
20
18
16
14
12
10
5 4 6 3 1 2
PECT. AS % STAND. SHAPE
30
25
20
15
5 4 6 2 3 1
0
1
2
3
4
5
6
7
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prior to the flightless period, something I did not detect (Fig. 12). This weight loss may have been due to the protein demanding prebasic body moult; this assumes that the gadwall diet was protein deficient. The other alternative is disuse atrophy prior to the wing moult. While this is not likely, Hay (1974) did note that gadwall drakes spent a great deal of time loafing and preening prior to dropping their remiges.

After weighing the feathers of several mallards in complete alternate plumage, I observed that the biomass of body feathers was 2.5 times that of the remiges and rectrices. Since most body feathers are replaced in m. c. 3, 6 and 7, one would expect a higher demand for sulphur amino acids during these periods. Furthermore, if the diet lacked sufficient protein, one would also expect body protein reserves to be mobilized to meet these requirements (Kendall et al. 1973, Evans and Smith 1975). The fact that neither pectoral nor carcass proteins decreased significantly during these periods suggests that the diet provided adequate protein.

The phenomenon of pectoral muscle decline during the flightless period (m. c. 4 and 5) could therefore be due to several factors: mobilization of protein reserves to provide sulfur amino acids for feather growth (this hypothesis assumes that the diet is protein deficient); disuse atropny, and/or breakdown of pectoral muscle to provide amino acids for the concurrent leg muscle hypertrophy.

If one examines the relationship between pectoral and leg musculature more closely, the net loss of muscle tissue amounts to 20 grams (2.5%) during the flightless period. A 2.5% loss to disuse atrophy is not unreasonable over 3-4 weeks (Goldberg 1972, Secord pers. comm.) and it is therefore likely that the balance of the 17 % decrease in pectoral muscle weight was due to degradation of these muscles to provide amino acids for leg muscle growth. Based on a 28-29 % decrease in pectoral muscle weights, Hay (1974) suggested degraded muscles were probably contributing to feather and leg muscle development in gadwalls. Hay (1974) neglected to discuss the net loss of muscle which amounted to 8.8%; since most was probably related to disuse atrophy, only a small amount would remain to contribute to feather development. This once again suggests that flightless gadwalls were obtaining sufficient protein in their diet, a fact that Hay (1974) alluded to in his discussion of dietary change.

Rather than relatively small net muscle losses of 2.5 and 8.8 %, Hanson (1962) reported that these muscles in flightless geese were 17-18% lighter than muscles in migrating geese. This substantial loss suggests that the diet of these breeding geese was protein deficient and that protein from the pectoral muscles was used in feather development and/or other processes such as leg muscle hypertrophy. In arctic nesting species, this may be an evolutionary development which enables breeding geese to complete the wing moult even if adverse weather limits food availability. This argument does not appear to hold true for prairie nesting and moulting ducks since the wing moult generally coincides with the greatest abundance and diversity of food in marshes.

Breeding birds have been emphasized in this discussion of muscle weights because there is evidence to suggest that net muscle loss is not nearly as dramatic in yearling (non-breeding) geese (11%, Hanson 1962). Non-breeding birds are probably in better "condition" before and during the prebasic moult because they are free to feed without the responsibilities of territorial defense and brood rearing. This reasoning may apply to most male ducks which do not actively participate in reproduction past the laying period.

The idea that brood-protection is time consuming and therefore decreases feeding opportunities is supported by the results of Harwood (1977). Harwood reported that female snow geese (Chen caerulescens) were able to feed for 85% of daylight hours because males spent twice as much time as the females watching for potential predators. As a result, females were able to gain weight during brood rearing while males' weights remained at late spring breeding levels (Ankney 1974). Since male mallards are not involved in brood rearing, they would have adequate time to feed, possibly explaining the continual weight gain during the post-breeding period.

SUMMARY

Using external and internal plumage characteristics, it was possible to describe seven discrete moult classes and trace the sequence of feather replacement in adult male mallards. As Hochbaum (1955) observed, there was considerable variation within the population in terms of timing of the moults. This situation ensures that a segment of the population is available to breed with late nesting or renesting females. This variation may also have been selected for to minimize the impact of localized disasters, for example, botulism.

In terms of their sequence and pattern, the moults were quite consistent. The prebasic moult was initiated antero-medially in tracts 1, 2, and 5 (capital, ventral and spinal) in m. c. 2. It radiated into all tracts in m. c. 3 and terminated medially in tract 5 in m. c. 4. The prealternate moult followed the same pattern in reverse: the first alternate pennae were observed in tract 5 and considerable numbers of down papillae were found in tracts 2 and 4 of m. c. 5. Alternate pennae and down were next found in tracts 4 and 6 (ventral and posterior spinal) of m. c. 6 and the last new alternate pennae were located anteriomedially in tracts 1, 2 and 3 (capital, mid- and anterior ventral) of m.c. 7.

While the remiges were not lost in any particular sequence, their replacement followed a general pattern, with the proximal primaries reaching their definitive length before the more distal ones.

The rectrices were not lost simultaneously; birds from the prebasic moult onwards, therefore, commonly possessed rectrices of both basic and alternate plumages.

This sequence of plumage replacement ensures that most feathers are renewed during the warmest part of the year. A minimum of body feathers are replaced during the flightless period when birds could potentially lose heat across vascularized papillae and therefore increase their energetic requirements. Furthermore, most down appears to be replaced only once, during the warmest part of the season, thereby reducing thermoregulatory costs.

The weight of breeding male mallards was lightest in the spring but increased significantly in post-breeding birds undergoing the prebasic body moult. Body weights were at their maximum prior to the wing moult and contrary to what most waterfowl literature has reported , did not decline significantly during moult of the remiges. Neither carcass nor lean carcass weight changed significantly during the period birds were collected. If one uses these weight parameters as indices of "condition", then it would appear that food intake in the Delta Marsh was sufficient to meet the average energy requirements of these moulting birds.

The weights of pectoral and leg muscles displayed an inverse relationship during the flightless period, a phenomenon probably related to the transfer of amino acids from the pectoral to leg muscles. As Hanson (1962) and Hay (1974) suggested, this increased leg musculature may be a passive response to increased exercise and/or an adaptation which increases swimming efficiency and predator avoidance.

A good correlation existed between testis regression and onset of the prebasic moult, suggesting that the cessation of breeding activity was at least indirectly linked to initiation of the prebasic moult. Examination of testis size also revealed that the breeding season spanned a period from early April to late June.

Heart weight declined significantly in flightless birds, probably because of decreased exercise associated with their inactive, secretive behaviour.

Liver weights increased in post breeding mallards, presumably associated with lipogenesis and lipolysis.

Components of the gastro-intestinal tract increased in weight-length characteristics during the moults. This probably reflected changes in quantity and/or quality of the diet to one containing a greater proportion of high fiber foods. The changes in the morphology of the gut were probably adaptations to insure efficient use of food items.

Lipids adhering to the skin decreased significantly in flightless birds but were not minimal when compared to breeding birds. On the other hand, carcass lipids did not decrease significantly in flightless birds which suggests that subcutaneous lipids are metabolized before carcass reserves. Pectoral muscle lipids were not depleted at all, probably because intramuscular lipid reserves are the last to be mobilized and were not required, at least in the birds I collected.

Total carcass proteins did not change significantly through the study. Although pectoral muscles, the largest single protein mass , declined significantly in flightless birds, leg muscles increased, resulting in a net tissue loss of only 2.5%. This loss was probably related to disuse atrophy and not a protein transfer for keratin synthesis. It therefore appeared that the protein demands during the moults were adequately met by the diet.

Some of my results differed from Hanson's (1962) work with Canada geese but because of differences in pair bond maintenance between geese and most ducks, it may not be accurate to draw comparisons between the physical condition of moulting males. Male geese which actively participate with all stages of reproduction are not able to accumulate lipid and protein reserves prior to the wing moult (Ankney 1974) and thus their body reserves are minimal during the moult of the remiges.

More energy is required to produce the greater biomass of body feathers than is required for the remiges, yet lipid build-up is compatible with the body moults. It therefore appears that the decline in lipid reserves during the flightless period was probably not due to greater energy requirements. The morphology of the gut suggests that the diet of flightless mallards contained a greater proportion of high fiber foods. This diet appeared to satisfy the protein requirements of the birds but total energy intake was insufficient resulting in depletion of lipid stores. This inadequate energy intake may be due to several factors. Since flightless mallards are relatively vulnerable during the flightless period, they are very secretive and seldom venture into open water. This behaviour may decrease feeding opportunities and perhaps result in insufficient energy intake. Secondly, the digestive tract may require some period of adjustment once the birds are flightless and presumably on a different diet. During this period of adjustment, the birds may not be efficiently using food items. The most likely possibility is that the birds are simply not ingesting sufficient amounts of food either because of a lack of appetite or because it is energetically more efficient to remain relatively inactive than constantly foraging for food. The build up of lipid reserves prior to the moult of the remiges probably has been selected for as an adaptation to provide flightless mallards with an energy reserve to supplement food intake.

MANAGEMENT IMPLICATIONS

The results of this study indicate the importance of marshes in providing good habitat for post-breeding ducks. Efforts to preserve waterfowl habitat have dealt almost entirely with breeding habitat. While the importance of this work cannot be overstated, the protection of moulting marshes has scarcely been considered. Furthermore, many drainage programs are directed towards large, potentially valuable moulting marshes. It is therefore apparent that studies quantifying post-breeding habitat are essential well organized program of waterfowl management. The stud of post-breeding waterfowl and their habitat has received little attention and many questions in this field of waterfowl biology remain unanswered.

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