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ASPECTS OF MALLARD NUTRITION DURING MOULT

BY

DAVID JOHN WIELICKI

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ABSTRACT

This study focused on the nutrient requirements for feather synthesis of adult and juvenile male mallards during different moulting periods. The adaptive significance of protein reserve fluctuations during the flightless period of adult males was also studied. The study was conducted at the Delta Waterfowl and Wetlands Research Station, Delta, Manitoba and the University of Manitoba, Winnipeg, Manitoba from 1984 through 1985.

Data on the nutrient composition of various plumages and feather types was combined with data on plumage weight and the lenght of moult to determine the total and average daily nutrient requirements for feather synthesis. Total and average daily requirements, for adults, increases from the prebasic to the prealternate moult. In contrast, juveniles have their highest requirements for feather synthesis during the prejuvenal moult.

Juveniles had significantly lighter alternate plumage weights and body protein levels after completing the prealternate moult. They expend a minimum of 5,004.9 Kj less than adults for the synthesis of feathers and protein during the prealternate moult.

Lighter alternate plumages may increase costs for thermoregulation in juveniles during the Fall, Winter, and Spring. This could decrease the amount of energy available for other maintenance and productive processes thus lowering the fitness of juvenile birds.

The study examined the use-disuse hypothesis of breast muscle

dynamics (i.e. breast muscles hypertrophy when heavily used and atrophy when little used) proposed to explain the breast muscle changes of flightless male mallards. The hypothesis was tested by examining breast muscle dynamics of 4 experimental groups of birds from October 2 to November 9, 1984. The groups consisted of wild and control birds which could fly, birds with their remiges clipped, and birds with their remiges pulled. These last two groups were incapable of flight. Breast muscle weights did not decline or increase in response to disuse or use, respectively.

It appears that changes in male mallard breast muscle dynamics during the annual cycle are ultimately, not proximately, related to use and disuse.

Data on the amino acid composition of breast and wing feather proteins was combined with information on the net loss of breast muscle protein during the flightless period to determine the biological value of breast muscle protein for producing wing feathers. The net loss of amino acids from the breast muscle could account for 20% of the amino acid requirements for feather synthesis during this period.

The ability to utilize endogenous protein during the flightless period ensures a steady supply of amino acids, for maximum rates of feather synthesis, even in the face of reduced food availability. This is probably an ultimate factor which has enabled waterfowl to undergo a synchronous wing moult.

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GENERAL INTRODUCTION

Obtaining information on the nutritional requirements of an individual species, throughout its annual cycle, should be a major priority in the development of population and habitat management plans. For the mallard (Anas platyrhynchos), nutritional requirements of breeding birds (Holm and Scott 1954, Foster 1976, Krapu 1979, 1981) have been examined fairly intensively while requirements of growing (Holm and Scott 1954, Sugden et al. 1981) and moulting birds (Foster 1976) have received less attention.

This study examined aspects of the nutrition of moulting male mallards. To understand nutritional requirements it is necessary to quantify the variables of this equation: $EC = [B + T + A \pm SDA] + [EF \pm BL \pm BP]$ where EC = the total daily energy costs; B = the energy cost of basal metabolism; T = the energy cost of thermoregulation; A = the energy cost of somatomotor and autonomic activity above the resting level; SDA = the specific dynamic action or the calorigenic effect of food; EF = the energy cost of feather replacement; BL = the energy increment or detriment due to body lipid catabolism or accretion, respectively, and; BP = the energy increment of detriment due to body protein catabolism or accretion, respectively. The variables of the equation are represented in terms of Kj which depict the energetic value of the various proteins, lipids, and carbohydrates required by moulting birds. This study has been divided into 3 chapters. Chapter I focuses on variable EF of the equation by quantifying the protein, amino acid,

ash, nitrogen, and sulphur content of various feather types and plumages of male mallards. Chapter II also focuses on variable EF by quantifying the total and average daily nutrient requirements, for feather synthesis, during different moults of adult and juvenile male mallards. Finally, Chapter III focuses on variable BP of the equation by examining the adaptive significance of protein reserve fluctuations during the flightless period and the biological value of breast muscle tissue for producing wing feathers.

To understand the information in these three chapters it is necessary to have a knowledge of the sequence of moults and plumages in male mallards. When a mallard hatches it is completely covered with downy feathers. This covering of feathers is known as the natal plumage. This plumage is replaced over the next 8 weeks during the prejuvenal moult (Rhymer 1982). During this moult, all of the body and wing feathers are replaced. The resulting plumage is called the juvenal plumage. Following the prejuvenal moult, the prebasic I moult begins. This is a partial moult in which only the head and neck feathers are replaced (Oring 1968). Following the prebasic I moult, the prealternate I moult begins. All of the body feathers are replaced during this moult which ends in October or November. This plumage is called the alternate plumage. Together the prebasic I and the prealternate I moults last approximately 12 weeks (Oring 1968, Rhymer 1982). In June or July of the next year, birds begin the prebasic II moult in which all of the body feathers (excluding down feathers) and the wing feathers are replaced (Young and Boag 1981). The resulting plumage is called the

basic plumage. In August or September, birds begin the prealternate II moult in which all of the body feathers are replaced. This moult results in the formation of the alternate plumage. This two moult cycle is repeated in subsequent years.

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CHAPTER I

NUTRIENT COMPOSITION OF THE PLUMAGES OF MALE MALLARDS

INTRODUCTION

The amounts of individual nutrients required for tissue synthesis is a function of the growth rate and composition of tissues. For the plumages of adult and juvenile male mallards (Anas platyrhynchos), data are available to calculate average daily feather growth rates during different moulting periods (Oring 1968, Rhymer 1982, Young and Boag 1981, chapter 2). Insufficient information is available concerning the nutrients composition of mallard plumages, feathers, or feather parts. These data are needed to estimate average daily nutrient requirements for feather synthesis throughout different moults.

In future studies, comparisons of nutrient requirements with the availability of endogenous and exogenous nutrients will provide a better understanding of the importance of these nutrient sources to birds during their annual cycle. These comparisons will also allow researchers to assess the quality of habitats in providing nutrients for maintenance and productive processes.

Components of nutrient composition of whole plumages, single feathers, feather parts, and purified keratins have been examined for a variety of species (Block 1939, Ward and Lundgren 1954, Schroeder and Kay 1955, Harrap and Woods 1964, 1967, Kelsall and Calaprice 1972, O Donnell and Inglis 1974, Busch and Brush 1979, Nitsan et al. 1981, Murphy and King 1982). Differences occur in the nutrient composition of feathers from each species as well as between feather parts within a single species (Schroeder and Kay 1955, Harrap and Woods 1964,1967, Myrcha and Pinowski

1970). As a result, the use of feather composition data from other species to estimate the nutrient requirements of feather synthesis for mallards would be unsubstantiated. In addition, the type and amount of feathers replaced by mallards can differ according to the particular moult in progress (see Palmer 1976, Weller 1980, chapter 2). In consideration of these factors, the amino acid, nitrogen, ash, and caloric density of several feather groups from plumages of adult and juvenile male mallards were measured in this study.

MATERIALS AND METHODS

Male mallards were collected from the wild in all plumage classes with the exception of the natal and basic 1 plumage of Humphrey and Parkes (1959) classification system. All birds were either shot with a shotgun or captured in a bait trap. The feathers of each bird were subsequently plucked and separated into three groups; the remiges, remaining feathers of the alar tract (hereafter refered to as 'alar'), and the body feathers. Feather groups were placed in cheesecloth, cleaned according to the methods of Harrap and Woods (1964), and dried at 90° C to a constant weight. After drying, feather groups were homogenized by grinding them in a Wiley mill with 1 mm mesh screen. This method provided homogeneous samples for further analysis.

Samples from homogenized feather groups were analyzed for % nitrogen (micro Kjeldahl technique according to Horwitz 1980), % ash (combustion of samples in a muffle furnace at 600 degrees celsius for 4 hours), amino acid content (Technicon AA Analyzer), and caloric density (oxygen bomb calorimetry). Percent sulfur content was estimated from the concentration of cystine/2 and methionine in the plumage according to equation 1;

$$\text{Eq. 1.} \quad PS = [GC(MSC/MC) + GM(MSM/MM)] \times 100$$

where PS = the percent sulfur in the sample, GC = the grams of cystine/2 per 100 grams of feathers, MSC = the molecular weight of sulfur in cystine/2, MC = the anhydrous molecular weight of cystine/2, GM = the grams of methionine per 100 grams of feathers, MSM = the molecular weight

of sulfur in methionine, and MM = the anhydrous molecular weight of methionine. Nitrogen and ash concentrations were analyzed by the feed analysis section of the Manitoba Department of Agriculture. Caloric densities were analyzed by the Animal Sciences laboratory, University of Manitoba. Amino acid concentrations were determined by hydrolysing 20-mg samples of homogenized feather groups in 2ml of 6N HCl for 24 hours (Murphy and King 1982), drying the hydrolysate, redissolving in distilled water, and analyzing the solutions on an NC-2P Technicon Amino Acid Analyzer System. Cystine was measured on duplicate samples as cystetic acid, after 24 hours of performic acid oxidation (Schram et al. 1954), and is reported as cystine/2.

In each different analysis, at least 10 samples were designated as duplicates. A paired t-test was employed to test for differences between duplicate and regular samples in each analysis (Steel and Torrie 1980). Procedures presented by Steel and Torrie (1980) were used in the analysis of regular sample data. A two-way ANOVA, according to feather group and plumage class, was conducted on all variables of nutrient composition. Data were also grouped according to feather type and analyzed with a one-way ANOVA. Fisher's protected lsd multiple paired comparison test was used to detect significant differences between means at the 95% confidence level.

RESULTS AND DISCUSSION

There were no significant differences between duplicate and regular samples for any of the analyses. Therefore, the analytical techniques were assumed to be accurate.

There were no significant interactions between plumage class and feather type for any of the feather nutrient parameters. As a result, factor effects are described separately.

For all feather nutrient parameters, there were no differences which could be attributed to plumage class. Thus, all data were grouped according to feather type.

The nitrogen content of the various feather groups did not differ significantly (Table 1). The overall mean value of 15.23 ± 0.27% is comparable to the 15.22 ± 0.07% nitrogen content reported for the total plumage of the white-crowned sparrow (Zonotrichia leucophrys gambelii) by Murphy and King (1982). The amino acid analysis of each feather group accounts for approximately 94-95% of its nitrogen content (Table 2). This is similar to a range of 90-101% reported for the plumages and feather parts of several other species by Harrap and Woods (1967) and Murphy and King (1982).

The ash content of the three feather groups did not differ significantly from each other and ranged between 0.86% ± 0.29% and 1.84 ± 0.48% (Table 1). These values are comparable to the 0.86 ± 0.08% ash content reported for white-crowned sparrow plumage (Murphy and King 1982).

Table 1. Some parameters of nutrient composition for feather groups of male mallards.

P[1]	Feather groups: Body	Remiges	'Alar'
C	22.53 ± 0.07a (14)[2]	22.89 ± 0.06b (9)	22.54 ± 0.14a (06)
N	15.26 ± 0.09a (14)	15.40 ± 0.06a (9)	15.06 ± 0.10a (11)
A	1.13 ± 0.37a (14)	0.86 ± 0.29a (9)	1.84 ± 0.48a (11)
S[3]	2.32	2.09	2.36

1. P. = parameter C = caloric density (kJ/g), N = percent nitrogen, A = percent ash, and S = percent sulfur.
2. Mean + SE (N). In rows, means not followed by the same letter are different ($P < 0.05$).
3. Estimated from the sulphur inherent in the sulphur amino acids.

Table 2. Amino acid composition of feather groups from male mallards

	FEATHER GROUPS											
	BODY				REMIGES				'ALAR'			
	umoles/g dry weight			mg/g dry weight	umoles/g dry weight			mg/g dry weight	umoles/g dry weight			mg/g dry weight
AMINO ACID	Mean	SE	(N)		Mean	SE	(N)		Mean	SE	(N)	
cystine/2	681	18a	(14)	82	616	8b	(9)	74	696	16a	(11)	83.6
aspartic acid	470	7a	(14)	54	481	14a	(9)	55	475	11a	(11)	54.7
threonine	401	5a	(14)	41	347	10b	(9)	35	395	6a	(11)	39.9
serine	914	12a	(14)	80	892	21a	(9)	78	904	19a	(11)	78.7
glutamic acid	572	12a	(14)	74	541	17a	(9)	70	560	14a	(11)	72.3
proline	958	14a	(14)	93	904	20a	(9)	88	897	21a	(11)	87.2
glycine	1001	15a	(14)	57	1200	16b	(9)	69	1007	15a	(11)	57.5
alanine	509	23a	(14)	36	639	15b	(9)	45	541	21a	(11)	38.4
valine	616	8a	(14)	61	617	16a	(9)	61	606	12a	(11)	60.1
methionine	43	6a	(14)	6	37	10a	(9)	5	40	5a	(10)	5.3
isoleucine	372	11a	(14)	42	338	11b	(9)	38	345	6ba	(10)	39.0
leucine	629	9a	(14)	71	714	14b	(9)	81	609	12a	(10)	68.9
tyrosine	267	5a	(14)	44	260	12a	(9)	43	245	5a	(11)	40.0
phenylalanine	256	5a	(14)	38	302	13b	(9)	45	251	6a	(11)	36.9
histidine	35	3a	(14)	5	40	9a	(9)	5	27	3a	(10)	3.7
lysine	86	7a	(03)	11	74	3a	(3)	10	106	4b	(04)	13.6
arginine	344	27a	(14)	54	355	9a	(9)	55	355	8a	(11)	55.4
NH3 released	895	19a	(03)	15	840	19a	(3)	14	830	14a	(04)	14.1
% nitrogen accounted for	= 94.0				95.1				94.7			
% dry weight accounted for	= 86.2				87.4				84.9			

1. In rows, means not followed by the same letter are different ($P < .05$)

Sulphur inherent in the sulphur amino acids accounted for 2.09% to 2.36% of the feather group weight (Table 1). The calculated sulfur content of the remiges was the lowest of all three feather groups. This value (2.09%) was higher than the 1.5% sulfur content of mallard primary feathers reported by Kelsall and Calaprice (1972). In comparison, the values for mallard feather groups in this study fall in the range of those reported for plumages, feathers, and feather parts of other species which range from 1.7% to 3.3% (Block and Bolling 1945, Harrap and Woods 1967, Murphy and King 1982).

The amino acids measured, for the three feather groups, accounted for 84.9% to 87.9% of the dry weight of different groups (Table 2). These values were higher than the 82% dry weight accounted for by the amino acids in the feathers of the white-crowned sparrow (Murphy and King 1982). The fraction of plumage weight not accounted for by constituent amino acids has been attributed to several components which are reviewed by Murphy and King (1982).

The remiges have significantly more umoles of the amino acids glycine, alanine, leucine, and phenylalanine than the body and 'alar' group feathers (Table 2). One the other hand, they have significantly fewer umoles of cystine/2 and threonine (Table 2). In comparison to the body feathers, there are significantly fewer umoles of isoleucine in the remiges. 'Alar' group feathers have significantly higher amounts of lysine in comparison to both the body and remigial feathers.

The nonessential amino acids (cys, asp, ser, glu, pro, gly, ala,

and tyr) account for 65.9, 66.2, and 66.1 molar percent (mol%) of the total amino acids in the body, remiges, and 'alar' group feathers, respectively. These values are similar to the 68 mol% accounted for by the nonessential amino acids of the white-crowned sparrow plumage (Murphy and King 1982). Glycine, proline, and serine were the most abundant amino acids in all feather groups (Table 2). Together, they accounted for approximately 35 mol% of all amino acids. In contrast to the white-crowned sparrow, glycine replaced serine as the most abundant amino acid in mallard plumages (Table 2) (Murphy and King 1982). The essential amino acids, lysine, methionine, and histidine account for approximately 2 mol% of the different feather groups. This is similar to the 3.4 mol% of these amino acids reported for the plumage of the white-crowned sparrow (Murphy and King 1982).

The caloric density of the remiges was significantly higher than that of the body and 'alar' group feathers (Table 1). The same relationship exists between the flight and body feathers of the European tree sparrow (Passer montanus) (Myrcha and Pinowski 1970). The mean heat of combustion value of 22.64 ± 0.25 KJ/g for mallard feather groups is comparable to the estimate of 22 KJ/g which Murphy and King (1982) suggested as a representative value for the average caloric density of bird feathers.

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CHAPTER II

ASPECTS OF FEATHER REPLACEMENT IN ADULT AND JUVENILE MALE MALLARDS

INTRODUCTION

Effective waterfowl management requires a knowledge of the relationships of individuals to their food supply during all periods of the annual cycle. For the mallard (Anas platyrhynchos), this data base is lacking in many areas. The nutrient requirements of breeding mallards (Holm and Scott 1954, Foster 1976, Krapu 1979, 1981) have been studied fairly intensively while requirements for growth (Holm and Scott 1954, Sugden et al. 1981), and moult (Foster 1976 have received less attention.

Exogenous energy in the form of lipids, protein, and carbohydrates required per unit time during moult and growth is regulated according to an organism's combined needs for basal methabolism, thermoregulation, locomotor activity, the synthesis of products such as feathers, lipid and protein reserves, and the availability of endogenous nutrient reserves. By modifying King's (1981) equation of moult energetics, these elements of energy flow and their interrelationships, for mallards, can be represented:

$$\text{EQ. 1} \quad EC = [B + T + A \pm SDA] + [EF \pm BL \pm BP]$$

where: EC = the total daily energy costs; B = the energy cost of basal metabolism; T = the energy cost of thermoregulation; A = the energy cost of somatomotor and automomic activity above the resting level; SDA = the specific dynamic action or the calorigenic effect of food; EF = the energy of feather replacement; BL = the energy

increment or detriment due to body lipid catabolism or accretion, respectively, and; BP = the energy increment or detriment due to body protein catabolism or accretion, respectively. A review of the data and methods needed to calculate the variables of this equation is provided by Ricklefs (1974), King (1981), and Robbins (1983). These authors also discuss relationships between SDA, T, and A. The terms in the first pair of brackets of the equation represent maintenance energy requirements while those in the second pair of brackets depict productive energy requirements.

Values for many of the variables of equation 1 have been determined by other researchers. Young and Boag (1981, 1982) described the sequence of moult and the dynamics of lipid and protein reserves during the prebasic and prealternate moult of adult male mallards. Prince (1979) reviewed aspects of the bioenergetics of postbreeding dabbling ducks and Wielicki (chapter 3) examined the importance of endogenous protein availability during the wing moult of adult male mallards. Sugden et al. (1981) studied the total energy requirement for growing mallards from hatch to 8 weeks of age. Rhymer (1982) and Oring (1968) provided information on aspects of the moult in juvenile mallards. Despite these studies, insufficient information is available to quantify the daily, average daily, or total nutrient requirements for maintenance and productive processes incurred by growing, moulting or breeding mallards of either sex. The objectives of this study were to: (1) quantify the variable EF, of equation 1, in terms of the total and average daily costs of

feather replacement for various plumages of adult and juvenile male mallards; (2) compare several energetic aspects of the prealternate moult in adults and juveniles, and; (3) relate these results to the ecological implications of alternate plumage weights between adult and juvenile males.

MATERIALS AND METHODS

For the purposes of this study, a juvenile bird is one that is within its first year of life prior to any breeding attempts. Plumage and moult classifications of Humphrey and Parkes (1959) are used throughout.

Twenty-seven male mallards were collected from the wild in various age and plumage classes. All birds were either shot with a shotgun or captured in a bait trap and killed. Thirteen adults and 5 juveniles in the alternate plumage were taken during the last week of October. Two adults in the alternate plumage were taken during the last week of May. Three adults in the basic plumage and 4 juveniles in the juvenal plumage were taken from late July to mid-August. Also, 6 males hatched and reared in captivity from wild eggs were killed in the alternate I plumage during the last week of October. Wild birds killed in the summer and fall were sexed and aged according to Hochbacum (1942). Adult males collected in May were aged according to techniques outlined by Gatti (1983). Plumage categories were assigned according to information from Oring (1968) and Young and Boag (1981).

All birds were weighed to the nearest gram on a Mettler PC4400 electronic balance. Measurements of the bill, tarsus, and keel were recorded to the nearest mm. With the exception of the 2 wild birds collected in May, in which only the down feathers were plucked, all of the feathers on each bird were plucked and separated into three

groups: the remiges, remaining feathers of the alar tract (hereafter refered to as 'alar'), and the body feathers. Feather groups were placed in cheesecloth, washed according to the methods of Harrap and Woods (1964), and dried to a constant weight at 90 °C . No birds were collected in the basic I plumage. Only the head and neck feathers are replaced during this moult (Oring 1968). The percent dry weight of these feather areas for the definitive basic plumage of a female mallard is 13.65 (Heitmeyer 1985). This value was multiplied by the weight of the juvenal plumage to estimate the weight of the basic 1 plumage.

After defeathering, a sample of birds in 'migrational body condition' (i.e. adult and juvenile birds taken during the last week of October in full alternate plumage) were reweighed and dissected immediately. The left pectoralis, supracoracoideus, coracobrachialis (breast muscles), and all of the leg muscles (i.e. muscles with their origin or insertion on the tibiotarsus or femur), along with the heart, gizzard, and liver were removed and cleaned of any adhering fatty tissues. All organs were weighed and then dried to a constant weight at 100 °C. Large and small intestines including the attached ceca were removed from the carcass. Large and small intestine were measured together as total intestine length. Ceca length was also measured. The contents of these organs were discarded and all adhering fatty tissues were removed. These organs were then weighed and dried to a constant weight at 100°C. All dried tissues and organs were subsequently frozen. The carcass, and any fat

removed from organs and tissues was weighed and frozen for later analysis.

The frozen carcass and remaining dried tissues and organs were combined and passed three times through a Hobart meat grinder. The entire homogenate was spread out in a aluminum pan and dried to a constant weight at 90°C. A sample of each carcass was sent to the Manitoba Agriculture Feed Analysis Section for protein analysis using the micro Kjeldahl technique according to Horwitz (1980) and ash determination by combusing samples in a muffle furnace at 600°C for 4 hours.

Dried breast and leg muscles from 6 wild adult males were separately passed twice through a Wiley mill equipped with a 1 mm mesh screen. Samples of each tissue were sent to the Manitoba Agriculture Feed Analysis Section were protein and ash content was determined as described above.

Wet and Dry body weight (WBW and DBW) represent the sum of the weight of all wet and dried body parts, respectively, excluding the feathers. DBW was subtracted from WBW to yield water content. Total crude protein content was determined by multiplying the nitrogen content was determined by multiplying the nitrogen content of the carcass X 6.25 and adding this value to the combined crude protein content of the left breast and leg muscles. These last two values were calculated by multiplying the average percent crude protein content of the dry breast and leg muscles from 6 wild males times the respective dry weight of these tissues for individual birds. Total

ash was added to total crude protein content to yield Lean Dry Weight (LDW). LDW was subtracted from DBW to yield an estimate of fat content.

Parameters from table 5 were computed using equations 2 through 6. The energy content of the feathers (ECF) was computed as:

$$\text{Eq. 2 } ECF = F \times CF$$

where F = grams of feathers produced and CF = caloric density of feathers on a per gram basis (chapter 1). The energy cost of feather production (ECFP) was caluclated as:

$$\text{Eq. 3 } ECFP = ECF/0.064$$

the constant 0.064 is the net energetic efficiency of feather synthesis for White-crowned Sparrows (Zonotrichia leucophrys gambelii) (Murphy and King 1984). This constant is the only value available in the literature and is assumed to be accurate for mallards. The energy cost of feather biosynthesis (ECFB) was computed as:

$$\text{Eq. 4 } ECFB = ECFP - ECF$$

Protein energy (PE) was calculated as:

$$\text{Eq. 5 } PE = P \times 23.6$$

where P = the grams of protein synthesized and the constant 23.6 is the Joule density of protein on a per gram basis (Brody 1945). Nonprotein energy (NPE) was calculated as:

$$\text{Eq. 6 } NPE = ECFP - PE$$

Average daily requirements (ADR) for NPE, PE, total energy, and grams of feather protein during different moulting periods was calculated as:

$$\text{Eq. 7 } ADR = X/LM$$

where X = the parameter of interest and LM = the estimated length, in days, of each moult. For adult males, the average length of three different moulting periods was 55, 28, and 55 days for the prebasic body, prebasic flightless, and the prealternate moult, respectively (Young and Boag 1981). For juvenile males, hatched on June 2, the average lengths of the prejuvenal and combined prealternate I and prebasic I moults were estimated to be 56 and 84 days, respectively (Rhymer 1982, Oring 1968).

The muscle protein parameters in table 6 were computed with equations 8-10. Muscle protein energy (MPE) was computed as:

$$\text{Eq. 8} \quad MPE = P \times 23.6$$

where: P = the grams of protein synthesized; the constant 23.6 is the Joule density of protein on a per gram basis (Brody 1945). The energy cost of muscle protein synthesis (ECMPS) was calculated as:

$$\text{Eq. 9} \quad ECMPS = MPE/0.75$$

the constant 0.75 is the net energetic efficiency of protein synthesis used by Ricklefs (1974). The nonprotein energy cost of muscle synthesis (NPECMS) was computed as:

$$\text{Eq. 10} \quad NPECMS = ECMPS - MPE$$

The analysis of data followed procedures outlined by Steel and Torrie (1980). For the nitrogen and ash determinations, a paired t-test was used to test for differences between ten duplicate and regular samples. This test was conducted to examine the accuracy of experimental procedures. Feather weight data (table 1) were submitted to a one-way ANOVA. Significant differences between means

were detected by using Fisher's protected lsd multiple paired comparison test. T-tests were used to determine if 8 carcass, 6 gut, and 3 structural parameters differed between adult and juvenile males in 'migrational body condition'.

RESULTS

There were no significant differences between duplicate and regular samples for any of the nitrogen and ash analyses. Therefore, the analytical techiques were assumed to be accurate.

The results from the analyses of feather weight data are presented in table 1. Mean definitive alternate plumage weights were significantly higher than definitive basic plumage weights, alternative I plumage weights of both captive and wild birds and the weight of the juvenal plumage ($P < 0.01$). Down is moulted only during the prealternate moult in adults (Young and Boag 1981). The average down feather weight of 2 adult birds in the alternate plumage (7.1 ± 0.1) was subtracted from the definitive basic body feather weight, which included the alternate down, to yield a corrected value of 34.3 grams. This value was significantly heavier ($P < 0.01$) than the weight of the juvenal body plumage. It was significantly lower ($P < 0.01$) than the weight of the alternate I of both wild and captive birds, and the definitive alternate body plumage. The remiges of adults in alternate plumage were heavier than those of young birds in juvenal captive or wild juvenal plumages ($P < 0.01$). Adult alternate 'alar' tract feathers were significantly heavier ($P < 0.01$) than those of the wild juvenal plumage but not of the captive juvenal plumage.

The results from the analyses of carcass, gut, and structural parameters for wild adult and juvenile birds are presented in tables

Table 1. Comparison of feather group weights (grams) for male mallards of different age classes.

Plum[1]	Feather Type		
	Body	Remiges	'Alar'
DA[2]	54.7 ± 1.0a (13)[3]		
DB[2]	34.3 ± 2.1c (3)	10.95 ± 0.2a (13)	11.30 ± 0.3a (13)
AI[2]	42.3 ± 0.7b (4)		
AIC[2]	43.6 ± 1.8b (6)		
JC[2]		8.90 ± 0.3b (6)	10.33 ± 0.7ab (6)
J[2]	24.9 ± 1.3d (4)	8.90 ± 0.4b (4)	9.13 ± 0.3b (4)

1. plumage.
2. DA = definitive alternate; DB = definitive basic; AI = alternate I; AIC = alternate I captive; JC = juvenal captive; J = juvenal.
3. Mean ± SE (N). In columns, means not followed by the same letter are different (P 0.01).

2, 3, and 4, respectively. Adults have significantly higher weights ($P < 0.05$) for breast muscle, crude protein, and WBW (table 2). The significantly heavier gizzards of adults ($P < 0.05$) was the only difference in gut parameters (table 3), while there were no significant differences in structural parameters (table 4).

Total and average daily energy and protein requirements of feather synthesis, for adults, increases form the prebasic to the prealternate moult. In contrast, juveniles have their highest requirements for feather synthesis during the prejuvenal moult (table 5). Juveniles expend a mininum of 5004.9 Kj less than adults for the synthesis of feathers and protein during the prealternate moult (table 6).

Table 2. Comparison of 8 carcass parameters (grams) for adult and juvenile wild mallards in 'migrational body condition.'

Parameter	Age	
	Adult	Juvenile
breast muscle	39.1 ± 0.7a (11)[1]	35.9 ± 0.7b (5)
leg muscle	11.4 ± 0.3a (11)	10.5 ± 0.6a (5)
crude protein	234.7 ± 5.4a (11)	214.4 ± 2.7b (5)
ash	51.5 ± 2.5a (11)	52.3 ± 2.3a (5)
lipid	192.2 ± 13.0a (11)	169.4 ± 11.8a (5)
water	752.5 ± 16.6a (11)	704.3 ± 30.7a (5)
WBW	1281.4 ± 23.2a (11)	1186.9 ± 27.0b (5)
DBW	528.9 ± 18.8a (11)	482.6 ± 14.9a (5)

1. Mean ± SE (N). In rows, means not followed by the same letter are different ($P < 0.05$)
2. WBW = Wetbody Weight
3. DBW = Drybody Weight

Table 3. Comparison of 6 gut parameters for different age wild mallards in 'migrational body condition'.

	Age	
Parameter	Adult	Juvenile
Weight (g)		
heart	2.9 ± 0.1a (11)	2.6 ± 0.1a (5)
liver	13.3 ± 1.2a (11)	11.4 ± 0.6a (5)
gizzard	12.0 ± 0.4a (11)	9.9 ± 0.2b (5)
intestine	6.0 ± 0.7a (11)	6.1 ± 0.4a (5)
Length (mm)		
intestine	176.5 ± 3.4a (11)	173.2 ± 3.4a (5)
ceca	31.0 ± 1.1a (11)	31.2 ± 0.7a (5)

1. Mean ± SE (N). In rows, means not followed by the same letter are different (P 0.05).

Table 4. Comparison of 3 structural parameters for different age wild mallards in 'migrational body condition.'

Parameter[2]	Age	
	Adult	Juvenile
tarsus	46.4 ± 0.6a (10)[1]	48.8 ± 3.1a (5)
keel	108.3 ± 1.0a (12)	108.3 ± 1.0a (4)
bill	63.2 ± 0.7a (10)	62.3 ± 0.7a (5)

1. Mean ± SE (N). In rows, means not followed by the same letter are different ($P < 0.05$).

2. Measurements in mm.

Table 5. Requirements for feather synthesis during the moults of adult and juvenile male mallards.

Parameter[2]	Moult[1] DPA	PAI	PBI	DPB	AFM	PJ
ECF (Mj)	1.231[3]	0.952	0.076	0.772	0.505	0.970
ECFB (Mj)	18.008	13.925	1.119	11.290	7.385	14.185
ECFP (Mj)	19.239	14.877	1.196	12.061	7.890	15.154
PE (Mj)	1.116	0.863	0.069	0.700	0.454	0.877
NPE (Mj)	18.123	14.015	1.128	11.362	7.436	14.277
GFP	47.2	36.5	2.9	29.6	19.2	37.1
ADR		PAI + PBI				
NPE (Kj)	329.7	180.3		206.7	265.7	254.8
PE (Kj)	20.1	11.3		12.6	16.3	15.5
TE (Kj)	349.8	191.6		219.2	282.0	270.3
GFP (g)	0.86	0.47		0.54	0.69	0.66

1. DPA = definitive prealternate; PAI = prealternate I; PBI = prebasic I; DPB = definitive prebasic (excluding the flightless part of the moult); AFM = adult flightless moult; PJ = prejuvenal.
2. ECF = energy content of the feathers; ECFB = energy cost of feather biosynthesis, ECFP = energy cost of feather production; PE = protein energy; NPE = non protein energy; GFP = grams of feather protein; ADR = average daily requirements; TE = total energy.
3. All values in Mj or kj unless otherwise specified as grams.

Table 6. Lower amount, in grams of tissue, produced by juveniles in 'migrational body condition' and the resulting savings in energy and protein requirements.

	Parameter[1]			
Tissue	GT	GP	PE	NPE
muscle protein	20.3	20.3	479.9	159.8
body feathers	12.4	10.7	253.1	4112.0
total			733.0	4271.89
total energy saved			5004.9	

1. GT = grams of tissue; GP = grams of protein; PE = protein energy energy in joules; NPE = nonprotein energy in joules.

DISCUSSION

The heavier weight of the the adult alternate body plumage in comparison to the adult basic can be related to two factors. First, the average ambient temperature during the period in the life cycle when the alternate plumage is worn is lower than that of the basic. A heavier and higher density alternate plumage presumable reduces the cost of thermoregulation (Gordon 1968, Robbins 1983). Second, the alternate plumage is worn for a much longer period than the basic (Young and Boag 1981). This longer period of wear, which includes two migrations, likely increases the loss of feather mass resulting from abrasive forces. Thus, heavier alternate plumages should minimize the effect of these losses of insulation capacity. These two factors, along with the smaller structural size reported for birds in the juvenal plumage (Rhymer 1982), could explain its lower weight in comparison to the alternate I plumage. The lighter weight of the juvenal plumage in comparison the the definitive basic plumage is partially due to the smaller structural size of juvenile birds. Although sample sizes are small, the data on remigial weights of the definitive basic and juvenal plumages (table 1) may provide an easier and more accurate method, than those currently available, for aging mallards in the fall, winter, and spring (Carney and Gesis 1960, Krapu et al. 1979, Gatti 1983).

The above factors cannot adequately explain the lighter weight of the alternate I plumage in comparison to the definitive alternate plumage. The data show that the structural size of adults and

juveniles are not significatly different. In addition, both plumages are worn for similar time periods (Weller 1980). These factors suggest that the alternate plumage weights of adults and juveniles should not differ.

Importance of plumage weight:

There is evidence to support the hypothesis that juveniles would incur a selective advantage by having adult weight plumages. The age-related differences in alternate plumage weights reported in this paper for male mallards and by Heitmeyer (1985) for female mallards suggess that, in comparison to adults, juveniles have a lower insulation capacity due to a lighter and lower density plumage (Gordon 1968, Robbins 1983). This would presumable cause juveniles to have higher costs for thermoregulation at comparable temperatures below the thermoneutral zone.

Increased thermoregulatory costs could reduce the energy available for dominance behavior, obtaining a mate, and productive processes such as body tissue and egg production. Previous studies of various waterfowl species, including the mallard, have shown that adult males are more successful at obtaining mates (Lebret 1961, Spurr and Milne 1976a, 1976b, Blohn 1982, Wishart 1983). Although there are no data for male mallards, adult male lesser snow geese (Anser caerulescens caerulescens) (Ankey 1977), shellduck (Tadorna tadorna) (Patterson 1977), gadwall (Anas strepera), (Paulus 1980) and Chilean

teal (Anas flavirostris flavirostris) (Standen 1980) are dominant over juvenile birds. Juvenile female mallards have lower body weight and nutrient reserves during the spring, lay fewer eggs, and attempt fewer renests than adult females (Krapu and Doty 1979). In addition to the possible relationship of these differences to insulation capacity, other factors such as courtship experience (Korschgen and Fredrickson 1976, Afton and Sayler 1982), body size (Wishart 1983), and foraging efficiency (Krapu and Doty 1979) may offer some additional understanding of these differences.

Increased costs for thermoregulation may help explain the higher mortality rates of immature mallards reported by Hickey (1952), Brakhage (1953), Lee et al. (1964), and Caswell et al. (1985). Reduced thermoregulatory capability may predispose juveniles to wintering in warmer and sometimes more southerly climates (Sugden et al. 1974, Jorde et al. 1984) to reduce energy costs. As a result, juveniles would presumabley suffer increased mortality due to the longer distances traveled during migration. Finally, in times of severe weather and decreased food availability, the added energy costs of thermoregulation could increase the loss of juveniles to mortality factors such as hypothermia, starvation, and predation.

Selection pressures during the prealternate moult:

Since mallards cannot overwinter on most of the breeding range, there is selection pressure for birds of all ages to attain a body

condition which will allow them to migrate to warmer areas. Thus, birds must develop sufficient body lipids and protein to provide enough energy and muscular strength for locomotion. Development of a high quality insulating plumage is important for reducing the cost of thermoregulation during the fall, winter,and spring (Weller 1980). There is also selection pressure on males to complete the alternate plumage as early as possible (Wishart 1983, Rhymer 1982). Males are unlikely to pair until they have acquired this plumage (Klint 1975, Paulus 1980) and since females are a limited resource (i.e. there are more males in the population) (Bellrose 1980), birds completing the alternate plumage earlier may be more likely to attain mates.

In comparison to juvenile males, the 'migrational body condition' of adult males is characterized by greater protein reserves and heavier plumages (tables 1,2). Based on the previous discussion it is assumed that the 'migrational body condition' attained by adults is the best possible response to selection pressures. Therefore, differences of juveniles from adult condition can be considered as compromises to evolutionary forces. A lighter alternate plumage and lower amounts of body protein are the compromises made by juveniles during the prealternate molt. The data indicate that juveniles do not compromise in terms of lipid deposition and time of completion of the prealternate moult. Therefore, for the juveniles examined in this study, it appears that selection pressures concerning lipid accretion and early completion of the alternate plumage overshadow those affecting body protein and feather production.

Nutritional and physiological constraints:

Juveniles probably have lower body protein, in the fall, and lighter alternate plumages as a result of their inability to secure and / or mobilize enough nutrients to produce adult weight tissues. At least two factors are likely to combine to bring about this result: 1) The prealternate 1 moult takes place while juvenile birds are still growing and the bird has to divide its productive energy between body growth, maintenance, and feather growth and; 2) juvenile birds are completely inexperienced at locating and obtaining adequate nutrition from the environment. Even as they find food resources, these are changing with the advance of the season.

For juvenile males to have the same response to selection pressures as adults, nutrient requirements must be temporally distributed so they do not exceed the physiological capability for tissue production or the nutrient availability required to produce these tissues. If time is limiting, the costs of an adult-like response will exceed one or both of these components. As a result, exogenous nutrient requirements must be lowered to within the limitations of these factors.

Exogenous nutrient requirements can be lowered by incorporating any or all of the following adjustments to the variables of equation 1: (1) alter behavior to conserve energy (Prince 1979); (2) utilize endogenous materials (King 1981); (3) decrease the amount of tissue

synthesis over time (e.g. produce a lighter alternate plumage); (4) alter the composition of tissues synthesized (e.g. produce feathers with a lower concentration of certain constituents), or; (5) decrease the rate of synthesis (see also Murphy and King 1982). When producing fewer grams of protein and feathers coupled with a decreased rate of feather synthesis relative to adults during the prealternate moult (tables 1,2), juvenile males are incorporating adjustments number 3 and 5 to decrease their daily nutrient requirements. In comparison to adults, this results in a significant decrease in the amount of nutrients required for tissue synthesis (Table 6). In terms of other adjustments, number 4 is not utilized in relation to feather production since no differences were found in the nutrient composition of various mallard feather groups from different plumages (Chapter 1). Data are not available to determine the importance of adjustments 1 and 2. The question arises as to whether the use of adjustment 3 and 5 is caused by a limitation in food or an insufficient physiological capability for producing adult amounts of tissues, given adequate food availability.

Food limitations:

Artificially reduced levels of aquatic invertebrates can limit growth of wild black duck (Anas rubripes) and mallard ducklings (Hunter et al. 1984). For captive wood ducks (Aix sponsa), low dietary protein levels have been shown to reduce growth rates

(Johnson 1971). Also, mallards grow much faster on a diet of blow fly larvae (Calliphora vulgaris) than on a diet composed of barley meal or mixed seeds (Street 1978). These studies indicate that decreased invertebrate availability can reduce protein ingestion to levels which are below the physiological requirements for maximum growth.

It appears that reduced invertebrate availability can limit growth, however, no quantitative information is available on whether food limitations actually occur under natural conditions. One way to examine this question would be to compare the growth rates of captive birds fed high quality diets ad libitum to those of wild birds in different habitats with natural variations in food abundance. By comparing the tissue production of captive juveniles, with that of wild adults and juveniles, the question of whether or not juveniles have physiological limitations which inhibit the production of adult amounts of tissues can also be analyzed.

Temporal considerations:

The nutrient requirements for maintenance and productive processes must always be expressed in terms of nutrients required per unit time. Thus, the amount of time available for a particular process is an important factor which would cause a birds to make compromises to enviromental pressures. The juveniles examined had around 5 months to develop before migration. This development time varies in southern Manitoba where hatching dates for mallards can

range from approximately May 20 to the end of July (Hochbaum 1944, Sowls 1955). With freeze up occurring around the end of October, juvenile mallards have approximately 3 to 5½ months to ready themselves for fall migration. This development time can also vary for adults, depending on when birds begin the prebasic molt (Young and Boag 1981).

The data indicate that there is no difference between the alternate plumage weights of wild mallards hatched in June and captive raised birds hatched one month later. Since the July birds were raised in captivity under ad libitum conditions, the possibility of plumage differences for wild birds of comparable hatching dates cannot be ruled out.

In conclusion, to improve the management of mallard populations further studies are necessary to quantify the nutritional requirements of mallards hatched at different dates and adults beginning moult at different times during the Spring and Summer. This information will help managers to provide optimum habitat for growing and moulting birds which are experiencing different environmental pressures while undertaking similar maintenance and productive processes. Future studies on the timing, rate, and pattern of tissue synthesis will also provide a better understanding of the reasons underlying the different mortality rates of various segments of the mallard population.

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CHAPTER III

EXAMINATIONS OF HYPOTHESES RELATING TO THE WING MOULT OF ADULT MALE MALLARDS

INTRODUCTION

All species of waterfowl studied show an inverse relationship between the weights of breast and leg muscle during flightless period (Hanson 1962, Hay 1974, Ankney 1979, 1984, Raveling 1979, Dubowy 1980, Bailey 1981, Young and Boag 1982, Reinecke et al. 1982, Austin 1983). The exact patterns vary with the species concerned. Breast muscle weights of mallards (Anas platyrhynchos) begin to decline just prior to the flightless period. These weights stabilize during the beginning of flightlessness and subsequently increase after flight is regained (Young and Boag 1982). Inversely, leg muscle weights increase just prior to, and during, the initial part of the flightless period. These weights then decline steadily throughout the fall premigatory period (Young and Boag 1982).

Several explanations have been offered for this inverse relationship between breast and leg muscle mass. Ankney (1979) suggested this phenomenon to be the result of simple use-disuse exercise relationships for snow geese (Chen caerulescens caerulescens) (i.e. these muscles hypertrophy when heavily used and atrophy when little used). Young and Boag (1982) also suggested that disuse atrophy could explain losses in the breast muscle mass of male mallards. With respect to mallards, a decreased use of breast muscle and an increased use of leg muscle if plausible during the flightless period. However, decreases in breast muscle mass and increases in leg muscle mass just prior to the flightless period along with decreases

in leg muscle mass prior to regaining flight capability appear more related to some sort of anticipatory change. The validity of the hypothesis in relation to female lesser scaup (Aythya affinis) (Austin 1983), male redheads (Aythya americana) (Bailey 1981), brant (Branta bernicla)(Ankney 1984), and gadwall (Anas strepera) (Hay 1974) is questionable, since various changes in breast and leg muscle dynamics occur, prior to, and during the flightless period, which do not coincide with the predictions of the use/disuse hypothesis.

Muscle tissue lost during the flightless period is possibly used as a protein source for feather growth (Hanson 1962, Hay 1974, Raveling 1979, Young and Boag 1982, Austin 1983) and leg muscle hypertrophy (Hay 1974, Hanson and Jones 1976, Ankney 1979, 1984, Raveling 1979, Young and Boag 1982). In the domestic fowl, if dietary protein or amino acids are inadequate for feather synthesis, protein for feather keratinazation may be withdrawn from the muscle of other tissues (Spearman 1971). This has also been show in gadwalls which were starved for 6 days during the flightless period. Feather growth was normal even though there was a 19% loss in body weight (Hay 1974). Body protein reserves apparently can be mobilized for feather growth and there is no reason the same situation should not exist for leg muscle. However, the biological value (see Scott et al. 1982) of the reserves used for these purposes is unknown.

The objectives of this study, which focuses on adult male mallards were: 1) to experimentally test the use-disuse hypothesis of breast muscle dynamics and; 2) to quantify the biological value

of nutrients released from breast muscle catabolism during the flightless period, for providing nutrients for feather growth and leg muscle hypertrophy.

MATERIALS AND METHODS

In order to test the use-disuse hypothesis of muscle dynamics, several carcass parameters were studied of captive adult male mallards assigned to a control group and 2 different treatments of remigial modification. These parameters were also examined on wild mallards during the experiment which lasted from October 2 to November 9, 1984. The experimental treatments consisted of one group with their remiges clipped (hereafter referred to as 'clipped') and another with their remiges pulled (hereafter referred to as 'pulled'). Both of these modifications rendered birds flightless throughout the experiment. The remiges were unaltered in the control group. Seventy-four birds were obtained from the Delta Marsh during the months of June and July 1985 by using bait traps. After capture and during the experiment, all birds were maintained outdoors in a 20' X 100' X 8' flight pen at the Delta Waterfowl and Wetlands Research Station. Birds were fed a maintenance diet recommended for captive waterfowl ad libitum (Ward and Batt 1973).

On October 2, 14 captive birds were randomly selected and killed. The remaining 60 birds were assigned to groups of three, stratified according to similar body weight and moult class. The different treatments were then randomly assigned to one member of each group. Differently colored nasal markers (Sugden and Poston 1968), one for each treatment, were attached to individual birds. All groups of three were paired according to similar body weight and moult class.

Each group of a pair was then randomly assigned to be killed on either October 21 or November 9. During October 2-9, 9 wild adult males were shot with a shotgun over decoys or captured in a bait trap. Also, from October 21 to October 27, eleven wild adult males were captured in a bait trap.

Captive birds were time-budgeted throughout the experiment using the scan sampling technique (Altmann 1974). Time-budget data were divided into two 19-day periods. Period 1 spanned from October 2-21, while period 2 lasted from October 22 through November 9. All of the birds from each treatment were scanned from an observation tower located directly adjacent to the flight pen. Scans were conducted once every 10 minutes during diurnal observation periods which lasted from 1 to 3 hours. The birds were time-budgeted for approximately 42 hours during each sampling period. Behaviours were broken down into 4 categories: locomotion (i.e. swimming or walking), flying, resting, and 'other' behaviors were grouped into one category. The locomotion, flying, and resting categories were analyzed using a chi-square test of homogeneity (Daniel 1978).

After being killed, all birds were weighed to the nearest gram on a Mettle PC 4400 balance, and frozen for later analysis. Upon thawing, the feathers were removed from the carcass. For the wild birds collected during the latter part of October, this was accomplished by plucking. Removal of feathers from remaining birds were accomplished by shearing the feathers of the alar tract, the gray belly feathers of the ventral tract, and the head and neck

feathers anterior to the ring of white feathers on the neck. The remaining feathers of each bird were plucked. Birds were dissected immediately after feather removal. The left breast muscles (pectoralis, supracoracoideus, coracobrachialis) and leg muscles (i.e. muscles with their origin or insertion on the tibiotarsus or femur) were removed and cleaned of any adhering fatty tissue. These muscles were dried to a constant weight at 100°C.

The remaining carcass was then passed three times through a Hobart meat ginder. The entire homogenate was placed in an aluminum pan and dried to a constant weight at 90° C. A sample of this tissue from each carcass was sent to the Manitoba Agriculture Feed Analysis Section for the determination of ash (combustion of samples on a muffle furnace at 600° C for 4 hours) and nitrogen (micro Kjeldahl technique according to Horwitz 1980) content. In each different analysis, ten duplicate samples were run to examine the accuracy of the analysis. A paired t-test was employed to test for differences between duplicate and regular samples in each analysis (Steel and Torrie 1980).

Dried leg and breast muscles from 6 wild birds collected during the latter part of October were separately passed twice through a Wiley mill with a 1 mm mesh screen. Samples of each tissue were analyzed by the Manitoba Agriculture Feed Analysis Section for nitrogen and ash as described above. Samples (20 mg) of homogenized lean dry breast and leg muscle tissue were also analyzed for amino acid content. The techniques used were identical to those outlined

in chapter 1 for the amino acid analyses of homogenized feather groups.

Total crude protein content of the body was determined by multiplying the nitrogen content of the carcass X 6.25 and adding this value to the combined crude protein content of the breast and leg muscles. These last two values were calculated by multiplying the average percent crude protein of the dry breast and leg muscles, determined for the wild males, times the respective dry weight of these tissues for individual birds. Carcass parameters were analyzed by using a two-way ANOVA according to treatment and date (Neter and Wasserman 1974). Fisher's protected lsd multiple paired comparison test was used to detect significant differences between means (Steel and Torrie 1980). Behavior data was analyzed using a chi-square test of homogeneity (Steel and Torrie 1980).

RESULTS

There were no significant differences beween duplicate and regular samples for any of the nitrogen and ash analyses. Therefore, the analytical techniques were assumed to be accurate.

No significant interactions between treatment and date, for any of the carcass parameters, were detected. As a result, the main factor effects are presented separately.

Breast muscle:

The type of treatment had no significant effect on breast muscle weight. Mean breast muscle weights of all captive birds were significantly higher at the end of the experiment than at the beginning ($P < 0.05$) (table 1). Wild birds did not differ from captive birds during the initial and middle parts of the experiment (table 1). Data were not collected for the November 9th sampling period.

Leg muscle:

Leg muscle dynamics for 'clipped' and 'pulled' birds did not differ throughout the experiment (table 1). In these groups, leg muscle weights increased significantly throughout period 1 ($P < 0.01$) and significantly decreased ($P < 0.01$), to levels similar to initial

Table 1. Mean dry weights (grams) of carcass parameters for the the various treatments.

Tr.[1]	October 2	October 21	November 9
		Breast Muscle	
1	37.8 ± 1.39a (14)[2]	40.6 ± 1.27ab (10)	43.9 ± 1.65b (10)
2	37.8 ± 1.39a (14)	38.6 ± 1.47ab (10)	43.0 ± 1.45b (10)
3	37.8 ± 1.39a (14)	37.6 ± 1.35a (10)	40.5 ± 1.13b (10)
W	36.5 ± 1.25a (9)	39.1 ± 0.72a (11)	----------
		Leg Muscle	
1	11.6 ± 0.30a (14)	11.9 ± 0.48a (10)	11.5 ± 0.17a (10)
2	11.6 ± 0.30a (14)	13.4 ± 0.51b (10)	11.8 ± 0.21a (10)
3	11.6 ± 0.30a (14)	13.6 ± 0.46b (10)	11.8 ± 0.31a (10)
W	10.9 ± 0.53a (9)	11.4 ± 0.25a (11)	----------
		Crude Protein	
1	223.0 ± 6.3a (13)	241.8 ± 7.5a (7)	221.7 ± 10.5a (9)
2	223.0 ± 6.3a (13)	228.0 ± 7.6a (8)	220.3 ± 5.3a (7)
3	223.0 ± 6.3a (13)	240.9 ± 11.7a (10)	221.5 ± 4.1a (8)
W	225.0 ± 8.7a (8)	234.7 ± 5.4a (11)	----------
		Ash	
1	45.2 ± 1.71a (13)	49.9 ± 2.57a (7)	46.1 ± 2.81a (9)
2	45.2 ± 1.71a (13)	49.5 ± 2.48a (8)	47.3 ± 1.45a (7)
3	45.2 ± 1.71a (13)	51.9 ± 2.62a (10)	45.1 ± 1.58a (8)
W	51.7 ± 1.80a (8)	51.5 ± 2.54a (11)	----------

1. Tr. = treatment, 1 = control, 2 = 'clipped', 3 = 'pulled', and W = wild.

2. Mean ± SE(N). In rows, means not followed by the same letter are different ($P < 0.05$).

weights, by the end of period 2. The control birds exhibited stable leg muscle weights throughout the experiment (table 1). Wild birds were similar to control birds (table 1), however, no data were collected for the November 9 sampling period. Within dates, treatments differed only for the October 21 sampling period. Here, leg muscle weights of 'clipped' and 'pulled' birds were significantly heavier than those of control and wild birds.

Ash and crude protein:

There were no significant differences in the ash and crude protein content of individual carcasses throughout the experiment (Table 1).

Amino acids:

The mol% (moles of individual amino acid/sum of moles of all amino acids analyzed) of amino acids in wing feathers (calculated from chapter 1) and breast and leg muscle are presented in table 2. In terms of utilizing breast muscle protein to produce leg muscle protein, arginine was the most limiting essential amino acid. There are no data available for lysine and tryptophan, however, based on the similar ratios of the breast and leg muscle amino acids analyzed, it is assumed they are equal. Assuming a 100% conversion efficiency of the amino acids in breast muscle protein

Table 2. The mol% of amino acids in leg and breast muscle protein and wing feather protein.

	Protein				
	Leg		Breast		Feather
Amino acid	Mean	SE	Mean	SE	Mean
cystine/2	1.1	0.07	1.2	0.10	8.1
aspartic acid	9.1	0.08	9.1	0.07	5.9
threonine	5.4	0.08	5.6	0.04	4.6
serine	4.5	0.12	4.5	0.12	11.1
glutamic acid	13.5	0.15	13.4	0.13	6.8
proline	5.8	0.08	5.1	0.09	11.1
glycine	9.8	0.07	9.0	0.11	13.6
alanine	9.8	0.12	10.2	0.09	7.3
valine	7.2	0.11	7.4	0.11	7.5
methionine	2.5	0.24	2.9	0.35	0.5
isoleucine	6.3	0.26	6.4	0.28	4.2
leucine	9.8	0.33	10.1	0.21	8.1
tyrosine	2.6	0.33	3.0	0.06	3.1
phenylalanine	4.0	0.02	4.0	0.07	3.3
histidine	2.7	0.04	2.6	0.07	0.4
arginine	5.8	0.09	5.5	0.07	4.4

to the amino acids in leg muscle protein, one gram of breast protein could provide enough essential amino acids to produce 0.95 grams of leg muscle protein. This value was calculated by dividing the arginine concentration in the breast muscle by the concentration of this amino acid in the leg muscle.

In terms of utilizing breast muscle protein to produce feathers, cystine/2 is the most limiting amino acid. There are no data available for the concentration of lysine and tryptophan in the breast muscle and tryptophan in the feathers. Scott et al. (1982) reported an average 9.3 and 0.9% concentration of lysine and tryptophan, respectively, in the carcass proteins of 6 different species of birds and mammals. Since there is little variation between the amino acid ratio of carcass proteins for these different species, these values are assumed to represent the breast muscle proteins of mallards. The percent lysine concentration of feather proteins is much lower than these values (chapter 1), thus, lysine is not a limiting amino acid in this case. Tryptophan concentrations in the feather rachis proteins of the domestic duck are ca. 0.19% (Harrap and Woods 1967), which is lower than the 0.90% concentrations estimated for breast muscle protein. Thus, tryptophan is not a limiting amino acid in this case. Assuming the same conversion efficiency as above, one gram of breast muscle protein could provide enough essential amino acids to produce 0.44 grams of feather protein. This value was calculated with the following equation:

$$\text{Eq 1.} \qquad FP = CB + (MB - MF) \times CF$$

FP = grams of feather protein produced; CB = cystine/2 concentration in the breast muscle; MB = methionine concentration of the breast muscle; MF = methionine concentration of the feathers; CF = cystine/2 concentration in the feathers.

Behaviour:

Overall, the percentage of time spent for locomotion differed between periods (X^2 = 198.6, $P < 0.001$) (table 3). 'Clipped' (X^2 = 87.6, $P < 0.001$), 'pulled' (X^2 = 58.3, $P < 0.001$), and control (X^2 = 54.2, $P < 0.001$) birds spent significantly less time for locomotion in period 2. Within period 1, the amount of time spent for locomotion differed between treatments (X^2 = 14.32, $P < 0.001$). The 'pulled' and 'clipped' treatments were not different. However, 'pulled' (X^2 = 4.3, $P < 0.05$) and 'clipped' (X^2 =14.3, $P < 0.001$) birds spent significantly more time for locomotion than control birds. Within period 2 the amount of time spent for locomotion did not differ between treatments.

Resting time differed significantly between periods (X^2 = 28.1, $P < 0.001$) (table 6). 'Clipped' (X^2 = 10.3, $P < 0.005$), 'pulled' (X^2 = 9.07, $P < 0.005$), and control (X^2 = 8.7, $P < 0.005$) birds rested significantly more in period 2 (Table 3). The amount of time spent resting did not differ significantly between treatments within period 1 or 2.

The control birds spent 0.18% and 0.31% of their time flying in periods 1 and 2, respectively. These values were not significantly different ($P < 0.05$). The percent of time spent for 'other' behaviours is listed in table 3.

Table 3. Percentage of time spent in various behaviours by captive birds.

	Period[1]	
Treatment	1 (October 2 -21)	2 (October 22 - November 9)
	Locomotion	
control	10.5a	3.2c
'clipped'	14.2b	3.7c
'pulled'	12.5b	4.1c
	Resting	
control	74.5a	85.0b
'clipped'	75.1a	86.5b
'pulled'	75.3a	86.1b
	Other[2]	
control	14.8	11.5
'clipped'	10.7	9.8
'pulled'	12.2	9.8

1. Within rows and columns, percentages not followed by the same letter are different ($P < 0.05$).
2. The 'Other' category was not of statistical interest to the study. Therefore, no statistical analysis was conducted.

DISCUSSION

The use-disuse hypothesis predicts that use and disuse are proximate factors controlling breast and leg muscle dynamics. To support this hypothesis, during the second and third sampling periods of the experiment the flightless 'clipped' and 'pulled' birds should have exhibited lower breast muscle weights, in comparison to mallards retaining flight capability (e.g. wild and control birds). According to the hypothesis, the breast muscle of flightless birds should have atrophied due to disuse. Also, since the wild and control birds were utilizing their breast muscle for flight, this tissue should have remained the same or even increased if these birds flew more after the beginning of the experiment. Since control birds utilized their breast muscle equally throughout the experiment, their muscle weights should have remained stable.

The lack of any significant difference between treatments coupled with a significant increase in breast muscle weights of captive birds during the experiment, regardless of use or disuse, does not support the use-disuse hypothesis. This increase in the breast muscle of mass of captive birds was probably in response to an increased need for muscular strength to complete the fall migration which was occuring at the time of the experiment. It is thus more plausible that changes in male mallard breast muscle dynamics, during the annual cycle, are ultimately, not proximately, related to use and disuse. This has also been suggested about the muscle dynamics of Atlantic Brant (Branta

bernicla hrota) during the moulting period of (Ankney 1984).

At the end of period 1, birds with significantly heavier leg muscle mass (i.e. the 'clipped' and 'pulled' treatments) had spent significantly more time using their leg muscles for locomotion. These treatments spent more time resting and less time locomoting in period 2. This coincided with a decline in leg muscle weights to values similar to the control group. These trends support the use-disuse hypothesis for leg muscle dynamics.

Increased use accounted for a 4-g increase in dry leg muscle mass during the experiment. This value is below the approximately 9-g dry weight increase in the leg muscle mass of flightless wild mallards over a similar time period (Young and Boag 1982). Since time-budget information is not available for wild flightless birds, one cannot determine if the difference in these values can be accounted for by an increased use of leg muscles for flightless birds. However, since the leg muscle mass of wild mallards begins to increase prior to the flightless period and decrease prior to regaining flight capability (Young and Boag 1982), it is likely that leg muscle dynamics are more ultimately, rather than proximately, related to use and disuse phenomenon.

Young and Boag (1982) examined the weight dynamics of adult male mallard breast and leg muscle during the flightless period and reported a net loss of approximately 9-g of breast muscle protein. Based on data presented in this thesis, this protein would provide enough amino acids to produce approximately 4-g of feather protein or about 4.6-g

of wing feathers based on the average 86.3% protein content of these feathers (chapter 1). Since adult male mallards produce an average of 22.25-g of feathers during the flightless period (chapter 2), the net loss of amino acids from the breast muscle could provide approximately 20% of the amino acid requirements for feather synthesis during this period.

Due to the loss of flight capability, birds are believed to be more susceptible to predation during the flightless period. The use of stored lipids and protein during this period (Young and Boag 1982) reduces the amount of foraging time needed to satisfy nutrient requirements. In turn, this could reduce their susceptibility to predation by allowing birds to spend more time in cover avoiding predators.

In conclusion, the ability to utilize endogenous protein during the flightless period ensures a steady supply of amino acids, for maximum rates of feather synthesis, even in the face of reduced food availability. This is probably an ultimate factor which has enabled waterfowl to undergo a synchronous wing moult.

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