Aspects of the energetics of greater scaup (Aythya marila) and lesser scaup (A. affinis) during migration

by

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ABSTRACT

Greater scaup (Aythya marila) and lesser scaup (A. affinis) were studied during their spring and fall migrations at Lake St. Louis, Québec (45° 24' N, 73° 50' W). Time-activity budgets were determined and nutrient reserve levels were monitored. Methods for estimating reserve lipids in migrating scaup were evaluated.

Comparisons of early and late spring scaup revealed changes in frequencies of behaviours over the migratory period. Time-activity budgets differed between sexes within a species. Behaviour appeared to be influenced by levels of stored nutrients, sex ratios and possible changes in the food resource. Greater scaup exhibited increased weights of fat deposits and total fat in late spring, whereas increases in protein and mean body weights were not significant. Lesser scaup had higher mean body weights in late spring, however, increases in fat deposits were only significant for adult males. Higher protein weights in late spring were only significant in adult females. Digestive organ size could not be explained by changes in feeding rates and may be related to protein storage and functional changes in the gut. All females of both species were undergoing body molt; in males molt was negligible.

During the fall the diurnal activity of migrating scaup was restricted to resting and preening. Increases in body weight over the migratory period were observed in greater scaup. No clear pattern of body weight change was evident in lesser scaup.

Percent body water and skin weight were the best predictors of reserve lipids in greater and lesser scaup. Body weight and body weight/body length provided reliable estimates of lipid reserves. A single equation using abdominal fat was derived to estimate reserve lipids for both species.

ABREGE

Le grand morillon (Aythya marila) et le petit morillon (A. affinis) ont été étudiés lors de leurs migrations au printemps et à l'automne au Lac St-Louis, Québec (45° 24' N, 73° 50' 0). Les budgets énergétiques ont été déterminés et les réserves de matières nutritives dans le corps ont été évaluées. On a également évalué des méthodes pour estimer les réserves de lipides des morillons en migration.

La fréquence de comportements était différente entre les individus migrant au début de la période de migration et les migrateurs tardifs.

Pour une même espèce, les budgets énergétiques étaient différents entre les deux sexes. Le comportement semblait être dépendant des quantités de réserves nutritives, du rapport de sexe et des changements dans le régime alimentaire.

Les poids des dépôts de graisse et des matières grasses totales étaient plus élevés vers la fin du printemps, alors que les variations du poids des protéines et du poids du corps n'étaient pas significatives.

Tard au printemps, le poids moyen du petit morillon était plus élevé; cependant, l'augmentation en dépôts de graisse n'était significatif que pour les mâles adultes. Vers la fin du printemps, les quantités de protéines sont significativement plus élevées chez les femelles adultes. Les dimensions du tube digestif ne s'expliquent pas par des modifications du taux d'alimentation mais plutôt par l'emmagasinage de protéines et les changements fonctionnels dans l'intestin. La mue chez les males était négligeable, toutefois toutes les femelles des deux espèces étaient en période de mue.

A l'automne, chez les morillons en migration, l'activité diurne se limite au repos et au lissage des plumes. Pendant la période migratoire, on observe des augmentations de poids chez le grand morillon. Pour le petit morillon, les changements de poids ne semblaient pas suivre un patron défini.

Chez les grands et petits morillons, les meilleurs indicateurs de réserves de lipides sont le pourcentage d'eau dans le corps et le poids de la peau. Le poids total et le rapport du poids total sur la longueur du corps procurent une bonne estimation de réserve de lipides. La graisse abdominale a servi de base pour dériver une simple équation pour estimer la réserve de lipide pour les deux espèces.

TABLE OF CONTENTS

Page

LIST OF TABLES vi

LIST OF FIGURES viii

ACKNOWLEDGEMENTS ix

PREFACE 1

Diurnal activity and nutrient storage in greater scaup (Aythya marila) and lesser scaup (A. affinis) during migration 2

ABSTRACT 3

INTRODUCTION 5

STUDY AREA 8

METHODS 9

Censuses 9

Behaviour 9

Condition and Physiology 10

Analyses 12

RESULTS 14

Censuses 14

Spring Behaviour 15

Fall Behaviour 16

Condition and Physiology 17

Contour Feather Molt 20

DISCUSSION 21

Behaviour 21

Condition and Physiology 28

Contour Feather Molt 36

Page

CONCLUSIONS 38

LITERATURE CITED 39

Estimating lipid reserves in greater scaup (*Aythya marila*) and lesser scaup (*A. affinis*) 70

ABSTRACT 71

INTRODUCTION 72

METHODS 73

RESULTS 75

DISCUSSION 77

LITERATURE CITED 80

LIST OF TABLES

Page

Diurnal activity and nutrient storage in greater scaup (*Aythya marila*) and lesser scaup (*A. affinis*) during migration.

Table 1. Ratios of males per female in greater and lesser scaup during spring migration on Lake St. Louis, Québec, 1980 45

Table 2. Percentages of greater scaup performing various activities during daylight hours in early and late spring and mean hours per day spent by each duck in these activities 46

Table 3. Percentages of lesser scaup performing various activities during daylight hours in early and late spring and mean hours per day spent by each duck in these activities 47

Table 4. Comparison of body parameters of early and late spring migrant greater scaup collected at Lake St. Louis, Quebec, 1980 48

Table 5. Comparison of indices of lipid reserves (body weight/ body length) of male and female adult greater scaup collected during spring, 1980 52

Table 6. Comparison of body parameters of early and late spring migrant lesser scaup collected at Lake St. Louis, Quebec, 1980 53

Table 7. Comparison of indices of lipid reserves (body weight/ body length) of male and female adult lesser scaup collected during spring, 1980 57

Table 8. Comparison of body weights (g) of early and late fall greater scaup collected and killed by hunters on Lake St. Louis, Quebec 58

Table 9. Comparison of body weights (g) of early and late fall lesser scaup collected and killed by hunters on Lake St. Louis, Quebec 59

Table 10. Total molt scores of greater and lesser scaup during early and late spring, 1980 60

Page

Table 11. Molt scores of greater scaup by body region during early and late spring, 1980 61

Table 12. Molt scores of lesser scaup by body region during early and late spring, 1980 62

Estimating lipid reserves in greater scaup (*Aythya marila*) and lesser scaup (*A. affinis*).

Table 1. Regression of ether-extractable body lipids (g) on independent variables for migrant greater scaup (*n* = 35) 82

Table 2. Regression of ether-extractable body lipids (g) on independent variables for migrant lesser scaup (*n* = 39) 83

Table 3. F values calculated by comparison of regression lines predicting ether-extractable lipids for migrant greater and lesser scaup 84

LIST OF FIGURES

Page

Diurnal activity and nutrient storage in greater scaup (*Aythya marila*) and lesser scaup (*A. affinis*) during migration.

Figure 1. Map of Lake St. Louis, Quebec, showing observation points from which behavioural data were collected 63

Figure 2. Combined numbers of greater and lesser scaup on Lake St. Louis during spring, 1980 64

Figure 3. Combined numbers of greater and lesser scaup observed in morning flights from Lake St. Louis to Lake of Two Mountains during fall, 1979 and 1980................ 65

Figure 4. Daily pattern of frequencies of activities of greater scaup in early spring, 1980 66

Figure 5. Daily pattern of frequencies of activities of greater scaup in late spring, 1980 67

Figure 6. Daily pattern of frequencies of activities of lesser scaup in early spring, 1980 68

Figure 7. Daily pattern of frequencies of activities of lesser scaup in late spring, 1980 69

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PREFACE

This thesis consists of 2 manuscripts concerned with aspects of the energetics of the spring and fall migrations of greater scaup (Aythya marila) and lesser scaup (A. affinis). Both manuscripts are in the form for submission for publication. The first is a draft; the second has been accepted for publication by the Canadian Journal of Zoology.

The first manuscript examines the importance of stopover areas for migrating greater and lesser scaup. Two approaches have been taken to gain understanding of this topic; behavioural and physiological. The behavioural approach examines the allocation of time in order to fulfill the physiological requirements of migration. Knowledge of behaviour provides an understanding of how an organism interacts with its environment. The physiological approach examines the use and storage of nutrients in the form of lipids and proteins and concurrent changes in digestive organs.

The second manuscript of this thesis examines methods of quickly and cheaply estimating reserve lipids in scaup. The aim was to provide a single index of reserve lipids which could be used for both species. The ability to evaluate lipid reserves in these birds will contribute to the understanding of nutrient reserve dynamics.

Diurnal activity and nutrient storage in greater scaup (*Aythya marila*) and lesser scaup (*A. affinis*) during migration.

ABSTRACT

The importance of stopover areas for greater scaup (Aythya marila) and lesser scaup (A. affinis) during migration was studied during the spring and fall at Lake St. Louis, Quebec (45° 24' N, 73° 50' W). Time budgets of diurnal behaviours were determined for each species separately from 23 March to 1 May, 1980. Comparisons of early and late spring migrants revealed that greater scaup exhibited an increased frequency of resting and decreased frequencies of feeding, swimming and flying in late spring. Frequencies of most behaviours differed between sexes during both time periods.

Male and female lesser scaup showed increases in resting and preening in late spring, however, slight increases in feeding in late spring were not significant. Other activities were performed less frequently in late spring. Similar to greater scaup, frequencies of behaviours differed between male and female lesser scaup. During the fall, diurnal behaviour of greater scaup and lesser scaup was restricted primarily to resting and preening. Feeding occurred almost entirely at night.

Comparisons of body parameters of early and late spring birds were made on 35 greater scaup and 51 lesser scaup collected by shooting. Greater scaup exhibited a slightly higher mean body weight in late spring. Mean weights of the skin, intestinal fat, abdominal fat and total fat were larger in late spring. Slight increases in protein weights and fat-free weights were not significant. Digestive organs of adult greater scaup did not change with the exception of large intestine length which decreased in late spring. Sample sizes of juveniles were small, but data suggested an increase in intestinal size. Mean body weights of lesser scaup were higher in late spring. Increases in fat deposit weights were observed but these were only significant for adult males. Higher protein weights in late spring were only significant for adult females, whereas higher mean values for fat-free weight were not significant in any age-sex class. Changes in digestive organ size in lesser scaup appeared to be limited to increases in intestinal weight. Adult and juvenile males of both species exhibited little body molt, whereas all females of both species were undergoing body molt. During the fall migrations in 1979 and 1980 body weights were obtained from hunter-killed birds. Weights of 192 greater scaup and 92 lesser scaup were measured during both years combined. All age-sex classes of greater scaup had higher mean body weights in late fall, however differences were not always significant. No clear pattern of body weight change was evident in lesser scaup.

Conclusions were that stopover areas such as Lake St. Louis were used by migrating scaup to replenish nutrient reserves. Behaviour appeared to be influenced by levels of stored lipids in birds, the ratio of males to females and possible changes in the food resource. Changes in digestive organs could not be explained by changes in feeding rates and may be related to protein storage and functional changes in the gut.

INTRODUCTION

Body weights of migrating ducks have been reported by many authors (including Bellrose and Hawkins 1947, Nelson and Martin 1953, Weller 1957, Mendall 1958, and Bellrose 1976). Ducks gain weight during the spring and fall as fat is being stored for migration (Weller 1957, Folk et al. 1966, Owen 1970, Erskine 1971, Ryan 1972, Peterson and Ellarson 1979). During the period of premigratory hyperphagia giant Canada geese (Branta canadensis maxima) exhibited large weight gains due to lipid and protein storage (McLandress and Raveling 1981). Weller (1957) showed that redhead ducks (Aythya americana) lose weight during the course of migration. Harris (in Fredrickson and Drobney 1979) believes that waterfowl use stopover areas to replenish reserves. Lesser snow geese (Anser caerulescens caerulescens) accumulate nutrients while staging at James Bay (Wypkema and Ankney 1979). Siegfried (1974) concluded that the Delta marsh in Manitoba is an important feeding and resting area for lesser scaup (Aythya affinis) during migration, however he made no attempt to determine if the birds were storing nutrients. Lipid reserves acquired before arrival on the breeding grounds have been shown to be important for reproduction (Harris 1970, Krapu 1974, 1981, Calverly and Boag 1977). During the course of migration it therefore seems reasonable that ducks should replenish the body lipids used as fuel during migratory flight. Since lipid and protein metabolism are interrelated (Hanson 1962), birds using stopover areas during migration should show an increase in body proteins concurrent with increasing lipids.

Siegfried (1974) stated that knowledge of a species behaviour at a given place contributes to the understanding of the species requirements and the importance of that place. Recently several studies have examined time-activity relations in breeding, postbreeding and wintering ducks (Klima 1966, Folk 1971, Siegfried 1974, Tamisier 1974, 1976, Dwyer 1975, Miller 1976, Siegfried *et al*. 1976a, b, Skead 1977, Seymour and Titman 1978, Afton 1979, Stewart and Titman 1980, Titman 1981, Bailey 1982). Time-activity studies of *Aythya* during migration are limited to Siegfried's (1974) work on lesser scaup as they approached the breeding grounds. Time-activity budgets monitored farther from the breeding grounds should provide greater understanding of the use of stopover areas along migratory routes.

Greater scaup (*A. marila*) and lesser scaup migrate long distances between wintering and breeding grounds. Greater scaup breed in the western arctic in North America and winter along the Atlantic and Pacific coasts, the Great Lakes and along the Gulf of Mexico. Lesser scaup breed in interior northwestern North America from central Alaska and western Canada north to the tree limit and east as far as the Laurentian Shield, south to Minnesota and northeastern California. Wintering areas include the Atlantic and Pacific coasts, the Gulf of Mexico and extend into Mexico and Central America. More detailed descriptions of the ranges of greater and lesser scaup are given by Bellrose (1976). During the migratory periods in spring and fall both species use the St. Lawrence River system in southwestern Quebec as a stopover area. The aim of this study was to gain an understanding of the importance of stopover areas for migrating scaup. It was hypothesized that birds using these areas replenish lipids and proteins spent to power migratory flight. Over the course of migration high levels of food intake should result in increased lipid deposits and protein reserves and heavier body weights. Protein is stored in digestive organs (Ankney 1977, Korschgen 1977, Bailey 1982) and in flight muscles (Kendall et al. 1973). Digestive organ size is also related to the level of food consumption (Fenna and Boag 1974, Miller 1975, Savory and Gentle 1976a, b, Ankney 1977), therefore interpretation of changes in these organs requires information on feeding rates. Time spent feeding by birds utilizing stopover areas should also reflect the quality and quantity of the food resource.

STUDY AREA

The study was conducted primarily on Lake St. Louis, Quebec (45° 24' N, 73° 50' W) which lies at the southwestern end of the island of Montreal (Figure 1). It is an enlargement of the St. Lawrence River where it is joined by waters from the Ottawa River and is therefore not a true lake. Approximately 18 km in length and 10 km at the widest point it is generally shallow. The substrate is principally silt and clay, and extensive beds of vegetation lie along the south shore and in the middle of the lake. Plant species are numerous and variable but dominant species include *Potamogeton richardsonii*, *Vallisneria americana*, *Anacharis canadensis*, *Alisma gramineum*, *Myriophyllum spicatum* and *Chara* spp. Pageau and Lévesque (1964) and Gravel and Lévesque (1977) provide a detailed description of the aquatic vegetation. There is a large human population (>2,000,000) surrounding the area, thus recreational use of the water is extremely high.

The eastern half of Lake of Two Mountains (45° 28' N, 73° 58' W) was included during fall hunter bag surveys. This is a long wide basin at the lower end of the Ottawa River immediately upstream from Lake St. Louis. It is shallow and turbid and lacks the extensive weed beds and heavy recreational use of Lake St. Louis.

METHODS

Censuses

Aerial censusing was conducted every 7-8 days from 27 March to 10 May, 1980, to assess numbers of scaup and to locate areas of use. All observations were made from a fixed-wing aircraft and the location and size of each flock was recorded. During the fall aerial surveys did not prove successful as birds were continually moving and often difficult to locate due to heavy hunting pressure.

An index of total fall numbers was obtained by estimating the numbers of birds observed flying from Lake St. Louis where they fed at night, to Lake of Two Mountains where they rafted during the day. Counts were made at the northwestern shore of Lake St. Louis and were attempted weekly, however successful counts were dependent on weather. Thornburg (1973) found that the magnitude of daily flights on Keokuk Pool, Iowa, was directly proportional to the population of diving ducks. Surveys made by airplane and by boat revealed that large numbers of birds seldom remained on Lake St. Louis during the diurnal period after the morning flights were completed. It was usually impossible to distinguish between greater and lesser scaup both from the air and during morning flight counts so values presented include both species.

Behaviour

Activity of unmarked greater and lesser scaup was sampled by continuous scanning (Altmann 1974). Observations were made with a spotting telescope and the activity of each duck was recorded on cassette tape. Behavioural activities were divided into the following categories: (1) feeding; (2) resting, including sleeping; (3) preening, including bathing and comfort movements; (4) swimming, including courtship and alert behaviour; and (5) flying. Scans were made every 10, 15, 20 or 30 minutes depending on the number of birds present. Scaup were observed so that all daylight hours were sampled every 2-4 days. Data were pooled from 4 separate locations during the spring to reduce bias associated with area related use. During the fall birds were difficult to observe due to their distance from shore and data were pooled from 2 locations only.

Condition and Physiology

Greater and lesser scaup were collected with a shotgun during their fall migrations in 1979 and 1980 and during their spring migration in 1980. Birds were aged by the bursa of Fabricius and by plumage characteristics (Palmer 1976). Birds were dried with paper towel, weighed fresh to 0.5 g and frozen within 1-2 hours in sealed polyethylene bags for later analyses.

Thawed birds were reweighed but weight loss rarely exceeded 1 g. Birds were skinned and dissected and the following wet weights to 0.01 g were taken: (1) unplucked skin including the subcutaneous fat but excluding wings and feet; (2) breast muscles (pectoralis, supracoracoideus, and coracobranchialis) from one side; (3) muscles of the femur and tibiotarsus including these bones from one leg; (4) gizzard; (5) small intestine disjoined at the junction with the gizzard and at the iliocaecalcolic axis; (6) large intestine severed at the visible junction with the cloaca; (7) combined cecae; (8) abdominal fat deposit; and (9) intestinal mesenteric fat. Prior to weighing all visible fat was removed from muscles and organs. Digestive organs were cut along their length, rinsed under running water to remove ingesta, patted dry with paper towel and weighed.

Measurements to 1.0 mm were taken of (1) small intestine length; (2) large intestine length; and (3) combined cecae length. Care was taken not to stretch these organs during rinsing and measuring.

Skins were scored for contour feather molt using a generalized pterylosis diagram described in Billard and Humphrey (1972). This was divided into 5 body regions: (1) head and neck; (2) sides and flanks; (3) upper breast and upper back; (4) lower breast and belly; and (5) mid-back and rump. It was not possible to distinguish between contour feather molt and down feather molt in the head and neck region, therefore this region was not included in the scoring. As in Billard and Humphrey (1972) each region was subdivided into smaller units of similar size to facilitate scoring.

The skins were scraped free of fat and numerical scores indicating molt intensity were entered in each subdivision. Scores were as follows: no molt, 0; light molt, 1; moderate molt, 2; and heavy molt, 3. The mean molt score for each region was calculated by adding the scores of the subdivisions within the region and then dividing by the number of subdivisions. Mean molt scores for the 4 regions were then added together to give the total mean molt score of each bird. The maximum total mean molt score for any skin was 12. Molt scoring was done on spring scaup only as fall sample sizes of whole birds were too small.

The skin was then plucked and the entire bird excluding the plumage, feet, bill, was ground in a meat grinder and thoroughly homogenized in a blender. Two 20 g samples of each homogenate were freeze dried at -50°C and 5 microns of pressure to a constant weight to estimate water content.

Dried samples were finely ground and washed in anhydrous ether for 18 hours in a modified Soxhlet apparatus capable of holding 20 samples. Samples were dried in a vacuum oven overnight then reweighed to estimate lipid content. The non-ether extractable residue of the samples was used as a protein index (Raveling 1979).

During the fall birds were difficult to collect due to heavy hunting pressure so additional data on body weight were obtained from hunter-killed scaup. Birds were weighed to 5.0 g on a Pesola spring scale.

Analyses

Physiological and behavioural data were categorized into the following periods for the purpose of statistical analyses: early spring - from 23 March to 13 April for greater scaup and from 23 March to 22 April for lesser scaup; late spring - from 14 April to May 1 for greater scaup and from 23 April to May 1 for lesser scaup; early fall - from 20 September to 24 October for both species; late fall - from 25 October to 2 December for both species. Different dates separating early from late spring were used for the two species because greater scaup arrived considerably earlier than lesser scaup. During the fall lesser scaup may have arrived earlier than greater scaup (Bellrose 1976), but this could not be verified as the first small flocks of early arrivals were difficult to locate or identify due to the large area of water and heavy boating pressure. Both greater and lesser scaup were seen during hunter bag checks from the third week of September until the beginning of December, therefore the same date was used to separate early from late fall for both species.

Behavioural data were compiled and sorted on an Amdahl V7 computer using the Statistical Analysis System (Barr _et_ _al_. 1979). Chi-square tests were performed on raw totals to test for differences in proportions (Siegel 1956). To compensate for increasing daylength the average number of hours of daylight (½ hour before sunrise to ½ hour after sunset) were calculated for early and late spring periods. The percentages of birds performing the various activities during daylight hours were multiplied by the average number of hours of daylight to estimate the mean number of hours per day spent by each duck in each activity.

Comparisons of body parameters of early and late migrants were made for spring and fall separately and between years in the fall with a two-tailed Wilcoxon rank-sum test using the Statistical Analysis System (Barr _et_ _al_. 1979).

RESULTS

Censuses

Peak numbers of combined greater and lesser scaup were observed on 3 April and 26 April, 1980 (Figure 2). The first peak consisted primarily of greater scaup; the first lesser scaup were seen on 25 March during behavioural observations but it was not until 6 April that they were seen regularly. Greater scaup were first recorded during the third week of March when the ice was beginning to break up on the lake. Both species were seen regularly until 1 May although lesser scaup seemed relatively more abundant than greater scaup towards the end of April. During the spring Lake of Two Mountains was of little importance to diving ducks and scaup were rarely seen there during aerial censuses.

Sex ratios were determined from observations made from shore (Table 1). The earliest greater scaup to arrive could not be observed as they were limited to ice-free water far from shore. By the time they could be observed greater scaup had been on the lake approximately 1 week and large numbers had arrived. Sex ratios of greater scaup favoured males throughout the spring, however this predominance showed a gradual decrease from late March to mid-April. After being lower initially, a similar pattern of decrease occurred among lesser scaup.

The largest fall concentrations occurred around mid-November in both years although the 1979 peak was lower and slightly earlier than in 1980 (Figure 3). Scaup were seen until mid-December in 1979 well after ice had formed in bays and along the shores. In 1980 no birds were observed after the first week in December.

Spring Behaviour

During 116 hours of observation from 23 March to 1 May, 1980, 30,191 instantaneous time-activity samples of greater scaup and 15,113 of lesser scaup were recorded. Frequencies of feeding decreased and frequencies of resting increased for both male and female greater scaup in late spring (Table 2; $\underline{P}<0.01$). Preening was observed more frequently in late spring but the increase was only significant for females ($\underline{P}<0.05$). Swimming and flying occurred with decreased frequency in late spring ($\underline{P}<0.01$).

More female greater scaup were observed feeding than males in early spring ($\underline{P}<0.05$), however no difference was found in late spring. Frequencies of resting and preening were greater for females than males throughout the spring ($\underline{P}<0.05$), whereas the frequency of swimming was less for females ($\underline{P}<0.01$). Females were also observed flying less frequently than males but this was only significant in early spring ($\underline{P}<0.01$).

Behavioural trends exhibited by lesser scaup (Table 3) during the spring migration were similar to those of greater scaup. However, both males and females showed increases in resting and preening in late spring ($\underline{P}<0.01$); slight increases in feeding in late spring by both sexes were not significant. Other activities were performed less frequently by both sexes in late spring ($\underline{P}<0.01$). Female lesser scaup were observed feeding and preening more frequently than males throughout the spring ($\underline{P}<0.05$). Although females were observed resting more than males in early spring ($\underline{P}<0.01$), no difference between sexes occurred in late spring. Frequencies of swimming and flying were greater for males than for females in both early and late spring ($\underline{P}<0.01$).

Figures 4 through 7 show the daily pattern of activity in 2 hour periods for greater and lesser scaup. Feeding occurred throughout the day suggesting that individual birds were feeding frequently. No strong daily activity pattern was apparent although swimming and flying were most frequently observed early in the day.

Fall Behaviour

Activity patterns of both greater and lesser scaup were entirely different during the fall. The birds rafted out in open water during the day restricting their activities primarily to resting and preening. Twenty-one hours of behavioural observations including all hours of daylight were conducted from 8 November to 19 November, 1979. Based on 45,261 instantaneous observations, 75.6% of the birds were observed resting and 21.0% preening. Only 4 individuals were seen feeding. Due to the distance of the birds from shore, scaup could not be identified as to species, sex, or age. The percentages given are based on all scaup with greater scaup forming the largest proportion. The largest daytime concentrations of scaup occurred on Lake of Two Mountains. Occasionally rafts of scaup were seen on Lake St. Louis, however hunter harassment and even the sound of a distant outboard motor would often cause these birds to fly to Lake of Two Mountains. Approximately one hour before sunset scaup would start to become restless, swimming alertly then flying off to the feeding areas in Lake St. Louis. This behaviour lasted until darkness with most birds flying between sunset and darkness. In the morning flocks of scaup would lift off the feeding areas and fly back to the resting areas. The morning flights would usually begin at first light and continue until approximately 1-2 hours after sunrise. The timing and duration of the morning flights often appeared to be influenced by the hunting pressure on Lake St. Louis. The sight and sound of motorboats and occasional chasing by hunters would result in earlier flights and reduced duration of the morning flight period. During late fall when hunting pressure was very light scaup often remained all day on Lake St. Louis.

Condition and Physiology

Comparisons of body parameters of early and late spring greater scaup are presented in Table 4. As efforts were concentrated on collecting adult males sample sizes for other age-sex classes are small. Statistical comparisons were therefore limited to adult males. Mean body weight of adult males was higher in late spring than early spring but this difference was not significant ($\underline{P}=0.10$). Adult females and juveniles of both sexes showed similar trends. Breast muscle weights and leg weights showed no change over the spring. Mean values of gizzard weight, small intestine length, small intestine weight, large intestine weight and combined caecae weight did not differ significantly between early and late spring for adult males, whereas large intestine lengths were shorter in late spring ($\underline{P}<0.01$). Adult female greater scaup showed similar organ measurements. Sample sizes of juveniles are small but the data suggest a possible increase in size of the intestines, particularly small intestine length. Large intestine length did not appear to decrease over spring. Mean weights of the skin, intestinal fat, abdominal fat and total fat were larger in late spring for all greater scaup. These differences were significant for adult males ($\underline{P}<0.05$). Slight increases in protein weights and fat-free weights were not significant.

Body length is highly correlated with fat-free weight in adult greater scaup and lesser scaup (Chappell 1982). Body weight was adjusted by body length to provide an index of lipid reserves to compare males and females within a species. Early spring male and female adult greater scaup could not be compared due to an insufficient sample size of females, however a comparison of indices of late spring males and females revealed no statistical difference (Table 5).

Body weights of migrant lesser scaup were significantly higher ($\underline{P}<0.05$) in late spring than early spring for adult males and females and juvenile males (Table 6). No juvenile females were obtained in early spring however the high body weight of the single late spring bird agreed with the above findings. Breast muscle weights were heavier in late spring but this increase was only significant for adult and juvenile males ($\underline{P}<0.05$). Leg weights did not change over the spring. Early and late spring adult males did not differ significantly in gizzard weight, small and large intestine lengths, or combined caecae weight and length. Increases were observed in the weights of the small and large intestines in late spring ($\underline{P}<0.01$). Adult females exhibited similar trends; small intestine weight was greater in late spring ($\underline{P}<0.05$) and a larger mean weight was obtained for the large intestine in late spring but this was not statistically significant. Other digestive organs did not differ between early and late spring for adult females although large intestine length appeared to be slightly greater in later spring. No statistical differences were found between digestive organ weights of juveniles in early and late spring although non-significant changes in the gut were similar to those of adults. The weights of the skin, abdominal and intestinal fat deposits and total fat were greater in late spring adult males ($\underline{P} < 0.05$). Increases in these parameters were observed for adult females and juvenile males but they were not significant. Weights of fat deposits and total fat of late spring juvenile females were similar to those of juvenile males collected in the same time period. Fat-free weights and protein weights of adult males had higher mean values in late spring but differences were not significant. Adult females showed a slight increase in fat-free weight ($\underline{P} = 0.08$) and a significant increase in protein weight ($\underline{P} < 0.05$). No difference in fat-free weights of juvenile males was observed, however protein weight increased slightly ($\underline{P} < 0.07$).

Comparisons of lipid reserves of adult males and females were made by adjusting body weight by body length (Table 7). No significant differences were found between sexes in either early or late spring.

Body weights of greater and lesser scaup obtained during fall migration in 1979 and 1980 are presented in Tables 8 and 9. All age-sex classes of greater scaup had higher mean body weights in late fall than in early fall, but differences were only significant for adult males and juvenile females in 1979 ($\underline{P} < 0.01$). A certain amount of variation between years was indicated by differences in mean body weights of early fall adult males in 1979 and 1980, and similarly in early fall juvenile females ($\underline{P} < 0.05$).

Body weights of adult male lesser scaup were not significantly different between early and late fall birds. Sample sizes of females were too small to compare statistically but data from both years indicate weight increases during their stay on Lake St. Louis. Body weight increases were significant for 1980 juveniles of both sexes ($\underline{P} < 0.05$), however in 1979 mean body weights of early and late fall juveniles did not differ.

Contour Feather Molt

During spring 1980 adult and juvenile males of both species exhibited little molt with most individuals not molting at all (Table 10). Of 7 adult male greater scaup scored in early spring only one showed light molt. Late spring adult males and juvenile males throughout the spring showed no evidence of contour feather molt. All adult and juvenile female greater scaup were undergoing body molt in early and late spring. Generally molt was observed in all body regions (Table 11).

Molt score patterns of lesser scaup were similar to those of greater scaup (Table 10). Of 13 early spring adult males scored, only 1 was molting lightly, and only 2 of 18 late spring adult males showed signs of molt. Similarly, of all juvenile males scored throughout the spring, only 1 was molting. All adult and juvenile females were molting during both spring periods. Most females exhibited contour feather molt in all body regions (Table 12).

DISCUSSION

Behaviour

Greater scaup arriving on Lake St. Louis in early spring spend over 25% of daylight hours feeding. A significant decrease in time spent feeding during the latter portion of spring passage may be due to several causes. The first greater scaup arrive when the lake is still partially ice covered; therefore certain areas are not accessible and birds may have to spend more time foraging in poorer quality habitats. Time spent feeding will be greater if birds are forced to feed in deeper water (Nilsson 1970a, b) or if food items are less abundant (Owen 1972). Food intake and therefore time spent feeding will increase if food quality decreases (Hill and Dansky 1954, McDonald _et_ _al_. 1973, Miller 1975). Greater scaup often began to utilize areas of Lake St. Louis as the ice broke up, particularly sheltered bays and shorelines. Although many areas were used by early and late spring birds, some areas were used in late spring that could not be used in early spring. Ice remained in sheltered bays used by the birds until the end of the first week of April. It is possible that the food resource improved qualitatively and quantitatively as additional areas became ice-free. The disappearance of the ice and the increase in daylength over the period of migration may have allowed for increased vegetative growth. An evaluation of food habits which would answer the questions posed above was not possible since very few birds had food in the esophagus when shot.

Folk (1971) suggested that the tufted duck (_Aythya_ _fuligula_) must devote most of its time to foraging in early spring as a result of short daylength and little available food. Although the average daylength was

1.1 hours longer in late spring, the average amount of time spent feeding diurnally by greater scaup was still less than in early spring (Table 2). If birds were feeding at night as well as during the day then increasing daylength may have had little effect on diurnal feeding rates. Scaup shot in the early morning generally had no food in their stomachs but I do not know if they were nocturnally active. Attempts to observe birds on moonlit nights were unsuccessful due to the distance of birds from shore. Klima (1966) found that diurnal and nocturnal activity did not differ for the European pochard (Aythya ferina). Canvasbacks (A. valisineria) were observed to be active on moonlit nights during the spring on Delta marsh (Hochbaum 1944). Contrary to this, Folk (1971) found the tufted duck (A. fuligula) showed marked diurnal feeding versus nocturnal resting. Nilsson (1970b) has shown that scaup, presumably the old world subspecies A. m. marila, are primarily nocturnal during the fall and winter, showing increased diurnal feeding behaviour during the spring months. Similar behavioural trends were observed for tufted ducks and pochards in the same study.

A change in ambient temperature may affect the caloric requirements of birds (Smith and Prince 1973) and therefore feeding intensity (Nilsson 1970b, Hickey 1980). The mean daily temperatures during early and late spring in the present study were 5.7^{o} and 7.7^{o}, respectively. Applying the mean body weights of male greater scaup (Table 4) to the equation provided by Kendeigh et al. (1977), $T_{1c} = 47.17\ W^{-0.1809} \pm 1.382$, the lower control temperature is calculated as approximately 13^{o}. As mean temperatures and especially nightly low temperatures were below the zone of thermo-neutrality, the warmer temperatures in late spring may have influenced the decreased feeding rates observed.

Presumably the main factor contributing to decreased feeding in late spring is that lipid stores had approached capacity in a large number of birds. Once lipid reserves have been replenished, food consumption and time spent feeding should decrease. Lepkovsky (1973) has shown that food intake is regulated by the size of fat deposits.

Female greater scaup were observed feeding more frequently than males in early spring but not in late spring. Sex ratios show that many females tend to arrive somewhat later in the spring compared to males. If arriving birds spend more time feeding that those which have had some time to replenish lipid reserves, then higher feeding rates for females should be observed.

In contrast with greater scaup, lesser scaup showed no significant changes in feeding rates over the spring. Lesser scaup tend to fly short distances between stopover areas during spring migration (Bellrose 1976), therefore birds arriving at Lake St. Louis should still have sizable lipid reserves. Little is known of the migratory habits of greater scaup, however their preference for larger waters (Bent 1923, Kortright 1942) may require longer flights between stopovers and the use of more stored energy than lesser scaup. Although both greater and lesser scaup showed increases in body lipids, greater scaup could not be collected for the first two weeks after arrival and therefore had ample time to replenish reserves. Early arrivals probably weighed considerably less than indicated in Table 4, necessitating a high feeding rate to replenish reserves used during migratory flight.

Female lesser scaup were observed feeding more than males throughout the spring passage; these results agree with the work of Siegfried (1974).

Observations of pre-territorial and pre-nesting spring dabbling ducks have shown that females feed more than males (Seymour and Titman 1978, Afton 1979, Dwyer _et al_. 1979, Stewart and Titman 1980). Gadwalls (_Anas strepera_) arriving on the breeding grounds showed no sex-related differences in feeding rates until the pre-nesting stage (Dwyer 1975). Weller (1957) found that female redheads showed rapid increases in weight upon arrival to the breeding grounds due to intensive feeding. The importance of lipid reserves acquired prior to arrival on the breeding grounds for dabbling ducks has been discussed by Harris (1970), Krapu (1974, 1981) and Calverly and Boag (1977). The fact that female greater scaup did not show a significantly higher feeding rate than males in late spring as seen in lesser scaup may be related to proximity to the breeding grounds. Lesser scaup migrating through this area are closer to their breeding grounds than are the majority of greater scaup (Bellrose 1976), and the need for lipid reserves for nesting may be of increasing importance for the former.

Female lesser scaup migrating through Delta marsh, Manitoba, in the southern portion of the breeding range spend 35% of their time feeding (Siegfried 1974). This is twice the time spent feeding by females at Lake St. Louis, suggesting increased feeding as nesting approaches. Males at Delta spent approximately the same amount of time feeding as males at Lake St. Louis.

Molt is an energy demanding function (King 1974) and may in part influence the higher feeding rates observed for females than males of both species. Also, since feathers have a higher concentration of sulphur-containing amino acids than do plant or animal foods, an increase in food intake is required (Kendeigh et al. 1977). Less efficient insulative properties of the plumage during the molt should result in females requiring more energy for thermoregulation. This would be most pronounced in early spring when air and water temperatures were colder. Also as new feathers develop the insulative properties of the plumage will improve compared to early stages of molt. Although female greater scaup exhibited higher molt scores than males in late spring, no significant difference in feeding rates was observed between sexes during that time. Energy required for molt may have been made available by reductions in other energy demanding activities as suggested by Ankney (1979) and Prince (1979).

Increased daylength was associated with increased resting on the feeding grounds by white fronted geese (Anser albifrons frontalis)(Owen 1972). Increases in the average number of hours spent resting in late spring by both species were greater than increases in daylight hours. Folk (1971) considered that time spent resting by the tufted duck was inversely related to the time spent foraging. Contrary to this, time spent resting by lesser scaup increased significantly in late spring although time spent feeding did not decrease suggesting that time spent resting may be inversely related to other activities.

McKinney (1965) has hypothesized that internal stimuli, such as a full crop, reduce the tendency to feed allowing other tendencies to be expressed. Comfort movements generally follow feeding in waterfowl (McKinney 1965, Nilsson 1974, Siegfried 1974). Time spent preening was greater in late spring than early spring for both species of scaup, however time spent feeding in late spring decreased for greater scaup but not for lesser scaup. This would suggest that time spent feeding and time spent preening are not directly related to each other. The fact that female greater and lesser scaup preened more than males throughout the spring is a reflection of heavier body feather molt in females (Table 10). Heavier molt in female greater scaup during March and April has also been demonstrated by Billard and Humphrey (1972). Siegfried (1974) also found that during spring migration male lesser scaup spent less time preening than females.

Active swimming by waterfowl may be due to disturbance, searching for food, seeking a potential mate or engaging in courtship. In preparation for flight scaup swim in the direction of take-off while performing chin-lifting (Johnsgard 1965). Resting and feeding birds were frequently carried away from a flock by the current and would periodically swim back. Decreases in frequencies of swimming by greater and lesser scaup in late spring may be influenced by the lower number of unpaired males present. The result should have been that fewer males were searching for and competing for mates and females thus spent less time avoiding unpaired males. Siegfried (1974) found that courtship behaviour by lesser scaup was normally initiated by unpaired males. More time spent in courtship by unpaired birds was also observed in ring-necked ducks (<u>Aythya collaris</u>) by Mendall (1958). Courtship by greater and lesser scaup was occasionally performed by pairs but was most frequently observed in courtship groups consisting of 1 or 2 females and several males. Often birds would dive in unison or make occasional courtship flights but most activity consisted of swimming and displaying.

Displays are described by Johnsgard (1965). Pre-flight swimming also decreased as a result of less time spent flying in late spring.

Estimating the amount of daylight spent flying is extremely difficult as birds disappear from sight and are no longer included in further behavioural observations. Understanding trends in the amount of flying done is important, particularly in constructing energy budgets, as flight is the most metabolically expensive activity that ducks engage in (Wooley and Owen 1978). Greater and lesser scaup showed significant decreases in time spent flying in late spring. As birds become familiar with the lake less time is required to seek feeding and resting areas so time spent flying should decrease. The fact that more males were observed flying than females throughout the spring is likely because unpaired males were seeking potential mates. Siegfried (1974) also found that unpaired male lesser scaup spent more time flying than paired males or females. In the present study it was generally impossible to distinguish between paired and unpaired males, however single males and small groups of males were frequently observed flying without accompanying females.

Nocturnal feeding habits of ducks during the fall and winter have been noted for several species (Owen 1970, Nilsson 1970b, Thornburg 1973, Tamisier 1974, 1976). Tamisier (1970, 1974) suggested that diurnal gregariousness and nocturnal feeding by common teal (Anas crecca crecca) is primarily an adaptation to predation pressure facilitated by other factors. Contrary to this Thornburg (1973) feels that diving ducks adapt to hunting disturbance by deviating from typical patterns of diurnal activity. Mallards have been shown to change feeding routines in response to hunting (Girard 1941). Increased nighttime feeding in response to hunting is also seen in geese (Owen 1972, Newton and Campbell 1973). Hunting and recreational activity on Lake St. Louis did frequently influence the timing and magnitude of diving duck flights, but increased diurnal activity did not occur as human disturbance decreased late in the fall. However, as Owen (1972) has pointed out in the case of geese, not only actual disturbance but also the tradition of disturbance in an area will influence behaviour.

Condition and Physiology

Weight gain by migrant birds in the form of stored lipid reserves is accomplished by active hyperphagia (King 1972). There are two distinct sources of lipids for storage: absorption of lipids in foods from the intestinal tract and synthesis from non-lipid compounds (Griminger 1976). Once lipid stores approach a particular maximum it is necessary to reduce food intake unless an increase in energy output occurs. Excessive reserves are maladaptive as they are obtained at the expense of the environment, increase the risk of predation and are metabolically expensive to maintain (Helms 1968). As lipid stores increase bulk and hence drag of the body in flight increases resulting in a decreased effective lift:drag ratio (Pennycuick 1969). This is obviously a consideration for long distance migrants.

Greater scaup gained weight and increased fat reserves over the spring migratory period. The fact that weight increases in late spring by greater scaup were not significant may suggest that maximum reserve levels were already being approached by a large proportion of individuals in the early spring period. Less time spent feeding in late spring also suggests this. Mean body weights of late spring greater scaup (Table 4) are higher than most provided in the literature for migrating or wintering birds (Nelson and Martin 1953, Ryan 1972, Johnsgard 1975, Palmer 1976, Bellrose 1976). Large increases in mean body weight would therefore seem unlikely. A significant difference between body weights of early and late spring greater scaup might have been found if birds could have been collected when the ice began to break up and the earliest arrivals were seen on Lake St. Louis. These birds started to arrive approximately 2 weeks before collecting could be started and therefore had time to build up lipid reserves.

Mean protein and fat-free weights were not significantly higher in late spring male greater scaup, although slightly higher values in late spring birds, especially adult females and juveniles, suggested some protein storage was occurring. Fry _et_ _al_. (1970) have shown that fat-free weights increased during the first few days of pre-migratory hyperphagia. Significant changes in protein and fat-free weight in greater scaup may have been obtained if more early arrivals had been collected. Proteins stored prior to and during migration may be used during periods of migrating flight when dietary intake of carbohydrates cannot supply the oxalacetate required for fat metabolism. Hanson (1962) states that a bird cannot use its fat deposits during migration or during periods of starvation without a simultaneous use of body protein. Peterson and Ellarson (1979) found that lipid and protein levels fluctuated together in wintering oldsquaw (_Clangula_ _hyemalis_). Scaup arriving at Lake St. Louis have used fat reserves to fuel migratory flight and in the process have presumably drawn on protein stores. As fat reserves are replenished during the stopover, proteins spent on fat metabolism must also be replaced in preparation for further flight.

As well as increases of stored fat, lesser scaup exhibited higher protein and fat-free weights in late spring. Increases may in part be explained by the larger size of breast muscles and some digestive organs. Heavier breast muscles may reflect use during migratory flight, suggesting that birds arriving later in the spring may have flown a longer distance than earlier arrivals. Breast muscles may be major storage organs for protein needed to metabolize lipids during migratory flight. Kendall *et al*. (1973) have shown that protein from the breast muscles of *Quelea quelea* is labile and used elsewhere. Increased lipid content of the breast will occur as body lipids are stored, however data from Raveling (1979) show that changes in lipid content can account for only part of changes in the weight of the entire breast.

The distance that could be flown by late spring greater scaup can be calculated. Applying the mean body weight of adult males in late spring to the equation provided by Owen and Reinecke (1979), basal metabolic rate (BMR) is calculated as:

$$\text{BMR} = 75\ (1.114)^{0.72} = 81.06\ \text{kcal day}^{-1}$$

Multiplying this value by 12.5, the multiple of BMR expended during flight (Wooley and Owen 1978), the cost of nonstop flying is calculated as approximately 1013.3 kcal day^{-1}. To determine the kcals available in stored lipids, total ~~available~~ fat weight is multiplied by 9.1 kcal g^{-1}, the caloric density of fat stored by migratory birds (Johnston 1970). Griminger (1976) states that even at the time of starvation to death a small percentage of body weight is made up of fat, therefore total fat weight does not equal the weight of fat available for metabolism. Wishart (1979) has shown that total lipids in starved American wigeon

(<u>Anas americana</u>) are less than 1% of body weight at death. Starvation weights of male greater scaup are not known but presumably are in the area of 800 g; therefore the weight of total lipids at death would be approximately 3 g. The mean weight of available stored lipids would then be 200 g which will provide 1820 kcal of energy, enough for 1.8 days of nonstop flying. As waterfowl migrate at an average speed of 80 km hr^{-1} (Bellrose 1976) the average nonstop distance late spring male greater scaup can fly is approximately 3500 km. The distance to major breeding areas from Lake St. Louis is 4000 km or more (Bellrose 1976). Although some birds could possibly fly nonstop to the breeding grounds they would arrive exhausted of lipid stores and would possibly be incapable of reproduction. However, most birds would not be able to fly the distance to the breeding grounds. These distances are based on a caloric density of stored lipids of 9.1 kcal g^{-1} based on burning. The actual energy available to a bird during lipid metabolism may be lower; therefore the distances calculated above may be an excess of what could be attained.

Applying the same logic to late spring male lesser scaup a value of 832.5 kcal day^{-1} is obtained for flight, and 1490 kcal is the energy available from stored lipids. Late spring male lesser scaup can therefore fly nonstop for approximately 1.8 days and for a distance of 3500 km, similar to that calculated for greater scaup. Major breeding areas begin less than 2000 km from Lake St. Louis, although important breeding grounds in Alaska and the Northwest Territories are still farther than could be reached by the majority of lesser scaup. Early spring male lesser scaup could on average fly 1.3 days and cover a distance of 2500 km. Having reached the breeding grounds in Manitoba or Saskatchewan, lipid stores would be depleted. The importance of stopover areas to greater and lesser scaup for replenishing spent body lipids is therefore evident.

The number of days required to replenish endogenous lipid reserves for migratory waterfowl weighing 1100 g has been calculated by Fredrickson and Drobney (1979) for various distances flown and caloric intakes. The amount of time needed to replenish reserves will be affected by several factors such as the condition of birds arriving, the quality and quantity of the food resources at the stopover area and weather. The average duration of stay by scaup on Lake St. Louis was not determined.

Several studies on gallinaceous birds have shown that the size of digestive organs is influenced by diet quality (Leopold 1953, Lewin 1963, Moss 1972, 1974, Pendergast and Boag 1973). More recent works have indicated that changes in the gut are more likely the result of changes in food consumption, which may vary in response to diet quality (Fenna and Boag 1974, Miller 1975, Savory and Gentle 1976a, b). Ankney (1977) has shown that changes in feeding activity by lesser snow geese (Anser caerulescens caerulescens) are positively correlated with changes in the average size of digestive organs. As migrating birds are constantly faced with varying habitat and food resources, changes in the gut should be made to rapidly accommodate changes in food intake and quality. Miller (1975) showed that mallards changing from a low fibre to a high fibre diet exhibited increases in digestive organ size within 3 weeks.

Although a decrease in feeding rates by greater scaup was observed in late spring, only large intestine length showed a significant decrease. In redheads (Aythya americana) large intestine length and weight show strong curvilinear correlations with seasonal feeding patterns, whereas gizzard weight, and small intestine and caecum weights and lengths are not significantly correlated (Bailey 1982). The equation predicting large intestine length in redheads from time spent feeding (Bailey 1982) was applied to data for greater scaup. Calculated large intestine lengths for adult males in early and late spring are 91.6 mm and 84.7 mm respectively. Observed values were 92.0 mm and 84.1 mm. Predicted values for adult females are 93.2 mm and 82.8 mm; observed values were 93.0 mm and 85.3 mm.

The fact that the weight of the large intestine did not appear to respond to feeding rates is difficult to explain. Several authors have shown that digestive organs may be used for protein storage (Ankney 1977, Korschgen 1977, Bailey 1982). Protein from the walls of the intestine may have been used to supply needs for lipid catabolism resulting in intestinal weight loss during migration prior to arrival at Lake St. Louis. Increases in intestinal weight may have occurred shortly after arrival in the earliest part of the spring before I was able to obtain samples. If the intestines are being used as a protein reserve for migratory flight then the weight should not respond to changes in food intake and should not decrease as the frequency of feeding decreases.

Sample sizes of juveniles are small, however slightly higher mean values for intestinal weights and lengths suggest that food intake may not necessarily parallel that of adults. Differences in chronology of migration and in behaviour will affect time spent feeding and food intake.

Studies dealing with the gut have primarily used length as the measurement of change (Lewin 1963, Moss 1972, 1974, Pendergast and Boag 1973, Savory and Gentle 1976a, b, Ankney 1977). Miller (1975) found that the weight of the gut was influenced by dietary fibre and increased concurrently with length. Late spring adult lesser scaup exhibited large gains in small and large intestine weight without concurrent changes in length. The lack of change in large intestine length agrees with the similar feeding rates observed in early and late ~~spring~~. The weight measures do not seem to be related to feeding rates, suggesting that protein was being stored in the intestines to replace what was used for the degradation of lipids during migratory flight.

Lewin (1963) found that the intestinal villi of California quail (*Lophortyx californicus*) lengthened in response to low quality bulky foods, which would presumably result in a higher intestinal weight. However increases in villi length were accompanied by longer small and large intestines and longer cacae. Lesser scaup showed a higher weight:length ratio in the intestines suggesting enhanced efficiency. Breitenbach *et al*. (1963) found that pheasants (*Phasianus colchicus*) on a protein restricted diet showed an increase in small intestine weight, presumably to enhance protein uptake from available food. Increases in protein weight and breast muscle weight may have required enhanced protein uptake by the intestines. Increases in protein over the spring occurring concurrently with intestinal weight increases may also suggest protein storage in these digestive organs. The fact that gizzard weight does not change along with the weights of the intestines is puzzling as this organ is believed to be a protein reserve (Ankney 1977, Korschgen 1977, Bailey

1982). Digestive organ measurements taken on the wintering grounds before and during premigratory hyperphagia with concurrent monitoring of feeding rates would provide more insight into changes in the digestive organs. Measurements of food consumption would provide more reliable data to explain changes in digestive organ size. Time spent feeding may increase if lower quality foods are consumed. Gadwalls exhibited increases in time spent feeding concurrent with declines in most gut measurements, indicating that feeding activity reflected a change in diet and can not entirely explain changes in gut size (Paulus 1982). Although food consumption can be monitored for captive birds such information is difficult to obtain for free living birds.

The use of stopover areas such as Lake St. Louis for nutrient replenishment by greater scaup migrating in the fall is indicated by heavier body weights in late season individuals, although certain variation between years was indicated. Contrary to this body weight increases in lesser scaup did not always occur over the fall. Distances between stopover areas may be shorter in the fall resulting in less weight loss between stops. Body weights of early fall adult males in 1980 indicated that fat and protein reserves had already been replenished in many birds. It is not possible to say whether these birds had arrived here fat or if increases in weight occurred during the stopover at Lake St. Louis. Similarly body weights of early and late fall juvenile lesser scaup were not different from each other in 1979. Mean body weights over 700 g indicate that many early juveniles had already established substantial reserves in early fall. An examination of raw data reveals that in the late fall period of 1979 there were many low weight birds, which were presumably late arrivals. The variation in body weights is indicated by the high standard errors associated with them (Table 9). A later migration by some birds may indicate regional differences in time of nesting or may be weather-related.

Contour Feather Molt

The extent of molt in greater scaup generally agrees with the results of Billard and Humphrey (1972). The majority of both adult and juvenile males appear to have completed the pre-alternate molt by the time the spring migration is underway. Billard and Humphrey (1972) found that 20% of juvenile males were still exhibiting light molt whereas in the present study no molt was observed in this age-sex class. The exclusion of the scapulohumeral feather tracts in the present study may have contribured to this discrepancy, however I would expect that the main reason is that the majority of Billard and Humphrey's (1972) samples were collected in Connecticut. Birds from that area would not be as advanced into the spring migration and many may not have even begun the northward journey.

Results of the present study and those of Billard and Humphrey (1972) indicate that the majority of female greater and lesser scaup are well into the pre-basic molt during the spring migration and that these 2 energy demanding events are not separated in time. Overlaps of energy demanding events may be attributed to pressures of time or shortages of energy (King 1974). Although molt is considered an energy demanding function (Billard and Humphrey 1972, King 1974) it is occurring during another energy demanding event, namely migration, and during a period of nutrient storage. There is obviously no nutritional stress on females at this time. However, increased food intake or adjustments in time-activity budgets may be necessary for molt and migration to occur simultaneously.

CONCLUSIONS

Greater and lesser scaup are utilizing stopover areas such as Lake St. Louis as feeding and resting areas during the course of migration. Changes in behaviour over the migratory period appear to be influenced by levels of stored lipids in the birds, the ratio of males to females and the birds familiarity with the area and possible changes in the food resource. During the spring both species exhibited increases in stored lipids. Calculations of flight ranges based on levels of stored lipids in spring birds show that scaup have to replenish lipids used during migration to reach the breeding grounds in good condition. Higher protein levels in late spring birds indicated that proteins were being accumulated concurrently with lipids. Changes in digestive organs could not be clearly explained by changes in feeding rates. Digestive organ changes may be related to protein storage and functional changes in the gut.

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Table 1. Ratios of males per female in greater and lesser scaup during spring migration on Lake St. Louis, 1980

	March 23-March 25	March 26-April 3	April 4-April 13	April 14-April 21	April 22-May 1
Greater scaup	3.9	3.0	2.6	1.8	2.0
Lesser scaup	2.3	3.6	1.9	1.8	1.6

Table 2. Percentages of greater scaup performing various activities during daylight hours in early[a] and late spring and mean hours per day spent by each duck in these activities

	Feed			Rest			Preen			Swim			Fly		
	Early		Late	Early		Late	Early		Late	Early		Late	Early		Late
	(3.56)[b]		(2.95)	(2.97)		(5.26)	(1.59)		(1.89)	(4.97)		(4.44)	(0.72)		(0.36)
Males	25.8[c]	**	19.8	21.5	**	35.3	11.5	N.S.	12.7	36.0	**	29.8	5.2	**	2.4
	*		N.S.	**		*	**		**	**		**	**		N.S.
Females	27.4	**	18.3	24.9	**	39.2	17.8	*	20.6	27.0	**	20.3	2.9	**	1.5
	(3.78)		(2.73)	(3.44)		(5.84)	(2.46)		(3.07)	(3.73)		(3.02)	(0.40)		(0.22)

[a] Average number of daylight hours (from 0.5 hour before sunrise to 0.5 hour after sunset) in early spring = 13.8 and in late spring = 14.9.

[b] Numbers in brackets are mean numbers of hours per day spent by each duck in each activity.

[c] Percentages of ducks observed performing each activity.

*$P<0.05$, statistical significance determined by chi-square test on raw totals.

**$P<0.01$, statistical significance determined by chi-square test on raw totals.

N.S. No significant difference determined by chi-square test on raw totals.

Table 3. Percentages of lesser scaup performing various activities during daylight hours in early[a] and late spring and mean hours per day spent by each duck in these activities

	Feed			Rest			Preen			Swim			Fly		
	Early		Late	Early		Late	Early		Late	Early		Late	Early		Late
	(2.19)[b]		(2.51)	(3.72)		(6.27)	(1.40)		(1.87)	(6.44)		(4.05)	(0.57)		(0.41)
Males	15.3[c]	N.S.	16.6	26.0	**	41.5	9.8	**	12.4	45.0	**	26.8	4.0	**	2.7
	**		*	**		N.S.	**		**	**		**	**		**
Females	17.5	N.S.	19.0	37.6	**	41.3	15.8	**	19.9	27.4	**	19.1	1.7	**	0.8
	(2.50)		(2.87)	(5.38)		(6.24)	(2.26)		(3.00)	(3.92)		(2.88)	(0.24)		(0.12)

[a] Average number of daylight hours (from 0.5 hour before sunrise to 0.5 hour after sunset) in early spring = 14.3, and in late spring = 15.1.

[b] Numbers in brackets are mean numbers of hours per day spent by each duck in each activity.

[c] Percentages of ducks observed performing each activity.

*$P < 0.05$, statistical significance determined by chi-square test on raw totals.

**$P < 0.01$, statistical significance determined by chi-square test on raw totals.

N.S. No significant difference determined by chi-square test on raw totals.

Table 4. Comparison of body parameters[a] of early and late spring migrant greater scaup collected at Lake St. Louis, Quebec, 1980

	Male		Female	
Parameter	Adult $\bar{x}$ ± SE (N)	Juvenile $\bar{x}$ ± SE (N)[b]	Adult $\bar{x}$ ± SE (N)[b]	Juvenile $\bar{x}$ ± SE (N)[b]
Body weight				
Early	1034.64±23.28 (7)	902.15±10.15 (2)	855.00 (1)	937.00 (1)
Late	1114.39±28.73 (16)	1079.35±48.47 (4)	1110.60±33.35 (3)	1047.70 (1)
Breast muscle weight				
Early	89.79± 1.21 (7)	82.05± 2.43 (2)	79.00 (1)	87.57 (1)
Late	91.47± 2.05 (16)	93.42± 1.51 (4)	90.52± 3.87 (3)	87.43 (1)
Leg weight				
Early	43.58± 1.19 (7)	39.86± 0.98 (2)	35.33 (1)	41.53 (1)
Late	44.11± 0.67 (14)	41.17± 1.05 (4)	40.32± 0.34 (3)	39.89 (1)
Gizzard weight				
Early	49.38± 2.19 (7)	46.44± 1.63 (2)	37.21 (1)	36.64 (1)
Late	46.02± 2.09 (16)	46.88± 4.18 (4)	43.61± 1.46 (3)	40.60 (1)
Small intestine length				
Early	1605.1 ±33.85 (7)	1590.0 ±59.00 (2)	1621.0 (1)	1500.0 (1)
Late	1651.9 ±37.42 (16)	1779.0 ±27.29 (4)	1690.0 ±11.24 (3)	1705.0 (1)

Continued.........

Table 4 (Continued)

Parameter	Male Adult $\bar{x}$ ± SE (N)	 Juvenile $\bar{x}$ ± SE (N)^b	Female Adult $\bar{x}$ ± SE (N)^b	 Juvenile $\bar{x}$ ± SE (N)^b
Small intestine weight				
Early	21.22± 1.38 (7)	19.23± 0.19 (2)	26.71 (1)	15.81 (1)
Late	21.21± 1.54 (16)	21.77± 1.36 (4)	21.56± 1.68 (3)	20.74 (1)
Large intestine length				
Early	92.0 ± 1.23 (7)	86.0 ± 2.00 (2)	93.0 (1)	81.0 (1)
Late	84.1 ± 1.86 (16)**	89.3 ± 3.68 (4)	85.3 ± 6.01 (3)	83.0 (1)
Large intestine weight				
Early	1.79± 0.06 (7)	1.50± 0.05 (2)	2.36 (1)	1.36 (1)
Late	1.92± 0.13 (16)	1.97± 0.19 (4)	2.21± 0.28 (3)	2.86 (1)
Combined ceca length				
Early	287.7 ± 9.23 (7)	286.0 ±17.00 (2)	271.0 (1)	226.0 (1)
Late	309.9 ± 5.44 (16)	308.5 ± 7.19 (4)	283.0 ± 7.23 (3)	249.0 (1)
Combined ceca weight				
Early	1.15± 0.08 (7)	1.04± 0.18 (2)	1.35 (1)	1.13 (1)
Late	1.17± 0.06 (16)	1.04± 0.08 (4)	1.40± 0.02 (3)	1.47 (1)

Continued..........

Table 4 (Continued)

Parameter	Male Adult $\bar{x}$ ± SE (N)		Male Juvenile $\bar{x}$ ± SE $(N)^b$	Female Adult $\bar{x}$ ± SE $(N)^b$	Female Juvenile $\bar{x}$ ± SE $(N)^b$
Skin weight					
Early	217.83±14.26 (7)	*	144.00± 2.93 (2)	121.64 (1)	185.95 (1)
Late	261.56±13.21 (16)		240.99±39.29 (4)	273.04±21.08 (3)	259.72 (1)
Abdominal fat weight					
Early	9.16± 1.39 (7)	*	2.66± 0.20 (2)	1.79 (1)	13.57 (1)
Late	18.21± 2.65 (16)		14.37± 4.56 (4)	16.30± 6.46 (3)	15.99 (1)
Intestinal fat weight					
Early	6.21± 1.06 (7)	*	1.75± 0.51 (2)	--	10.35 (1)
Late	12.11± 2.04 (16)		9.68± 2.59 (4)	11.23± 3.50 (3)	14.26 (1)
Total fat weight					
Early	142.35±14.63 (7)	*	56.12± 1.94 (2)	42.09 (1)	135.22 (1)
Late	203.17±17.25 (16)		171.70±44.86 (4)	178.47±39.85 (3)	172.20 (1)

Continued..........

Table 4 (Continued)

Parameter	Male			
	Adult $\bar{x}$ ± SE (N)	Juvenile $\bar{x}$ ± SE (N)[b]	Adult $\bar{x}$ ± SE (N)[b]	Juvenile $\bar{x}$ ± SE (N)[b]
Protein weight[c]				
Early	215.23± 2.75 (7)	198.60± 3.45 (2)	194.14 (1)	200.53 (1)
Late	219.09± 4.44 (16)	211.71± 3.39 (4)	205.32± 3.50 (3)	199.15 (1)
Fat-free carcass weight				
Early	755.17±11.18 (7)	716.73± 6.41 (2)	682.51 (1)	678.58 (1)
Late	765.64±14.17 (16)	754.42± 9.75 (4)	755.76± 8.83 (3)	713.50 (1)

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[a] Weights are in grams and lengths are in millimeters.

[b] When $N \leq 2$ no statistical test is performed.

[c] Lean dry weight: see text.

* $P<0.05$

** $P<0.01$

Table 5. Comparison of indices of lipid reserves (body weight/body length) of male and female adult greater scaup collected during spring 1980

	Early spring			Late spring		
	Male		Female	Male		Female
	$\bar{x}$ ± SE (N)		$\bar{x}$ ± SE (N)	$\bar{x}$ ± SE (N)		$\bar{x}$ ± SE (N)
Body weight/body length	2.251±0.04 (7)	N.T.	1.934 (1)	2.416±0.05 (16)	N.S.	2.501±0.06 (3)

N.T. No test.

N.S. Not significant ($P>0.05$).

Table 6. Comparison of body parameters[a] of early and late spring migrant lesser scaup collected at Lake St. Louis, Quebec, 1980

	Male		Female	
Parameter	Adult $\bar{x}$ ± SE (N)	Juvenile $\bar{x}$ ± SE (N)	Adult $\bar{x}$ ± SE (N)	Juvenile $\bar{x}$ ± SE (N)
Body weight				
Early	778.54±13.18 (13)	728.28±12.97 (5)	769.13±43.26 (3)	-
Late	847.88±18.90 (18) *	802.45±21.93 (8) *	907.53±27.26 (3) *	833.40 (1)
Breast muscle weight				
Early	68.78± 0.98 (13)	64.57± 1.03 (4)	62.59± 4.57 (2)	-
Late	72.11± 1.15 (18) *	68.87± 1.40 (8) *	72.56± 3.96 (3)	68.29 (1)
Leg weight				
Early	31.94± 0.55 (13)	31.00± 0.67 (5)	28.73± 1.27 (3)	-
Late	31.84± 0.41 (16)	31.10± 0.59 (7)	30.45± 0.58 (3)	29.99 (1)
Gizzard weight				
Early	28.26± 1.06 (13)	26.70± 1.89 (5)	30.02± 2.21 (3)	-
Late	29.61± 1.20 (18)	30.81± 2.74 (8)	26.46± 1.39 (3)	34.94 (1)
Small intestine length				
Early	1697.5 ±48.95 (13)	1658.4 ±82.29 (5)	1803.7 ±113.78 (3)	-
Late	1695.6 ±26.70 (18)	1702.5 ±55.13 (8)	1830.0 ±75.14 (3)	1998.0 (1)

Continued.........

Table 6 (Continued)

	Male			Female		
Parameter	Adult $\bar{x}$ ± SE (N)		Juvenile $\bar{x}$ ± SE (N)	Adult $\bar{x}$ ± SE (N)		Juvenile $\bar{x}$ ± SE (N)
Small intestine weight						
Early	16.78± 0.88 (13)	**	14.98± 1.72 (5)	17.76± 0.81 (3)	*	-
Late	20.56± 0.63 (18)		18.40± 1.44 (8)	24.91± 1.65 (3)		20.59 (1)
Large intestine length						
Early	75.8 ± 1.70 (13)		76.2 ± 2.71 (5)	72.7 ± 4.98 (3)		-
Late	78.9 ± 1.10 (18)		80.9 ± 3.01 (1)	76.3 ± 3.18 (3)		82.0 (1)
Large intestine weight						
Early	1.10± 0.07 (13)	**	1.09± 0.10 (5)	1.24± 0.17 (3)		-
Late	1.39± 0.06 (18)		1.28± 0.17 (8)	1.52± 0.10 (3)		1.70 (1)
Combined ceca length						
Early	256.6 ± 7.93 (13)		260.0 ±15.05 (5)	248.0 ±26.63 (3)		-
Late	265.3 ± 6.19 (18)		246.0 ±18.36 (8)	253.7 ±15.68 (3)		276.0 (1)
Combined ceca weight						
Early	0.90± 0.05 (13)		0.88± 0.07 (5)	0.97± 0.17 (3)		-
Late	1.00± 0.05 (18)		1.02± 0.06 (8)	1.09± 0.11 (3)		1.28 (1)

Continued..........

Table 6 (Continued)

Parameter	Male Adult x̄ ± SE (N)	 Juvenile x̄ ± SE (N)	Female Adult x̄ ± SE (N)	 Juvenile x̄ ± SE (N)
Skin weight				
Early	165.47± 7.12 (13)	146.31±13.19 (5)	171.34±21.06 (3)	-
Late	205.50±10.34 (18)*	176.99±13.04 (8)	247.47±32.23 (3)	190.58 (1)
Abdominal fat weight				
Early	7.92± 1.13 (13)	5.91± 1.11 (5)	8.16± 3.34 (3)	-
Late	13.79± 1.80 (18)*	11.22± 1.92 (8)	17.40± 5.14 (3)	10.06 (1)
Intestinal fat weight				
Early	4.30± 0.42 (13)	3.32± 0.80 (5)	3.78± 1.10 (3)	-
Late	9.46± 1.51 (17)*	7.09± 1.40 (8)	12.32± 4.19 (3)	7.99 (1)
Total fat weight				
Early	111.31± 8.01 (13)	95.95±13.11 (5)	108.49±23.85 (3)	-
Late	165.83±14.04 (16)*	131.13±17.45 (8)	195.85±40.10 (3)	125.40 (1)

Continued..........

Table 6 (Continued)

	Male		Female	
Parameter	Adult $\bar{x}$ ± SE (N)	Juvenile $\bar{x}$ ± SE (N)	Adult $\bar{x}$ ± SE (N)	Juvenile $\bar{x}$ ± SE (N)
Protein weight				
Early	162.09± 2.79 (13)	149.56± 2.86 (5)	151.09± 4.76 (3)*	-
Late	167.42± 2.65 (16)	162.62± 4.01 (8)	166.12± 4.25 (3)	150.61 (1)
Fat-free weight				
Early	569.27± 8.78 (13)	535.37±10.43 (5)	552.78±15.64 (3)	-
Late	581.17± 8.62 (16)	571.49±13.69 (8)	584.71±10.52 (3)	556.50 (1)

Weights are in grams and lengths are in millimeters.

Lean dry weight: see text.

*$P<0.05$

**$P<0.01$

Table 7. Comparison of indices of lipid reserves (body weight/body length) of male and female adult lesser scaup collected during spring 1980

	Early spring		Late spring	
	Male	Female	Male	Female
	$\bar{x}$ ± SE (N)	$\bar{x}$ ± SE (N)	$\bar{x}$ ± SE (N)	$\bar{x}$ ± SE (N)
Body weight/body length	1.873±0.03 (13)	N.S. 1.885±0.09	2.016±0.04 (18)	N.S. 2.196±0.07 (3)

N.S. Not significant ($\underline{P}>0.05$).

Table 8. Comparison of body weights (g) of early and late fall greater scaup collected and killed by hunters on Lake St. Louis, Quebec

	Adult male		Adult female	
	1979 $\bar{x}$ ± SE (N)	1980 $\bar{x}$ ± SE (N)	1979 $\bar{x}$ ± SE (N)[a]	1980 $\bar{x}$ ± SE (N)
Early	915.80±29.65 (14)	996.32±24.24 (19)	896.00 (1)	917.71±27.11 (10)
	**			
Late	1077.34±24.51 (29)	1065.83±55.38 (6)	1044.26±33.68 (5)	1025.00±56.57 (4)

	Juvenile male		Juvenile female		
	1979 $\bar{x}$ ± SE (N)	1980 $\bar{x}$ ± SE (N)	1979 $\bar{x}$ ± SE (N)		1980 $\bar{x}$ ± SE (N)
Early	946.52±28.17 (15)	943.89±45.54 (9)	810.78±27.47 (6)	*	902.00±29.19 (10)
			**		
Late	991.42±24.92 (30)	1048.75±27.53 (8)	955.39±23.46 (12)		961.07±22.14 (14)

[a] When N $\leq$ 2 no statistical test is performed.

*$P<0.05$

**$P<0.01$

Table 9. Comparison of body weights (g) of early and late fall migrant lesser scaup collected and killed by hunters on Lake St. Louis, Quebec

	Adult male			Adult female	
	1979 $\bar{x}$ ± SE (N)		1980 $\bar{x}$ ± SE (N)	1979 $\bar{x}$ ± SE (N)[a]	1980 $\bar{x}$ ± SE (N)[a]
Early	767.57±23.17 (14)	*	881.25±30.71 (4)	602.20 (1)	687.50± 7.22 (4)
Late	803.57±33.38 (7)		823.33±19.22 (3)	793.43±72.25 (3)	877.50±47.50 (2)

	Juvenile male			Juvenile female	
	1979 $\bar{x}$ ± SE (N)		1980 $\bar{x}$ ± SE (N)	1979 $\bar{x}$ ± SE (N)	1980 $\bar{x}$ ± SE (N)
Early	732.49±19.41 (13)		661.67±38.44 (3)	713.64±18.62 (7)	678.33±24.04 (3)
			*		*
Late	712.51±51.35 (7)	*	827.50±22.76 (8)	731.63±51.41 (4)	800.00±23.61 (9)

[a] When N ≤ 2 no statistical test is performed.

*P<0.05

Table 10. Total molt scores of greater and lesser scaup during early and late spring 1980

Greater scaup	Adult male			Juvenile male			Adult female			Juvenile female		
	Early (n=7)		Late (n=16)	Early (n=2)		Late (n=4)	Early (n=1)		Late (n=3)	Early (n=1)		Late (n=1)
Mean score	0.17	N.S.	0.00	0.00	N.S.	0.00	2.50	a	7.80	4.70	a	8.00
Minimum score	0.00		0.00	0.00		0.00	-		6.00	-		-
Maximum score	1.20		0.00	0.00		0.00	-		9.50	-		-

Lesser scaup	Adult male			Juvenile male			Adult female			Juvenile female		
	Early (n=13)		Late (n=18)	Early (n=5)		Late (n=8)	Early (n=3)		Late (n=3)	Early (n=0)		Late (n=1)
Mean score	0.04	N,S.	0.46	0.71	N.S.	0.00	7.17	N.S.	6.37	-		6.20
Minimum score	0.00		0.00	0.00		0.00	3.93		4.50	-		-
Maximum score	0.57		5.50	3.57		0.00	11.23		8.74	-		-

[a] Sample size too small for statistical test.

N.S. No significant difference between scores.

Table 11. Molt scores of greater scaup by body region during early and late spring, 1980

	Adult male		Juvenile male		Adult female		Juvenile female	
	Early (n=7)	Late (n=16)	Early (n=2)	Late (n=4)	Early (n=1)	Late (n=3)	Early (n=1)	Late (n=1)
Sides and flanks								
Mean	0.03	0.00	0.00	0.00	0.60	2.27	1.80	3.00
Minimum	0.00	0.00	0.00	0.00	-	1.80	-	-
Maximum	0.20	0.00	0.00	0.00	-	3.00	-	-
Upper breast and upper back								
Mean	0.14	0.00	0.00	0.00	1.33	2.67	0.67	2.67
Minimum	0.00	0.00	0.00	0.00	-	2.67	-	-
Maximum	1.00	0.00	0.00	0.00	-	2.67	-	-
Lower breast and belly								
Mean	0.00	0.00	0.00	0.00	0.17	1.33	0.83	0.33
Minimum	0.00	0.00	0.00	0.00	-	0.50	-	-
Maximum	0.00	0.00	0.00	0.00	-	1.83	-	-
Mid-back and rump								
Mean	0.00	0.00	0.00	0.00	0.40	1.53	0.20	2.00
Minimum	0.00	0.00	0.00	0.00	-	1.00	-	-
Maximum	0.00	0.00	0.00	0.00	-	2.00	-	-

Table 12. Molt scores of lesser scaup by body region during early and late spring, 1980

	Adult male		Juvenile male		Adult female		Juvenile female	
	Early (n=13)	Late (n=18)	Early (n=5)	Late (n=8)	Early (n=3)	Late (n=3)	Early (n=0)	Late (n=1)
Sides and flanks								
Mean	0.03	0.19	0.20	0.00	2.73	2.33	-	2.40
Minimum	0.00	0.00	0.00	0.00	2.40	2.00	-	-
Maximum	0.40	2.20	1.00	0.00	3.00	2.20	-	-
Upper breast and upper back								
Mean	0.00	0.15	0.33	0.00	2.00	1.89	-	3.00
Minimum	0.00	0.00	0.00	0.00	1.33	1.33	-	-
Maximum	0.00	1.67	1.67	0.00	3.00	2.67	-	-
Lower breast and belly								
Mean	0.01	0.06	0.10	0.00	1.39	0.61	-	0.00
Minimum	0.00	0.00	0.00	0.00	0.00	0.17	-	-
Maximum	0.17	0.83	0.50	0.00	2.83	1.00	-	-
Mid-back and rump								
Mean	0.00	0.07	0.08	0.00	1.07	1.53	-	0.8
Minimum	0.00	0.00	0.00	0.00	0.20	0.80	-	-
Maximum	0.00	0.80	0.40	0.00	2.40	2.60	-	-

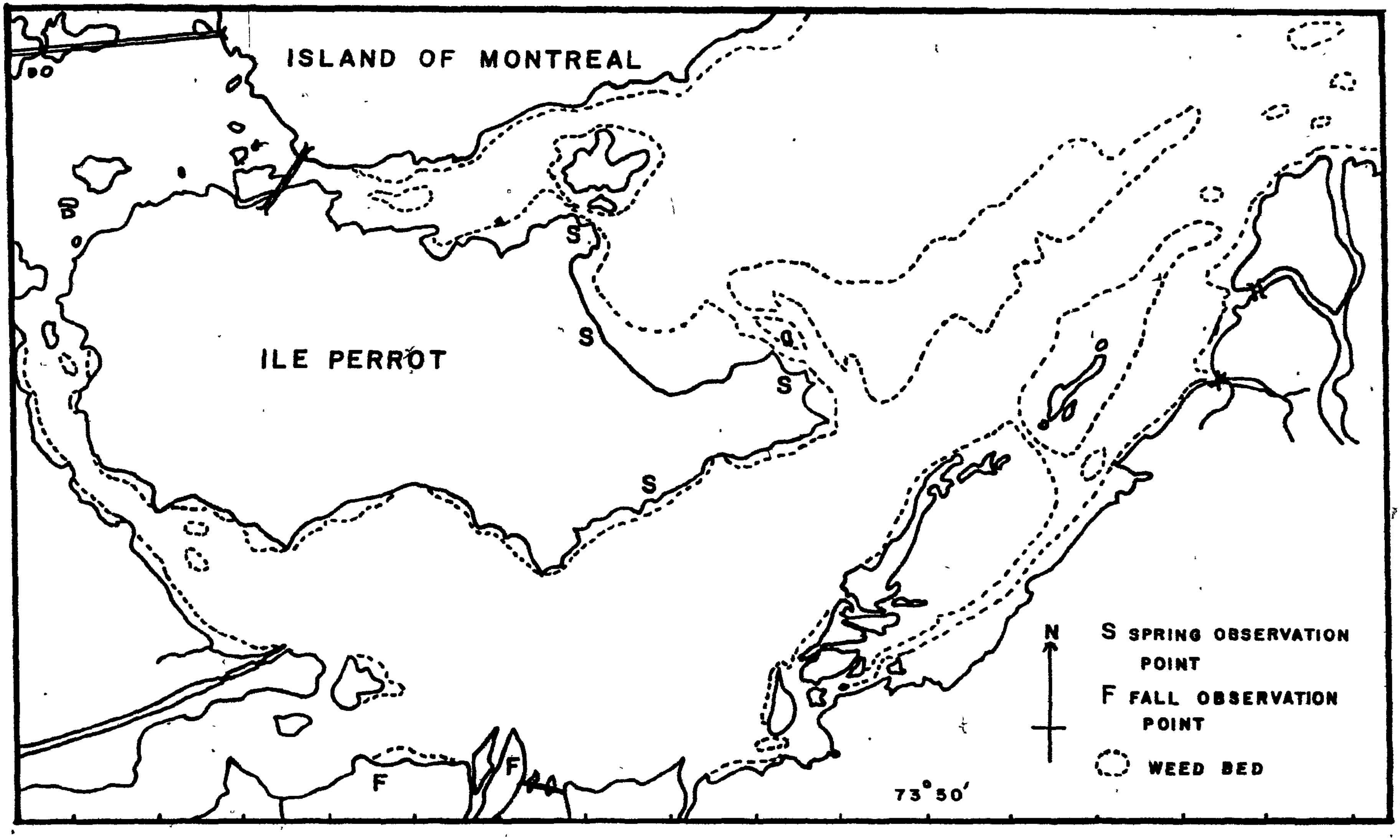

Figure 1. Map of Lake St. Louis, Quebec, showing observation points from which behavioural data were collected.

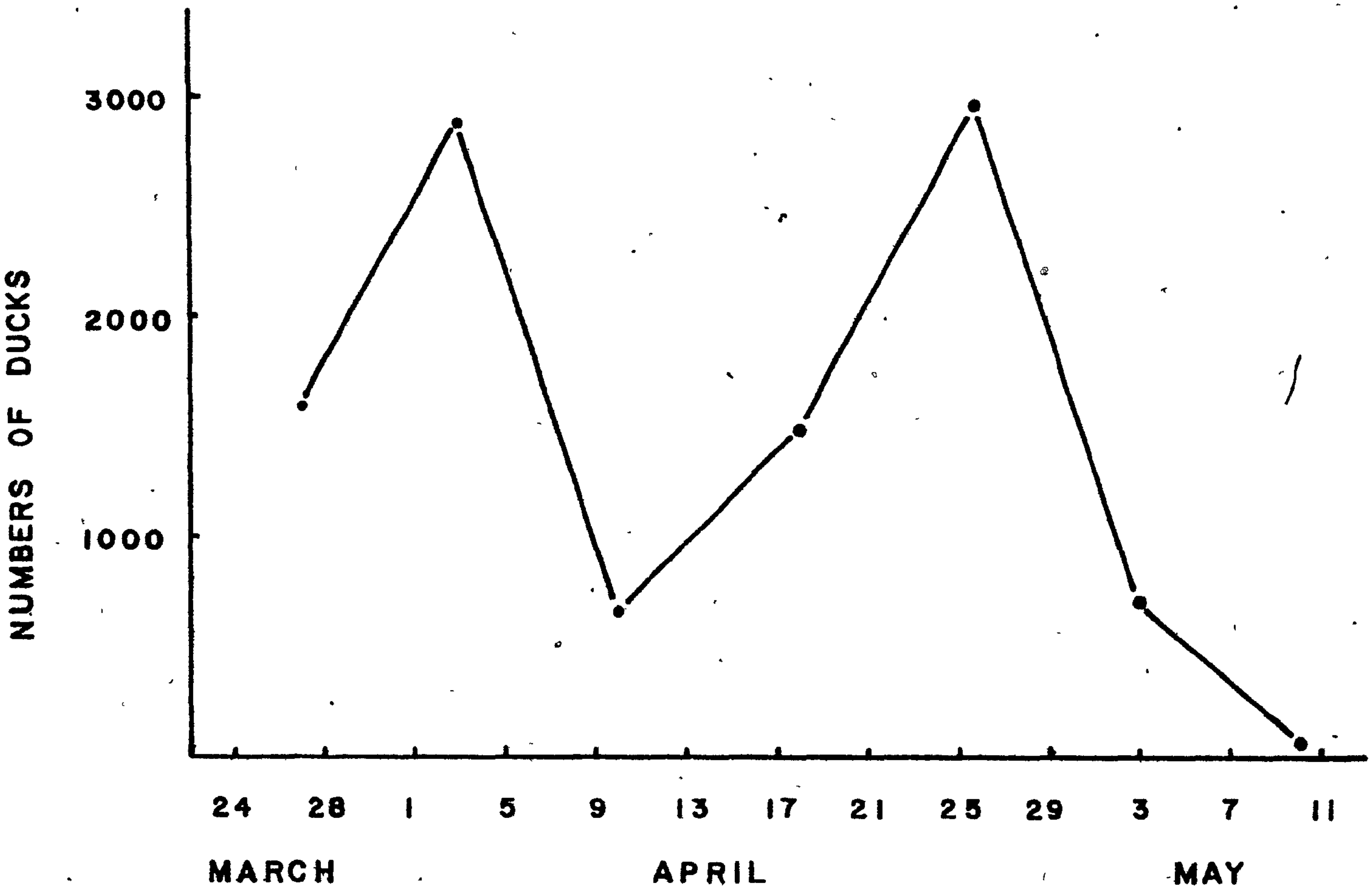

Figure 2. Combined numbers of greater and lesser scaup on Lake St. Louis during spring, 1980.

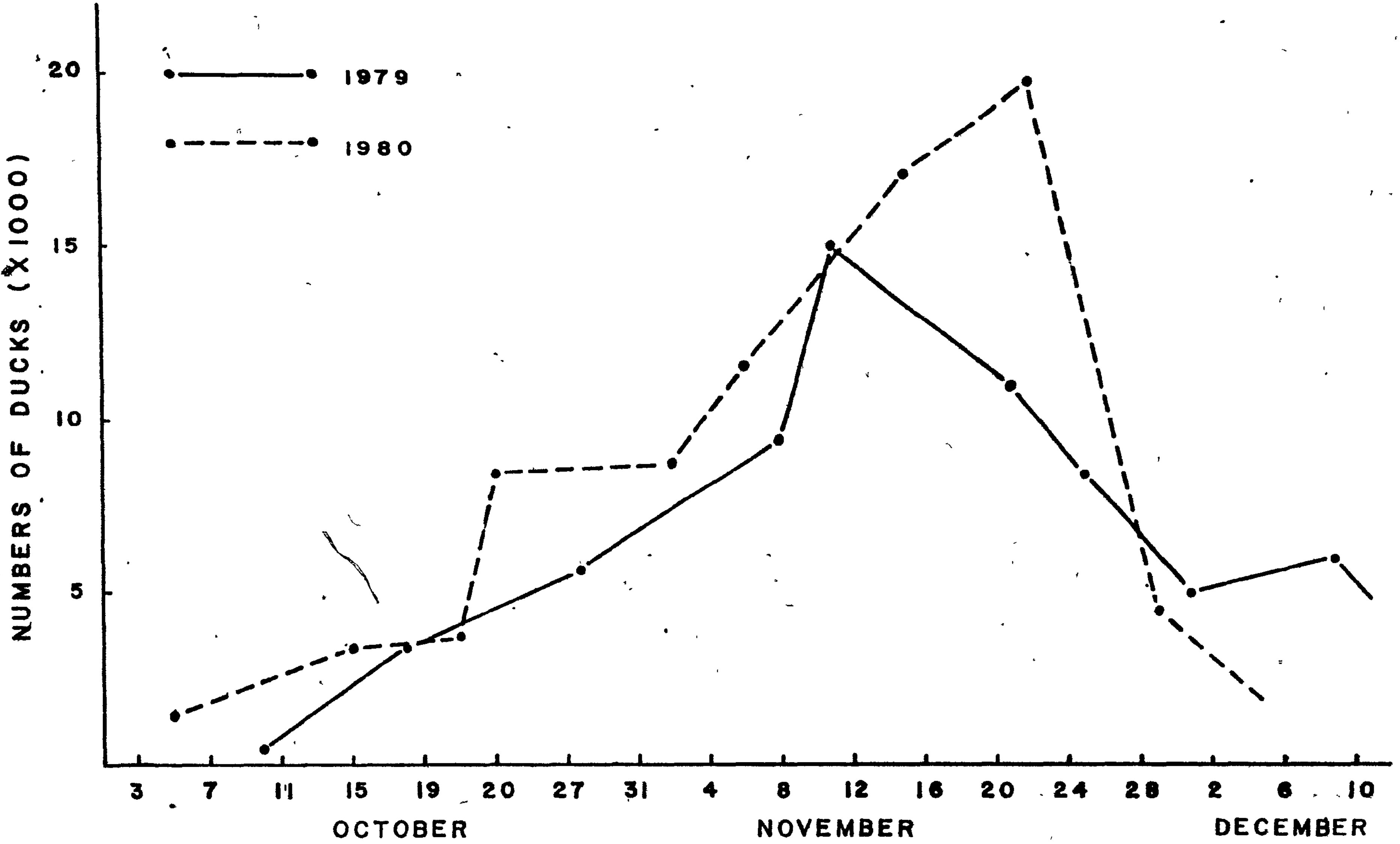

Figure 3. Combined numbers of greater and lesser scaup observed in morning flights from Lake St. Louis to Lake of Two Mountains during fall, 1979 and 1980.

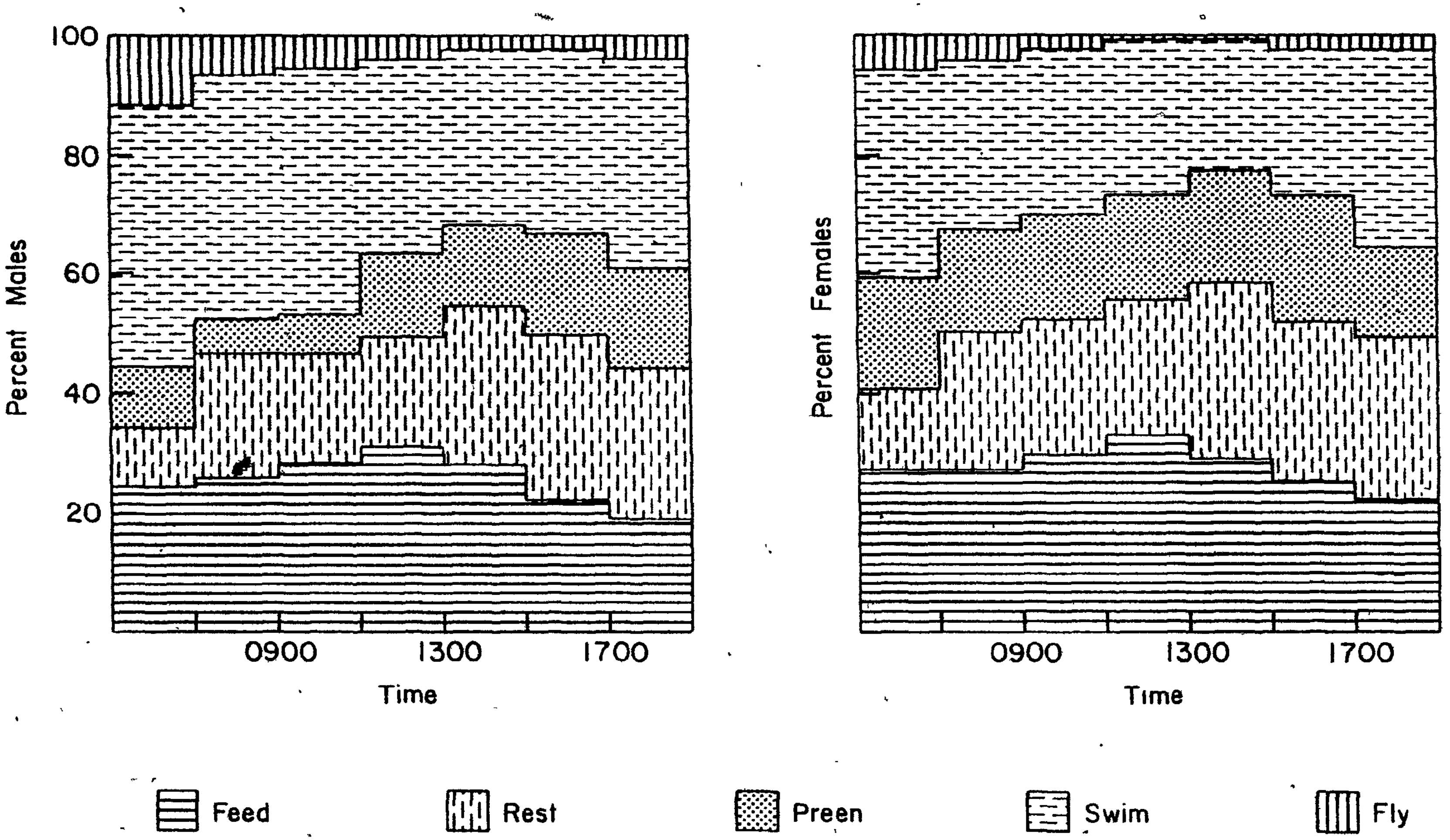

Figure 4. Daily pattern of frequencies of activities of greater scaup in early spring, 1980.

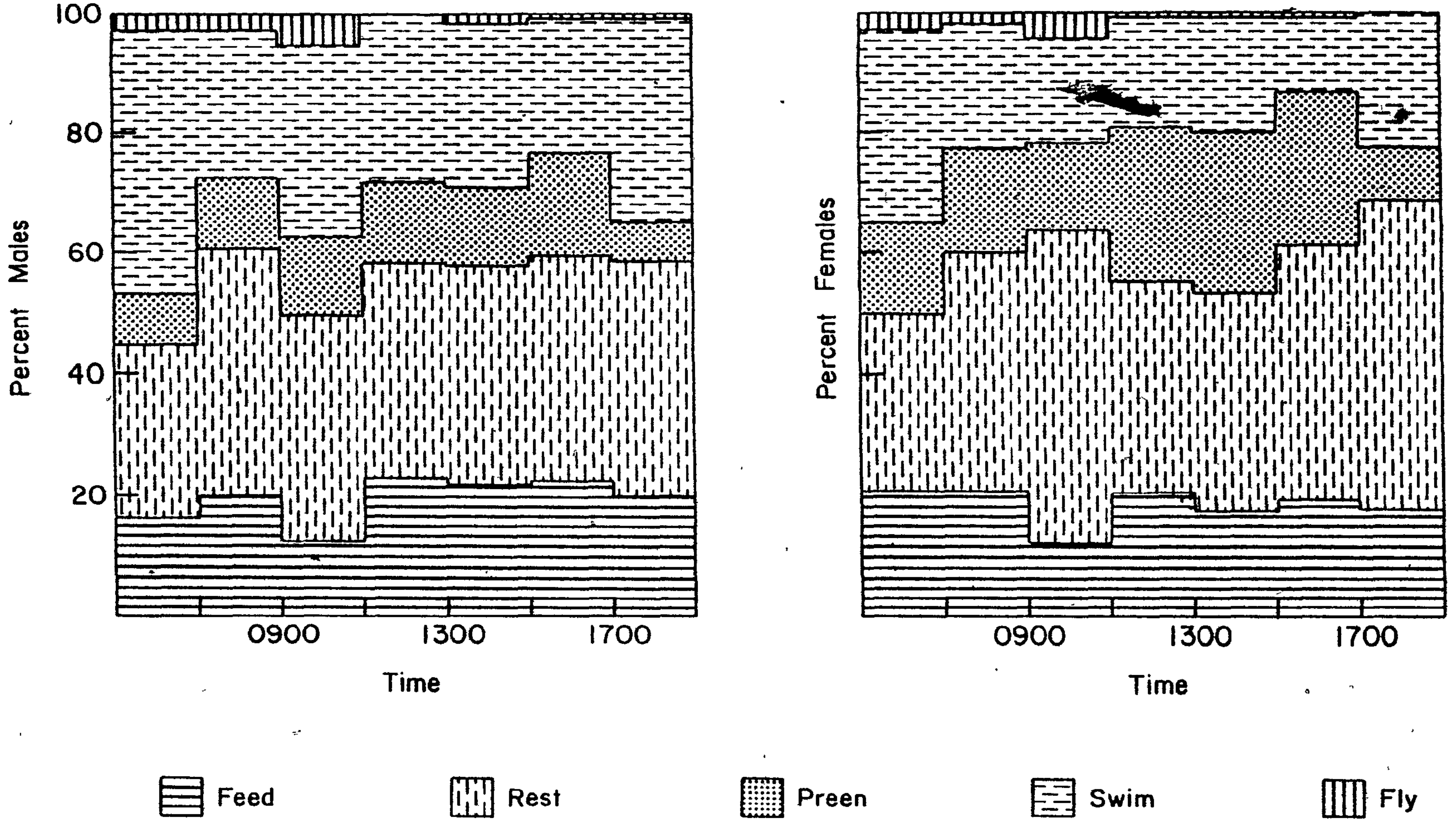

Figure 5. Daily pattern of frequencies of activities of greater scaup in late spring, 1980.

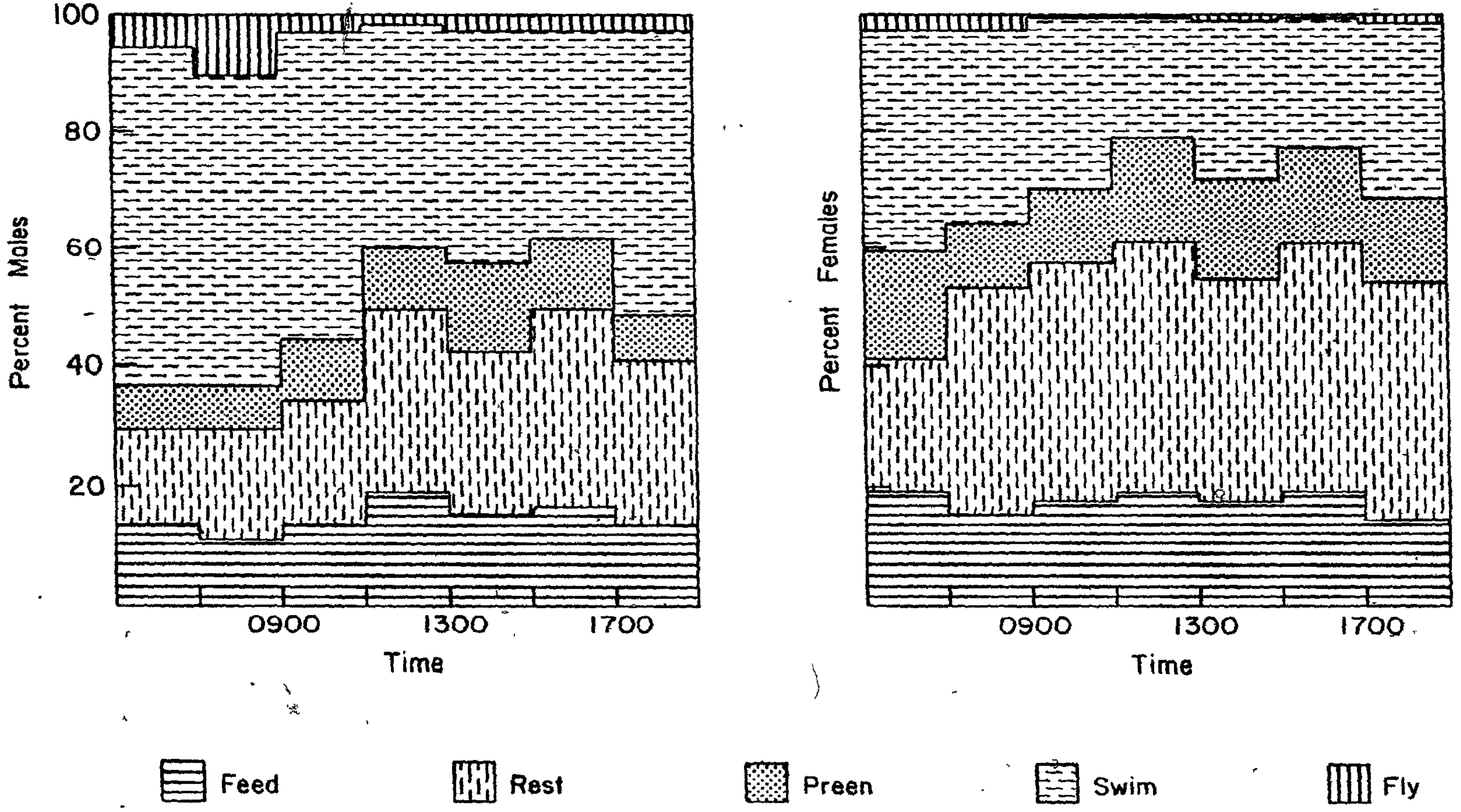

Figure 6. Daily pattern of frequencies of activities of lesser scaup in early spring, 1980.

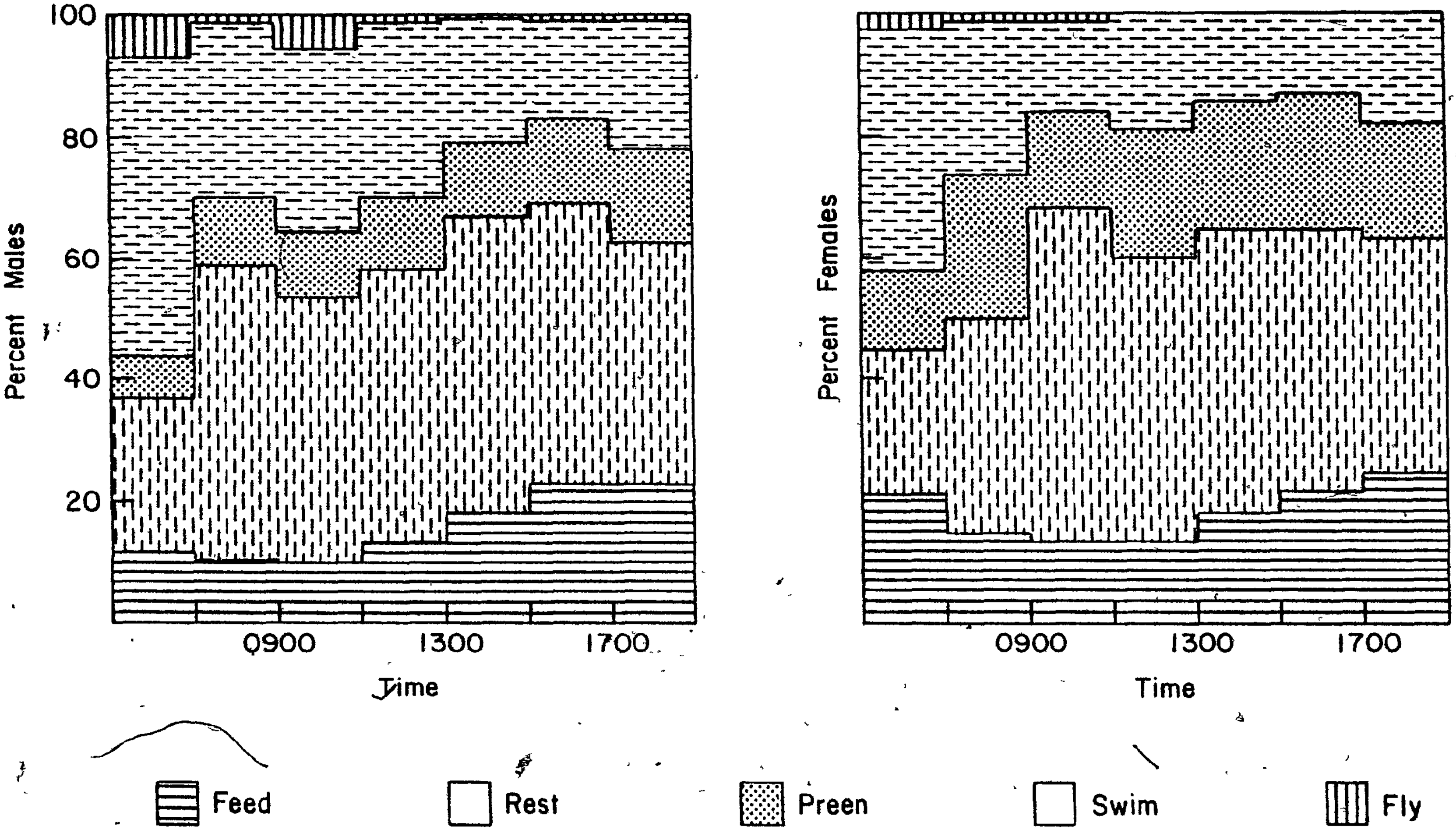

Figure 7. Daily pattern of frequencies of activities of lesser scaup in late spring, 1980.

Estimating reserve lipids in greater scaup (Aythya marila) and lesser scaup (A. affinis).

ABSTRACT

Greater scaup (Aythya marila) and lesser scaup (A. affinis) were collected during their spring and fall migrations at Lake St. Louis, Quebec, in 1979 and 1980. Body measurements and weights of fat deposits were obtained for 35 greater scaup and 39 lesser scaup. Carcasses were homogenized and analyzed for lipid and water content. Percent body water and skin weight were the best predictors of ether-extractable body lipids. Body weight and body weight/body length were good predictors of ether-extractable lipids but may provide less reliable estimates if used for scaup at other stages of their annual cycle. Only abdominal fat weight could be used to derive a single predictive equation estimating ether-extractable lipids for both species. Regression lines with body weight or body weight/body length as the independent variables had the same slope for both species but these differed in elevation.

INTRODUCTION

Measurements of specific fat deposits have been used as indices of reserve lipids in geese (Hanson 1962, Ankney 1977, Ankney and MacInnes 1978). Campbell and Leatherland (1980) have described a method for estimating body lipids and proteins in lesser snow geese (Anser c. caerulescens) using measurements of body weight and body water. Various indices including body water and individual fat deposits, have been used to derive predictive equations for estimating reserve lipids in ducks (Woodall 1978, Bailey 1979, Wishart 1979). Bailey (1979) has suggested that the predictive equations he presented for the redhead (Aythya americana) may provide reliable estimates of reserve lipids for other species of Aythya.

The primary objective of this study was to derive and compare predictive equations for estimating extractable lipids of greater and lesser scaup. These equations provide fast and inexpensive methods of estimating ether-extractable lipids. The underlying hypothesis was that extractable lipids may be predicted for more than one species using the same equation if the species considered are structurally similar. The ability to do this adds greater evidence that the species in question are closely related.

METHODS

Adult greater and lesser scaups were collected by shooting under permit from the Canadian Wildlife Service at Lake St. Louis, Quebec (45^{o} 24' N, 73^{o} 50' W), during spring and fall migrations in 1979 and 1980. During both years birds were collected during the month of April and from the last week in September to the first week of December. Numbers of each sex and species were as follows: 29 male greater scaup; 6 female greater scaup; 31 male lesser scaup; and, 8 female lesser scaup. Birds were weighed fresh to the nearest 0.5 g and were frozen within 2 hours of collection in sealed polyethylene bags for later analyses.

Measurements were taken on indices of structural size and ether-extractable lipids which have been used by other authors (Woodall 1978, Bailey 1979, Wishart 1979). The following measurements to 0.5 mm were taken with a ruler on thawed birds: (1) body length from the tip of the bill to the end of the longest retrix with the bird firmly flattened on its back and the neck straightened but not stretched; (2) wing chord with the wing flattened and straightened as described by Carney (1964); bill length from the commissural point to the tip of the upper mandible; and (4) culmen length from the tip of the nail to the "V" of feathers on the forehead (Harris 1970).

Birds were skinned and dissected, and wet weights to 0.01 g were taken of: (1) unplucked skin, including the subcutaneous fat but excluding the wings which were severed at the distal end of the humerus, and the feet which were severed at the junction of the tibiotarsus and the tarsometatarsus; (2) plucked skin; (3) abdominal fat deposit which lies in the abdominal cavity, under the subcutaneous fat and partially surrounded by the pubic bones; and (4) intestinal mesenteric fat. Keel length was measured to 0.5 mm with a clear plastic ruler.

The entire bird excluding plumage, feet and bill, was ground in a meat grinder, thoroughly mixed then homogenized in a blender. The feet and bill were not included due to difficulties with grinding. Two 20 g samples of each homogenate were freeze-dried at -50°C and 5 microns of pressure to a constant weight to estimate water content. Dried samples were finely ground and washed in petroleum ether for 18 hours in a modified Soxhlet apparatus capable of holding 20 samples. Samples were dried in a vacuum oven at 105°C then reweighed to obtain estimates of their lipid content. All samples were weighed to 0.005 g throughout the procedure. Forward selection, backward elimination, and stepwise multiple regression analyses (Barr _et_ _al_. 1979) were performed to determine the best predictors of fat-free weight. Simple linear regression (Barr _et_ _al_. 1979) was used to determine relationships between various indices and extractable lipids. Comparisons of regression lines between species was done using analyses of covariance (Snedecor and Cochran 1967).

RESULTS

Several independent variables were good predictors of ether-extractable body lipids (Tables 1 and 2). Fresh body weight alone explained 81% of the variation in total lipids for both species. The best predictor was percent body water ($\underline{R}^2 = 0.95$), which varied inversely with stored lipids. Whole skin weight provided reliable estimates for both greater scaup ($\underline{R}^2 = 0.91$) and lesser scaup ($\underline{R}^2 = 0.95$). Plucking only slightly improved the predictive value of skin weight. Abdominal and intestinal fat deposits were good predictors, however, the latter explained more variation in extractable lipids for lesser scaup ($\underline{R}^2 = 0.85$) than for greater scaup ($\underline{R}^2 = 0.77$).

The only structural parameter selected as a predictor of fat-free carcass weight was body length. The equation for greater scaup is: fat-free weight (g) = -693.60 + 3.18 x body length (mm), ($\bar{x} = 456.81$ mm ± 1.69 mm (SE), $\underline{R}^2 = 0.47$, $\underline{P} < 0.0001$). For lesser scaup the equation is: fat-free weight (g) = -361.56 + 2.24 x body length (mm), ($\bar{x} = 416.13$ mm ± 1.65 mm (SE), $R^2 = 0.39$, $\underline{P} < 0.0001$).

Fresh body weight was adjusted for individual differences in fat-free weight by dividing by body length. Although this method corrects for structural differences between sexes, body weight/body length explained 82% of the variation in extractable lipids for both species, an increase of only 1% over body weight alone.

Regression equations predicting extractable lipids were compared between species for each independent variable (Table 3). The only pair of regression lines which could not be considered different for both species were those with abdominal fat weight as the independent variable.

A single equation derived from pooled data from both species is: body lipid (g) = 64.99 + 7.11 x abdominal fat (g), ($\bar{x}$ = 12.61 g ± 0.98 g (SE), $\underline{R}^2 = 0.86$, $\underline{P} < .0001$). Regression lines using body weight or body weight/body length as the independent variable had the same slope for both species, however, elevations were significantly different ($\underline{P} < .01$).

DISCUSSION

The condition of an individual may be evaluated by relating nutrient reserves to nutrient requirements at the stage of the annual cycle. Therefore indices of body lipids must provide reliable estimates of lipid reserves and should be easily obtained. Several of the parameters tested satisfy these requirements. Skin weight, whole or plucked, is a good predictor but careful removal of the skin and subcutaneous fat deposits from a large bird is time consuming. The abdominal fat deposit provides slightly less reliable estimates but is much quicker to disect and can be readily obtained from hunter-killed birds.

Measurements of body weight and body weight/body length are the easiest indices of body lipids to collect and may be the only data available. These values can be obtained from both living and dead birds. The correlation between fresh body weight and extractable lipids is particularly high. This is because increases in fat weight over the period of migration were greater in magnitude than changes in fat-free body weight (Chappell 1982). Applying the predictive equations based on body weight (Tables 1 and 2) to scaup at a different stage of the annual cycle may result in less accurate estimates if non-fat components (eg. protein reserves) are different.

Child and Marshall (1970) used water content to estimate body lipids and fat-free weights of small birds. Redheads (Bailey 1979) and wigeon (Wishart 1979) showed strong correlations between percent body water and reserve lipids. Similarly percent body water provided the best estimates of total lipids in migrant greater and lesser scaup. This relationship is logical. Since fat-free weight changes were relatively small in magnitude (Chappell 1982), any increase in lipids will cause a decrease in body water expressed as a percentage of body weight. Birds used by Bailey (1979) and Wishart (1979) were collected over various stages of the annual cycle but it appears that the variation in water content between individuals was not enough to greatly reduce the correlation between percent body water and body lipids. Although body water provides reliable estimates of lipids, its value is tedious to obtain and the mutilation procedure limits the use of specimens for other purposes.

Several waterfowl researchers have used morphological measurements to correct body weights for variation in structural size (Harris 1970, Owen and Cook 1977, Bennett and Bolen 1978). Since changes in fat-free weights of scaup over migration were relatively small, this was a good measure of structural size. Concurring with the work of Bailey (1979), body length explained most of the variation in fat-free weight. Wing length has been shown to have a strong relationship with fat-free weight in passerines (Connell _et_ _al_. 1960). Although wing length also showed a strong correlation with skeletal weight of American wigeon (Wishart 1979), it was not included as a significant variable in the model predicting fat-free weight of scaup.

Of the indices tested, only abdominal fat provided an equation that could be used for predicting lipids of both greater and lesser scaup. This equation does not resemble the one calculated by Bailey (1979) for redheads, (body lipid = 53.90 + 9.37 x abdominal fat weight), although these were not compared statistically. These results suggest that a single equation with abdominal fat as the independent variable could be used to estimate body lipids in more than one species only if they are closely related. Johnsgard (1965) divides *Aythya* into 3 distinct subgroups: the true pochards, the white eyes, and the scaup-like ducks. The equation using abdominal fat in the present study may therefore provide reliable estimates of lipids for the tufted duck (*A. fuligula*) and the New Zealand scaup (*A. novae-seelandiae*) as it did for greater and lesser scaup. Similarly, Bailey's (1979) equation for redheads may provide reliable estimates of body lipids for the canvasback (*A. valisineria*), European pochard (*A. ferina*) and the ring-necked duck (*A. collaris*). Further testing is required to substantiate this.

The fact that other indices of body lipids could not be used to derive single equations for greater and lesser scaup may be due to species-related differences in morphology and body size. Lipid content as a function of body weight produces almost identical slopes for both species. However, a significant difference in elevations precludes the use of a single equation to estimate body lipids in live-trapped greater and lesser scaup.

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Table 1. Regression of ether-extractable body lipids (g) on independent variables for migrant greater scaup (n = 35)

Independent variable	Mean ± SE	Coefficient of determination[a]	Equation
Body weight (BW)	1071.16g±18.41g	0.81	$\hat{Y} = -462.50 + 0.59\ (BW)$
Percent body water (PW)	58.75%± 0.74%	0.95	$\hat{Y} = 1109.58 - 15.98\ (PW)$
Skin whole (SW)	239.59g± 9.87g	0.91	$\hat{Y} = -109.73 + 1.17\ (SW)$
Skin plucked (SP)	172.22g± 9.53g	0.94	$\hat{Y} = -40.84 + 1.23\ (SP)$
Abdominal fat (AF)	14.20g± 1.61g	0.87	$\hat{Y} = 71.70 + 6.96\ (AF)$
Intestinal fat (IF)	9.36g± 1.13g	0.77	$\hat{Y} = 83.24 + 9.33\ (IF)$
Body weight/body length (BW/L)		0.82	$\hat{Y} = -536.63 + 302.26\ (BW/L)$

---

[a] All correlation coefficients were significant ($\underline{P}<0.0001$).

Table 2. Regression of ether-extractable body lipids (g) on independent variables for migrant lesser scaup (n = 39)

Independent variable	Mean ± SE	Coefficient of determination[a]	Equation
Body weight (BW)	814.92g±13.42g	0.81	$\hat{Y} = -346.57 + 0.60\ (BW)$
Percent body water (PW)	57.74%± 0.72%	0.96	$\hat{Y} = 840.99 - 12.13\ (PW)$
Skin whole (SW)	189.15g± 7.41g	0.95	$\hat{Y} = -80.60 + 1.17\ (SW)$
Skin plucked (SP)	138.96g± 6.62g	0.95	$\hat{Y} = -41.60 + 1.31\ (SP)$
Abdominal fat (AF)	11.19g± 1.14g	0.84	$\hat{Y} = 60.91 + 7.12\ (AF)$
Intestinal fat (IF)	7.24g± 0.88g	0.85	$\hat{Y} + 72.80 + 9.35\ (IF)$
Body weight/body length (BW/L)		0.83	$\hat{Y} = -398.91 + 275.83\ (BW/L)$

[a] All correlation coefficients were significant ($\underline{P}<0.0001$).

Table 3. F values calculated by comparison of regression lines predicting ether-extractable lipids for migrant greater and lesser scaup

Independent variable, X	Comparison of residual variances (df=33,37)[a]	Comparison of slopes (df=1,70)	Comparison of elevations (df=1,71)
Body weight, g (BW)	1.66	0.01	127.28**
Percent body water (BW)	1.73	27.97**	--[c]
Skin whole, g (SW)	2.72**	--[b]	--
Skin plucked, g (SP)	2.10*	--[b]	--
Abdominal fat, g (AF)	1.35	0.05	2.31
Intestinal fat, g (IF)	2.50**	--[b]	--
Body weight/body length (BW/L)	1.69	0.65	85.85**

[a] All residual mean squares for greater scaup were larger than those for lesser scaup.

[b] Comparison of slopes was not done because residual variances were significantly different from one another.

[c] Comparison of elevations was not done because slopes were significantly different from one another.

$^{*}P<0.05$

$^{**}P<0.01$