

BODY COMPOSITION OF WINTERING CANVASBACKS IN LOUISIANA: DOMINANCE AND SURVIVAL IMPLICATIONS¹

WILLIAM L. HOHMAN

U.S. Fish and Wildlife Service, National Wetlands Research Center,
700 Cajundome Blvd., Lafayette, LA 70506-3152

Abstract. I studied effects of sex, age, and month on body mass and composition of Canvasbacks (*Aythya valisineria*) at Catahoula Lake (CL) and the Mississippi River Delta (MRD), Louisiana, in winter 1987-1988. Size-adjusted body mass and fat varied by age, month, and site. Fat levels in immatures were greater at MRD than at CL, but changed similarly at both sites. Adults at MRD were also fatter than those at CL in early winter, especially in December, but fat levels of all birds increased from early to late winter and were equivalent by late winter. Body protein adjusted for structural size varied by age, month, and site, and sex, month, and site. Protein levels by site were higher in adults and males than in immatures and females, but sex- and age-related differences averaged < 11 g (5%). Changes in size-adjusted leg muscle protein (index of feeding activity) and body fat were positively associated. This relation (my measure of feeding efficiency) was not affected by sex or age of Canvasbacks, implying that all birds at CL or MRD fed at similar efficiencies by month. At both sites, females were fatter than males; thus, although males were larger and potentially dominant to females, it appears that females were not disadvantaged in their acquisition of nutrients during the year of study. Body mass of CL and MRD birds in winter 1987-1988 was greater than that of Canvasbacks wintering elsewhere. If overwinter and annual survival of Canvasbacks are related to their relative body mass during winter, then survival probabilities of CL and MRD birds may be high compared to other wintering populations.

Key words: *Aythya valisineria*; Canvasback; Anatidae; body mass; composition; behavior; nonbreeding; Louisiana.

INTRODUCTION

Overwinter and annual survival probabilities of waterfowl may be influenced by their relative body mass in winter (Haramis et al. 1986, Hepp et al. 1986; but see Kremetz et al. 1989). It is commonly assumed that large energy reserves (correlate of body mass) enhance survival during winter when birds may experience food shortages and increased thermoregulatory costs. Indeed, Haramis et al. (1986) determined that survival probabilities (defined as recapture rates at the same site) of adult male Canvasbacks (*Aythya valisineria*) were positively associated with body mass in early winter. It has also been suggested that breeding performance of waterfowl is correlated with their physiological condition during winter (Heitmeyer and Fredrickson 1981, Kaminski and Gluesing 1986). Canvasbacks delay pairing until spring migration (Weller 1965); thus, in March and April they simultaneously incur energy costs of both migration and courtship.

Moreover, spring-migrating females initiate pre-basic molt (Lovvorn and Barzen 1988) and storage of energy and nutrients for reproduction (Barzen and Serie 1990). Energy reserves maintained in late winter may be used to offset these costs.

Male Canvasbacks are dominant to females and control access to limited food resources during nonbreeding periods (Alexander and Hair 1979, Alexander 1980). Nichols and Haramis (1980) suggested that male dominance was responsible for sexual differences in winter distributions (males wintering further north than females), location within flocks (females found more frequently on peripheral areas of rafts), and habitat use (proportion of females on smaller bodies of water exceeding that on large open water bodies). Competition between the sexes and age classes during winter is assumed to be deleterious to females and immatures; however, effects of competition on survival and reproductive performance (or correlates thereof) have not been demonstrated.

Here I examine the influence of sex, age, and

¹ Received 8 October 1992. Accepted 6 January 1993.

month on body mass and composition of wintering Canvasbacks at two sites in Louisiana. Because of its potential implication for survival, I compare patterns of change in Canvasback body composition between Louisiana study sites and populations wintering in the Mississippi and Atlantic Flyways. I also use these data to assess the potential influence of dominance relations on nutrient acquisition by Canvasbacks.

STUDY AREA AND METHODS

I conducted this study at Catahoula Lake (CL) in central Louisiana (31°15'N, 92°00'W) and at the Mississippi River Delta (MRD) in coastal southeastern Louisiana (29°15'N, 89°15'W) (see Hohman et al. [1990a] for site description). Sixty-eight to 74% of all Canvasbacks observed on monthly statewide surveys in winter 1987–1988 were recorded at these two sites (D. W. Woolington, unpubl. data). Maximum numbers of Canvasbacks censused were 58,000 on CL and 14,000 on MRD.

I shot Canvasbacks from flocks of ≥ 3 birds between the 10th and 20th of each month from November 1987 through February 1988. Birds were collected at night from boats equipped with spotlights or from natural blinds during the daytime without use of artificial decoys. Measurements taken in the field included body mass (± 5 g), bill length from the commissural point to tip of nail (± 0.1 mm), maximum bill width distal to nares (± 0.1 mm), keel length (± 0.1 mm), tarsal bone length (± 0.1 mm), and body length measured from the tip of the bill to the base of the middle rectrix (± 0.5 cm), with the bird held on its back. Culmen and head length, culmen height, and head width were measured (± 0.1 mm) in the laboratory. Birds were categorized as hatch-year (HY = immature) or after-hatch-year (AHY = adult) based on plumage (Haramis et al. 1982) or cloacal characteristics (Hochbaum 1942).

Gizzard (emptied), liver, omental fat, and right leg muscles (all muscles having either origin or insertion on the femur or tibiotarsus) were excised and weighed (± 0.01 g). Contents of the digestive tract were removed either in the field (esophagus and proventriculus) or from thawed carcasses in the laboratory (gizzard, intestine, and caeca). Gizzard contents were washed into individually labeled plastic containers, frozen, and examined radiologically for metal particles (Montalbano and Hines 1978). Samples testing positive were inspected manually for steel or lead

shotshell pellets. All tissues, except omental fat, liver, and leg muscle, were combined and passed through a Hobart meat grinder twice using 10 and 5 mm plates. A 100-g sample of homogenate and one of leg muscle were dried (90°C) separately to constant mass (Kerr et al. 1982). Dried carcass homogenate and leg muscle were homogenized separately in an electric coffee grinder. Fat was extracted from subsamples (ca. 10 g) of each constituent with petroleum ether (Dobush et al. 1985) in a modified Soxhlet apparatus. Fat content of each constituent was determined by multiplying dry mass of each constituent by the proportion of fat that it contained. Fat content was subtracted from dry mass of each constituent to calculate its lean dry mass. Samples of lean dry carcass homogenate (ca. 6–9 g) were ashed in a muffle furnace at 550°C for ≥ 6 hr. Proportion of ash in each sample was used to calculate total ash in the carcass. Carcass ash was subtracted from lean dry mass of each carcass to obtain ash-free lean dry mass, an index of protein. Proximate analyses of carcass homogenate were replicated until results agreed to $\pm 5\%$. Results from proximate analyses of individual constituents (replicates averaged) and mass of omental fat (assumed to be 100% fat) were summed to determine total body fat (FAT) and protein (PROTEIN) for each bird. Note that estimates of FAT and PROTEIN did not include composition of livers which were analyzed separately for trace elements.

I examined the influence of sex, age, month, and site on body mass and composition of Canvasbacks by using analysis of covariance models with type III sums of squares (PROC GLM, SAS Institute, Inc. 1981). First, I subjected the correlation matrix of nine measurements (culmen, tarsus, keel, bill, body, and head lengths, bill and head widths, and culmen height) to principal components analysis (PROC PRINCOMP, SAS for calculations). The first principal component accounted for 61% of the variance in the original measures, described positive covariation among all measures, and had fairly consistent loading factors that ranged from 0.27 to 0.37. Following Alisaukas (1988:Appendix 5), I used scores along the first principal component as a measure of body size (SIZE) and, hence, as a covariate in analyses of factors affecting body mass, FAT, PROTEIN, and leg muscle protein (LEG). Because of its significant association with ingesta-free body mass of Canvasbacks (Hohman et al.

1990b), presence (1) or absence (0) of ingested lead shot was included in my models of body mass and composition. Analysis of variance was used to test for effects of sex, age, month, and site on SIZE (PROC GLM, SAS Institute, Inc. 1981).

To test for sex- and age-related differences in foraging efficiencies (here defined as fat accumulation relative to locomotory effort) of Canvasbacks, I examined relations between FAT and LEG, an index of locomotory or foraging activity (cf. Hanson 1962). Canvasback diets at both Louisiana study sites contained >97% plant material (>80% subterranean plants parts) and did not vary among sex-age classes or months (Hohman et al. 1990a), but CL and MRD birds were analyzed separately because foraging modes (diving vs. tipping-up) differed between study sites (Hohman and Rave 1990). LEG was related to SIZE as follows:

$$\text{LEG}_{\text{CL}} = 9.495 + 0.248(\text{SIZE}),$$

$$\text{df} = 200, r^2 = 0.293, P < 0.001$$

$$\text{LEG}_{\text{MRD}} = 10.715 + 0.232(\text{SIZE}),$$

$$\text{df} = 198, r^2 = 0.300, P < 0.001.$$

Following Ankney and Alisauskas (1991:801), residuals from these regressions were used to calculate size-adjusted values of LEG (ADJLEG) for Canvasbacks. Analysis of covariance with type I sums of squares was used to test for heterogeneity of slopes (PROC GLM, SAS Institute, Inc. 1981; Model: FAT = ADJLEG, month, sex, age, and all interactions). Significance level was set a priori at $P = 0.05$.

RESULTS

SIZE AND BODY MASS

I collected 202 Canvasbacks at CL and 200 at MRD (Table 1). I detected no differences in SIZE of Canvasbacks at the two sites ($P = 0.993$), but there was a significant sex effect ($P < 0.001$) and month \times age interaction ($P = 0.024$; Appendix 1). Males were larger than females (Table 2). Whereas SIZE of immatures was greater in January–February than in November–December, adult Canvasbacks collected in December–January were larger than those shot in November or February (Table 2).

Body mass varied by age, month, and site, and sex and month ($P \leq 0.025$; Appendix 1). Throughout winter 1987–1988, Canvasbacks at

MRD were heavier than CL birds of the same age class (Table 1). Site differences were greatest in adult birds collected in December. At both sites, females were heavier than males in December and January (Table 2).

FAT

FAT was highly correlated with body mass ($r^2 = 0.69$, $\text{df} = 400$, $P < 0.001$) and, like body mass, varied by age, month, and site, and sex and month ($P < 0.001$; Appendix 1). Levels of FAT in immatures were greater at MRD than at CL, but changed similarly at the two sites (Table 1, Fig. 1). Adult Canvasbacks at MRD were also fatter than those at CL in early winter, especially in December, but FAT levels of all birds increased from early to late winter and were equivalent by late winter (Table 1, Fig. 1). At both sites, females were fatter than males in December and January (Table 2).

PROTEIN

Canvasback PROTEIN varied by age, month, and site, and sex, month, and site ($P \leq 0.017$; Appendix 1). PROTEIN levels by site were higher in adults and males than in immatures and females, but sex- and age-related differences averaged <11 g (5%; Table 1). Furthermore, except for immatures at CL, levels of PROTEIN by sex- or age-class and site were similar at the beginning and end of winter (Table 1).

LEG MUSCLE PROTEIN

Canvasback LEG varied by month and site ($P = 0.039$; Appendix 1). LEG was greater at MRD than at CL, especially in December, but was reduced in immatures relative to adults (Table 1, Appendix 1). Female Canvasbacks had relatively higher levels of LEG than males (Table 1, Appendix 1).

ADJLEG was positively related to FAT of Canvasbacks at both study sites ($P < 0.001$; Appendix 2). Interactions between sex and/or age, and ADJLEG were nonsignificant ($P > 0.1$; Appendix 2), indicating that relations (i.e., regression slopes) between ADJLEG and FAT were not affected by sex or age of Canvasbacks at either study site.

DISCUSSION

SEX AND AGE DIFFERENCES

FAT levels of both adult and immature females were greater than those of males, suggesting that,

TABLE 1. Body mass, fat, and leg muscle protein (g) of Canvasbacks collected at Catahoula Lake (CL) and the Mississippi River Delta (MRD), Louisiana, in winter 1987-1988.

Month	n	Body mass			Fat			Body protein			Leg muscle protein		
		CL	MRD	CL	MRD	CL	MRD	CL	MRD	CL	MRD	CL	MRD
November	46	51	1,178.86 (14.19) ^a	1,236.62 (13.90)	169.89 (9.81)	192.95 (9.61)	214.22 (2.26)	214.00 (2.21)	9.45 (0.11)	10.44 (0.11)			
Sex													
Male	23	26					215.93 (3.27)	217.92 (3.47)					
Female	23	25					212.50 (3.46)	210.07 (3.19)					
Age													
Adult	16	33	1,199.93 (22.49)	1,281.47 (16.40)	172.57 (15.55)	206.89 (11.34)	218.34 (3.58)	221.19 (2.61)					
Immature	30	18	1,157.79 (17.35)	1,191.77 (22.40)	167.22 (12.00)	179.01 (15.49)	210.09 (2.76)	206.80 (3.57)					
December	53	51	1,153.40 (13.72)	1,294.89 (13.78)	156.70 (9.49)	238.57 (9.53)	211.49 (2.18)	212.40 (2.19)	9.18 (0.11)	10.57 (0.11)			
Sex													
Male	27	22					220.70 (3.19)	214.62 (3.50)					
Female	26	29					202.27 (3.32)	210.17 (3.17)					
Age													
Adult	21	33	1,104.29 (19.96)	1,367.53 (16.86)	129.44 (13.80)	274.83 (11.66)	209.48 (3.18)	219.43 (2.69)					
Immature	32	18	1,202.51 (18.64)	1,222.26 (21.90)	183.95 (12.89)	202.31 (15.14)	213.50 (2.97)	205.36 (3.49)					
January	51	48	1,228.63 (13.60)	1,317.60 (13.56)	208.72 (9.40)	242.36 (9.37)	215.60 (2.16)	215.95 (2.16)	9.81 (0.11)	10.83 (0.11)			
Sex													
Male	27	23					218.89 (3.31)	220.29 (3.36)					
Female	24	25					212.30 (3.09)	211.61 (3.16)					
Age													
Adult	29	24	1,254.10 (18.09)	1,328.14 (19.13)	219.77 (12.51)	246.66 (13.23)	225.05 (2.88)	218.01 (3.05)					
Immature	22	24	1,203.15 (20.10)	1,307.07 (19.24)	197.66 (13.90)	238.06 (13.30)	206.14 (3.20)	213.88 (3.06)					
February	52	50	1,253.17 (13.75)	1,312.64 (13.21)	235.95 (9.51)	238.18 (9.13)	211.61 (2.19)	214.14 (2.10)	9.74 (0.11)	10.48 (0.11)			
Sex													
Male	22	24					213.41 (3.63)	222.42 (3.26)					
Female	30	26					209.82 (3.06)	205.87 (3.11)					
Age													
Adult	26	28	1,293.48 (18.38)	1,321.90 (17.58)	254.55 (12.71)	240.89 (12.15)	222.41 (2.93)	219.03 (2.80)					
Immature	26	22	1,212.87 (20.47)	1,303.38 (19.91)	217.36 (14.15)	235.47 (13.77)	200.82 (3.26)	209.26 (3.17)					
Nov-Feb	202	200	1,203.51 (6.85)	1,290.44 (6.86)	192.82 (4.74)	228.02 (4.75)	213.23 (1.09)	214.12 (1.09)	9.54 (0.05)	10.58 (0.05)			

^a Least Squares Mean (SE) based only on factors contributing significantly to models.

TABLE 2. Size, body mass, and fat of Canvasbacks collected at Catahoula Lake and the Mississippi River Delta, Louisiana, in winter 1987–1988.

Month	<i>n</i>	Size ^a	Body mass (g)	Fat (g)
November	97			
Sex				
Male	49		1,208.55 (15.62) ^b	178.83 (10.80)
Female	48		1,206.93 (15.75)	184.01(10.89)
Age				
Adult	49	0.07 (0.18)		
Immature	48	-0.39 (0.19)		
December	104			
Sex				
Male	49		1,203.83 (15.63)	173.22 (10.81)
Female	55		1,244.46 (15.40)	222.05 (10.65)
Age				
Adult	54	0.65 (0.17)		
Immature	50	-0.62 (0.18)		
January	99			
Sex				
Male	50		1,243.41 (15.91)	195.11 (11.00)
Female	49		1,302.82 (14.38)	255.96 (9.94)
Age				
Adult	53	0.69 (0.17)		
Immature	46	0.01 (0.18)		
February	102			
Sex				
Male	46		1,288.78 (16.25)	240.22 (11.23)
Female	56		1,277.03 (14.66)	233.91 (10.13)
Age				
Adult	54	0.14 (0.17)		
Immature	48	-0.05 (0.19)		
November–February	402			
Sex				
Male	194	1.98 (0.09)		
Female	208	-1.85 (0.09)		

^a Size = scores along the first principal component: a linear combination of 9 structural measurements based on their correlation matrix.

^b Least Squares Mean (SE) based only on factors contributing significantly to model.

although males were larger and potentially dominant to females, females were not disadvantaged in their access to foods during the year of study. The potential for site defense by Canvasbacks exists whenever food is appropriately distributed (Lovvorn 1989a). Shallow water depth, patchy distribution of foods (e.g., tubers of Banana Water-lily, *Nymphaea mexicana*), considerable time and energy expenditures required to access individual food items, and large potential gain from foraging effort, favored defense of feeding sites by Canvasbacks wintering in coastal South Carolina (Alexander 1987). The potential for defense of feeding sites by Canvasbacks clearly exists at wintering sites in Louisiana where birds feed almost exclusively on energy-rich, subterranean

plant parts (Hohman et al. 1990a). Indeed, aggression associated with feeding was commonly observed in wintering Canvasbacks at CL and MRD (Hohman and Rave 1990). Hohman and Rave (1990), however, found little evidence of male dominance of females in Louisiana. Female-female aggression was elevated at MRD. At CL, male aggression towards females was higher than predicted, but Canvasbacks at that site fed in flocks, and aggressive encounters commonly occurred when a feeding (i.e., diving) bird resurfaced close to another bird (aggressor). Because females fed more than males at that site, they were more likely than males to be subject to aggression (Hohman and Rave 1990).

Dominance relations (and experience) poten-

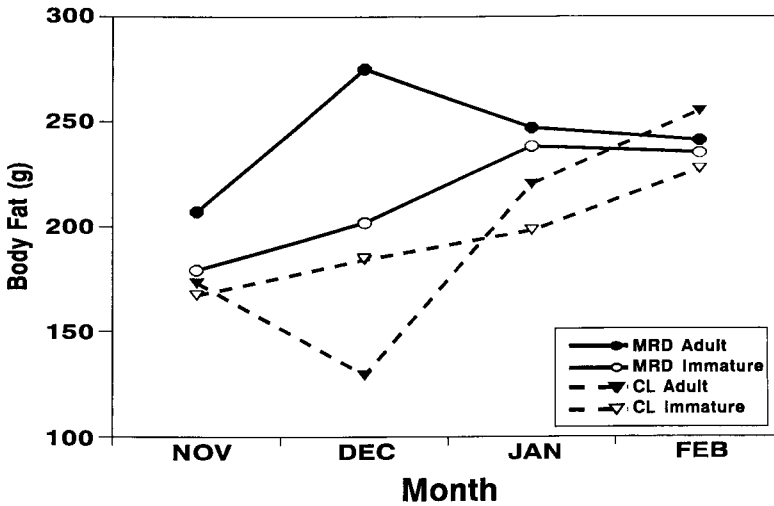


FIGURE 1. Changes in body fat of Canvasbacks collected at Catahoula Lake (CL, $n = 202$) and the Mississippi River Delta (MRD, $n = 200$), Louisiana, in winter 1987–1988. Least squares means depicted here are based only on factors contributing significantly to model. Sample sizes given in Table 1.

tially influence foraging efficiency of waterfowl (Raveling 1970, Paulus 1983). In Louisiana, Canvasbacks that fed more were fatter. This was suggested by the positive association between ADJLEG and FAT of Canvasbacks at both CL and MRD, and is based on the assumption that ADJLEG was related to locomotory (primarily feeding) activity. Sexual differences in FAT (female > male), LEG (female > male), PROTEIN (female < male), and diurnal time spent feeding (female > male, Hohman and Rave 1990) support this interpretation. Relations between ADJLEG and FAT were not affected by sex (or age) of Canvasbacks. Thus it appears that all birds at CL or MRD fed with similar efficiencies by month. This result supports my argument that nutrient acquisition by female Canvasbacks wintering in Louisiana (1987–1988) was unaffected by male-female dominance relations. Temporal and spatial variability in dominance relations between sexes is further evident during spring migration when females were reported to be dominant to males (Lovvorn 1990).

Age-related differences in condition (here defined as size-adjusted fat or protein levels) were evident at both Louisiana study sites. Differences in condition were not related to diet, because adult and immature Canvasbacks ate the same foods (Hohman et al. 1990a). Similarities between age-classes in the relation between ADJLEG and FAT suggest that adults and immatures

fed at the same efficiency. Condition differences, therefore, apparently were not the result of age-related differences in foraging experience. Rather, reduced LEG in immatures suggests that they fed less than adults. This difference might have resulted from interference competition with adults. In coastal South Carolina where Canvasbacks defended feeding sites, immatures were subordinate to adults (Alexander 1987). Hohman and Rave (1990) speculated that adult dominance may have contributed to elevated female-female aggression at MRD; however, in spite of the potential adult interference with feeding by immatures and related differences in fat levels from early to mid-winter, all Canvasbacks achieved similar levels of condition in late winter.

SITE DIFFERENCES

CL Canvasbacks, especially adults collected in December, were lighter (leaner) than MRD birds. Species composition of Canvasback diets at CL and MRD were somewhat different, but birds at both sites consumed primarily plant material (>97%), including >80% subterranean plant parts (Hohman et al. 1990a). Selected foods were abundant at CL and MRD relative to other migrational or wintering habitats (Hohman et al. 1990a), so it was unlikely that site differences were related to diet. As indicated previously, foraging mode differed between study sites. Can-

canvasbacks at MRD used deltaic splays (i.e., accreting mudflats receiving shallow, intermittent flooding) almost exclusively. At MRD, birds foraged independently and seldom dove. Feeding was most intensive during low to intermediate tidal conditions (or river stage) when water depths were shallow enough to permit birds to feed by tipping-up. Canvasbacks used their feet as well as their bill to excavate subterranean plant parts. In contrast, Canvasbacks at CL fed in flocks by diving. Water depth at the center of CL ranged from 0.2 m to 5.5 m and averaged 3.1 ± 0.22 m ($\bar{x} \pm SE$) during the study. Diving is an energetically costly activity, e.g., Takekawa (1987) estimated diving costs of Canvasbacks to be 7.7 times basal metabolic rate. Foraging costs of Canvasbacks at CL likely increased in late November when lake levels increased 3.9 m in four days following locally heavy rains (W. L. Hohman, unpubl. data). However, November to December increases in FAT levels of CL immatures and reduction in LEG of CL adults (i.e., reduced feeding) indicate that other factors (e.g., hunting disturbance) contributed to FAT depletion in CL adults.

POPULATION DIFFERENCES

Patterns of change in Canvasback body composition apparently differ between populations wintering in the Atlantic (Perry et al. 1986, Lovvorn 1987) and Mississippi Flyways (this study). Canvasbacks wintering in coastal North Carolina (Lovvorn 1987) and Chesapeake Bay (Nichols and Haramis 1980) exhibited a mid-winter decline in body mass (mass not adjusted for body size) and were lighter in late winter than birds collected in Louisiana in winter 1987–1988 (this study). Perry et al. (1986) argued that mid-winter declines in body mass, feed intake, and activity of captive Canvasbacks fed *ad libitum* rations were evidence for endogenous control of body composition. They further speculated that such changes increased the probability of survival in ducks by decreasing maintenance energy costs during periods of cold stress.

Reductions in body mass (and fat) of Canvasbacks in North Carolina in mid- to late winter corresponded to a dietary shift from American wildcelery (*Vallisineria americana*) tubers to clams (*Macoma* spp.; Lovvorn 1987). Although fat declined from November to January, body protein increased during this period (Lovvorn 1987). Lovvorn (1987) concluded that gains in

body protein had no clear function and seemed to be an incidental result of the protein : energy ratio of the tuber vs. clam diet.

I submit that high relative body mass of Canvasbacks wintering in Louisiana resulted from their having access to abundant, energy-rich subterranean plant foods throughout winter. Canvasbacks are specialized behaviorally and morphologically for feeding on subterranean plant parts (Goodman and Fisher 1962; Tome and Wrubleski 1988), as evidenced by diets of Canvasbacks throughout the annual cycle (see Hohman et al. 1990a). Densities of subterranean plant foods at CL (Wills 1965) and MRD (Hohman et al. 1990a; Bielefeld and Afton, in press) are high compared to those at other major Canvasback wintering areas. Moreover, unlike Lake Mattamuskeet, North Carolina, where the standing crop of American wildcelery tubers apparently was depleted (Lovvorn 1989b), waterfowl grazing seemed to have minimal affect on density of plant foods at MRD (Hohman et al. 1990a).

The significance of high fat levels for Canvasback survival and recruitment is unknown. In theory, large reserves may handicap birds, increasing risk of predation by interfering with birds' ability to escape from predators (Lima 1986). Although immature Herring Gulls (*Larus argentatus*) were observed harassing feeding Canvasbacks at MRD, Hohman and Rave (1990) concluded that predation risks at the two sites were low. High fat levels, therefore, probably do not increase risks of predation to wintering Canvasbacks in Louisiana as they might in coastal North Carolina or Chesapeake Bay, where predation risks apparently are greater (Lovvorn 1989a).

If Haramis et al.'s (1986) suggestion that overwinter and annual survival probabilities of Canvasbacks are related to their relative body mass in winter applies across populations, then survival probabilities of Canvasbacks wintering in Louisiana may be high relative to those of other wintering populations. Louisiana has become a major wintering area for Canvasbacks, providing habitat since 1985 for over 25% of the continental population (U.S. Fish. and Wildl. Serv., Off. Migratory Bird Manage., unpubl.). Sex ratios of wintering Canvasbacks in Louisiana are more balanced (<2 males : female; Woolington, in press) than those recorded in the Atlantic Flyway (1.7–4.0 male : female; Haramis et al. 1985). Increased population size and balanced sex ratio

imply high female survival and lend support to the above speculation, but additional studies examining survival and recruitment in relation to condition of Canvasbacks at different wintering locations are needed.

ACKNOWLEDGMENTS

I am grateful to H. A. Bateman and J. W. Tarver, Louisiana Department of Wildlife and Fisheries (LDWF); B.D.J. Batt, former Scientific Director, Delta Waterfowl and Wetlands Research Station; and C. F. Bryan and S. K. Joyner (deceased), U.S. Fish and Wildlife Service (USFWS), for their support of the Canvasback research project. I was aided in the field and laboratory by J. M. Collucy, T. J. Meis, R. D. Pritchert, D. P. Rave, and D. W. Woolington. The LDWF provided lodging at both study sites. I thank personnel of Pass-a-Loutre and Saline Wildlife Management Areas, and Catahoula and Delta-Breton National Wildlife Refuges for their assistance throughout this study. R. M. Pace, USFWS, Louisiana State University, and D. A. Fuller, USFWS, National Wetlands Research Center, provided statistical advice. Helpful reviews of the draft manuscript were provided by G. S. Farris, G. M. Haramis, D. G. Jorde, J. R. Lovvorn, and J. L. Moore. S. M. Lauritzen prepared the figure.

LITERATURE CITED

- ALEXANDER, W. C. 1980. The behavioral ecology and sociobiology of nonbreeding diving ducks (Aythyini). Ph.D.diss., Clemson Univ., Clemson, SC.
- ALEXANDER, W. C. 1987. Aggressive behavior of diving ducks (Aythyini). *Wilson Bull.* 99:38-49.
- ALEXANDER, W. C., AND J. D. HAIR. 1979. Wintering foraging behavior and aggression of diving ducks in South Carolina. *Proc. Annu. Conf. Southeast. Assoc. Fish and Wildl. Agencies* 31:226-232.
- ALISAUSKAS, R. T. 1988. Nutrient reserves of lesser snow geese during winter and spring migration. Ph.D.diss., Univ. Western Ontario, London, Ontario, Canada.
- ANKNEY, C. D., AND ALISAUSKAS, R. T. 1991. Nutrient-reserve dynamics and diets of breeding female Gadwalls. *Condor* 93:799-810.
- BARZEN, J. A., AND J. R. SERIE. 1990. Nutrient reserve dynamics of breeding Canvasbacks. *Auk* 107:75-85.
- BIELEFELD, R. R., AND A. D. AFTON. In press. Habitat related variation in Canvasback food on the Mississippi River Delta, Louisiana. *Proc. Annu. Conf. Southeast. Assoc. Fish and Wildl. Agencies* 46.
- DOBUSH, G. R., C. D. ANKNEY, AND D. G. KREMENTZ. 1985. The effect of apparatus, extraction time, and solvent type on lipid extractions of Snow Geese. *Can. J. Zool.* 63:1917-1920.
- GOODMAN, D. C., AND H. I. FISHER. 1962. Functional anatomy of the feeding apparatus in waterfowl (Aves: Anatidae). Southern Illinois Univ. Press, Carbondale, IL.
- HANSON, H. C. 1962. The dynamics of condition factors in Canada Geese and their relation to seasonal stresses. *Arctic Inst. N. Am. Tech. Paper No. 12.*
- HARAMIS, G. M., E. L. DERLETH, AND D. G. MCAULEY. 1982. Techniques for trapping, aging and banding wintering canvasbacks. *J. Field Ornithol.* 53:342-351.
- HARAMIS, G. M., J. R. GOLDSBERRY, D. G. MCAULEY, AND E. C. DERLETH. 1985. An aerial photographic census of Chesapeake and North Carolina Canvasbacks. *J. Wildl. Manage.* 49:449-454.
- HARAMIS, G. M., J. D. NICHOLS, K. H. POLLOCK, AND J. E. HINES. 1986. The relationship between body mass and survival of wintering Canvasbacks. *Auk* 103:506-514.
- HEITMEYER, M. E., AND L. H. FREDRICKSON. 1981. Do wetland conditions in the Mississippi Delta hardwoods influence Mallard recruitment? *Trans. N. Am. Wildl. and Nat. Resour. Conf.* 46:44-57.
- HEPP, G. R., R. J. BLOHM, R. E. REYNOLDS, J. E. HINES, J. D. NICHOLS. 1986. Physiological condition of autumn-banded Mallards and its relationship to hunting mortality. *J. Wildl. Manage.* 50:177-183.
- HOCHBAUM, H. A. 1942. Sex and age determination of waterfowl by cloacal examination. *Trans. N. Am. Wildl. and Nat. Resour. Conf.* 7:299-307.
- HOHMAN, W. L., AND D. P. RAVE. 1990. Diurnal time-activity budgets of wintering Canvasbacks in Louisiana. *Wilson Bull.* 102:645-654.
- HOHMAN, W. L., D. W. WOOLINGTON, AND J. H. DEVRIES. 1990a. Food habits of wintering Canvasbacks in Louisiana. *Can. J. Zool.* 68:2605-2609.
- HOHMAN, W. L., R. D. PRITCHERT, R. M. PACE III, D. W. WOOLINGTON, AND R. HELM. 1990b. Influence of ingested lead on body mass of wintering Canvasbacks. *J. Wildl. Manage.* 54:211-215.
- KAMINSKI, R. M., AND E. A. GLUESING. 1986. Density and habitat related recruitment in Mallards. *J. Wildl. Manage.* 51:141-148.
- KERR, D. C., C. D. ANKNEY, AND J. S. MILLAR. 1982. The effect of drying temperature on extraction of petroleum ether soluble fats of small birds and mammals. *Can. J. Zool.* 60:470-472.
- KREMENTZ, D. G., J. E. HINES, P. O. CORR, AND R. B. OWEN, JR. 1989. The relationship between body mass and annual survival in American Black Ducks. *Ornis Scand.* 20:81-85.
- LIMA, S. L. 1986. Predation risk and unpredictable feeding conditions: determinants of body mass in birds. *Ecology* 67:377-385.
- LOVVORN, J. R. 1987. Behavior, energetics, and habitat relations of Canvasback ducks during winter and early spring migration. Ph.D.diss., Univ. of Wisconsin, Madison.
- LOVVORN, J. R. 1989a. Food defendability and antipredator tactics: implications for dominance and pairing in Canvasbacks. *Condor* 91:826-836.
- LOVVORN, J. R. 1989b. Distributional responses of Canvasbacks to weather and habitat change. *J. Appl. Ecol.* 26:113-130.
- LOVVORN, J. R. 1990. Courtship and aggression in Canvasbacks: influence of sex and pair-bonding. *Condor* 92:369-378.
- LOVVORN, J. R., AND J. A. BARZEN. 1988. Molt in the annual cycle of Canvasbacks. *Auk* 105:543-552.

- MONTALBANO, F., AND T. C. HINES. 1978. An improved X-ray technique for investigating ingestion of lead by waterfowl. Proc. Annu. Conf. Southeast. Fish and Wildl. Agencies 32:364-368.
- NICHOLS, J. D., AND G. M. HARAMIS. 1980. Sex-specific differences in winter distribution patterns of Canvasbacks. Condor 82:406-416.
- PAULUS, S. L. 1983. Dominance relations, resource use, and pairing chronology of Gadwalls in winter. Auk 100:947-952.
- PERRY, M. C., W. J. KUENZEL, B. K. WILLIAMS, AND J. A. SERAFIN. 1986. Influence of nutrients on feed intake and condition of captive Canvasbacks in winter. J. Wildl. Manage. 50:427-434.
- RAVELING, D. G. 1970. Dominance relationships and agonistic behavior of Canada Geese in winter. Behaviour 37:291-319.
- SAS INSTITUTE, INC. 1981. SAS for linear models: a guide to the ANOVA and GLM procedures. SAS Institute, Inc., Cary, NC.
- TAKEKAWA, J. Y. 1987. Energetics of Canvasbacks staging on the Upper Mississippi River pool during fall migration. Ph.D.diss., Iowa State Univ., Ames, IA.
- TOME, M. W., AND D. A. WRUBLESKI. 1988. Underwater foraging behavior of Canvasbacks, Lesser Scaups, and Ruddy Ducks. Condor 90:168-172.
- WELLER, M. W. 1965. Chronology of pair formation in some Nearctic *Aythya* (Anatidae). Auk 82:227-235.
- WILLS, D. W. 1965. An investigation of some factors affecting waterfowl and waterfowl habitat on Catatoula Lake. M.Sc.thesis, Louisiana State Univ., Baton Rouge, LA.
- WOOLINGTON, D. W. In press. Sex ratios of wintering canvasbacks in Louisiana. J. Wildl. Manage. 57.

APPENDIX 1. General linear models used to describe differences in size, body mass, fat, and body and leg muscle protein of Canvasbacks collected at Catahoula Lake and the Mississippi River Delta, Louisiana, in winter 1987–1988.

Source	df	Size ^a			df	Body mass		
		Sum of squares ^b	F-value	P > F		Sum of squares	F-value	P > F
Model ^c	31	1,611.61	32.73	<0.001	33	4,794,768.89	16.96	<0.001
Error	370	587.68			368	3,151,816.85		
Corrected Total	401	2,199.30			401	7,946,585.75		
Lead ^d					1	394,485.12	46.06	<0.001
Size					1	562,140.70	65.63	<0.001
Month	3	12.84	2.69	0.045	3	366,340.51	14.26	<0.001
Site	1	0.00	0.00	0.993	1	672,571.83	78.53	<0.001
Month*Site	3	9.81	2.06	0.105	3	102,757.60	4.00	0.008
Sex	1	1,368.94	861.87	<0.001	1	13,127.69	1.53	0.216
Month*Sex	3	4.61	0.97	0.407	3	80,567.61	3.14	0.025
Site*Sex	1	0.13	0.08	0.771	1	1,761.66	0.21	0.650
Month*Site*Sex	3	2.89	0.61	0.610	3	36,020.50	1.40	0.241
Age	1	40.51	25.51	<0.001	1	160,030.93	18.68	<0.001
Month*Age	3	15.06	3.16	0.024	3	22,348.84	0.87	0.456
Site*Age	1	0.00	0.00	0.966	1	57,485.01	6.71	0.010
Month*Site*Age	3	1.27	0.27	0.848	3	331,302.08	12.89	<0.001
Sex*Age	1	0.62	0.40	0.530	1	160.48	0.02	0.891
Month*Sex*Age	3	4.39	0.92	0.429	3	57,113.02	2.22	0.085
Site*Sex*Age	1	0.16	0.10	0.746	1	12,174.92	1.42	0.233
Month*Site*Sex*Age	3	6.76	1.42	0.236	3	36,817.69	1.43	0.232

^a Size = scores along the first principal component: a linear combination of nine structural measurements based on their correlation matrix.

^b Type III Sums of Squares (SAS Inst., Inc. 1981).

^c Explained variance for full models: size, $r^2 = 0.73$; body mass, $r^2 = 0.60$; fat, $r^2 = 0.41$; body protein, $r^2 = 0.62$; and leg muscle protein, $r^2 = 0.62$.

^d Lead = presence/absence of ingested lead shotshell pellets in individual gizzards.

APPENDIX 2. General linear models used to describe relation of fat to size-adjusted leg muscle protein (ADJLEG) of Canvasbacks collected at Catahoula Lake and the Mississippi River Delta, Louisiana, in winter 1987–1988.

Source	Catahoula Lake			
	df	Sum of squares ^a	F-value	P > F
Model ^b	31	855,301.54	6.57	<0.001
Error	170	714,235.80		
Corrected total	201	1,569,537.34		
ADJLEG	1	565,151.91	134.52	<0.001
Month	3	101,062.62	8.02	<0.001
Sex	1	3,512.76	0.84	0.361
Age	1	12.38	0.00	0.956
Month*sex	3	82,718.51	6.56	<0.001
Month*age	3	18,184.32	1.44	0.232
Sex*age	1	16,233.45	3.86	0.051
Month*sex*age	3	17,075.28	1.35	0.258
ADJLEG*Month	3	33,451.80	2.65	0.050
ADJLEG*Age	1	2,430.86	0.58	0.447
ADJLEG*Sex	1	20.87	0.00	0.943
ADJLEG*Month*Age	3	705.66	0.06	0.982
ADJLEG*Month*Sex	3	657.81	0.05	0.984
ADJLEG*Sex*Age	1	3,734.56	0.89	0.347
ADJLEG*Month*Sex*Age	3	10,348.69	0.82	0.483

^a Type I Sum of Squares (SAS Inst., Inc. 1981).

^b Explained variance for full models: Catahoula Lake, $r^2 = 0.54$; and Mississippi River Delta, $r^2 = 0.51$.

APPENDIX 1. Extended.

Fat			Body protein			Leg muscle protein		
Sum of squares	F-value	P > F	Sum of squares	F-value	P > F	Sum of squares	F-value	P > F
1,061,534.14	7.85	<0.001	130,526.74	18.16	<0.001	361.02	18.35	<0.001
1,507,154.97			80,148.87			219.35		
2,568,689.11			210,675.62			580.32		
143,135.82	34.95	<0.001	5,499.18	25.25	<0.001	14.79	24.83	<0.001
37,178.29	9.08	0.002	13,002.73	59.70	<0.001	51.29	86.06	<0.001
175,992.26	14.32	<0.001	748.98	1.15	0.330	10.65	5.96	<0.001
110,288.63	26.93	<0.001	70.84	0.33	0.568	95.18	159.69	<0.001
76,818.22	6.25	<0.001	96.92	0.15	0.930	5.00	2.80	0.039
20,587.89	5.03	0.025	2,114.96	9.71	0.002	3.82	6.42	0.011
75,181.16	6.12	<0.001	454.63	0.70	0.555	3.27	1.83	0.141
21.37	0.01	0.942	43.60	0.20	0.654	0.02	0.04	0.850
6,505.42	0.53	0.662	2,236.76	3.42	0.017	2.93	1.64	0.179
20,256.78	4.95	0.026	9,907.70	45.49	<0.001	10.86	18.23	<0.001
1,789.84	0.15	0.932	1,346.34	2.06	0.105	0.31	0.18	0.911
15,767.90	3.85	0.050	8.02	0.04	0.847	1.90	3.20	0.074
88,806.82	7.23	<0.001	4,232.05	6.48	<0.001	3.94	2.21	0.086
97.25	0.02	0.877	449.02	2.06	0.151	0.03	0.06	0.811
17,150.19	1.40	0.243	497.57	0.76	0.516	0.51	0.29	0.834
13,403.37	3.27	0.071	201.25	0.92	0.337	0.89	1.50	0.221
29,264.59	2.38	0.069	738.04	1.13	0.337	0.62	0.35	0.788

APPENDIX 2. Extended.

Mississippi River Delta			
df	Sum of squares	F-value	P > F
31	397,751.56	5.55	<0.001
168	388,043.00		
199	785,794.57		
1	171,686.82	74.33	<0.001
3	63,706.39	9.19	<0.001
1	2,444.28	1.06	0.305
1	16,174.71	7.00	0.008
3	21,830.56	3.15	0.026
3	16,310.26	2.35	0.073
1	5,954.10	2.58	0.110
3	32,594.39	4.70	0.003
3	19,355.50	2.79	0.042
1	3,253.57	1.41	0.237
1	1.73	0.00	0.978
3	12,413.08	1.79	0.150
3	13,752.35	1.98	0.118
1	5,630.68	2.44	0.120
3	12,643.08	1.82	0.144