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BODY MASS AND COMPOSITION OF RING-NECKED DUCKS WINTERING IN SOUTHERN FLORIDA

WILLIAM L. HOHMAN[1] AND MILTON W. WELLER[1]

ABSTRACT.—We studied effects of sex, age, and date on body mass and composition of Ring-necked Ducks (*Aythya collaris*, hereafter Ring-necks) in southern Florida in winter 1979–1980. We conducted this analysis to assess the potential influence of dominance relations among sex-age classes on nutrient acquisition and to elucidate factors influencing patterns of change in body mass and composition of diving ducks in winter. Size-adjusted body mass (ADJMASS) was greater in adult than in immature Ring-necks, but ADJMASS of all birds increased during winter. Body fat (FAT) also increased through the winter but, unlike ADJMASS, was not affected by age. Size-adjusted protein (ADJPROT) varied by age and by sex and date. ADJPROT was greater in adults than in immatures. ADJPROT remained unchanged in females and increased (14%) in males, but sex-related differences averaged less than 2% for the entire winter period. Size-adjusted leg mass (ADJLEG, an index of feeding activity) increased through winter in immatures only and was equivalent in adults and immatures by late winter. Changes in ADJLEG and FAT were positively related, suggesting that Ring-necks gained fat through increased feeding. This relation (our measure of feeding efficiency) was not affected by sex or date, but the relation between ADJLEG and FAT was influenced by age. We found limited evidence that dominance relations influenced nutrient acquisition by Ring-necks in Florida during the year of study. Patterns of change in winter body mass and composition of Ring-necks and other diving ducks vary geographically. We argue that local environmental conditions, especially ambient temperature and food availability, are proximately responsible for observed variation. We further suggest that geographic differences are ultimately related to waterfowl mating systems. *Received 23 Sept. 1993, accepted 17 Dec. 1993.*

Body mass and composition of waterfowl (Anatidae) change substantially in winter. Many species exhibit midwinter declines in mass or composition (e.g., Canada Goose [*Branta canadensis*] [Raveling 1979]; Oldsquaw [*Clangula hyemalis*] [Peterson and Ellarson 1979]; Green-winged Teal [*Anas crecca*] [Baldassarre et al. 1986]; Northern Pintail [*A. acuta*] [Miller 1986]; Blue-winged Teal [*A. discors*] [Thompson and Baldassarre 1990]). The extent of mass loss varies among species and within species by latitude, social status, sex, age, and year (e.g., Paulus 1980, Thompson and Baldassarre 1990). Nonetheless, similarities in patterns of change during winter have led some investigators to speculate that body mass was endogenously controlled (Reinecke et al. 1982, Baldassarre et al. 1986, Perry et al. 1986, Thompson and Baldassarre 1990). Changes in body masses of wintering diving ducks (Tribe Aythyini) do not show

[1] Dept. of Entomology, Fisheries, and Wildlife, Univ. of Minnesota, 1980 Folwell Ave., St. Paul, Minnesota 55108. (Present address WLH: National Biological Survey, National Wetlands Research Center, 700 Cajundome Blvd., Lafayette, Louisiana 70506-3152. Present address MWW: Dept. of Wildlife and Fisheries Sciences, Texas A&M Univ., College Station, Texas 77843.)

declines consistently. Diving ducks wintering in New York, Chesapeake Bay, and coastal North Carolina show midwinter declines in body mass (Kaminsky and Ryan 1981, Perry et al. 1986, Lovvorn 1987), but Canvasbacks (*Aythya valisineria*), Redheads (*A. americana*), and Ring-necked Ducks (*A. collaris,* hereafter Ring-necks) in the Gulf of Mexico gain weight through winter (Jeske 1985, Hohman et al. 1988, Moore 1991, Hohman 1993).

In coastal South Carolina, dominance relations among wintering Ring-necks influenced access to limited food resources (Alexander 1987). Alexander (1987) determined adults to be dominant to immatures within sexes and, between sexes, males to be dominant to females. Alexander (1983) suggested that male dominance was responsible for sexual differences in winter distributions of Ring-necks (males wintering farther north than females). Similarly, Nichols and Haramis (1980) argued that male dominance was responsible for sexual differences in winter distribution, location within flocks, and habitat use of Canvasbacks. 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 (Hohman 1993).

Here we examine the influence of sex, age, and date on body mass and composition of wintering Ring-necks in southern Florida. We conducted this analysis in part to assess the potential influence of dominance relations on nutrient acquisition by Ring-necks. Specifically, we tested the predictions that (1) mass and composition of subordinates (females, immatures) were different from those of dominants (males, adults) and (2) that subordinates fed less efficiently than dominants. Results from this study were interpreted in the context of similar studies and used to elucidate factors influencing patterns of change in body mass and composition of diving ducks in winter.

STUDY AREAS AND METHODS

This study was conducted at the Arthur R. Miller Loxahatchee National Wildlife Refuge (Loxahatchee NWR), a 60,000-ha impoundment located in Florida's northern Everglades (see Maffei [1991] for site description). Waterfowl hunting was permitted (morning only) on approximately 25% of Loxahatchee NWR, 22 November 1979 to 20 January 1980. Foods were rarely found in the esophagi of birds killed before 12:00 h (Hohman 1984). To minimize interference with hunting and increase our sample of birds with foods in their esophagi, we shot birds in the evening (>16:00 h) as they returned to roosting areas within or adjacent to the sanctuary portion of Loxahatchee NWR.

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 on its back. Birds

were categorized as hatch-year (immature) or after-hatch-year (adult) based on plumage (Hohman and Cypher 1986) or cloacal characteristics (Hochbaum 1942).

Carcasses were sheared to remove feathers (cf. Raveling 1979). Skin (including all associated fat) and omental fat were excised and weighed (±0.01 g). After the eviscerated carcass was weighed (±0.01 g), the right leg (masses of femur and tibiotarsus bones and all muscles having either origin or insertion on the femur or tibiotarsus) was excised and weighed (±0.01 g). The combined mass of skin and omental fat was positively correlated with total body fat ($r^2 = 0.96$; $P < 0.001$), and the eviscerated carcass was positively related to ash-free lean dry mass of Ring-necks ($r^2 = 0.69$, $P < 0.001$; Hohman and Taylor 1986). Consequently, we used the sum of skin and omental fat masses and eviscerated carcass mass as indexes of body fat (FAT) and protein (PROTEIN), respectively.

We examined the influence of sex, age, and date (1 November = day 1; 28 February = day 120) on body mass and composition of Ring-necks by using analysis of covariance models with type III sums of squares (PROC GLM, SAS Instit., Inc. 1987). First, we subjected the correlation matrix of five structural measurements (tarsus, keel, bill, body length, and bill width) to principal components analysis (PROC PRINCOMP, SAS for calculations). To characterize size of Florida Ring-necks more accurately, we included, in this analysis only, 27 birds collected in west central Florida, winter 1979–1980 (Hohman 1984). The first principal component accounted for 61% of the variance in the original measures, described positive covariation among all measurements, and had loadings ranging from 0.39 to 0.48. We used scores along the first principal component as a measure of body size (SIZE) and, therefore, as a covariate in analyses of factors affecting body mass, FAT, PROTEIN, and leg mass (LEG) (Ankney and Alisauskas 1991). Analysis of variance was used to test for effects of sex, age, and date on SIZE (PROC GLM, SAS Instit., Inc. 1987).

To test for sex- and age-related differences in foraging efficiencies of Ring-necks (here defined as fat accumulation relative to an index of locomotory effort), we examined relations between FAT and LEG. We assumed that changes in LEG were related to level of locomotory or foraging activity as in molting Canada Geese (Hanson 1962). Examination of sex and age effects on the relation between FAT and LEG was possible because Ring-neck diets (esophageal contents only) contained >98% plant material (almost exclusively seeds of white water-lily [*Nymphaea odorata*]) and did not vary among sex-age classes or months (Weller, unpubl. data). LEG was related to SIZE as follows:

$$\text{LEG} = 25.94 + 0.651(\text{SIZE}),$$
$$\text{df} = 175, \quad r^2 = 0.220, \quad P < 0.001.$$

Following Ankney and Alisauskas (1991:801), we used residuals from this regression to calculate size-adjusted values of LEG (ADJLEG) for Ring-necks. Analysis of covariance with type I sums of squares was used to test for heterogeneity of slopes (SAS Instit., Inc. 1991:229–246; Model: FAT = ADJLEG, date, sex, age, and all interactions). Factors not contributing significantly to the model were removed in a stepwise manner. Significance level was set a priori at $P = 0.05$.

RESULTS

We collected 177 Ring-necks at Loxahatchee NWR between 9 November 1979 and 28 February 1980. Our sample included 85 males (40 adults, 45 immatures) and 92 females (57 adults, 35 immatures). Males were structurally larger than females, and adults were larger than immatures, but SIZE was not affected by date or any interactions (Table 1, Appendix I). Size-adjusted body mass (ADJMASS) was greater in adult than in

TABLE 1

SIZE, SIZE-ADJUSTED BODY MASS (ADJMASS) AND PROTEIN (ADJPROT) OF RING-NECKED DUCKS COLLECTED IN FLORIDA, WINTER 1979–1980

Variable	N	Size[a]	ADJMASS (g)	ADJPROT (g)
Sex				
Male	85	1.30 (0.13)[b]		347.1 (2.8)
Female	92	−1.26 (0.13)		342.0 (2.7)
Age				
Adult	97	0.42 (0.13)	713.7 (4.5)	353.0 (2.2)
Immature	80	−0.37 (0.14)	685.6 (4.8)	336.1 (2.3)

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

[b] Least squares mean (SE) based only on factors contributing significantly to model.

immature Ring-necks (Table 1), but ADJMASS of all birds increased through winter (Fig. 1, Appendix I). FAT also increased through winter (Fig. 1), but, unlike ADJMASS, was not affected by age (Appendix I).

Size-adjusted protein (ADJPROT) varied by age and by sex, and date (Appendix II). ADJPROT was greater in adults than in immatures (Table 1). Whereas ADJPROT remained unchanged in females through the winter, it increased (14%) in males (Fig. 2).

Size-adjusted leg mass increased through the winter in immatures only and was equivalent in adults and immatures by late winter (Fig. 2, Appendix II). ADJLEG was positively related to FAT ($F = 27.95$, df = 1, 161, $P < 0.001$). Interactions between sex and/or date and ADJLEG were nonsignificant (F's = 0.09–1.40, df = 1, 161, P's > 0.239), but relations between ADJLEG and FAT were affected by age ($F = 3.91$, df = 1, 161, $P = 0.049$). Increases in FAT per unit measure of foraging effort (i.e., ADJLEG [g]) were greater in immatures than in adults (Fig. 3).

DISCUSSION

Influence of dominance relations on nutrient acquisition.—The potential for defense of feeding sites by diving ducks exists whenever food is

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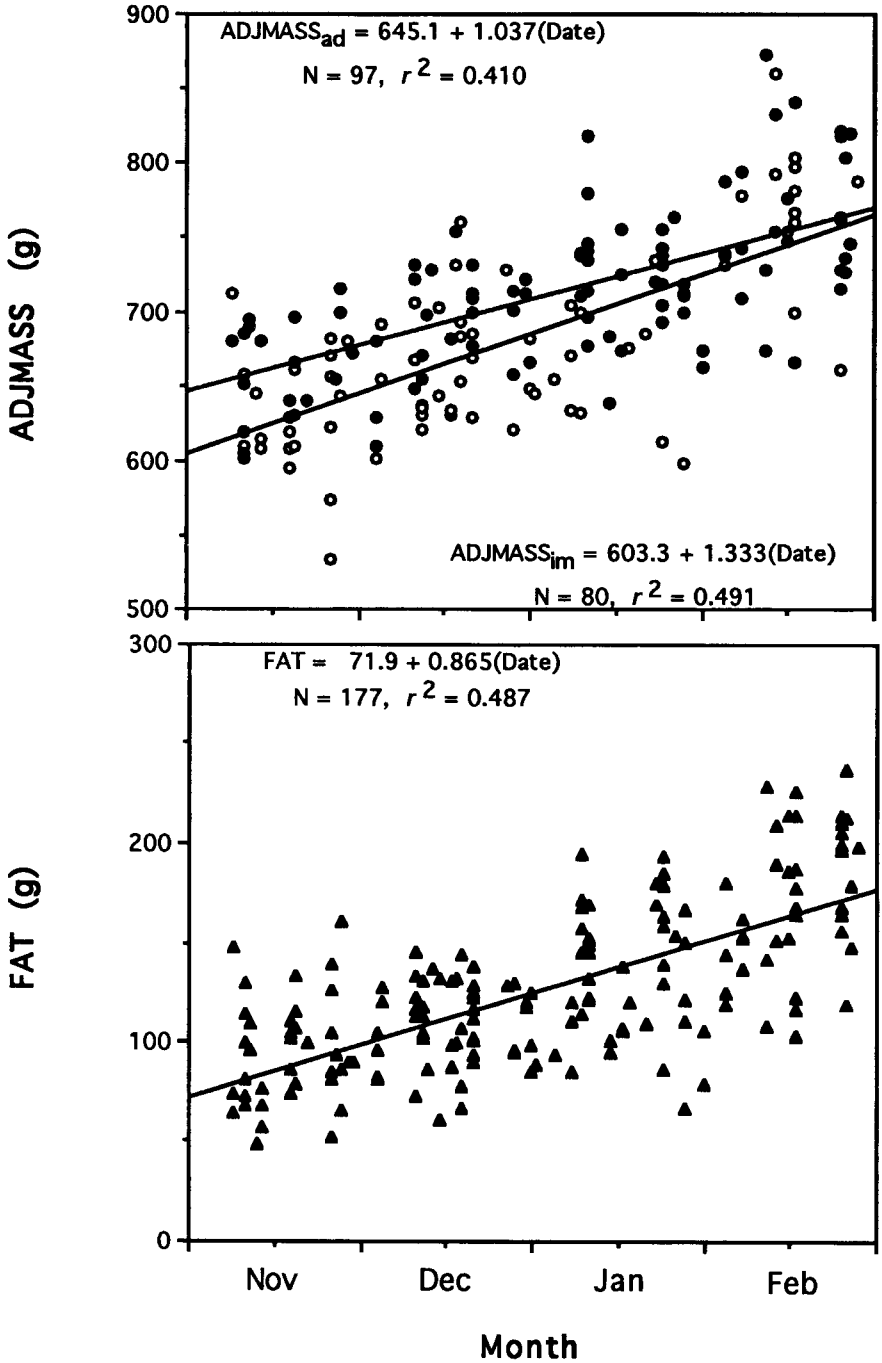
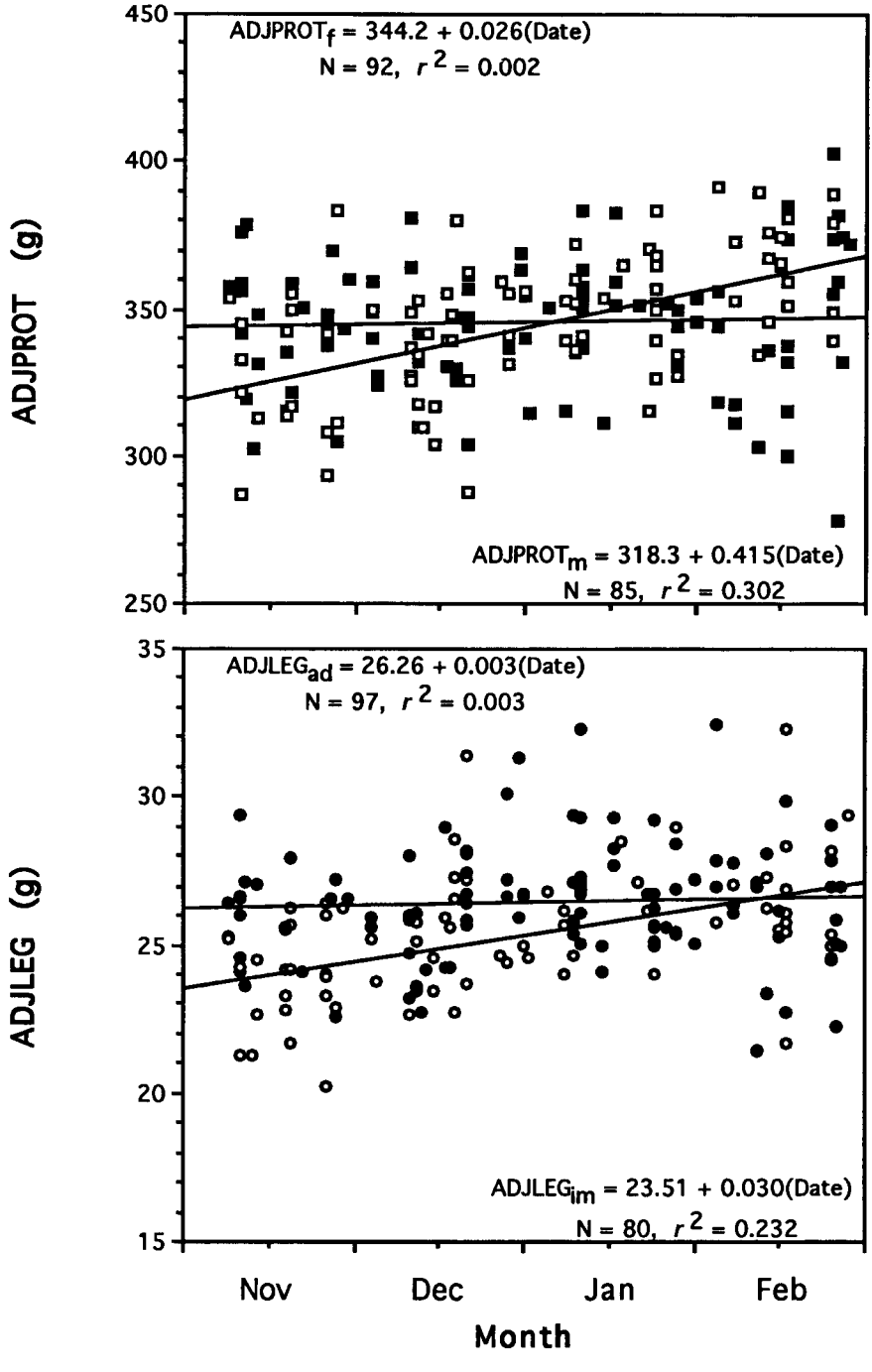
FIG. 1. Changes in size-adjusted body mass (ADJMASS) and fat of Ring-necked Ducks collected in southern Florida in winter 1979–1980. Date: 1 November = day 1. Adult (solid circle), immature (open circle), and combined (solid triangle).

FIG. 2. Changes in size-adjusted protein (ADJPROT) and leg mass (ADJLEG) of Ring-necked Ducks collected in southern Florida in winter 1979–1980. Date: 1 November = day 1. Adult (solid circle), immature (open circle), male (open square), and female (solid square).


ADJMASS (g)
900
800
700
600
500
ADJMASS$_{ad}$ = 645.1 + 1.037(Date)
N = 97, r^2 = 0.410
ADJMASS$_{im}$ = 603.3 + 1.333(Date)
N = 80, r^2 = 0.491
FAT (g)
300
200
100
0
FAT = 71.9 + 0.865(Date)
N = 177, r^2 = 0.487
Nov
Dec
Jan
Feb
Month


ADJPROT (g)
450
400
350
300
250
ADJPROT$_f$ = 344.2 + 0.026(Date)
N = 92, r^2 = 0.002
ADJPROT$_m$ = 318.3 + 0.415(Date)
N = 85, r^2 = 0.302
ADJLEG (g)
35
30
25
20
15
ADJLEG$_{ad}$ = 26.26 + 0.003(Date)
N = 97, r^2 = 0.003
ADJLEG$_{im}$ = 23.51 + 0.030(Date)
N = 80, r^2 = 0.232
Nov
Dec
Jan
Feb
Month

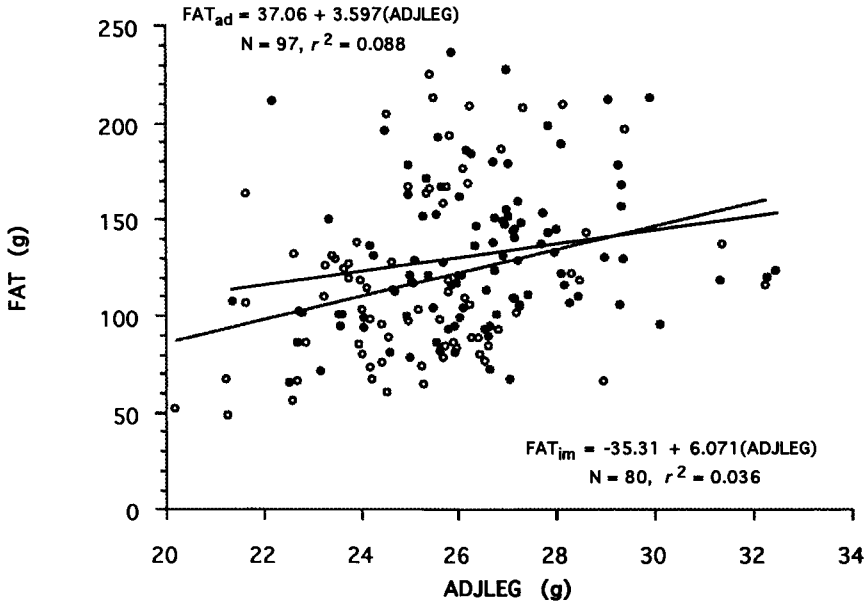


FIG. 3. Relation of body fat (FAT) to size-adjusted leg mass (ADJLEG) of adult (solid circle) and immature (open circle) Ring-necked Ducks collected in southern Florida in winter 1979–1980.

appropriately distributed (cf. Lovvorn 1989). In coastal South Carolina, where birds fed on tubers of banana water-lily (*Nymphaea mexicana*), site defense by diving ducks was favored by shallow water depth, irregular distribution of foods, substantial investments of time and energy required to excavate tubers, and high nutritional value of tubers (Alexander 1987). We believe that the potential for site defense by wintering Ring-necks also existed in southern Florida. There, Ring-necks fed diurnally on seeds of white water-lily in water depths less than 1.5 m (Weller, unpubl. data). They probably located submersed flower heads visually and fed on flower heads before seed dispersal. This interpretation was supported by large food volumes found in esophagi (i.e., high rates of ingestion) and presence of immature seeds and miscellaneous flower head fragments in food samples (Hohman 1984). Although we have no data on the distribution or abundance of water-lily flower heads, we believe that considerable search time was required to find submersed flower heads and that, once located, flower heads represented defendable resources.

In spite of the likelihood of site defense and potential asymmetries in

social interactions related to size differences between sex-age classes, there was limited evidence in our data to indicate that nutrient acquisition by wintering Ring-necks was influenced by dominance relations during the year of study. Sex had little or no effect on body mass and composition of Ring-necks wintering in southern Florida. ADJMASS and FAT changed similarly in males and females. ADJPROT was affected by sex, remaining constant in females and increasing (14%) in males; however, differences between sexes averaged less than 2% for the entire winter period (Table 1). Speculation that adults interfered with feeding by immatures was supported by our finding that immatures were lighter and had less ADJPROT than adults; however, we found no evidence of age-related differences in FAT or late-winter ADJMASS and ADJLEG of Ring-necks. Moreover, agonistic behavior among wintering Ring-necks at two nearby sites in central Florida was rarely observed (Hohman 1984, Jeske 1985).

Likewise, there was no indication that females or immatures fed less efficiently than males or adults. Assuming that changes in ADJLEG were related to locomotory (primarily feeding) activity, the positive association between ADJLEG and FAT suggested that Ring-necks gained fat through increased feeding. This relation was not influenced by sex, which we interpret to indicate that males and females fed with the same efficiency. However, feeding efficiencies of adult and immature Ring-necks apparently differed. ADJLEG explained less than 9% of the variation in FAT of immatures or adults, but, contrary to prediction, fat gained per measure of foraging effort (ADJLEG) was greater for immatures than adults. Age-related differences in foraging efficiency were not related to diet because adults and immatures selected the same foods (Weller, unpubl. data). We are unable to explain apparent differences in feeding efficiencies of adults and immatures, but we are confident in our conclusion that adults did not interfere with nutrient acquisition by immatures.

Proximate and ultimate controls of body mass and composition.—Patterns of change in body mass and composition of diving ducks during winter vary geographically. Ring-necks and other diving ducks in the Gulf of Mexico region gain body mass during winter, whereas diving ducks wintering at more northerly sites exhibit midwinter declines in body mass. Midwinter declines in body mass, feed intake, and activity of captive Canvasbacks fed ad libitum rations led Perry et al. (1986) to speculate that body mass of Canvasbacks was endogenously controlled. They argued that these changes increased the probability of survival in ducks by decreasing maintenance energy costs during periods of cold stress. However, geographic variation in body mass changes of diving ducks during winter does not support their argument for endogenous control. We be-

lieve that local environmental conditions, especially ambient temperature and food availability, are proximately responsible for observed geographic variation. Declines in body masses of Canvasbacks and Redheads wintering in New York from January to March were attributed to increased thermoregulatory costs and reduced food availability (Ryan 1972, Kaminsky and Ryan 1981). Canvasbacks wintering in coastal North Carolina (Lovvorn 1987) and Chesapeake Bay (Nichols and Haramis 1980) also exhibited midwinter declines in body mass. Reductions in body mass (and fat) of Canvasbacks in North Carolina corresponded to a dietary shift from American wild celery (*Vallisneria americana*) tubers to clams (*Macoma* spp.; Lovvorn 1987). In contrast, high relative body mass of Canvasbacks wintering in Louisiana resulted from their having access to abundant, energy-rich plant foods throughout winter (Hohman 1993).

Overwinter survival probabilities of some waterfowl are influenced by their relative body mass (Haramis et al. 1986, Hepp et al. 1986; but see Krementz et al. 1989). Large energy reserves (correlate of body mass) enhance survival when birds experience food shortages and increased thermoregulatory costs. Further, energy and nutrient reserves maintained in late winter may be used to offset costs (i.e., courtship, migration, prebasic molt [females only], and energy and nutrient storage for reproduction) incurred by diving ducks in spring (Hohman et al. 1988, Hohman 1993).

If it is advantageous for diving ducks to maintain high levels of endogenous reserves during winter, then why do some birds winter at northern latitudes where, because of greater maintenance energy costs and reduced feeding opportunities, they are lighter than birds at more southerly sites? Most diving ducks wintering in northern portions of their winter ranges are males (Nichols and Haramis 1980, Alexander 1983, Haramis et al. 1985, Woolington 1993). Factors responsible for sexual differences in winter distributions of diving ducks thereby contribute to observed geographic variation in body mass. Speculation offered by Nichols and Haramis (1980) and Alexander (1983) that females are subordinate to males and competitively excluded from northern wintering areas is not supported by this study nor by studies of wintering or migrating Canvasbacks (Lovvorn 1989, Hohman and Rave 1990, Hohman 1993). Dominance relations are temporally and spatially dynamic (e.g., Lovvorn 1989). Although structurally smaller, female ducks are sometimes dominant to males (e.g., Canvasbacks, Lovvorn 1989; Blue-winged Teal, Thompson and Baldassarre 1990).

We speculate that geographic differences in mass and composition changes are related ultimately to waterfowl mating systems. Waterfowl form pair-bonds well in advance of breeding, but there is considerable

variation among taxa (Rohwer and Anderson 1988). In general, dabbling ducks (*Anas* spp.) pair in fall and winter, whereas diving ducks form pair-bonds in late-winter or spring (Weller 1965). Delays in pair formation by diving ducks have been attributed to advantages of remaining in flocks (antipredator tactic) and dispersion of foods that commonly preclude site defense (Lovvorn 1989). Regardless of its causes, a major implication of delayed pair formation in diving ducks is that males and females are able to exploit winter habitats independently.

Costs and benefits to diving ducks occupying various portions of their winter range probably differ between sexes. Wintering at northern sites may be favored in males because they are more numerous than females (Bellrose et al. 1961) and must compete for mates. If proximity to spring-staging and breeding areas (i.e., sites where birds initiate courtship and pair-bond formation) influences time of arrival and pairing success, then males wintering in the north may gain a competitive advantage over those wintering to the south (Nichols and Haramis 1980). Because of their lower body mass, survival rates of birds wintering at more northerly sites may be reduced relative to those at southern latitudes; however, the abundance of males relative to females would seem to suggest that survival risks to males wintering at northern latitudes are minimal.

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LITERATURE CITED

ALEXANDER, W. C. 1983. Differential sex distributions of wintering diving ducks (Aythyini) in North America. Am. Birds 37:26–29.

———. 1987. Aggressive behavior of diving ducks (Aythyini). Wilson Bull. 99:38–49.

ANKNEY, C. D. AND ALISAUSKAS, R. T. 1991. Nutrient-reserve dynamics and diet of breeding female Gadwalls. Condor 93:799–810.

BALDASSARRE, G. A., R. J. WHYTE, AND E. G. BOLEN. 1986. Body weight and carcass composition of nonbreeding Green-winged Teal on the southern High Plains of Texas. J. Wildl. Manage. 50:420–426.

BELLROSE, F. C., T. G. SCOTT, A. S. HAWKINS, AND J. B. LOW. 1961. Sex ratios in North American ducks. Ill. Nat. Hist. Surv. Bull. 27:391–474.

HANSON, H. C. 1962. The dynamics of condition factors and their relation to seasonal stresses. Arctic Inst. N. Am. Tech. Paper No. 26.

HARAMIS, G. M., J. R. GOLDSBERG, D. G. MCAULEY, AND E. C. DERLETH. 1985. An aerial photographic census of Chesapeake and North Carolina Canvasbacks. J. Wildl. Manage. 49:449–454.

———, J. D. NICHOLS, K. H. POLLACK, AND J. E. HINES. 1986. The relationship between body mass and survival of wintering Canvasbacks. Auk 103:506–514.

HEPP, G. R., R. J. BLOHM, R. E. REYNOLDS, J. E. HINES, AND 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. Nat. Resour. Conf. 7:299–307.

HOHMAN, W. L. 1984. Diurnal time-activity budgets for Ring-necked Ducks wintering in central Florida. Southeast. Assoc. Fish and Wildl. Agencies 38:158–164.

———. 1993. Body mass and composition changes of wintering Canvasbacks in Louisiana: dominance and survival implications. Condor 95:377–387.

——— AND B. L. CYPHER. 1986. Age-class determination of Ring-necked Ducks. J. Wildl. Manage. 50:442–445.

——— AND D. P. RAVE. 1990. Diurnal time-activity budgets of wintering Canvasbacks in Louisiana. Wilson Bull. 102:645–654.

——— AND T. S. TAYLOR. 1986. Indices of fat and protein for Ring-necked Ducks. J. Wildl. Manage. 50:209–211.

———, ———, AND M. W. WELLER. 1988. Annual body weight change in Ring-necked Ducks (*Aythya collaris*). Pp. 257–269 *in* Waterfowl in winter (M. W. Weller, ed.). Univ. Minnesota Press, Minneapolis, Minnesota.

JESKE, C. L. 1985. Time and energy budgets of wintering Ring-necked Ducks *Aythya collaris* (L.) in north-central Florida. M.S. thesis, Univ. Florida, Gainesville, Florida.

KAMINSKY, S. AND R. A. RYAN. 1981. Weight changes in Red Heads and Canvasbacks during the winter. N.Y. Fish Game J. 28:215–222.

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.

LOVVORN, J. R. 1987. Behavior, energetics, and habitat relations of Canvasback ducks during winter and early spring migration. Ph.D. diss., Univ. Wisconsin, Madison, Wisconsin.

———. 1989. Food defendability and antipredator tactics: implications for dominance and pairing in Canvasbacks. Condor 91:826–836.

MAFFEI, M. D. 1991. Malaleuca control on Arthur R. Marshall Loxahatchee National Wildlife Refuge. Pp. 197–207 *in* Proceedings of symposium on exotic pest plants (T. D. Center, R. F. Doren, R. L. Hofstetter, R. L. Meyers, and L. D. Whiteaker, eds.). U.S. Dept. Interior, Natl. Park Serv., Washington, D.C.

MILLER, M. R. 1986. Northern Pintail body condition during wet and dry winters in the Sacramento Valley, California. J. Wildl. Manage. 50:189–198.

MOORE, J. L. 1991. Habitat-related activities and body mass of wintering Redhead Ducks on coastal ponds in South Texas. M.S. thesis, Texas A&M Univ., College Station, Texas.

NICHOLS, J. D. AND G. M. HARAMIS. 1980. Sex specific differences in winter distribution patterns of Canvasbacks. Condor 82:406–416.

PAULUS, S. L. 1980. The winter ecology of the Gadwall in Louisiana. M.S. thesis, Univ. North Dakota, Grand Forks, North Dakota.

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.

PETERSON, S. R. AND R. S. ELLARSON. 1979. Changes in Oldsquaw carcass weight. Wilson Bull. 91:288–300.

RAVELING, D. G. 1979. The annual cycle of body composition of Canada Geese with special reference to the control of reproduction. Auk 96:234–252.

REINECKE, K. J., T. L. STONE, AND R. B. OWEN, JR. 1982. Seasonal carcass composition and energy balance of female Black Ducks in Maine. Condor 84:420–426.

ROHWER, F. C. AND M. G. ANDERSON. 1988. Female-biased philopatry, monogamy, and the timing of pair formation in migratory waterfowl. Current Ornithol. 5:187–221.

RYAN, R. A. 1972. Body weight and weight changes of wintering diving ducks. J. Wildl. Manage. 36:759–764.

SAS INSTITUTE, INC. 1987. SAS/STAT Guide for personal computers, Version 6 ed. SAS Inst. Inc., Cary, North Carolina.

———. 1991. SAS system for linear models. 3rd ed. SAS Inst. Inc., Cary, North Carolina.

THOMPSON, J. D. AND G. A. BALDASSARRE. 1990. Carcass composition of nonbreeding Blue-winged Teal and Northern Pintails in Yucatan, Mexico. Condor 92:1057–1065.

WELLER, M. W. 1965. Chronology of pair formation in some Nearctic *Aythya* (Anatidae). Auk 82:227–235.

WOOLINGTON, D. W. 1993. Sex ratios of wintering canvasbacks in Louisiana. J. Wildl. Manage. 57:751–758.

APPENDIX I

GENERAL LINEAR MODELS USED TO DESCRIBE DIFFERENCES IN SIZE, BODY MASS, AND FAT (G) OF RING-NECKED DUCKS COLLECTED IN FLORIDA, WINTER 1979–1980

		Size[a]				Body mass			Fat[b]		
Source	df	Sum of squares[c]	*F*-value	*P* > *F*	df	Sum of squares	*F*-value	*P* > *F*	Sum of squares	*F*-value	*P* > *F*
Model[d]	7	293.09	29.32	<0.001	8	656,254.8	48.59	<0.001	156,272.4	23.89	<0.001
Error	169	241.33			168	283,647.2			137,357.3		
Corrected total	176	534.43			176	939,902.0			293,629.7		
Size					1	75,914.4	44.96	<0.001	1407.7	1.72	0.191
Date	1	1.69	1.19	0.277	1	267,488.3	158.43	<0.001	135,268.4	165.45	<0.001
Sex	1	13.35	9.35	0.003	1	5.1	0.00	0.956	1652.2	2.02	0.157
Date*sex	1	0.66	0.47	0.495	1	124.0	0.07	0.787	2126.6	2.60	0.109
Age	1	8.95	6.27	0.013	1	8371.5	4.96	0.027	966.6	1.18	0.278
Date*age	1	4.61	3.23	0.074	1	3887.5	2.30	0.131	692.9	0.85	0.359
Sex*age	1	5.06	3.54	0.062	1	2469.1	1.46	0.228	1996.5	2.44	0.120
Date*sex*age	1	4.61	3.23	0.074	1	4878.5	2.89	0.091	2037.5	2.49	0.116

[a] Size = scores along the first principal component: a linear combination of five structural measurements based on their correlation matrix.
[b] Fat = sum of sheared skin and omental fat mass.
[c] Type III Sums of Squares (SAS Inst., Inc. 1987).
[d] Explained variance for full models: size, $r^2 = 0.55$; body mass, $r^2 = 0.70$; and fat, $r^2 = 0.53$.

APPENDIX II

GENERAL LINEAR MODELS USED TO DESCRIBE DIFFERENCES IN PROTEIN AND LEG MASS (G) OF RING-NECKED DUCKS COLLECTED IN FLORIDA, WINTER 1979–1980

		Protein[a]			Leg mass		
Source	df	Sum of squares	*F*-value	$P > F$	Sum of squares	*F*-value	$P > F$
Model[b]	8	115,611.0	36.83	<0.001	403.55	13.49	<0.001
Error	168	65,919.4			628.01		
Corrected total	176	181,530.5			1031.56		
Size	1	27,779.7	70.80	<0.001	143.82	38.47	<0.001
Date	1	7623.0	19.43	<0.001	56.35	15.08	<0.001
Sex	1	3380.9	8.62	0.004	9.78	2.62	0.108
Date*sex	1	4394.8	11.20	0.001	4.67	1.25	0.265
Age	1	2191.1	5.58	0.019	28.89	7.73	0.006
Date*age	1	846.7	2.16	0.144	20.89	5.59	0.019
Sex*age	1	965.3	2.46	0.119	4.87	1.30	0.255
Date*sex*age	1	1115.5	2.84	0.094	5.08	1.36	0.245

[a] Protein = eviscerated carcass mass.
[b] Explained variance: protein, $r^2 = 0.64$; leg muscle mass, $r^2 = 0.39$.