

# CHANGES IN BODY COMPOSITION OF AMERICAN BLACK DUCKS WINTERING AT CHINCOTEAGUE, VIRGINIA<sup>1</sup>

JOHN M. MORTON AND ROY L. KIRKPATRICK

Department of Fisheries and Wildlife Sciences, Virginia Polytechnic Institute and  
State University, Blacksburg, VA 24061

MICHAEL R. VAUGHAN

Virginia Cooperative Fish and Wildlife Research Unit, Virginia Polytechnic Institute and  
State University, Blacksburg, VA 24061

**Abstract.** Fifty-nine American Black Ducks (*Anas rubripes*) were collected during early, mid-, and late winter 1985-1986 at Chincoteague, Virginia to assess overwinter changes in physiological condition. Lipid Index (LI = grams lipid/gram nonlipid dry carcass  $\times$  100) values of adult males were relatively high throughout winter, whereas LI values of both female age classes were low in early winter, peaked by midwinter, and remained high into late winter. Juvenile females had consistently lower LI values than adult females, indicating that juvenile females may be physiologically disadvantaged during winter. Protein mass did not vary over winter, but tended to be less in juvenile females than adult females. In contrast, Reinecke et al. (1982) found that lipid and protein masses of female American Black Ducks (both age classes) wintering in Maine decreased between fall and winter. This disparity may be explained by latitudinal differences in winter severity and diet. We argue that improved physiological condition, as a result of wintering farther south, may influence overwinter survivorship more strongly than reproductive potential during the subsequent spring.

**Key words:** American Black Duck; *Anas rubripes*; condition; lipid; migration; protein; Virginia; wintering waterfowl.

## INTRODUCTION

Concern for declining populations of American Black Ducks (*Anas rubripes*; Steiner 1984) prompted us to investigate their physiological condition during winter. Environmental factors outside the breeding season may be crucial in regulating populations of migratory birds (Fretwell 1972). The condition of wintering waterfowl influences overwinter survival (Haramis et al. 1986, Conroy et al. 1989; but see Kremenz et al. 1989), vulnerability to hunter harvest (Greenwood et al. 1986, Hepp et al. 1986, Conroy et al. 1989), pairing chronology (Hepp 1986), and reproductive potential during the subsequent spring (Ankney and MacInnes 1978, Raveling 1979, Krapu 1981).

Physiological condition of homeotherms is generally considered to be a function of total body lipids relative to body size. Lipid has twice the caloric density of protein (Ricklefs 1974), and only 0.2-0.3 g lipid/g nonlipid tissue are needed to maintain functional homeostasis in birds

(Odum et al. 1964). In waterfowl, however, labile protein also may constitute a source of endogenous energy. Gizzards lose weight in some waterfowl species during nesting (Korschgen 1977, Reinecke et al. 1982), and flight muscles lose weight during wing molt (Korschgen 1977, Ankney 1979, Raveling 1979, Bailey 1985) and during winter (Reinecke et al. 1982). Work by Jones and Ward (1976) on the Red-billed Quelea (*Quelea quelea*), by Bailey (1985) on Redheads (*Aythya americana*), and by Austin and Fredrickson (1987) on Lesser Scaups (*A. affinis*) suggest that at least some of the gizzard and pectoral muscle weight losses may be due to active mobilization of endogenous protein for energy.

The winter distribution of American Black Ducks extends from maritime Canada to the Gulf Coast (Bellrose 1980). This wide range in latitudes may promote high intraspecific variability in body condition during winter, but American Black Duck body composition has been studied only in Maine (Reinecke et al. 1982). In this study, we investigated the body composition of American Black Ducks wintering in tidal Virginia. Objectives were to determine changes in body lipid and protein over winter, and to com-

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pare the body composition of American Black Ducks wintering in Virginia (37°53'N) with that of American Black Ducks wintering in Maine (43°20'N).

## STUDY AREA AND METHODS

Body composition, habitat use, and behavior of wintering American Black Ducks were concurrently studied on 25,600 ha on Virginia's eastern shore of the Delmarva Peninsula (Morton 1987; Morton et al. 1989a, 1989b). This area included the Chincoteague National Wildlife Refuge (NWR) and was composed of 26% upland, 42% estuarine water, 18% salt marsh, 5% tidal flat, 4% brackish impoundment, and 5% other habitats. At least 3,000 American Black Ducks, which approximated 8% of the 1986 wintering population in Virginia (Serie 1986), wintered on the study area (Morton et al. 1989a). Mean monthly temperatures were 1.9°C and 4.4°C above the 15-year mean for October and November, respectively, but were average during December through February (NOAA, unpubl. data).

Fifty-nine American Black Ducks were collected during early (12 October–11 November), mid- (16–30 December), and late (31 January–13 February) winter in 1985–1986. Ducks were shot in all major habitat types, either on the wing or over water; no decoys, traps, or baits were used. Ducks were sexed and aged using plumage and cloacal characteristics (Anonymous 1977; Larson and Taber 1980, p. 157–160), double-bagged in plastic, and frozen.

In the laboratory, ducks were weighed to the nearest 0.5 g and partially thawed. The carcass was plucked, and bill, tarsi, liver (for heavy metal analysis), and the entire gastrointestinal tract were removed; mesentery fat was stripped from the viscera and returned to the carcass. Flight muscles (i.e., pectoralis, supracoracoideus, and coracobrachialis) on the left side of the sternum were removed (Owen and Cook 1977). Wet weights of flight muscles, liver, and emptied gizzard were obtained after returning external fat to the carcass. The gizzard, flight muscles, and remaining carcass (i.e., excluding liver, intestines, tarsi, and bill) were combined and weighed to the nearest gram to obtain mass of the wet homogenate.

Dry weights of the flight muscles, gizzard, and liver were recorded after freeze drying for  $\geq 48$  hr. Carcass components (excluding the liver) were then pooled, ground twice with a commercial Waring blender, freeze-dried again for 24 hr, and

weighed to the nearest gram to obtain mass of the dry homogenate.

Lipids in two 7- to 10-g samples of each carcass homogenate were extracted for  $\geq 12$  hr using ethyl ether in a Soxhlet apparatus after oven drying the replicates at 55°C for 12 hr. A 2-g sample of each homogenate was analyzed for percent protein ( $6.25 \times N$ ) using the Kjeldahl method. A 1- to 2-g sample of each homogenate was combusted in a muffle furnace at 450°C for 12 hr to determine percent ash.

Paired lipid replicates were not different ( $t = -0.09$ ,  $P = 0.931$ ); therefore, mean values were used in subsequent analyses. Wet weights of esophagus and proventriculus contents (if any) were subtracted from laboratory weights of intact carcasses to standardize measurements of body mass. Water mass was the difference between wet and dry homogenate masses.

A Lipid Index (LI = grams lipid/gram nonlipid dry carcass  $\times 100$ ) was used to assess physiological condition (Johnson et al. 1985, Servello and Kirkpatrick 1987). LI accounts for individual differences in body size among American Black Ducks. Changes in LI are proportional to incremental changes in lipid mass for a given nonlipid dry mass (NLDM). However, percent lipid changes at a decreasing rate as lipid mass increases incrementally for a given NLDM.

We had initially planned to assess the effects of sex, age, and time (i.e., early, mid-, and late winter) on body composition in a three-way analysis of variance (ANOVA). However, due to a small sample of juvenile males ( $n = 5$ ), we eliminated this cohort from statistical analyses. We used a two-way ANOVA model (PROC GLM, SAS 1985) to test the effects of age and time on female body composition ( $n = 36$ ) and a one-way ANOVA model to test the effect of time on adult male body composition ( $n = 23$ ). Variances associated with least square means were used to interpret ANOVA models (PDIF option) because of unequal cell sizes, although arithmetic means and variances are reported. Significance was  $P \leq 0.05$  for all statistical inference unless otherwise indicated.

## RESULTS

Whole body mass of female American Black Ducks ( $n = 36$ ) differed by age ( $P < 0.01$ ) but not over winter ( $P = 0.16$ ; Table 1). Mean body masses of adult and juvenile females were 1,204 g (SE = 20,  $n = 18$ ) and 998 g (SE = 17,  $n = 18$ ),

TABLE 1. Body and organ masses of American Black Ducks collected during early, mid-, and late winter, 1985-1986, at Chincoteague, Virginia.

Time period <sup>a</sup>	Sex	Age	n	Body															
				Whole wet <sup>b</sup>			Nonlipid dry <sup>c</sup>			Flight muscle			Gizzard			Liver			
				$\bar{x}$	SE	n	$\bar{x}$	SE	n	Dry	Wet	SE	$\bar{x}$	SE	n	Dry	Wet	SE	$\bar{x}$
Early	F	J	6	949	19	196	3	28	2	98	3	11.5	1.6	38.2	2.4	6.2	0.6	21.4	2.2
	A	A	4	1,182	41	226	4	32	1	114	2	12.3	1.7	43.9	4.7	9.8	0.2	33.1	0.7
	M	A	8	1,303	48	250	5	43	4	127	4	19.5	3.2	47.7	4.1	8.7	1.1	26.9	2.7
Mid	F	J	7	992	31	197	6	32	2	101	3	11.3	0.8	35.6	1.6	6.9	0.7	22.5	1.8
	A	A	8	1,219	27	225	2	35	1	115	2	13.0	0.6	43.9	1.6	7.8	0.4	25.6	1.1
	M	A	4	1,322	48	256	6	40	2	127	2	15.2	2.6	45.3	2.7	8.1	0.6	27.3	2.0
Late	F	J	5	1,066	14	209	3	32	1	109	2	11.4	1.8	30.0	1.5	8.5	0.5	29.6	2.3
	A	A	6	1,200	46	226	6	42	2	121	4	15.9	1.5	35.7	1.3	9.8	0.8	31.5	2.3
	M	A	11	1,311	23	262	6	44	2	133	4	16.4	0.8	41.0	2.2	9.7	0.7	31.2	1.9

<sup>a</sup> Collections were made during three periods in winter 1985-1986: 12 October-11 November (early), 16-30 December (mid), and 31 January-13 February (late).

<sup>b</sup> Wet body mass (with feathers) — wet mass of proventriculus and esophagus contents.

<sup>c</sup> Feathers, bill, tarsi, liver, intestines, and lipids removed.

respectively. Protein mass did not change over winter ( $P = 0.93$ ) but tended to differ between ages ( $P = 0.09$ ; Table 2). Similarly, weights of NLDM and water mass differed by age ( $P < 0.01$ ) but did not change over winter ( $P > 0.23$ ). These two components account for 69.2% (SE = 0.6,  $n = 36$ ) of whole body mass (the remaining portion is lipid), which partly explains the apparent constancy of whole body mass (within age class) over the winter.

LI and lipid mass of females differed over time ( $P < 0.01$ ) and between age classes ( $P < 0.01$ ), with no significant interaction ( $P > 0.84$ ). Mean lipid masses of adult and juvenile females were 151 g (SE = 13,  $n = 18$ ) and 73 g (SE = 10,  $n = 18$ ), respectively, and ranged from 21-226 g. Mean LI values of adult and juvenile females were 67 (SE = 6,  $n = 18$ ) and 36 (SE = 5,  $n = 18$ ), respectively, and ranged from 11-104. Lipid levels in both female age classes were low in early winter and highest in midwinter (Table 2), but did not differ between mid- and late winter ( $P > 0.56$ ). Mean LI values of adults increased from 45 (SE = 10,  $n = 4$ ) in October-November to 73 (SE = 6,  $n = 14$ ) after mid-December (mid- and late winter data pooled), while LI values for juveniles increased from 16 (SE = 2,  $n = 6$ ) to 46 (SE = 5,  $n = 12$ ) over the same period.

Ash mass of females differed by age ( $P = 0.03$ ). A significant time-age interaction ( $P = 0.03$ ) indicated that juvenile ash mass increased between early and late winter while adult ash mass remained relatively constant (Table 2).

Livers ( $\bar{x} = 69.6\%$ , SE = 0.2,  $n = 59$ ) and flight muscles ( $\bar{x} = 68.3\%$ , SE = 0.6,  $n = 59$ ) consisted of proportionately more water than whole carcasses ( $\bar{x} = 62.3\%$ , SE = 0.6,  $n = 59$ ) and gizzards ( $\bar{x} = 64.1\%$ , SE = 1.3,  $n = 59$ ). Only dry weights of flight muscle, liver, and gizzard are discussed, although both wet and dry masses are reported (Table 1) for comparison with other studies (e.g., Reinecke et al. 1982).

Dry masses of flight muscles, gizzard, and liver were higher in adult than juvenile females ( $P < 0.03$ ). Dry flight muscle mass of all females differed over winter ( $P < 0.01$ ), but dry gizzard mass did not ( $P = 0.36$ ). However, there was a significant time-age interaction ( $P = 0.05$ ); flight muscles of adult females increased from 32 g in early winter to 42 g in late winter (Table 1), while those of juveniles remained at 31 g (SE = 1,  $n = 18$ ). Dry liver mass increased in midwinter ( $P = 0.01$ ) but did not vary between early and late winter.

TABLE 2. Body composition of American Black Ducks collected during early, mid-, and late winter, 1985–1986, at Chincoteague, Virginia.

Winter <sup>a</sup>	Sex	Age	n	Lipid index <sup>b</sup>		Lipid		Protein		Water		Ash	
				$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE
Early	F	J	6	16	2	32	3	161	3	505	9	31	3
	A	4	45	10	101	22	176	8	595	15	49	5	
	M	A	8	59	11	148	29	199	4	629	13	55 <sup>c</sup>	7
Mid	F	J	7	45	6	91	14	155	5	496	11	40	4
	A	8	76	7	170	16	176	4	575	8	39	2	
	M	A	4	65	13	166	35	198	8	634	14	47	2
Late	F	J	5	48	8	99	16	168	3	532	15	44	2
	A	6	70	10	159	24	164	15	581	18	46	3	
	M	A	11	51	5	132	14	207	5	621	15	52	5

<sup>a</sup> Collections were made during three periods in winter 1985–1986; 12 October–11 November (early), 16–30 December (mid), and 31 January–1 February (late).

<sup>b</sup> LI = (grams lipid/gram nonlipid dry carcass) × 100.

<sup>c</sup> n = 7.

Whole body mass, NLDM, LI, lipid, protein, water, and ash of adult male American Black Ducks (n = 23) did not differ over winter (P > 0.34). Similarly, dry masses of flight muscles, gizzard and liver did not vary over winter (P > 0.43). Mean body mass of adult male American Black Ducks was 1,310 g (SE = 21, n = 23). Mean lipid mass of adult males was 144 g (SE = 13, n = 23) and ranged from 75–314 g. Mean LI value was 56 (SE = 5, n = 23) and ranged from 32–123.

DISCUSSION

Our data suggest that American Black Ducks leaving Chincoteague wintering grounds in spring were in as good, if not better, condition than when they arrived there in the fall (winter temperatures in 1985–1986 were not atypical). Adult males maintained high levels of lipids throughout winter, varying from 148 g in early winter to 132 g in late winter (Table 2). Female American Black Ducks were in relatively poor condition in October–November (minimum body lipids during this period were 21 g for juveniles and 58 g for adults); presumably, juvenile and postbreeding adult females had insufficient time to accumulate extensive lipid reserves on the breeding grounds. Lipids peaked by late December in both female age classes and were maintained into late winter (Table 2). Maximum lipid levels in both adult (226 g, LI = 104) and juvenile (148 g, LI = 66) females occurred during mid-winter.

Reinecke et al. (1982) also found that juvenile female American Black Ducks had lower lipid levels than adult females throughout winter, sug-

gesting that juveniles are physiologically disadvantaged during severe winter weather. Both Reinecke et al. (1982) and Albright et al. (1983) estimated that adult females, based on caloric values of lipid and protein reserves, had survival times approximately twice that of juveniles under starvation conditions during the winter. Additionally, different ash levels found in our study (contrary to Reinecke et al. 1982) suggest that juvenile American Black Ducks must divert some dietary nutrients to a maturing skeletal structure while wintering at Chincoteague. Energetic demands on juveniles are further compounded by behavioral differences; they used core and range areas two to three times larger than adults on wintering grounds in Virginia (Morton et al. 1989b). These factors may cumulatively help explain the findings of Conroy et al. (1989) that age and early winter body mass of American Black Ducks were predictive of overwinter survival.

Age differences in lipid levels further suggest that second-year females may be disadvantaged during egg laying. Adult females collected in late winter carried 60 g more lipid than juvenile females (Table 2). Peak vernal migration at Chincoteague typically occurs in late February to early March (Meanley 1982, Morton 1987), shortly after our last collection period. As clutch size is highly correlated with prenesting lipid levels in Mallards (*Anas platyrhynchos*; Krapu 1981), second-year American Black Duck females may have lower productivity if they arrive at breeding grounds with relatively low lipid levels. Furthermore, Owen and Reinecke (1979) pointed out that lipid deposition prior to egg laying may be critical in reducing the exogenous energy re-

quirement of egg production to a level within foraging capabilities.

Body protein of female American Black Ducks collected at Chincoteague did not vary over winter but did tend to vary by age. Mean protein masses of adult and juvenile females were 172 g (SE = 4,  $n = 18$ ) and 161 g (SE = 4,  $n = 18$ ), compared with 203 g (SE = 3,  $n = 23$ ) in adult males. Flight muscle and gizzard dry mass of females also differed between ages (Table 1). However, a 25-g difference in mean dry muscle mass (flight muscles and gizzard) between juvenile and adult females in late winter did not contribute to any appreciable difference in body protein during that same period ( $P = 0.75$ ). Our data suggest that protein reserves of second-year females leaving the Chincoteague wintering grounds may be less than those of older females but the evidence is not clear.

#### COMPARISON OF VIRGINIA AND MAINE DATA

Carcass analysis procedures used in our study were similar to those used by Reinecke et al. (1982) to investigate carcass composition of female American Black Ducks in Maine. Contrary to their analysis, however, the liver, intestines, tarsi, and bill were excluded from the homogenate in our study. Reinecke et al. (1982) accounted for 93% of body weight by summing the slopes of fat, protein, water, and ash regressed on body weight. Using the same approach, we accounted for 83% of body weight; therefore, direct comparisons of absolute values for NLDM, protein, fat, water, and ash are not appropriate. However, qualitative comparisons can be made.

Female American Black Ducks wintering in Virginia generally did not differ structurally from ducks wintering in Maine (Albright 1981). Tarsus, keel, culmen, and bill lengths were similar but wings of adult females collected in Virginia were longer (Morton 1987). However, adult and juvenile females collected in fall at Chincoteague had 21% and 52% less lipid mass than adult and juvenile females collected in Maine (Table 3); presumably the caloric cost of migrating farther south depleted energy reserves.

Female American Black Ducks collected at Chincoteague during late January and early February were as heavy and fat as ducks collected in the fall, whereas those collected during late winter in Maine were in poor condition relative to the fall sample (Table 3). Body condition

peaked by early December in Maine and by late December in Virginia. Reinecke et al. (1982) reported adult females with as much as 250 g lipid in fall and maximum lipid levels in both age classes of females at Chincoteague occurred in late December. Similar patterns of peak body lipids in midwinter have been observed in Northern Pintails (*A. acuta*; Mora et al. 1987) and in some shorebirds (Charadriidae and Scolopacidae; Pienkowski et al. 1984).

Differences in winter severity explains much of this disparity in body condition between American Black Ducks collected in Maine and Virginia. Estimates of daily energy expenditure by American Black Ducks wintering in Maine (Albright et al. 1983) and Virginia (Morton et al. 1989a) were similar at a given temperature; however, average winter temperatures are much lower in Maine than in Virginia. Increased snow and ice cover, as a consequence of lower temperatures, also reduce access to high carbohydrate foods (i.e., vegetation). As much as 95% (by volume) of the diets of American Black Ducks wintering in coastal Maine and New Hampshire is animal matter, and this proportion diminishes to 1.6% in South Carolina (Lewis and Garrison 1984). This change from a protein-rich diet at high latitudes to a carbohydrate-rich diet at lower latitudes may significantly increase fat deposition in wintering American Black Ducks (cf. Griminger 1986).

Captive American Black Ducks (Hepp 1986) and Canvasbacks (*Aythya valisineria*; Perry et al. 1986) lost weight and reduced food intake after midwinter despite being fed ad libitum, suggesting endogenous factors may ultimately regulate metabolism in wintering waterfowl (see Meier and Burns 1976). However, differences between Virginia and Maine data indicate that proximate factors, such as winter temperatures and diet, influence timing and extent of lipid deposition in American Black Ducks. Whyte et al. (1986) similarly suggested that a high carbohydrate diet (i.e., waste corn) and milder winters explained findings that wintering Mallards in Texas carried more lipid mass than wintering Mallards in Missouri or Nebraska. The energetic cost of migrating farther south is apparently mitigated by the energy accrued in a milder climate.

It seems unlikely, however, that American Black Ducks wintering farther south are able to maintain these high energy reserves during northward migration. For example, female Mal-

TABLE 3. Adult and juvenile carcass components (g) of female American Black Ducks wintering in Maine and Virginia.

Age	Component	Maine <sup>a</sup>						Virginia <sup>b</sup>					
		Fall			Winter			Fall			Winter		
		n	$\bar{x}$	SE	n	$\bar{x}$	SE	n	$\bar{x}$	SE	n	$\bar{x}$	SE
Adult	Whole carcass <sup>c</sup>	7	1,166	51	11	989	28	12	1,206	22	6	1,200	46
	Nonlipid dry carcass	5	281	13	11	259	4	12	225	2	6	226	6
	Protein	5	206	8	11	189	4	12	176	3	6	164	15
	Water	5	619	23	11	519	13	12	582	8	6	581	18
	Lipid	5	187	27	11	128	18	12	147	16	6	159	24
	Ash	5	49	3	11	42	2	12	43	3	6	46	3
	Gizzard	7	40	3	11	34	2	12	44	2	6	36	1
	Flight muscle	7	227	9	11	191	5	12	229	3	6	242	7
Juvenile	Whole carcass	25	1,112	22	20	890	22	13	972	19	5	1,066	14
	Nonlipid dry carcass	14	269	7	20	243	5	13	197	3	5	209	3
	Protein	14	202	4	20	177	3	13	158	3	5	168	3
	Water	14	633	15	20	505	11	13	500	7	5	532	15
	Lipid	14	133	21	20	69	11	13	64	11	5	99	16
	Ash	14	46	1	20	41	1	13	36	3	5	44	2
	Gizzard	25	36	2	20	31	2	13	37	1	5	30	2
	Flight muscle	25	226	4	20	179	6	13	200	5	5	218	4

<sup>a</sup> Data from Reinecke et al. (1982). Fall carcasses collected in October, November, and early December. Winter carcasses collected in late January and early February.

<sup>b</sup> Direct comparisons with Maine data cannot be made for nonlipid dry mass, protein, fat, water, and ash. Virginia analyses excluded liver, intestines, tarsi, and bill from homogenate. Mass of flight muscles multiplied by 2 (only left side weighed). Fall carcasses collected 12 October–11 November and 16–30 December. Winter carcasses collected 31 January–13 February.

<sup>c</sup> All carcass components except nonlipid dry carcass are expressed as wet weights.

lards arriving on North Dakota breeding grounds (Krapu 1981) had 50% less lipid mass than female Mallards collected on Missouri wintering grounds in late spring (Heitmeyer 1988); Heitmeyer (1988) argued that this difference was mostly related to the energetic costs of spring migration. Using the method of Whyte and Bolen (1988), we estimated that American Black Ducks would minimally consume 64–80 g of lipid to fly (at 64 km/hr; Tucker and Schmidt-Koenig 1971) the 960-km linear distance between Virginia and Maine, which is more than twice the difference in lipid mass between late winter ducks collected in Maine and Virginia (Table 3).

Perhaps the major advantage of wintering farther south, then, is in increased winter survivorship rather than increased energy reserves carried to the breeding grounds. Conroy et al. (1989) estimated that overwinter survival from both nonhunting and all (i.e., hunting and nonhunting combined) risks was significantly higher for radio-tagged ducks trapped at Chincoteague NWR than for those trapped at Brigantine NWR in New Jersey (39°20'N). Although this is suggestive of a relationship between latitude and overwinter survivorship, Conroy et al. (1989) found only a weak relationship between average daily temperature and survival probability. However,

these authors suggested that differences in the extent of ice cover at critical periods may explain these differences in survivorship.

In 1986, 9,000 and 36,700 American Black Ducks were recorded in Maine and Virginia, respectively, during the Midwinter Waterfowl Inventory (Serie 1986). This distribution may reflect large scale differences in habitat suitability (sensu Baker 1978). Baker (1978) postulated that individuals migrate when the habitat suitability of the breeding or natal site is less than the suitability of the winter site, after accounting for migration costs. In this context, habitat suitability is density-dependent; departure of individuals from a given habitat improves the suitability of that habitat for those that remain. The geographic distribution should stabilize when potential reproductive success is the same for all individuals within a species. Band recovery data applied to Baker's model (Ketterson and Nolan 1983) showed that overwinter survival of Juncos (*Junco hyemalis*) improved with distance migrated, which was attributed to the latitudinal climatic gradient. If this is true of American Black Ducks, there must be a proportionately increasing cost associated with distance migrated for average reproductive potential to be equal at all latitudes. That cost could be manifested as expended en-

ergy reserves (see previous discussion) or delayed arrival on the breeding grounds.

Krementz et al. (1989) found no relationship between late winter (January–March) body mass of captured American Black Ducks and the probability of recapture (i.e., annual survival) the subsequent winter. However, we do not believe that this finding negates our conclusions. We argue that winter body condition primarily affects survival during that winter, not the subsequent year.

Our discussion also is not meant to imply that habitat conditions on wintering grounds do not affect reproductive potential. Raveling and Heitmeyer (1989), for example, demonstrated a positive relationship between Northern Pintail recruitment and precipitation the previous winter under certain conditions, and feeding at stopover areas while en route to breeding grounds may compensate for some of the costs of migration (M. E. Heitmeyer, pers. comm.). However, we suggest that intraspecific variation in geographic use of wintering areas may influence overwinter survival of American Black Ducks more strongly than reproductive potential during the subsequent spring (i.e., increased endogenous energy carried to the breeding grounds).

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