CARCASS COMPOSITION OF NONBREEDING BLUE-WINGED TEAL AND NORTHERN PINTAILS IN YUCATAN, MEXICO[1]

JOHN D. THOMPSON AND GUY A. BALDASSARRE
Environmental and Forest Biology, State University of New York,
College of Environmental Science and Forestry,
Syracuse, NY 13210

Abstract. We studied the carcass composition of Blue-winged Teal (*Anas discors*) and Northern Pintails (*A. acuta*) wintering in Yucatan, Mexico from October through March 1986–1987 and 1987–1988. Patterns of body mass and lipid reserves in Yucatan were similar to patterns reported in ducks (including conspecifics) wintering farther north. However, on average, ducks in Yucatan weighed 5–22% less and carried smaller energy reserves. We argue that an endogenous mechanism is the primary factor controlling the cyclic pattern of body mass and carcass composition of ducks during winter, but that environmental conditions are the proximate cause responsible for the observed geographical variation in the amplitude of changes.

Key words: Anas discors; Anas acuta; Blue-winged Teal; Northern Pintail; carcass composition; body mass; Yucatan; Mexico.

INTRODUCTION

Waterfowl tend to lose weight during winter, which usually reflects use of lipid reserves (Peterson and Ellarson 1979, Kaminsky and Ryan 1981, Reinecke et al. 1982, Baldassarre et al. 1986, Miller 1986). However, factors controlling the regulation of lipid stores throughout winter are unclear. Recent studies on carcass composition have suggested that an endogenous mechanism largely controls changes in winter body mass and/or lipid reserves (Reinecke et al. 1982, Baldassarre et al. 1986, Perry et al. 1986), whereas others have suggested that environmental conditions such as declining food supply or temperature cause observed patterns (Ryan 1972, Kaminsky and Ryan 1981, Joyner et al. 1984). However, most studies do not distinguish between different levels of causation. For example, although an endogenous mechanism may be the primary factor controlling weight patterns during winter, temperature and other environmental stresses probably act as the important proximate causes responsible for the amplitude of observed seasonal and annual variations (King and Farner 1966).

If temperature does affect changes in carcass composition, then conspecifics wintering at different latitudes should be exposed to differing

environmental stresses and may be expected to exhibit differences in body mass and carcass composition (Kendeigh 1969, King and Mewaldt 1981, Nolan and Ketterson 1983). This hypothesis has been tested using various species, but with conflicting results for migratory birds. For example, Nolan and Ketterson (1983) found that northern populations of the Dark-eyed Junco (*Junco hyemalis*) had higher body mass and fat stores than birds from more southerly populations. Pienkowski et al. (1975) and Dick and Pienkowski (1979) reported similar results with shorebirds. Conversely, neither White-crowned Sparrows (*Zonotrichia leucophrys gambelii*; King and Mewalt 1981) nor American Goldfinches (*Carduelis tristis*; Wiseman 1975) exhibited a latitudinal correlation with body mass, and European Starlings (*Sturnus vulgaris*; Blem 1981) carried more fat at midlatitudes than to the north or south.

Mexico annually is the winter home of several million ducks that breed in the Nearctic, and is a major wintering area for the Blue-winged Teal (*Anas discors*) (Voelzer 1985). In addition, Mexico is the southern end of the wintering range for several North American species (e.g., Northern Pintails *A. acuta*; Bellrose 1980). We examined body mass and carcass composition of Blue-winged Teal and Northern Pintails wintering in Yucatan, Mexico, where temperatures are milder than at more northerly wintering sites used by

these species. Our objective was to better explore the factors controlling carcass composition of wintering waterfowl by examining their body mass and carcass composition in Yucatan relative to the hypothesis that they vary with latitude.

METHODS

Blue-winged Teal and Northern Pintails were collected by shooting without the use of decoys during four phenological seasons from October–March, 1986–1988. However, in 1987–1988, some birds were donated by hunters who used decoys. Research and collecting permits (No. 413,700,4857) were obtained from the Secretaria de Desarrollo Urbano y Ecologia in Mexico, D.F., Mexico. All birds were collected from wetlands adjacent to the Laguna de Celestun (Celestun Estuary) located on the western coast of the Yucatan Peninsula. This area was described in detail elsewhere (Thompson 1989). Seasons were differentiated by migration chronology and weather as: (1) Arrival, arrival of birds on the study area (October–November); (2) Early Winter, populations stable but prior to most winter storm activity (December); (3) Late Winter, stable populations and increased winter storm activity (i.e., strong winds and cooler temperatures; 1 January–15 February); and (4) Departure, departure from the area (16 February–31 March). Birds were aged and sexed using plumage and cloacal characteristics (Hochbaum 1942, Carney 1964). Plumage was dried and birds weighed (nearest gram), plucked, and reweighed to determine plucked mass. Ingesta were removed from the esophagus, gizzard, and intestine, and weighed (nearest 0.1 g). Body mass and carcass mass were determined by subtracting ingesta mass from feathered body mass, and plucked body mass, respectively.

A carcass homogenate was obtained by repeatedly passing the carcass, minus the feet and bill, through a meat grinder equipped with a 5-mm sieve plate. A 100-g sample then was used for carcass component determination. Water content was determined by drying samples in individual aluminum pans at 85–90°C for 72–84 hr or until constant mass, and subtracting residue from wet mass. Dried samples then were ground twice in a Molinex coffee grinder and hand mixed to obtain maximum homogeneity.

A subsample weighing 6–10 g was taken from each sample and lipids were extracted in a Soxh-

let apparatus for 8–10 hr using petroleum ether (Dobush et al. 1985). Ash content was determined by combustion of lean samples in a Pyradia Muffle furnace at 550°C for 6 hr to burn off organic matter, leaving a mineral ash. Protein content was assumed to be ash-free lean mass. All weights were to the nearest 0.01 g. All techniques followed those outlined in Alisauskas and Ankney (1985).

Differences in body mass and percentage of each carcass component between adults and immatures were determined for each sex by season combination using analysis of variance; Tukey's studentized range test separated means where appropriate (Steel and Torrie 1980). We used the percentage of each carcass component to correct for differences in body size. Differences between years within seasons, and differences among seasons were determined for body mass, lipid, protein, water, and ash content using analysis of variance and Tukey's studentized range test. Data were pooled where differences were not significant ($P > 0.05$).

Daily environmental data were collected from a portable weather station erected at the southern end of the study area. Long-term weather data collected in Celestun were obtained from the Secretaria de Recursos Hidraulicos, Oficina de Climatologia, in Merida, Yucatan.

Energy budgets were calculated for both species using activity budget data (Thompson 1989) and estimates of basal metabolic rate for each activity (Wooley and Owen 1977, 1978).

RESULTS

We collected 192 Blue-winged Teal (110 males, 82 females), and 39 Northern Pintails (18 males, 21 females). The percentage of each carcass component did not differ ($P > 0.05$) between adults and immatures in each sex by season combination, therefore adults and immatures were combined for all further analyses. There were no differences (t-test; $P > 0.05$) in body mass or carcass composition between birds collected by pass shooting and those collected over decoys as suggested by Greenwood et al. (1986) and Reinecke and Shaiffer (1988). Therefore data for both collection methods were combined.

BODY MASS

Except for two instances, body masses for both species were similar ($P > 0.05$) between years and, did not vary ($P > 0.05$) among seasons with-
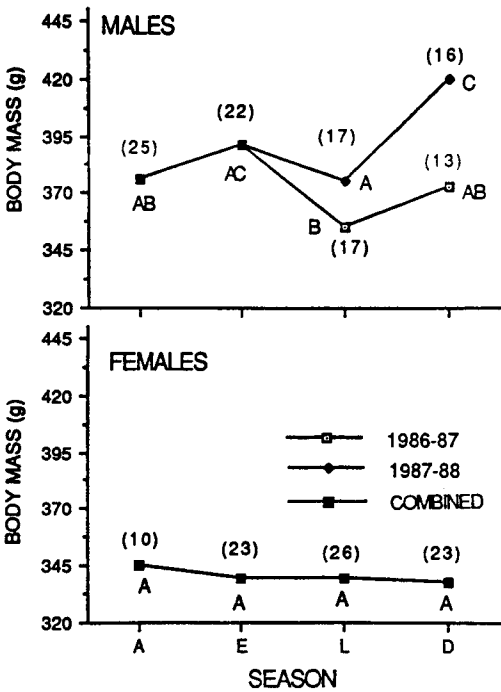
FIGURE 1. Body mass of Blue-winged Teal wintering in Yucatan, Mexico, 1986–1988. A = Arrival (1 October–30 November), E = Early Winter (1–31 December), L = Late Winter (1 January–15 February), D = Departure (16 February–30 March). Sample size in parentheses. Within sexes, means sharing the same letter are not different (Tukey's test; $P > 0.05$).

FIGURE 2. Body mass of Northern Pintails wintering in Yucatan, Mexico, 1986–1988. A = Arrival (1 October–30 November), E = Early Winter (1–31 December), L = Late Winter (1 January–15 February), D = Departure (16 February–30 March). Sample size in parentheses. Within sexes, no means are different (Tukey's test; $P > 0.05$).

in years ($\bar{x} = 380.4$ g, SE = 3.4, $n = 110$ for male and $\bar{x} = 339.7$ g, SE = 3.1, $n = 82$ for female Blue-winged Teal; $\bar{x} = 853.0$ g, SE = 24.8, $n = 18$ for male and $\bar{x} = 763.6$ g, SE = 22.3, $n = 18$ for female Northern Pintails). The exceptions were for male Blue-winged Teal during Late Winter ($\bar{x} = 375.5$ g, SE = 5.1, $n = 17$; $P = 0.001$) and Departure ($\bar{x} = 419.8$ g, SE = 9.1, $n = 13$; $P = 0.001$) 1987–1988 (Figs. 1, 2).

Generally, male Blue-winged Teal and Northern Pintails exhibited similar mass cycles throughout winter. Masses of males increased from Arrival to Early Winter (4.0% for Blue-winged Teal, 8.5% for Northern Pintails) and then decreased from Early through Late Winter (6.0% for Blue-winged Teal, 7.0% for Northern Pintails) before stabilizing or increasing during Departure.

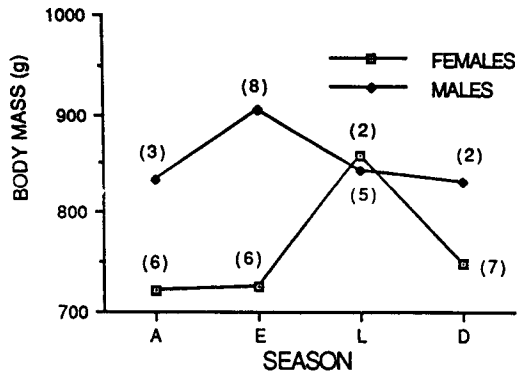Female Northern Pintails exhibited a cycle similar to males, but maximum body mass was not reached until Late Winter, a delay of one season (Fig. 2). Body mass of female Northern Pintails increased 18.2% between Early and Late Winter followed by a 13% decline during Departure. No such pattern in body mass was evident for female Blue-winged Teal.

CARCASS COMPOSITION

Blue-winged Teal. In females, all carcass components remained constant ($P > 0.05$) throughout the winter of 1987–1988. Among males, however, lipid, ash, and water levels remained constant ($P > 0.05$) from Arrival through Late Winter ($\bar{x} = 48.0$ g, SE = 3.6 lipids; $\bar{x} = 20.5$ g, SE = 0.6 ash; $\bar{x} = 220.1$ g, SE = 2.5 water), but increased ($P < 0.05$) during Departure ($\bar{x} = 71.6$ g, SE = 4.4 lipids; $\bar{x} = 25.2$ g, SE = 1.3 ash; $\bar{x} = 227.1$ g, SE = 5.7 water). Both sexes exhibited declines ($P < 0.05$) in lipid and ash content from Early to Late Winter during 1986–1987. These Late Winter declines in body lipids averaged 57.2% (29.8 g) for males and 39.8% (15.8 g) for females. Annual differences in lipid content averaged 20.0 g for males and 21.0 g for females during Late Winter, and 46.0 g for males and 33.9 g for females during Departure.

Protein levels remained constant ($P > 0.05$) across all seasons in females in 1986–1987 and 1987–1988, and in males during 1987–1988 ($\bar{x} = 55.8$ g, SE = 1.0 for males; $\bar{x} = 51.4$ g, SE = 0.9 for females). However, average protein levels in males during 1986–1987 increased 16.3% (8.4 g) during Late Winter, and 5.5% (3.3 g) during
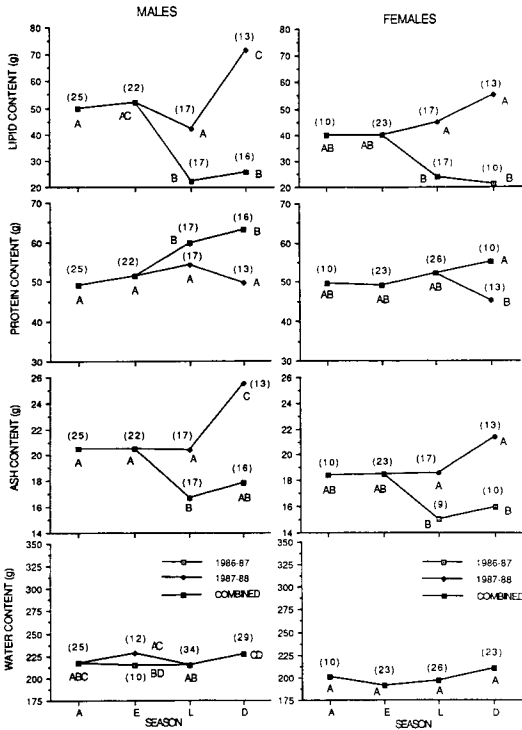
FIGURE 3. Carcass composition of Blue-winged Teal wintering in Yucatan, Mexico, 1986–1988. A = Arrival (1 October–30 November), E = Early Winter (1–31 December), L = Late Winter (1 January–15 February), D = Departure (16 February–30 March). Sample size in parentheses. Within sexes, means sharing the same letter are not different (Tukey's test; $P > 0.05$).

Departure. Water content differed ($P < 0.05$) among seasons only in males, but fluctuations were slight (<4%; Fig. 3).

Northern Pintails. Male body lipids ($\bar{x} = 102.4$ g, SE = 12.4), ash ($\bar{x} = 47.6$ g, SE = 2.4), and water ($\bar{x} = 474.0$ g, SE = 14.3) content increased from Arrival to Early Winter, decreased during Late Winter, and then increased again during Departure. Male lipid increases during Early Winter and Departure were 11.7% (11.3 g) and 49.7% (41.0 g), respectively, with Late Winter decreases of 23.2% (24.9 g). Females exhibited seasonally delayed changes in carcass composition that were similar to delayed body mass cycles. Body protein ($\bar{x} = 117.3$ g, SE = 3.8 for males, $\bar{x} = 100.6$ g, SE = 3.8 for females) varied little among seasons, but showed a general decline throughout winter.

DISCUSSION
BODY MASS

Seasonal changes in body mass are common in wild anatids, and many species exhibit similar mass cycles throughout winter. The general pattern is for body mass to increase during fall followed by midwinter declines and increases in spring. Such changes have been reported for Northern Pintails in California (Miller 1986), Green-winged Teal (*A. crecca*) in Texas and Louisiana (Baldassarre et al. 1986, Rave 1987), Mallards (*A. platyrhynchos*) in Great Britain and Texas (Owen and Cook 1977, Whyte et al. 1986), and Gadwalls (*A. strepera*) in Louisiana (Paulus 1980). The mass cycles of Blue-winged Teal and Northern Pintails in Yucatan were comparable to these other species, however, all sex and age classes of both species tended to weigh less than reported elsewhere. For example, Blue-winged Teal during Arrival in Yucatan, weighed 6.3–16.9% less than Blue-winged Teal during fall (September–October) in Missouri and Texas and, excepting adult males (5.1% greater), 5.4–11.9% less during Departure than during spring (April) from these more northerly areas (White et al. 1981). Overall mean masses were from 9.5–19.2% less than those reported by Bellrose (1980). Northern Pintail males were 9.9–21.9% lighter, and females 4.9–22.0% lighter during all seasons in Yucatan than in California (Miller 1986), and both sexes were 8.3–13.6% lighter than reported by Bellrose (1980). Additionally, during October and November, Northern Pintails weighed 13% less in Yucatan than in Texas (Baldassarre and Bolen 1986), but generally were equal or slightly heavier (6.7% for males) in January and February.

Changes in body mass often reflect changes in levels of body lipids, which are the primary energy reserve for birds (Blem 1976). Thus, reduced body masses of ducks during Arrival in Yucatan probably reflects use of lipids due to added migration costs (Heitmeyer 1988), but this does not explain midwinter differences.

CARCASS COMPOSITION

The pattern of seasonal variation in lipid reserves in Yucatan also is similar to those of birds in other areas, but the magnitude of changes was different. For example, Miller (1986) reported variation in lipid reserves in Northern Pintails in California with lows of 11–15% of carcass mass

in August and September and peaks of 22–39% of carcass mass in November. In Yucatan, lipid levels of Northern Pintails exhibited similar lows of 11.0–12.6% during Arrival for females and during Late Winter for males, but markedly reduced highs of 16.1–17.3% of carcass mass during Late Winter and Departure for females and males, respectively. Data for Blue-winged Teal in midwinter were not found, but Green-winged Teal, a slightly smaller duck, had midwinter lipid stores of 64–73 g (21.7–22.0% of carcass mass) in Texas (Baldassarre et al. 1986), and 32–44 g (11.4–14.0%) in coastal Louisiana (Rave 1987). This deviates somewhat from Late Winter reserves of Blue-winged Teal in Yucatan of only 22.2–44.9 g (6.8–14.1%), and demonstrates a general pattern of smaller lipid reserves at more southerly latitudes.

It has been argued that midwinter declines in body mass and lipids are caused by cold temperatures and/or food shortages (Ryan 1972, Owen and Cook 1977, Kaminsky and Ryan 1981, Whyte and Bolen 1984) as well as annual cycle events (Heitmeyer 1988). Perry et al. (1986) also suggested that birds feeding on low-energy diets store less lipid than those using higher energy foods. This was supported by Rave (1987), who noted that Green-winged Teal feeding on a lower-energy (natural food) diet in coastal Louisiana carried smaller lipid reserves than did Green-winged Teal feeding on a high-energy (agricultural food) diet in Texas (Baldassarre et al. 1986).

Waterfowl in Yucatan consumed only natural foods, using a low-energy (gastropod) diet during Arrival and Early Winter but shifting to a high energy (95% nitrogen-free extract; Swiderek et al. 1988) diet (tubercles of Chara sp.) beginning in mid-December (Thompson, unpubl. data), which is before birds began to lose weight and lipid reserves in Late Winter. In addition, temperatures in Yucatan are very mild compared to those in more northerly wintering areas, whereby both species in this study spent <4.2% of time below their lower critical temperature (Thompson 1989). We further note that activity budgets of waterfowl in Yucatan varied little throughout winter (Thompson 1989). Therefore, declines in body mass and lipid reserves probably did not result from increased energy expenditure for behavioral requirements as suggested by Miller (1986) for Northern Pintails in California. Few paired birds were observed on the study area (Thompson 1989), thus changes in body mass

and carcass composition probably were not influenced by pairing as suggested by Heitmeyer (1988). Therefore, we believe that an endogenous mechanism rather than diet or temperature is the ultimate factor controlling the overall cyclic pattern of body mass and carcass composition observed in waterfowl during winter. Indeed, ducks lost mass and exhibited seasonal changes in carcass composition despite mild temperatures and a high energy diet. However, the proximate cues of temperature and diet may influence the amplitude of these differences and cause intraspecific geographic variation in body mass and carcass composition, which agrees with Blem (1981) and Nolan and Ketterson (1983).

The fact that the cycle of change in carcass composition of female Northern Pintails was delayed in comparison to that of males may have been due to a delay in the timing of annual cycle events as suggested by Heitmeyer (1988). Census data (Thompson, unpubl. data) suggest that female Northern Pintails arrive in Yucatan later than males which may account for the delayed timing of the winter cycle.

Protein levels of both species changed little throughout winter (Figs. 3, 4), except for increases in body protein of male Blue-winged Teal during Late Winter and Departure of 1986–1987. This is interesting because lipid levels were decreasing at this time. Availability of protein during the breeding season can limit waterfowl productivity (Swanson and Meyer 1973, Krapu 1981, McLandress and Raveling 1981, Drobney and Fredrickson 1985). Stored protein also may buffer or replace inadequate dietary protein intake by postbreeding birds (Bailey 1985). However, the role of protein in the physiology of wintering waterfowl is unclear. Reinecke et al. (1982) reported decreasing protein levels in winter in female American Black Ducks (A. rubripes) and suggested that this may permit reduction of daily energy requirements and increase the effective amount of energy reserves (i.e., lipids). Why body protein increased while lipid reserves decreased is unclear, however, at least one hypothesis should be considered. As noted, waterfowl in Yucatan fed on a low-energy (gastropod) diet during Arrival and Early Winter, but shifted to the higher energy diet in mid-December. Data are available only for 1987–1988, as the esophagi of birds collected during 1986–1987 were empty. However, if birds fed only on the higher-protein gastropod diet throughout the winter of 1986–1987, then
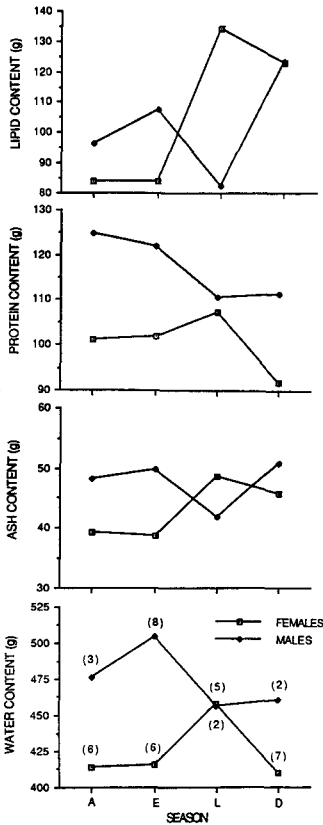
FIGURE 4. Carcass composition of Northern Pintails wintering in Yucatan, Mexico, 1986–1988. A = Arrival (1 October–30 November), E = Early Winter (1–31 December), L = Late Winter (1 January–15 February), D = Departure (16 February–30 March). Sample size in parentheses. Within sexes, no means are different (Tukey's test; $P > 0.05$).

carcass protein may have increased and lipids decreased as shown for captive Canvasbacks on a high-protein, low-energy diet (Perry et al. 1986).

Influence of environmental conditions. Lipid stores serve both as energy reserves and insulation for wintering birds (King 1972, Blem 1976, Raveling 1979, Nolan and Ketterson 1983) and can increase the probability of survival during periods of stress associated with cold, food shortage, or fasting (e.g., overnight or during snow cover). In addition, heavier ducks may exhibit greater overwinter survival, presumably due to larger lipid reserves (Haramis et al. 1986). However, the energetic costs of maintaining and carrying excessive fat loads may place birds at a selective disadvantage (King 1972, Blem 1976, Reinecke et al. 1982, Nolan and Ketterson 1983).

TABLE 1. Energy budget of Blue-winged Teal wintering in Yucatan, Mexico, 1986–1988.

Activity	Time activity (hr)[a]	Multiple of BMR[b]	Energy/ activity kJ/bird/ hr[c]	Energy expended kJ/day
Feeding	10.39	1.8	12.35	128.32
Resting	4.99	1.4	9.63	48.05
Swim	6.40	2.3	15.78	100.99
Flight	0.50[d]	12.5	85.83	42.92
Preen	1.35	1.8	12.35	16.67
Courtship	0.01	2.8	19.26	0.19
Comfort	0.25	1.8	12.35	3.09
Alert	0.06	2.0	13.73	0.82
Aggression	0.05	2.0	13.73	0.69
Totals	24.00			341.74

[a] Based on activity budgets (Thompson 1989).
[b] Modified from Wooley and Owen (1978).
[c] BMR = $0.5224W^{0.7347} \pm 1.237$ where W = body mass (g) (Wooley and Owen 1977).
[d] Estimated maximum time spent/day.

Mild temperatures in Yucatan reduced the need for insulation because the probability that birds would experience stress associated with low temperatures was reduced. However, high tides due to windstorms throughout winter often caused water in the Celestun Estuary to rise to levels at which ducks could not reach submerged vegetation. During these periods, birds apparently fasted, as they were usually observed resting in large flocks away from feeding areas. Storm tides never lasted over 2 days during this study, and birds had lipid reserves sufficient to survive these periods. For example, using average body masses and activity budgets for these species (Thompson 1989), we calculated energy budgets (Tables 1, 2). Assuming that activity budgets were similar between diurnal and nocturnal periods, energetic requirements for ducks were 341.7 kJ/day for Blue-winged Teal and 613.5 kJ/day for Northern Pintails. Using these estimates and assuming that 1 g lipid = 37.7 kJ energy (Blem 1976), then Blue-winged Teal and Northern Pintails would need 18.1 g and 32.6 g of lipid, respectively, to survive a 2-day fast. Averaging years, Blue-winged Teal and Northern Pintails in Yucatan stored no less than 34.4 and 82.5 g of lipids, respectively, across all seasons. This is a 3.8-day reserve for Blue-winged Teal, and a 5.1-day reserve for Northern Pintails. Thus, both species should have had little trouble surviving a 2-day fast. Additionally, average maximum lipid levels of 52 g and 134 g suggest that these species could survive fasts in Yucatan of up to 5.7 and 8.2 days, respectively.

TABLE 2. Energy budget of Northern Pintails wintering in Yucatan, Mexico, 1986–1988.

Activity	Time activity (hr)[a]	Multiple of BMR[b]	Energy/activity kJ/bird/hr[c]	Energy expended kJ/day
Feeding	10.81	1.8	22.48	243.01
Resting	5.03	1.4	17.50	88.03
Swim	4.91	2.3	28.72	141.02
Flight	0.50[d]	12.5	156.13	78.07
Preen	2.08	1.8	22.48	46.76
Courtship	0.07	2.8	34.71	2.43
Comfort	0.33	1.8	22.48	7.42
Alert	0.23	2.0	25.04	5.76
Aggression	0.04	2.0	25.00	1.00
Totals	24.00			613.50

[a] Based on activity budgets (Thompson 1989).
[b] Modified from Wooley and Owen (1978).
[c] $BMR = 0.5224W^{0.7347} \pm 1.237$ where W = body mass (g) (Wooley and Owen 1977).
[d] Estimated maximum time spent/day.

Yearly differences in carcass composition. Blue-winged Teal exhibited yearly differences ($P <$ 0.05) in carcass composition, with lower lipid and ash content during 1986–1987 than 1987–1988. These differences possibly were due to differences in tidal patterns between years. High water levels associated with tides $\geq 80\%$ of mean maximum high tide made it difficult for the small-bodied Blue-winged Teal to reach submerged vegetation and food resources. Strong winds associated with intense winter storm activity during Early Winter 1986–1987 caused tides to be above the 80% level 23.4% of the time as compared to only 2.8% in 1987–1988 (Table 3). Therefore, birds may have been forced to use stored lipid reserves to meet daily energetic requirements more often during the winter of 1986–1987 than 1987–1988.

Cost of migration and overwintering. Migration is an energetically costly event, however, energy expenditure during migration can be compensated for by wintering in warmer climates and thus reducing thermal stress (Kendeigh et al. 1977). For example, using the equation for total energy expenditure during migration (Kendeigh et al. 1977, p. 165), and assuming a round-trip

TABLE 3. Percentage of time when tide was >80% of mean maximum high tide in the Laguna de Celestun, Yucatan, Mexico.

Season	1986–1987	1987–1988
Arrival	9.5	14.4
Early winter	23.4	2.8
Late winter	10.1	13.3
Departure	40.0	22.4

distance of 1,800 km (coastal Louisiana to coastal Yucatan), then Blue-winged Teal and Northern Pintails would spend 4,530 kJ and 6,632 kJ, respectively, in migration costs (Table 4). This, when compared to the added thermoregulatory cost for both species to winter in Louisiana, a well-known wintering area with a mean daily temperature difference of around 10°C (NOAA 1985), yields a savings of 7,725 and 8,872 kJ for Blue-winged Teal and Northern Pintails, respectively (Table 4). Based on daily energy budgets (Tables 1,2), this is equivalent to about a 22.6- and 14.5-day energetic requirement in Yucatan, respectively. Thus, it appears that both species in this study would realize an energetic savings by flying to and wintering in Yucatan vs. coastal Louisiana, which may compensate for other costs (e.g., mortality in transit) associated with migration to a more southerly wintering area.

ACKNOWLEDGMENTS

LITERATURE CITED

ALISAUSKAS, R. T., AND C. D. ANKNEY. 1985. Nutrient reserves and the energetics of reproduction in American Coots. Auk 102:133–144.
BAILEY, R. O. 1985. Protein reserve dynamics in postbreeding adult male Redheads. Condor 87: 23–32.

TABLE 4. Relative cost of migration to Yucatan Mexico vs. overwintering in coastal Louisiana for Blue-winged Teal and Northern Pintails.

Species	Mass (g)	Migration (kJ)	Overwintering (kJ)	Difference (kJ)
Blue-winged Teal	360	4,530	12,255	+7,725
Northern Pintails	810	6,632	15,504	+8,872

BALDASSARRE, G. A., AND E. G. BOLEN. 1986. Body weight and aspects of pairing chronology of Green-Winged Teal and Northern Pintails wintering on the Southern High Plains of Texas. Southwest. Nat. 31:361–366.

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. 1980. Ducks, geese, and swans of North America. Stackpole Books, Harrisburg, PA.

BLEM, C. R. 1976. Patterns of lipid storage and utilization in birds. Am. Zool. 16:671–684.

BLEM, C. R. 1981. Geographic variation in the mid-winter body composition of Starlings. Condor 83:370–376.

CARNEY, S. M. 1964. Preliminary keys to waterfowl age and sex identification by means of wing plumage. U.S. Bur. Sport Fish. and Wildl. Spec. Sci. Rep. Wildl. 82:1–47.

DICK, W.J.A., AND M. W. PIENKOWSKI. 1979. Autumn and early winter weights of waders in northwest Africa. Ornis Scand. 10:117–123.

DOBUSH, G. R., C. D. ANKNEY, AND D. G. KREMENTZ. 1985. The effect of apparatus, extraction time, and solvent type on lipid extraction of Snow Geese. Can. J. Zool. 63:1917–1920.

DROBNEY, R. D., AND L. H. FREDRICKSON. 1985. Protein acquisition: a possible proximate factor limiting clutch size in Wood Ducks. Wildfowl 36:122–128.

GREENWOOD, H., R. G. CLARK, AND P. J. WEATHERHEAD. 1986. Condition bias of hunter shot Mallards (Anas platyrhynchos). Can. J. Zool. 64:599–601.

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. 1988. Body composition of female Mallards in winter in relation to annual cycle events. Condor 90:669–680.

HOCHBAUM, H. A. 1942. Sex and age determination of waterfowl by cloacal examination. Trans. N. Am. Wildl. Nat. Resour. Conf. 7:299–307.

JOYNER, D. E., R. D. ARTHUR, AND B. N. JACOBSON. 1984. Winter weight dynamics, grain consumption and reproductive potential in Canada Geese. Condor 86:275–280.

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.

KENDEIGH, S. C. 1969. Tolerance of cold and Bergmann's rule. Auk 86:13–25.

KENDEIGH, S. C., V. R. DOL'NIK, AND V. M. GAVRILOV. 1977. Avian energetics, p. 127–204. In J. Pinowski and S. C. Kendeigh [eds.], Granivorous birds in ecosystems. Cambridge Univ. Press, London.

KING, J. R. 1972. Adaptive periodic fat storage by birds. Proc. Int. Ornithol. Congr. (1970):200–217.

KING, J. R., AND D. S. FARNER. 1966. The adaptive role of winter fattening in the White-crowned Sparrow with comments on its regulation. Am. Nat. 100:403–418.

KING, J. R., AND L. R. MEWALDT. 1981. Variation of body weight in Gambel's White-crowned Sparrows in winter and spring: latitudinal and photoperiodic correlates. Auk 98:752–764.

KRAPU, G. L. 1981. The role of nutrient reserves in Mallard reproduction. Auk 98:29–38.

MCLANDRESS, M. R., AND D. G. RAVELING. 1981. Changes in diet and body composition of Canada Geese before spring migration. Auk 98:65–79.

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

NATIONAL OCEANIC AND ATMOSPHERIC ADMINISTRATION. 1985. Environmental data service, climatological data. 90:10–12. Asheville, NC.

NOLAN, V., JR., AND E. D. KETTERSON. 1983. An analysis of body mass, wing length, and visible fat deposits of Dark-eyed Juncos wintering at different latitudes. Wilson Bull. 95:603–620.

OWEN, M., AND W. A. COOK. 1977. Variations in body weight, wing length and condition of Mallard Anas platyrhynchos platyrhynchos and their relationship to environmental changes. J. Zool. (Lond.) 183:377–395.

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

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.

PIENKOWSKI, M. W., C. S. LOYD, AND C. D. T. MINTON. 1975. Seasonal and migrational weight changes in Dunlins. Bird Study 26:134–148.

RAVE, D. P. 1987. Time budget and carcass composition of Green-winged Teal wintering in coastal wetlands of Louisiana. M.Sc.thesis, Auburn Univ., Auburn, AL.

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

REINECKE, K. J., AND C. W. SHAIFFER. 1988. A field test for differences in condition among trapped and shot Mallards. J. Wildl. Manage. 52:227–232.

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.

RYAN, R. A. 1972. Body weight and weight changes of wintering diving ducks. J. Wildl. Manage. 36:759–765.

STEEL, R.G.D., AND J. H. TORRIE. 1980. Principles and procedures of statistics. 2nd. ed. McGraw-Hill Book Co., New York.

SWANSON, G. A., AND M. I. MEYER. 1973. The role of invertebrates in the feeding ecology of Anatidae during the breeding season, p. 143–185. In Proceedings Waterfowl Habitat Management Symposium at Moncton, New Brunswick, Canada.

SWIDEREK, P. K., A. S. JOHNSON, P. E. HALE, AND R. L. JOYNER. 1988. Production, management, and waterfowl use of sea purslane, gulf coast muskgrass, and widgeongrass in brackish impoundments, p. 441–457. *In* M. W. Weller [ed.], Waterfowl in winter. Univ. of Minnesota Press, Minneapolis.

THOMPSON, J. D. 1989. Behavioral ecology and carcass composition of waterfowl wintering in Yucatan, Mexico. Ph.D.diss., State Univ. of New York, Syracuse.

VOELZER, J. F., COMPILER. 1985. Mexico winter waterfowl survey. U.S. Fish and Wildl. Serv. 42 pp.

WHITE, D. H., K. A. KING, C. A. MITCHELL, AND A. J. KRYNITSKY. 1981. Body lipids and pesticide burdens of migrant Blue-winged Teal. J. Field Ornithol. 52:23–28.

WHYTE, R. J., G. A. BALDASSARRE, AND E. G. BOLEN. 1986. Winter condition of Mallards on the Southern High Plains of Texas. J. Wildl. Manage. 50:52–57.

WHYTE, R. J., AND E. G. BOLEN. 1984. Impact of winter stress on Mallard body composition. Condor 86:477–482.

WISEMAN, A. J. 1975. Changes in body weight of American Goldfinches. Wilson Bull. 87:390–411.

WOOLEY, J. B., JR., AND R. B. OWEN, JR. 1977. Metabolic rates and heart rate-metabolism relationships in the Black Duck (*Anas rubripes*). Comp. Biochem. Physiol. 57:363–367.

WOOLEY, J. B., JR., AND R. B. OWEN, JR. 1978. Energy costs of activity and daily energy expenditure in the Black Duck. J. Wildl. Manage. 42:739–745.