

CARCASS MASS, COMPOSITION AND GUT MORPHOLOGY DYNAMICS OF MOTTLED DUCKS IN FALL AND WINTER IN LOUISIANA¹

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Abstract. We studied carcass mass, composition, and gut morphology of Mottled Ducks (*Anas fulvigula*) during fall (≈1 October–16 November) and winter (≈17 November–28 February) in southwestern Louisiana during 1987–1988 and 1988–1989. During fall, Mottled Ducks replaced mass and endogenous reserves used during reproduction and molt. From fall through late winter, carcass mass of adult male Mottled Ducks increased 92–115 g, while carcass mass of adult females increased 120 g. Lipid mass of adult males increased 55 g and 71 g from fall through middle winter in 1987–1988 and 1988–1989, respectively. Lipid stores of adult females increased 85 g from fall through late winter. Carcass protein content of both sexes generally did not differ among winter periods within years, but some differences of up to 39 g occurred between years. These yearly differences were associated with changes in gizzard mass and intestine length, and probably were related to different habitat conditions and/or diets. Immature Mottled Ducks generally exhibited patterns in mass, composition, and gut morphology similar to adults. We suggest that mass and lipid patterns in fall and winter reflect the nonmigratory status of Mottled Ducks and earlier breeding opportunities due to the mild climate in coastal Louisiana.

Key words: fall; Mottled Duck; *Anas fulvigula*; carcass composition; gut morphology; Louisiana; winter.

INTRODUCTION

The identification of factors influencing patterns of carcass mass and composition of migratory waterfowl during winter is important because variation in mass and lipid reserves in winter may affect survival (Haramis et al., 1986, Hepp et al. 1986) and reproductive potential (Ankney and MacInnes 1978, Raveling 1979, Krapu 1981). For example, the quality of wetland habitat in winter might influence recruitment of Mallards (*Anas platyrhynchos*) and Northern Pintails (*A. acuta*; Heitmeyer and Fredrickson 1981, Raveling and Heitmeyer 1989) because these species acquire lipid reserves during late winter or spring migration that are used for reproduction (Krapu 1981, LaGrange and Dinsmore 1988).

However, most wintering ducks are highly mobile in response to changing wetland conditions and vary in migration chronology to wintering areas (Bellrose 1980). For example, Mallards wintering in the Mississippi Alluvial Valley responded to increased ice cover by moving farther south into Louisiana (Nichols et al. 1983). Similarly, Green-winged Teal (*A. crecca*) banded during fall and winter on the Southern High Plains of Texas exhibited only limited site fidelity to that area (Baldassarre et al. 1988). Such mobility weakens the assumption that repeatedly sampling from the same geographical area is synonymous with repeatedly sampling the same population. To overcome these potential sources of variation samples should be taken from the same population, but such a sampling scheme has not yet been achieved among the ducks.

Mottled Ducks (*A. fulvigula*) are well suited for study of winter carcass mass, composition, and gut morphology dynamics because their movements are extremely limited relative to those

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of other Nearctic ducks. For example, Stutzenbaker (1988) reported that 82% of direct and indirect band recoveries of Mottled Ducks banded in February and March occurred in the Texas county in which they were banded. Consequently, the same population can be sampled repeatedly during a given winter. Furthermore, Mottled Ducks relied entirely on natural foods on our study area (Moorman 1991), and 83% of females are paired by October (Paulus 1984, 1988a). Thus, variation attributable to these factors also might be reduced by repeatedly sampling this nonmigratory population. Additionally, Paulus (1984, 1988a, 1988b) has determined the behavioral ecology of Mottled Ducks in winter, which in combination with carcass mass, composition, and gut morphology data, allows a more holistic assessment of the ecology of Mottled Ducks during winter. Finally, carcass mass, composition, and gut morphology dynamics are poorly documented for subtropically or tropically distributed ducks in general and nonmigratory species in particular. Such data are valuable for comparison with temperate-dwelling species because the effect of winter severity is removed, which may allow clearer resolution of the effect of annual cycle events on patterns of mass and composition. In this paper we describe patterns of carcass mass, composition, and gut morphology of Mottled Ducks in fall and winter, compare and contrast observed patterns with those reported for other species, and discuss our results in light of the behavioral observations presented by Paulus (1984, 1988b).

STUDY AREA AND METHODS

Collection of specimens. We collected Mottled Ducks by shooting on Rockefeller State Wildlife Refuge in southwestern Louisiana during the fall and winter (1 October–28 February) of 1987–1988 and 1988–1989. Paulus (1982) provides a description of the study area. We did not use decoys, traps or bait to attract Mottled Ducks, nor did we include hunter-killed birds in the sample (Greenwood et al. 1986, Reinecke and Shaiffer 1988). Rockefeller Refuge is not hunted, thus our sample might have included some birds seeking refuge from hunted agricultural lands 30 km north of the refuge. However, the low mobility of Mottled Ducks and complete absence of agricultural grains (i.e., rice; *Oryza sativa*) in esophageal contents of birds collected during our study suggests this was not the case (Moorman 1991).

We did not consider pair status as a potential source of variation because of the small number of Mottled Ducks ($n = 3$ adult males, 1 adult female, 3 immature females in fall, and $n = 2$ immature females in early winter) that were believed to be unpaired. Paulus (1988a) also found that a high proportion of female Mottled Ducks were paired in fall (83% by October) and early winter (93% by December) in our study area.

Laboratory methods. We determined the age and sex of the birds via cloacal examination (Stutzenbaker 1988), allowed their plumage to dry, and then weighed, plucked and reweighed them to determine both fresh body mass and plumage mass to the nearest 0.1 g. We dissected the birds to determine ingesta-free gizzard mass to the nearest 0.1 g and the total lengths of the intestines (small and large combined) and ceca (left and right combined) to the nearest 0.1 cm. The bill, tongue and feet were removed and weighed to the nearest 0.1 g. We calculated body mass by subtracting mass of ingesta from fresh body mass, whereas we determined carcass mass by subtracting the combined masses of ingesta, bill, tongue, feet, and plumage from fresh body mass. After the dissection, we froze the carcasses, allowed them to partially thaw, and then passed each three times through a commercial meat grinder equipped with a 5-mm sieve plate to obtain a carcass homogenate. We removed a 90–100 g sample from each bird for use in carcass component determination.

The samples were dried to constant mass at 90°C to determine water content (Kerr et al. 1982). The dried samples were homogenized further by passing them repeatedly thorough a coffee grinder and then mixing by hand to maximize homogeneity. A 6–10 g subsample was used for proximate analysis of carcass composition. Lipid content of each subsample was determined by petroleum ether extraction in a modified Soxhlet apparatus (Dobush et al. 1985). Lipid-free subsamples were incinerated in a muffle furnace at 550°C for six hours to determine mineral ash content. We used ash-free lean mass as an index to carcass protein content. Masses of carcass components were determined to the nearest 0.001 g. Methods of carcass composition followed Aisauskas and Ankney (1985).

Statistical methods. We divided winter into four phenological periods based on the 30-year mean daily minimum ambient temperature (T_a ; NOAA 1982) and lower critical temperatures (LCT) of the birds (Fig. 1). The LCT was esti-

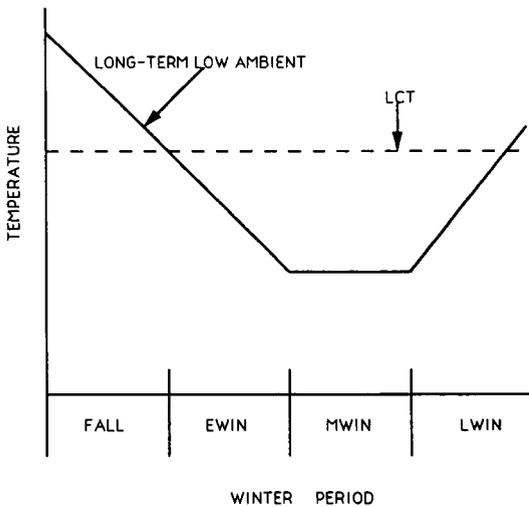


FIGURE 1. Schematic diagram of the division of winter into four periods based on the lower critical temperature (LCT) of Mottled Ducks collected in this study, and the 30-year mean daily minimum ambient temperature (T_a) from 1 October through 28 February at Rockefeller Refuge, Louisiana. The LCT was calculated separately for each sex and age class combination; LCT = 8.4°C for adult males, LCT = 8.7°C for immature males, LCT = 9.1°C for adult females, and LCT = 9.8°C for immature females. Minimum T_a = 5.6°C during MWIN. For chronological reference, FALL was \approx 1 October–16 November, EWIN was \approx 17 November–28 December, MWIN was \approx 29 December–27 January, and LWIN was \approx 28 January–28 February. Dates are approximate because the beginning or end of some periods varied (<4 days) among sex and age classes.

mated with the equation for non-passerine birds presented by Kendeigh et al. (1977:136). We calculated the LCT separately for each sex and age class combination using the mean, ingesta-free, plumed body mass of each group. We identified fall (FALL) as the period when T_a was declining but still $>$ LCT. We defined early winter (EWIN) as the period when T_a was $<$ LCT and still declining over time, middle winter (MWIN) as the period when T_a was $<$ LCT but stable over time, and late winter (LWIN) as the period when T_a was $<$ LCT but increasing over time (Fig. 1). This method avoided potential problems associated with a chronological classification as discussed by Heitmeyer (1988). Also, our method of classification seemed more appropriate because of the potential for temperature (as a measure of winter severity) to act as an ultimate factor that determines body and endogenous reserve mass of birds in winter (Blem 1990).

We used analysis of covariance (ANCOVA) to test for differences between years within periods in carcass mass, composition, and gut morphology; grams of carcass ash was the covariate to control for variation due to structural size (Packard and Boardman 1988, Blem 1990). We used analysis of variance (ANOVA) when the assumption of homogeneity of regressions was not fulfilled (Zar 1984). We combined data when differences were not present and then tested for differences among winter periods in carcass mass, carcass components, and gut morphology variables with ANCOVA. We applied Tukey's studentized range test where appropriate. Differences were considered significant when $P < 0.05$.

We analyzed the data by sex because of the differences in the timing and nature of annual cycle events for each sex (Heitmeyer 1988, Thompson and Baldassarre 1990, Moorman 1991). Also, we analyzed data on immature birds separately and did not make comparisons between years because no immature birds were collected within some year-period-sex combinations. We combined data on immature birds from both years and tested by sex for differences among periods in carcass mass, composition, and gut morphology using analysis of variance (ANOVA). We used ANCOVA to compare carcass mass, composition, and gut morphology between immature and adult mottled Ducks, but Student's t -tests were used to make this comparison when the assumption of homogeneity of regressions was not fulfilled (Zar 1984).

RESULTS

We collected 179 Mottled Ducks (69 adult males, 48 adult females, 21 immature males, 41 immature females) from fall through late winter, 1987–1988 and 1988–1989. Sample sizes of immature birds declined as winter progressed. This was probably a function of early hatching dates and associated early attainment of adult plumage and anatomical characteristics (i.e., absence of bursa of Fabricius, presence of sheathed penis) by immature Mottled Ducks (Stutzenbaker 1988). Consequently, we might have misclassified some immature birds as adults, especially in the middle and late winter periods, but this probably had only a limited effect on the variance because our data indicate that immature Mottled Ducks differed little from adults in carcass mass, composition, or gut morphology during this portion of the annual cycle (see below).

MASS

Body mass. Body mass of adult males was lower in fall 1988–1989 (\bar{x} = 942 g, SE = 18) versus late winter (\bar{x} = 1,056 g, SE = 13). Annual differences in body mass of adult males occurred during fall (\bar{x} = 1,013 g, SE = 22 in 1987–1988) and middle winter (\bar{x} = 1,068 g, SE = 34 in 1987–1988, and \bar{x} = 1,038 g, SE = 70 in 1988–1989). Body mass of adult males during early winter (\bar{x} = 995, SE = 19) did not differ between years or from the other periods. Body mass of immature males did not differ among winter periods (\bar{x} = 1,003 g, SE = 42 in fall, \bar{x} = 962 g, SE = 76 in early winter, \bar{x} = 1,000 g, SE = 28 in middle winter, \bar{x} = 999 g, SE = 49 in late winter). However, immature males averaged 61 g heavier than adult males in fall 1987–1988.

Body mass of adult females increased 112 g from fall (\bar{x} = 888 g, SE = 11) to late winter (\bar{x} = 1,000 g, SE = 26), but no other differences occurred among periods or between years (\bar{x} = 920 g, SE = 28 in early winter, \bar{x} = 935 g, SE = 33 in middle winter). Body mass of immature female Mottled Ducks did not differ among winter periods (\bar{x} = 884 g, SE = 14 in fall, \bar{x} = 835 g, SE = 27 in early winter, \bar{x} = 871 g, SE = 62 in middle winter, \bar{x} = 846 g, SE = 46 in late winter). However, immature females averaged 153 g lighter than adult females in late winter.

Carcass mass. Mean carcass mass of adult male Mottled Ducks increased 92–115 g from fall (\bar{x} = 890 g, SE = 23 in 1987–1988, and \bar{x} = 867 g, SE = 17 in 1988–1989) to late winter (\bar{x} = 982 g, SE = 12), but means from adjacent periods were not different (Fig. 2). Carcass mass of adult males differed by up to 24 g between years during fall and middle winter (Fig. 2). Carcass mass of immature males did not differ among winter periods, but immature males (\bar{x} = 941 g, SE = 62) were 74 g heavier than adult males (\bar{x} = 867 g, SE = 16) in fall 1988–1989 (Fig. 2).

Carcass mass of adult females increased 120 g from fall (\bar{x} = 809 g, SE = 11) to late winter (\bar{x} = 929 g, SE = 24), but means in adjacent periods were not different (Fig. 3). Carcass mass of adult females differed by up to 16 g between years during middle winter (Fig. 3). Mean carcass mass of immature females did not differ among winter periods, but immature females (\bar{x} = 781 g, SE = 44) were 148 g lighter than adult females in late winter (Fig. 3).

CARCASS COMPOSITION

Lipid. Lipid mass of adult males increased 55 g and 71 g from fall (\bar{x} = 96 g, SE = 14 in 1987–1988, and \bar{x} = 91 g, SE = 10 in 1988–1989) to middle winter (\bar{x} = 151 g, SE = 14 in 1987–1988, and \bar{x} = 162 g, SE = 38 in 1988–1989) in 1987–1988 and 1988–1989, respectively. Lipid stores of adult males were also greater in late winter (\bar{x} = 130 g, SE = 7) than in fall (Fig. 2). Lipid content of immature males did not differ among winter periods or from levels of adults (Fig. 2).

Lipid content of adult females increased 56 g from fall (\bar{x} = 81 g, SE = 11) to middle winter (\bar{x} = 137 g, SE = 12), and 85 g from fall to late winter (\bar{x} = 166 g, SE = 14) (Fig. 3). Lipid content of immature females did not differ among periods, but immatures (\bar{x} = 81 g, SE = 24) averaged 85 g less lipid than adults in late winter (Fig. 3).

Protein. Adult males did not differ in protein content among winter periods in 1987–1988; however, there were differences between years within periods (Fig. 2). Adult males had 28 g more protein during fall of 1987–1988 (\bar{x} = 191 g, SE = 6) than in fall 1988–1989 (\bar{x} = 163 g, SE = 2), and 39 g more in middle winter of 1987–1988 (\bar{x} = 189 g, SE = 11) versus 1988–1989 (\bar{x} = 150 g, SE = 8) (Fig. 2). Protein content of immature males did not differ among periods, but during middle winter immature males (\bar{x} = 152 g, SE = 8) had 37 g less protein than adult males collected in middle winter, 1987–1988 (Fig. 2).

Protein content of adult females did not differ among winter periods within years, but it was 21 g greater during middle winter 1987–1988 (\bar{x} = 165 g, SE = 4) versus 1988–1989 (\bar{x} = 144 g, SE = 5) (Fig. 3). Protein content of immature females did not differ among periods, but their middle winter protein level (\bar{x} = 139 g, SE = 2) was 26 g lower than that of adults collected in middle winter 1987–1988 (Fig. 3).

GUT MORPHOLOGY

Gizzard mass. Gizzard mass of males did not differ among winter periods, between years, or between age classes, except that it was greater in adults during middle winter 1987–1988 (\bar{x} = 36 g, SE = 2) versus 1988–1989 (\bar{x} = 32 g, SE = 2) (Fig. 4). Gizzard mass of adult females was greater in fall (\bar{x} = 37 g, SE = 3) than early winter (\bar{x} = 29 g, SE = 2) or late winter (\bar{x} = 28 g, SE =

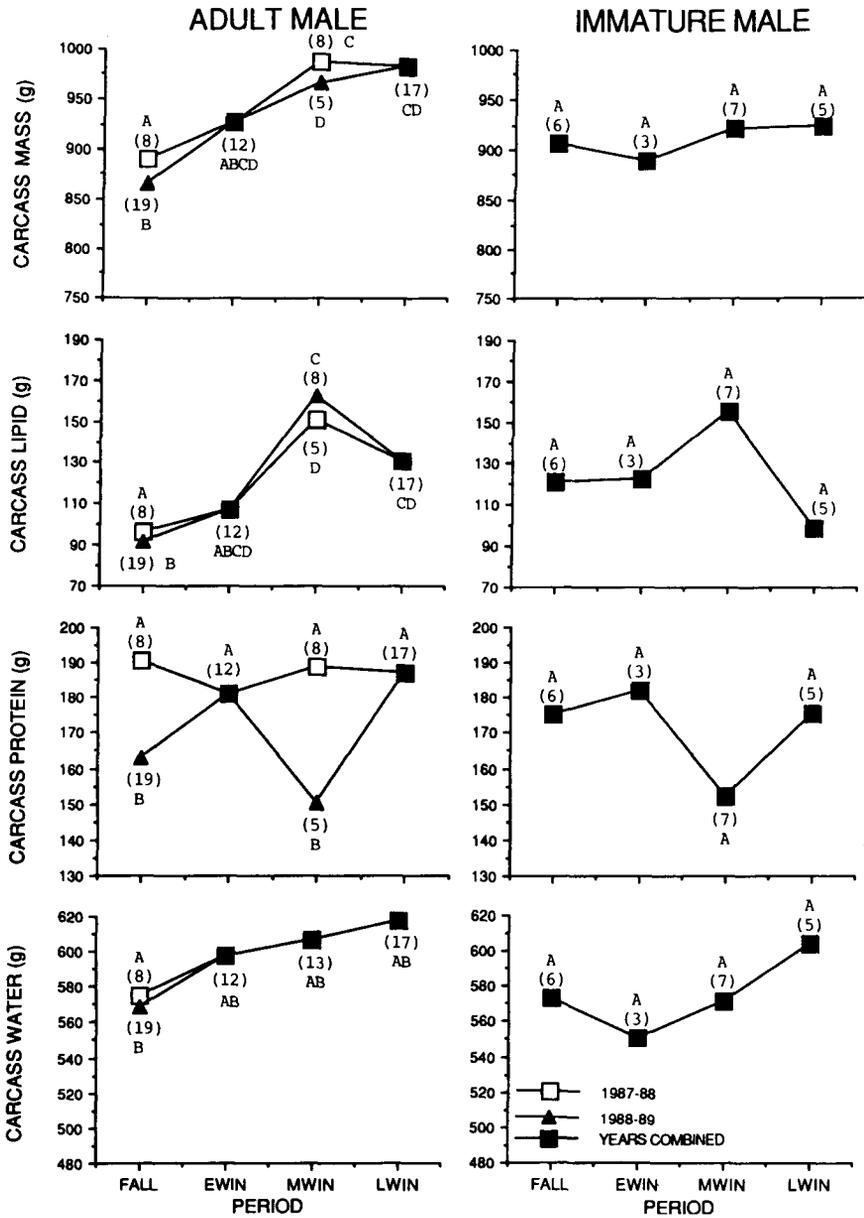


FIGURE 2. Carcass mass and composition of adult and immature male Mottled Ducks in coastal Louisiana in winter, 1987-1988 and 1988-1989. FALL was ≈1 October-16 November, EWIN was ≈17 November-28 December, MWIN was ≈29 December-27 January, and LWIN was ≈28 January-28 February. Sample size in parentheses. Within age classes, all means sharing the same letter do not differ (Tukey's test; $P > 0.05$).

6), but it did not differ between years (Fig. 5). Gizzard mass of immature females did not differ among winter periods, but it differed from adult females during early winter ($\bar{x} = 38$ g, SE = 1) (Fig. 5).

Intestine length. Intestine length of adult males did not differ among periods, but it averaged 24 cm longer in middle winter 1987-1988 ($\bar{x} = 151$ cm, SE = 3) versus middle winter 1988-1989 ($\bar{x} = 127$ cm, SE = 4) (Fig. 4). Intestine length of

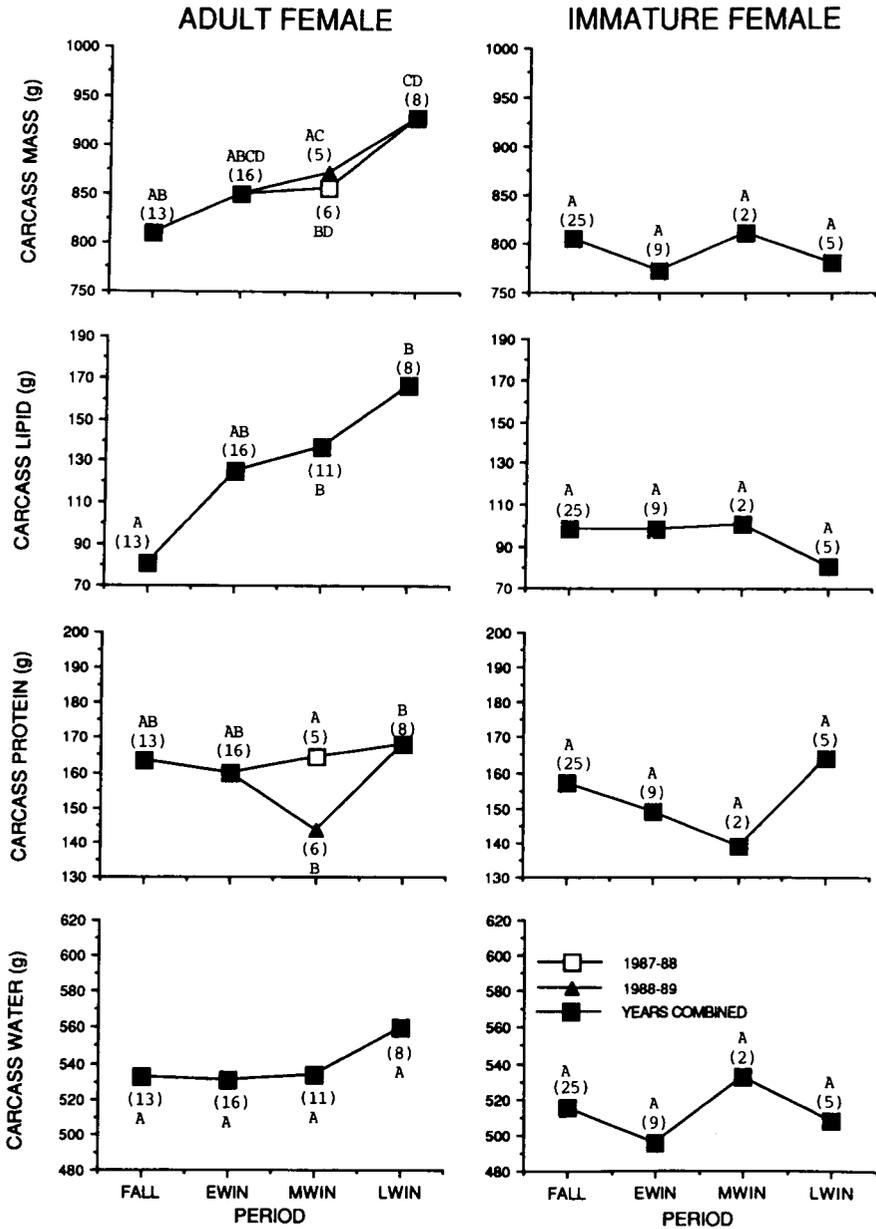


FIGURE 3. Carcass mass and composition of adult and immature female Mottled Ducks in coastal Louisiana in winter, 1987–1988 and 1988–1989. FALL was ≈1 October–16 November, EWIN was ≈17 November–28 December), MWIN was ≈29 December–27 January, and LWIN was ≈28 January–28 February. Sample size in parentheses. Within age classes, means sharing the same letter do not differ (Tukey’s test; $P > 0.05$).

immature males did not differ among periods, but it averaged 22 cm shorter during middle winter ($\bar{x} = 129$ cm, SE = 4) than adults collected in middle winter 1987–1988 (Fig. 4). Intestine length of females did not differ among periods, between years, or between age classes, except that it was 22 cm longer in adults during fall ($\bar{x} = 151$

cm, SE = 9) versus middle winter ($\bar{x} = 129$ cm, SE = 7) (Fig. 5).

Ceca length. Ceca length of adult males was 7 cm longer in fall of 1987–1988 ($\bar{x} = 32$ cm, SE = 2) versus both middle winter ($\bar{x} = 25$ cm, SE = 1) and late winter ($\bar{x} = 25$ cm, SE = 1); their ceca length also differed between years during

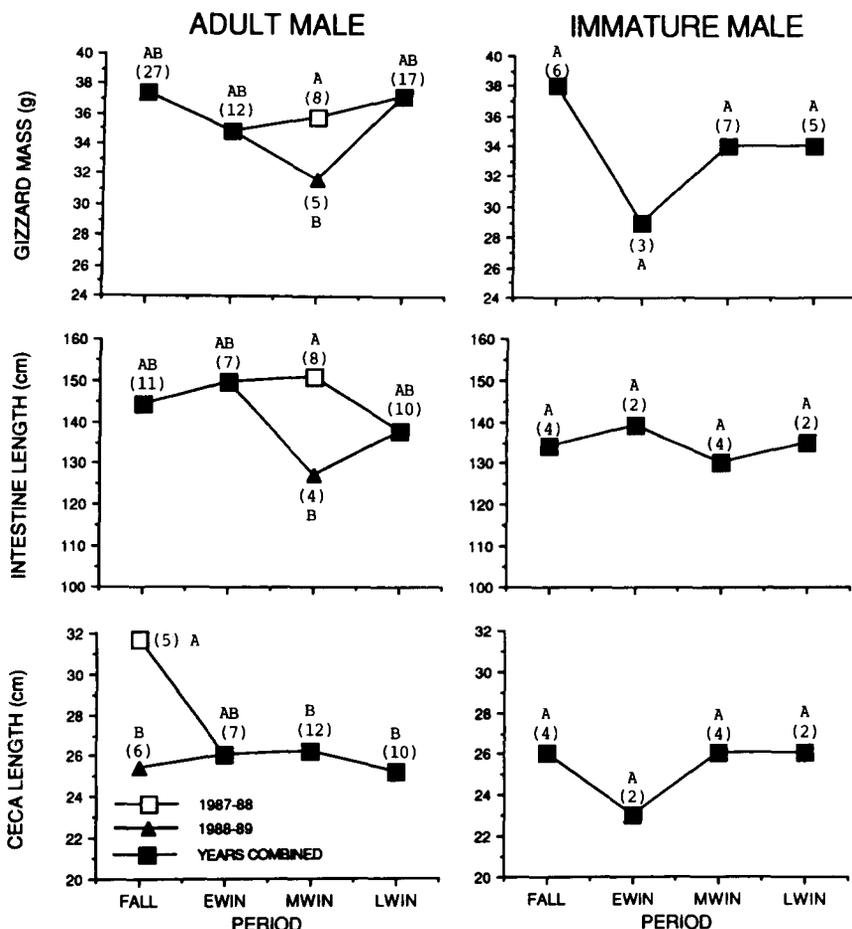


FIGURE 4. Gut morphology of adult and immature male Mottled Ducks in coastal Louisiana in winter, 1987–1988 and 1988–1989. FALL was \approx 1 October–16 November, EWIN was \approx 17 November–28 December, MWIN was \approx 29 December–27 January, and LWIN was \approx 28 January–28 February. Sample size in parentheses. Within age classes, means sharing the same letter do not differ (Tukey's test; $P > 0.05$).

fall ($\bar{x} = 25$ cm, $SE = 1$ in 1988–1989) (Fig. 4). Ceca length of immature males did not differ among periods or from those of adult males (Fig. 4). Ceca length of adult females did not differ among periods, between years, or between age classes, except during fall when immature females ($\bar{x} = 23$ cm, $SE = 1$) had ceca 5 cm shorter than adult females ($\bar{x} = 28$ cm, $SE = 1$) (Fig. 5).

DISCUSSION

Observed patterns and potential causes. Both sexes of Mottled Ducks gradually increased or maintained mass and lipid reserves from fall through late winter and did not exhibit a mid-winter decline like that reported in Mallards (Delnicki and Reinecke 1986, Whyte et al. 1986, Heitmeyer 1988), Northern Pintails (Miller 1986), Black

Ducks (*A. rubripes*; Reinecke et al. 1982), and Canvasbacks (*Aythya valisineria*; Perry et al. 1986) wintering at more northern latitudes. Mottled Ducks surprisingly maintained lipid reserves that would meet existence energy requirements (EER) for 5–9 days in early winter and middle winter (EER based on the equation for nonpasserines, 0°C , and 10-hr photoperiod; Kendeigh et al. 1977:143). Such reserves are comparable to those maintained by Mallards wintering farther north on the Southern High Plains of Texas (Whyte and Bolen 1984) and seem more than adequate to meet energy demands during periods of extremely cold weather. Periods of extreme winter weather are very uncommon and rarely persist for >2 –3 days in coastal Louisiana (Rave and Baldassarre 1991). Additionally, Paulus

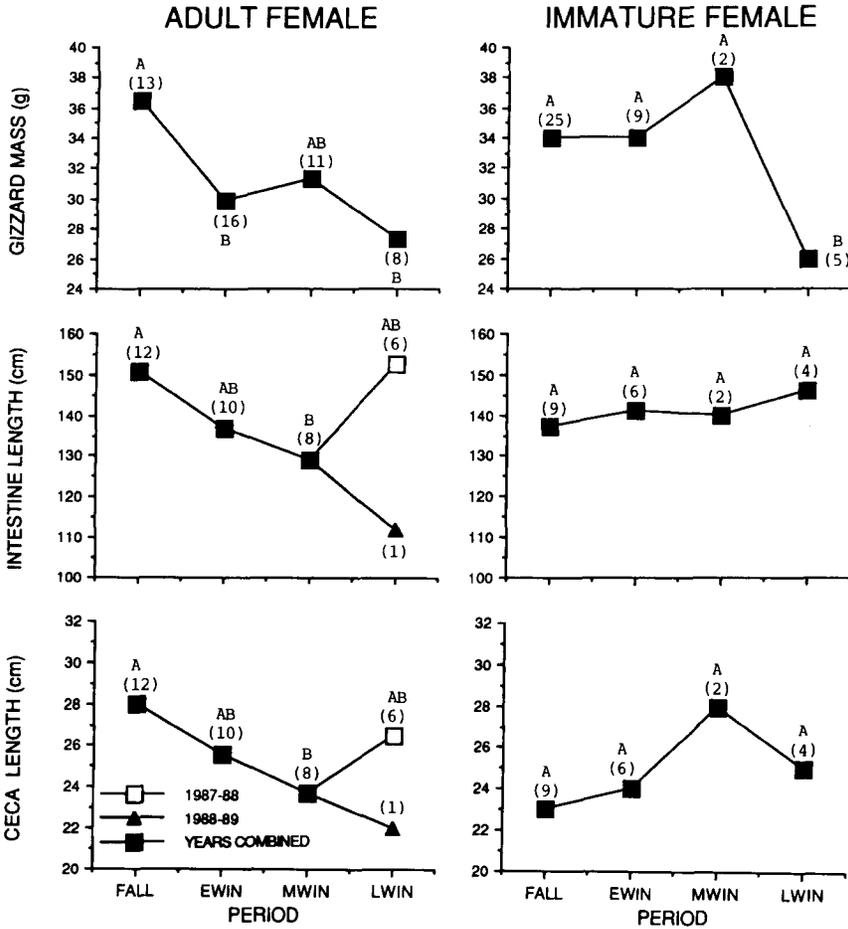


FIGURE 5. Gut morphology of adult and immature female Mottled Ducks in coastal Louisiana in winter, 1987–1988 and 1988–1989. FALL was ≈ 1 October–16 November, EWIN was ≈ 17 November–28 December), MWIN was ≈ 29 December–27 January, and LWIN was ≈ 28 January–28 February. Sample size in parentheses. Within age classes, all means sharing the same letter do not differ (Tukey’s test; $P > 0.05$).

(1984, 1988b) observed that Mottled Ducks respond to declining ambient temperature by increasing feeding rates and cease feeding only during periods of extreme cold (-15°C).

Thus, considering the relatively mild winter climate in coastal Louisiana, and assuming that Mottled Ducks meet increased energetic demands during periods of cold weather by increasing foraging effort (Paulus 1988b), why should they gradually increase or maintain lipid reserves during winter? Also, why should their reserves be adequate to meet EER for 5–9 days, when at worst, reserves are required for about three days, and then only rarely? Such a pattern does not appear to be adaptive because (1) large reserves seem unnecessary due to the mild winters in coastal Louisiana, (2) the risk of predation

might increase with increasing mass and lipid reserves (Lima 1986), particularly in Louisiana where Northern Harriers (*Circus cyaneus*) persistently harass wintering ducks (Tamisier 1976, Paulus 1984), (3) maintenance energy requirements would be increased unnecessarily (Reinecke et al. 1982), and (4) the probability of severe weather events and associated energy deficit lessens as winter progresses (Baldassarre et al. 1986).

We believe the gradual increase in mass and lipid reserves exhibited by Mottled Ducks during winter has little to do with increasing the probability of winter survival per se; rather, it is probably related to late winter and early spring breeding opportunities available due to the mild climate in coastal Louisiana. Furthermore, Mottled

TABLE 1. Mean daily minimum temperature (°C) and precipitation (cm) in fall and winter in Louisiana.

Year	Period ¹							
	Fall		Early winter		Middle winter		Late winter	
	Temp	Precip	Temp	Precip	Temp	Precip	Temp	Precip
1987–1988	11.6	16.3	9.5	13.6	4.0	8.1	7.2	24.8
1988–1989	13.1	10.1	6.9	11.8	8.9	14.0	9.4	0.9
Long-term ²	11.0	14.8	7.0	15.2	5.6	9.9	6.7	11.6

¹ Chronological reference for periods as in Figure 1.

² Long-term data are 30-year averages taken from National Oceanic and Atmospheric Administration (1982).

Ducks probably are able to take advantage of earlier breeding opportunities because they have eliminated migration from their annual cycle, an adaptation that allows reserves attained during the period of premigratory fattening that occurs in other ducks to be used for reproduction by Mottled Ducks.

For example, female Mottled Ducks peaked in lipid reserves in late winter (February), which is about the time many other migratory species of ducks are undergoing premigratory fattening (Baldassarre et al. 1986, Whyte et al. 1986, Heitmeyer 1988, Thompson and Baldassarre 1990, Rave and Baldassarre 1991). This may enable Mottled Ducks to begin nesting in February and March with a peak of nesting activity occurring in early April (Baker 1983, Stutzenbaker 1988), 4–6 weeks earlier than prairie-nesting Mallards, which do not begin to initiate nests until mid-April and do not peak until mid-May (Bellrose 1980, Krapu 1981). Mottled Ducks may benefit from breeding earlier because it allows more time for females to reneest and for both sexes to recover reserves in the interim prior to wing molt (Moorman 1991). Additionally, associated earlier hatching dates would allow more time for duckling growth and development before the onset of fall, which might enhance their survival and recruitment. These advantages apparently outweigh the previously discussed costs associated with acquisition and maintenance of the reserve during winter.

Relationship to time spent feeding. Our data support the conclusion of Paulus (1988b) that feeding rates of Mottled Ducks were higher in early fall (61% of daily activity budget [DAB] in September) because they were replacing mass and endogenous reserves used during reproduction and/or molt. For example, male Mottled Ducks averaged 10–13% heavier, had 87–97% more lipid, and 4–22% more protein in fall than during the late portion of the flightless period (Moorman 1991). Similarly, females were 16% heavier, had

60% more lipid and 15% more protein in fall than during the late portion of the flightless period (Moorman 1991).

Lower feeding rates in late fall and early winter (29–31% DAB in October–December) observed by Paulus (1984, 1988b) might reflect the mild climate of coastal Louisiana (Table 1). After Mottled Ducks attain a level of reserves adequate to meet the relatively brief (≤ 3 days) periods of cold weather or high tides (i.e., inaccessible food), they probably feed at a rate suitable to maintain or slowly increase their reserves and meet daily energy requirements.

Additionally, Paulus (1984, 1988b) observed that Mottled Ducks increased feeding rates (45–49% DAB) in late winter (January and February), and females apparently foraged selectively for invertebrates. He suggested that increased feeding time was necessary to meet protein demands of upcoming reproductive activities. However, we found that carcass protein remained unchanged in both sexes during the winter of 1987–1988, did not change in females in 1988–1989, and fluctuated $\leq 10\%$ in males in 1988–1989. Also, Mottled Ducks continue to increase their lipid reserves during winter. Therefore, we suggest that Mottled Ducks increase feeding time to increase lipid reserves in preparation for reproduction. Female Mottled Ducks observed selectively foraging for invertebrates probably were early-nesting birds engaged in rapid follicle growth or egg laying when dietary protein is required for hypertrophy of the ovary and oviduct, and for albumen production (Drobney 1980, Krapu 1981, Moorman 1991). Alternatively, it is possible that food resources were depleted by late winter, which could have resulted in higher feeding rates.

Carcass protein and gut morphology. The cause of the lower levels of carcass protein that occurred during 1988–1989 is unclear. However, differences occurred in adults of both sexes, which suggests they were real. Lower gizzard mass and shorter intestine lengths of adult Mottled Ducks

coincided with, and contributed to, the lower levels of protein. These changes in gut morphology suggest a possible linkage between habitat conditions and diet. The winter of 1988–1989 was drier than average (Table 1) and caused marsh and impoundment water levels to recede, which could have allowed Mottled Ducks both continuous and greater access to both seed banks and invertebrates (Swanson and Meyer 1977, Baldassarre 1980, Fredrickson and Taylor 1982). Consequently, diet diversity of Mottled Ducks might have been greater in 1988–1989; such increases in dietary diversity can cause decreases in the size and mass of digestive organs of ducks (Kehoe and Ankney 1985, Kehoe et al. 1988).

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