The Condor 90:669–680

BODY COMPOSITION OF FEMALE MALLARDS IN WINTER IN RELATION TO ANNUAL CYCLE EVENTS[1]

MICKEY E. HEITMEYER[2]
Gaylord Memorial Laboratory, School of Forestry, Fisheries and Wildlife,
University of Missouri–Columbia, Puxico, MO 63960

Abstract. Body mass and carcass composition were determined from 267 female Mallards (*Anas platyrhynchos*) collected during the winters of 1980–1981, 1981–1982, and 1982–1983 in the Mingo Basin of southeastern Missouri. Changes in carcass composition were related to annual events, such as migration, molt, and pairing. Body and carcass masses were similar between adults and immatures within status groups. The first females arriving in the Mingo Basin in fall were mostly adults engaged in the prealternate molt; body (1,010 g) and lipid (65 g) masses of these females in mid-prealternate molt were low compared to females collected at other times during winter. Females gained body and lipid mass following the completion of the prealternate molt and most became paired in November and December. Paired females had greater lipid masses than unpaired females throughout fall and winter. Body and carcass masses of nonmolting females remained constant over winter. Females initiated the prebasic molt with relatively large body (1,118 g) and lipid (168 g) masses. Lipid mass declined curvilinearly through the middle of the prebasic molt but then increased to 188 g and 219 g by late prebasic molt and premigratory stages, respectively. Adults proceeded through annual events earlier than immatures and both immatures and adults proceeded through annual events earlier in the wet winter of 1982–1983 than in the drier winters of 1980–1981 and 1981–1982. Mallards complete annual events earlier than most other ducks and female Mallards that complete annual events early in winter may have, at least historically, realized survival and reproductive potential advantages, especially following wet winters.

Key words: Mallard; Anas platyrhynchos; *body composition; molt; migration; pair formation; winter; lowland hardwood wetlands.*

INTRODUCTION

Resources on wintering grounds may be limiting for many migrant birds, especially those inhabiting highly dynamic and seasonal environments (Fretwell 1972). Wetlands are among the most dynamic of North American ecosystems (Mitsch and Gosselink 1986) and resource dynamics during winter influence both survival and recruitment characteristics of many aquatic bird species (Nilsson 1979, Den Held 1981, Heitmeyer and Fredrickson 1981, Nichols and Hines 1987). Body and lipid masses are important determinants of survival (Haramis et al. 1986, Hepp et al. 1986) and reproductive potential (Ankney and MacInnes 1978, Raveling 1979, Krapu 1981) in waterfowl and potentially vary with climatic and wetland conditions. Consequently, several investigators have attempted to quantify patterns of carcass composition in waterfowl during winter (e.g., Raveling 1979, Delnicki and Reinecke 1986, Miller 1986, Whyte et al. 1986 and references within).

Most studies of body composition of waterfowl in winter have presented data on a chronological basis and have not related results to events in the annual cycle that are undertaken during winter, such as molt and pairing (but see McLandress and Raveling 1981a). These annual events require different quantities and qualities of nutrients and involve different levels of physical exertion, thus, they potentially impose different constraints on body composition. The chronology of these events varies not only among species (e.g., Weller 1965) but also within a species in relation to age, sex, and habitat condition (Heitmeyer 1987). Therefore, data presented only on a chronological basis may be misleading and obscure the importance of different events and demands placed on waterfowl during winter.

The purpose of the present paper is to document the body composition dynamics of wintering female Mallards (*Anas platyrhynchos*) in

---

[1] Received 4 January 1988. Final acceptance 1 April 1988.

[2] Present address: Department of Wildlife and Fisheries Biology, University of California, Davis, CA 95616.

relation to events in the annual cycle. Such data are needed to understand mechanisms and evolutionary strategies of nutrient acquisition and use.

STUDY AREA AND METHODS

Data presented are from 267 female Mallards collected from January through March 1981 (*n* = 73) and October through March 1981–1982 (*n* = 114) and 1982–1983 (*n* = 80) from the Mingo Basin in southeastern Missouri. Description of the study area, and of climatic and wetland conditions during this study, are provided in Heitmeyer (1985). Precipitation, river overflows, and flooding of lowland hardwood wetlands during winter in the Mingo Basin ranged from wet (57.9 cm of precipitation falling from October to March) in 1982–1983 to drier in 1981–1982 and 1980–1981 (49.7 cm and 40.3 cm of precipitation, respectively).

Birds selected for collection were observed immediately prior to collecting to obtain data on time budgets, habitat use, and feeding ecology (Heitmeyer 1985). Relatively equal numbers (20 to 30 females in most months) of birds were collected throughout winter in each year. Collections were random with respect to status and age except that the pairing status of females (paired or unpaired) was determined before collection. Pair status of females was determined by associations and displays (Lebret 1961, Johnsgard 1965). Attempts were made to collect both paired and unpaired females during all months of the study, however, few females remained unpaired after late December; consequently few (*n* = 10) unpaired birds were collected from January through March. Cold temperatures (mean daily temperatures were <0° C during December and January) and ice cover caused most Mallards to leave the Mingo Basin in midwinter 1981–1982 and reduced access to remaining birds, therefore few (*n* = 19) birds were collected from mid-December 1981 to late January 1982. Absence of the investigator from the study area further limited collections in early December 1982.

Only foraging birds were collected; no birds were collected from traps, by shooting over decoys, or by pass-shooting because of biases introduced from such collections (see Greenwood et al. 1986). Additionally, females that had wounds indicative of past hunting or natural accidents, showed signs of lead poisoning (Bellrose 1959), and/or contained lead shot in their gizzards were not included.

Immediately after each bird was collected, its esophagus, proventriculus, and gizzard were removed for analysis of food consumption. External measurements and fresh body mass were recorded in the laboratory before the birds were sealed in plastic bags and frozen. All birds were thawed, plucked, dissected, and prepared for analysis of carcass composition within 9 months of collection. Age (immature or adult) of females was determined by presence or absence of a bursa of Fabricius (Hochbaum 1942) and wing feather characteristics (Krapu et al. 1979, Gatti 1983a).

Only birds collected in 1981–1982 and 1982–1983 were analyzed for carcass composition. Carcasses were analyzed similar to the methods described in Drobney (1982). The eviscerated carcass was ground in a Globe meat grinder. Each carcass was passed through the grinder at least five times and mixed thoroughly after each grinding. A random sample of the homogenate (ca. 10 to 15% of the eviscerated carcass mass) was removed for analysis (Brisbin 1968). Each sample was dried to a constant weight in a vacuum oven at 40°C. Water content was determined by subtraction. Lipids were extracted from the dry residue using a 2:1 mixture of petroleum ether. The dry extracted material was subsequently combusted in a muffle furnace at 500°C to determine ash content. Ash-free lean dry mass (AFLDM) was used as the estimate of protein content of the carcass (Raveling 1979:241) and determined by subtracting the weight of the ash from the weight of the dry extracted material. All chemical analyses were performed by the University of Missouri Agricultural Experiment Station Chemistry Laboratory using standard laboratory techniques (Horwitz 1975).

Lipid masses were obtained from the above described chemical analyses with two exceptions. First, for 26 females from the 1981–1982 group, 0.1- to 2.2-g samples of fat adhering to the right leg and 0.4- to 6.5-g samples of the peritoneal fat depot were removed along with the entire plucked skin for analyses of fatty acid composition (Heitmeyer 1985) before the eviscerated carcass was prepared for analysis. The weight of the fat removed from the right leg, peritoneum, and skin was added to the weight of the lipid extracted from the remaining eviscerated carcass to obtain the total grams of fat for these 26 females. Secondly, all of the 1982–1983 females had 0.3- to

TABLE 1. Migration, pair, and molt status categories of female Mallards collected in the Mingo Basin of southeastern Missouri.

Status category (acronym)	Criteria
Fall—middle prealternate molt (FMPA)	Prealternate molt 40 to 75% completed.
Fall—late prealternate molt (FLPA)	Prealternate molt 76 to 99% completed.
Early-fall migrants—alternate plumage—unpaired (FAUP); or paired (FAP)	Early migrants (November) into the Mingo Basin, nonmolting in alternate plumage, unpaired; or paired.
Midwinter—alternate plumage—unpaired (WAUP); paired (WAP)	Birds present in midwinter (December–January), nonmolting in alternate plumage, unpaired; or paired.
Initiation of prebasic molt—paired (IPB)	Prebasic molt 1 to 15% completed.
Early prebasic molt—paired (EPB)	Prebasic molt 16 to 40% completed.
Middle prebasic molt—paired (MPB)	Prebasic molt 41 to 75% completed.
Late prebasic molt—paired (LPB)	Prebasic molt 76 to 99% completed.
Prebasic molt complete—prespring migration departure (PD)	Nonmolting in basic plumage, immediately preceding their migration departure in spring.

6.0-g samples of the peritoneal fat depot removed for analyses of fatty acid composition and the weights of these samples were added to the weight of the lipid extracted from the remaining eviscerated carcass to obtain the total grams of fat for the individual.

Data on body mass exclude the esophagus and proventriculus and their contents, ovaries and oviducts, and contents of the gizzard, intestines, and ceca. Eviscerated carcass mass does not include the weight of feathers, heart, liver, kidneys, spleen, intestines (including the ceca and their contents), and ovary.

Data were not adjusted for structural size nor were condition indices used because morphological measurements were similar within age groups and the use of existing predictors of body fat for Mallards (Ringleman and Szymczak 1985) and other ducks (Harris 1970, Woodall 1978, Wishart 1979) predicted body fat poorly (Heitmeyer 1985:165). Additionally, prediction equations that included morphological measurements to adjust for structural size predicted body fat more poorly than did unadjusted equations (Heitmeyer 1985:165–166).

Data were analyzed based on the migration, pair, and molt status (Table 1) of individual birds (see Heitmeyer 1985, 1987 for data on migration chronologies of Mallards into and out of the Mingo Basin, and for methods determining molt completion).

The chronology of females engaged in the above status groups, with the exception of pairing, was determined from collections. Chronology of pairing was determined by observation of Mallards in the Mingo Basin from October to March. Randomly selected flocks of Mallards were scanned and an assessment of pairing status of each female was made based on associations and displays. Results are presented as the percentage of total females paired. Additional data on pairing chronology in relation to habitat use are presented in Heitmeyer (1985:268–269).

RESULTS

TIMING OF ANNUAL EVENTS

Small numbers of Mallards began arriving in the Mingo Basin in mid-October in 1981 and 1982. Collections began shortly thereafter and indicated that most females present were adults engaged in the prealternate molt. All 15 females collected in October were adults; 13 of these 15 were engaged in the prealternate molt. No females engaged in the prealternate molt were paired or collected later than 24 November. The majority of Mallards migrated into or through the Mingo Basin in November.

Pairing by Mallards apparently occurred from prior to arrival in the Mingo Basin through early March (Table 2). One unpaired female was collected as late as 3 March. The majority of females present in the Mingo Basin became paired in November and December (Table 2). Based on collections, adults paired earlier (Mann-Whitney *U*-test, $P < 0.05$) than immatures (mean dates of nonmolting paired females was 21 December for adults and 14 January for immatures). Females paired earlier (chi-square test, $P < 0.05$) in 1982–1983 than in 1981–1982 (Table 2). The

TABLE 2. Percentage of female Mallards randomly observed in the Mingo Basin of southeastern Missouri during 1981-1982 and 1982-1983 that were paired in relation to month.

Month	1981–1982		1982–1983	
	n	%	*n*	%
October	89	14.6	12	16.7
November	78	51.3	164	62.2
December	66	69.7	253	81.8
January	50	76.0	168	95.2
February	471	87.9	168	89.3
March	576	84.5	252	84.5

slight decline in the percentage of females paired from February through March 1982 and from January through March 1983 (Table 2) may indicate that some paired females migrated from the Mingo Basin earlier in spring than did the few remaining unpaired females. The chronology of the prebasic molt has been previously reported (Heitmeyer 1987) and indicated that adults molt earlier than immatures and that molt by all females occurred earlier in the wetter winter of 1982–1983 than in the drier winters of 1980–1981 and 1981–1982.

Individuals, within age groups, were extremely variable in the chronology of undertaking annual events. For example, of five adult females collected on 22 January 1981, two were unpaired and in alternate plumage, two were paired and in alternate plumage, and one was paired and had initiated the prebasic molt. Similarly, of three immatures collected on 1 March 1983, one was paired and in alternate plumage, one had initiated the prebasic molt, and one was in middle stages of the prebasic molt.

BODY COMPOSITION

Body and carcass masses were similar between adults and immatures within status groups (Mann-Whitney *U*-tests, *P*s > 0.05) in 64 (97%) of the 66 (11 status groups × 6 body and carcass masses) possible tests. The two exceptions were lipid masses for MPB females (116 ± 8 [SE] g for adults vs. 76 ± 16 g for immatures) and ash masses for FAUP females (41 ± 5 g for adults vs. 29 ± 2 g for immatures). Because of the similarities between age groups, data are subsequently presented as adults and immatures combined.

Body and carcass masses of female Mallards within status groups were also similar among years (Mann-Whitney *U*-tests, $P > 0.05$) in 141 (97%) of 146 (11 status groups × 2 years × 4 carcass components + 4 status groups × 2 years × 2 body masses + 7 status groups × 3 years × 2 body masses) possible tests. The five exceptions were fresh body mass for FAP (1,142 ± 17 g in 1981–1982 vs. 1,038 ± 23 g in 1982–1983) and EPB (1,013 ± 21 g in 1980–1981 vs. 1,126 ± 37 g in 1982–1983) females and eviscerated carcass mass for FAUP (738 ± 6 g in 1981–1982 vs. 856 ± 16 g in 1982–1983), IPB (796 ± 15 g in 1980–1981 vs. 911 ± 26 g in 1982–1983), and EPB (763 ± 25 g in 1980–1981 vs. 877 ± 34 g in 1982–1983) females. Because of the similarities among years, data are subsequently presented as all years combined.

TABLE 3. Changes in body and carcass composition masses (g, $\bar{x}$ ± SE) of female Mallards wintering in the Mingo Basin of southeastern Missouri in relation to status.

Status[a]	*n*	Fresh body	Eviscerated carcass	Water
FMPA	11/11[c]	1,010 ± 24AB[d]	726 ± 25A	480 ± 12AB
FLPA	17/17	1,093 ± 35CD	817 ± 32BC	506 ± 12BC
FAP	12/12	1,137 ± 30D	863 ± 21C	518 ± 24BC
FAUP	9/9	1,083 ± 37CD	823 ± 30BC	497 ± 22B
WAP	29/19	1,085 ± 18CD	829 ± 16BC	504 ± 17BC
WAUP	21/14	983 ± 20A	745 ± 20A	453 ± 12A
IPB	44/32	1,118 ± 21D	865 ± 24C	522 ± 14BC
EPB	34/24	1,068 ± 22BC	829 ± 20BC	506 ± 13BC
MPB	45/26	1,048 ± 12B	793 ± 11B	504 ± 8BC
LPB	35/23	1,193 ± 15E	920 ± 13D	529 ± 12BC
PD	10/6	1,280 ± 13F	1,001 ± 16E	554 ± 15D

[a] FMPA = fall—middle prealternate molt, FLPA = fall—late prealternate molt, FAP = early fall migrants—alternate plumage—paired, FAUP = early fall migrants—alternate plumage—unpaired, WAP = midwinter—alternate plumage—paired, WAUP = midwinter—alternate plumage—unpaired, IPB = initiation prebasic molt, EPB = early prebasic molt, MPB = middle prebasic molt, LPB = late prebasic molt, PD = basic plumage, prespring migration departure.

[b] Ash-free lean dry mass.

[c] Sample size for fresh body and eviscerated carcass masses/sample size for water, lipid, AFLDM, and ash.

[d] Means within a column followed by the same letter are not significantly (LSD multiple comparisons tests, *P*s > 0.05) different.

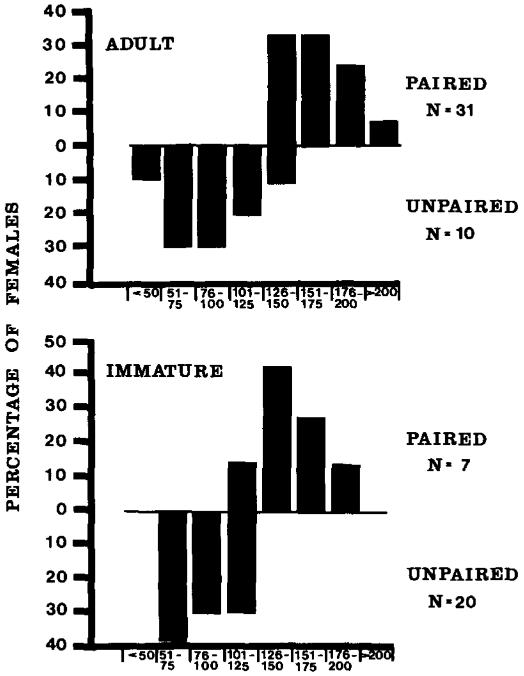

FIGURE 1. Frequency distribution of the pairing status of nonmolting adult and immature female Mallards in relation to their body lipid masses.

Fresh body, eviscerated carcass, water, lipid, and ash-free lean dry masses of female Mallards were different (Kruskal-Wallis tests, Ps < 0.001) among status groups (Table 3). In contrast, ash mass was not different ($P > 0.05$) among status groups.

TABLE 3. Extended.

Lipid	AFLDM[b]	Ash
65 ± 14A	148 ± 6A	32 ± 4A
104 ± 10B	163 ± 4B	39 ± 3A
134 ± 7C	167 ± 8BC	41 ± 4A
111 ± 8B	159 ± 6AB	32 ± 5A
145 ± 7CD	162 ± 7B	37 ± 3A
102 ± 12B	145 ± 6A	36 ± 4A
168 ± 8DE	163 ± 4B	35 ± 3A
141 ± 13C	166 ± 3B	33 ± 6A
110 ± 11B	162 ± 2B	35 ± 2A
188 ± 13E	173 ± 2C	34 ± 3A
219 ± 13E	187± 4D	41 ± 3A

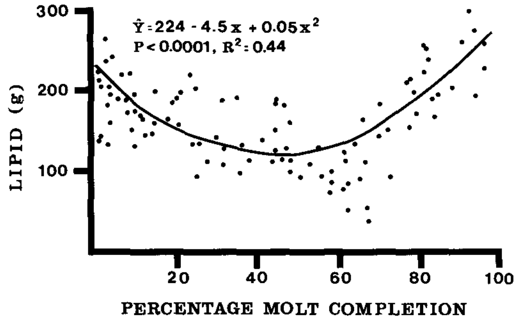

FIGURE 2. Relationship between percentage of prebasic molt completion and lipid mass of female Mallards.

Females in FMPA had low body and carcass masses (Table 3). Body and carcass masses increased after females completed the prealternate molt; females gained 127 g (13%) of body mass and 69 g (106%) of lipid mass between FMPA and FAP. Nonmolting females that were paired in both fall (FAP) and winter (WAP) had larger lipid reserves than unpaired females in the same periods (i.e., FAUP and WAUP) (Table 3). Frequency distributions of lipid reserves for paired and unpaired females indicated that females with <125 g of lipid mass were seldom paired (Fig. 1). Body and carcass masses were not different between FAP and WAP females, however, FAUP females had heavier body and eviscerated carcass masses than WAUP females.

Females initiated the prebasic molt with relatively large body and lipid masses (Table 3). Lipid mass declined an average of 58 g (35%) from IPB to MPB and accounted for 83% of the 70-g loss in body mass at this time. Lipid mass was curvilinearly related to molt completion (Fig. 2). Body mass increased an average of 145 g (14%), lipid mass increased 78 g (71%), and AFLDM increased 11 g (7%) between MPB and LPB. Females that completed the prebasic molt before migrating from the Mingo Basin in spring (all were adults) were heavy (1,280 g fresh body mass) and fat (219 g lipid mass).

DISCUSSION

CHRONOLOGICAL VS. BIOLOGICAL ANALYSES

Part of the dynamics of carcass composition of female Mallards in winter is related to annual cycle events in which individuals are engaged. Different biological events undertaken by dabbling ducks during spring and summer (i.e., laying, incubation, brood rearing) also impose different physiological constraints on breeding birds (e.g., Drobney 1980, Gatti 1983b) and recognition of adaptations of body composition and dietary intake to production of young has been facilitated by analyses based on these biological events (e.g., Krapu 1974, 1981; Swanson et al. 1979; McKinney 1986). Likewise, correct interpretation of winter biology seems dependent upon analyzing data based on biological events and not solely by chronological time. While the sequence of events for female Mallards from prealternate molt to pairing to prebasic molt was discernible from November through February during this study, analyses based solely on chronology would be extremely misleading. For example, during December females ranged from being unpaired in alternate plumage to being paired in middle stages of the prebasic molt. Consequently, calculation of a mean body mass in December would have included both very heavy (FAP, WAP, and IPB) and very light (FAUP, WAUP, MPB) individuals and had a large associated standard error, therefore masking true biological changes.

Changes in body and carcass masses of nonbreeding ducks, when analyzed solely by chronological time, have been attributed to "endogenous annual rhythms" (e.g., Reinecke et al. 1982, Baldassarre et al. 1986:425). When analyzed from a biological perspective, however, similar data from this study of female Mallards suggest that at least part of the endogenous aspect of annual body mass cycles may be the changing nutritional and physiological requirements associated with annual events such as molt, migration, and pairing (the specific requirements are discussed below). Studies of dabbling ducks that have indicated losses of body and lipid masses in midwinter (e.g., Baldassarre et al. 1986, Delnicki and Reinecke 1986, Miller 1986, Whyte et al. 1986) may have simply been documenting the progression of, or changes related to, pairing, the prebasic molt, and weather related stress rather than endogenously controlled "clock" mechanisms. Pen studies that have attempted to document endogenous annual weight cycles have yielded equivocal results (cf. Wise 1960, Joyner et al. 1984, Hepp 1986, Perry et al. 1986) perhaps because of the unacknowledged effects of captivity (through alterations in geographical location, diet, photoperiod, activity, and behavioral stimulus) on molt and pairing (see West 1968, Blackmore 1969, King 1974, Chilgren 1978, Murphy and King 1987) and/or the failure to recognize that molt and pairing did or did not occur.

NUTRIENT RESERVES AND BIOLOGICAL EVENTS

Fall migration and prealternate molt. Most female Mallards initiate the prealternate molt while on northern migration staging areas, but complete it during fall migration or on wintering areas (Palmer 1976; Young and Boag 1981; Heitmeyer 1985, 1987). Protein (Heitmeyer 1988) and energy (Blem 1980) requirements increase greatly during molt and migration, respectively. Most birds do not have annual events that overlap, especially when the major nutrients required for the events are substantial and different (King 1974). Mallards may be able to molt and migrate simultaneously in fall because they migrate when large quantities of foods that supply both protein and energy (e.g., seeds from moist-soil plants) become available in traditionally used floodplain marshes and forests (Bellrose et al. 1979, Heitmeyer and Vohs 1984).

Even though nutrients are often readily available on northern fall migration areas, some female Mallards (primarily adults) migrate to the Mingo Basin early in fall and arrive with low body masses, presumably because of high nutritional demands of molting and migrating simultaneously. Although these early arriving females nearly deplete their lipid reserves, they may ultimately receive nutritional and social advantages once they reach wintering areas by being first to exploit available foods and to become familiar with habitats and disturbances (see e.g., Ketterson 1979). These advantages are countered, however, by dynamic fall and winter precipitation and flooding, and thus food availability, in southern lowland forests. Flooding in southern forested wetlands usually does not begin until late October (Heitmeyer 1985), therefore females that arrived too early would find little available habitat. In conjunction, cross-seasonal habitat influences (such as chronology and success of nesting and migration habitat conditions) cause variation in migration chronologies of Mallards, within and among years.

Pairing. The factors controlling the timing of courtship and pairing in ducks are not entirely known. It seems likely that acquisition of seasonally dynamic resources necessary to survive and reproduce in relation to advantages or disadvantages of being accompanied by a mate ultimately controls chronology of pair formation. Many of these advantages (see e.g., Paulus 1983, Hepp 1984, Heitmeyer 1985) are realized by individuals in winter when pairing takes place in dabbling ducks.

Several factors such as food abundance, body mass, dominance, behavioral stimulation, experience, and photoperiod have been suggested to proximately control courtship and pair formation in waterfowl (Akesson and Raveling 1981, Dittami 1981, Patterson 1982, Balthazart 1983, Ottinger 1983, Wishart 1983, Hepp 1986, McKinney 1986). Many of these nutritional and behavioral factors are inextricably intertwined. For example, dominance is determined by aggressiveness and associated increases in testosterone production (Scott 1958, Thiessen 1976), body and reserve mass (see review in Gauthreaux 1978), experience (Raveling 1981 and references therein), and plumage characteristics (Ewald and Rohwer 1980). All of these factors have at least some influence on pair formation in Mallards (Lebret 1961, Donham 1979, Klint 1980, Haase 1983). Photoperiod does not seem to be the proximate control of pairing in wild Mallards, however, because females initiate pairing in both decreasing and increasing daylengths around the winter solstice (see also Wishart 1983:1739).

Female Mallards that were paired were heavier and fatter than unpaired females throughout winter in the Mingo Basin. These data have at least three possible explanations, (1) that storage of lipid reserves preceded pair formation, (2) that increased storage of lipid reserves followed pair formation, or (3) that a combination of (1) and (2) occurred. Data from captive Mallards indicate that females fed restricted diets have low body masses and delay initiation of courtship and pairing and decrease the number of permanent pair bonds formed compared to females with larger body masses (Pattenden and Boag, in press). Captive female Black Ducks (*Anas rubripes*) fed restricted diets also delay pairing (Hepp 1986). In the Mingo Basin, ca. 90% of wild female Mallards are paired by early January; most pair formation occurs in November and December. Body masses of paired females collected in both November (FAP) and December–January (WAP) were high. If FAP females represented birds that were more likely to be newly paired, then these data also suggest that high body mass preceded pairing.

The mechanism whereby high body and lipid masses might facilitate pairing in female Mallards may include the greater endurance and physical strength of heavy birds. Pairing by dabbling ducks is accompanied by testing dominance and potential fitness by intense courtship and temporary associations, which are costly both in time and energy use (McKinney 1975, 1986; Daly 1978; Wishart 1983). Attainment of large body masses, especially lipids, before engaging in courtship and pairing may give a female the advantage of greater endurance, which is important to assess male quality, and vice versa for males to assess female quality (McKinney 1975, 1986; Wishart 1983).

Data from this study also suggest that pair formation may enable female Mallards to store lipids beyond that necessary for pairing. Paired Mallards (both males and females in the pair) are dominant over unpaired Mallards and have increased foraging potential (Heitmeyer 1985). Female Mallards seldom initiate the prebasic molt before they become paired (Heitmeyer 1987) or while they are in poor condition. The fitted regression curve of lipid mass on molt completion indicated that females beginning the prebasic molt contained an average of >200 g of lipid stores, an average increase of 60+ g of lipid from fall and winter levels. In total, it appears that deposition of lipid reserves precedes pair formation in wild female Mallards and that females increase lipid storage following pairing, while females that are not paired do not accumulate large lipid reserves in midwinter.

Prebasic Molt. Female Mallards require ca. 84 g of protein in excess of maintenance requirements for replacement of body feathers during the prebasic molt (Heitmeyer 1988). Costs/day are substantial and greatest (ca. 3 g/day) during midmolt. Feather replacement rate (Heitmeyer 1987), protein cost (Heitmeyer 1988), daily time spent foraging (Heitmeyer 1985), and consumption of invertebrates (Heitmeyer, in press) increase during 40 to 80% completion of the prebasic molt, while body lipid mass decreases greatly during this same time. These data indicate that female Mallards meet protein costs of the prebasic molt by using endogenous lipid reserves to provide daily energy requirements while increasing dietary intake of protein-rich invertebrates obtained by extensive time spent foraging (Heitmeyer 1985). This strategy of obtaining exogenous protein when using endogenous lipid is similar to the strategy that female Mallards and Northern Pintails (*Anas acuta*) use to obtain protein for egg laying on prairie breeding grounds (Krapu 1974, 1981; Swanson et al. 1979).

Female Mallards apparently obtained proteins for feather production largely from dietary sources and not from interconversion of fat to amino acids or use of labile protein reserves; protein mass did not decrease during molt. Furthermore, only the ketogenic amino acids (lysine, phenylalanine, isoleucine, tyrosine, leucine) can be constructed from fat whereas essential amino acids such as cystine, methionine, threonine, tryptophan, and valine needed for feather synthesis (Wielicki 1987) must be obtained from the diet.

Lipid and protein masses of females increased during the last 30 to 40% of the prebasic molt as molt intensity (Heitmeyer 1987) and nutrient requirements (Heitmeyer 1988) decreased. The onset of spring migration was also near and some females may have begun premigratory hyperphagia and fattening (common among many anatids, see Owen 1970; McLandress and Raveling 1981a, 1981b; Drobney 1982). Winter molt may, however, inhibit prevernal fat deposition and nocturnal activity in ducks (Owen 1970). Therefore, females that molted and migrated concurrently might not be able to accumulate substantial reserves for either efficient migration or eventual reproduction early in that breeding season. This might be especially important for immatures which seldom, if ever, completed the prebasic molt while on wintering grounds. In contrast, adults that completed the prebasic molt in the Mingo Basin attained the highest body masses observed during winter immediately preceding spring migration.

Reserves and reproduction. Endogenous reserves obtained prior to arrival on breeding grounds are utilized to varying degrees for egg production, defense of the female and nest, and incubation by geese (Ankney and MacInnes 1978, Raveling 1979, McLandress and Raveling 1981a), Northern Pintails (Krapu 1974), and Mallards (Krapu 1981, Gatti 1983b). Most geese obtain much of the reserves used during nesting from migrational areas (see Raveling 1979, Wypkema and Ankney 1979, Davies and Cooke 1983). In contrast, it seems that many female Mallards may obtain similar reserves, especially during wet winters, from wintering on more southerly migration areas.

Adult female Mallards that completed the prebasic molt while in the Mingo Basin weighed nearly 1,300 g with 220 g of lipid and 185 to 190 g of protein. Female Mallards arriving on prairie breeding grounds in North Dakota during 1974 to 1977 weighed only 1,150 to 1,200 g with 110 g of lipid (Krapu 1981). Body masses of breeding Mallards in Krapu's (1981) study also included ingesta which would make actual body mass of these breeding females even lower (ingesta weights of female Mallards in the Mingo Basin averaged 43 ± 16 g). Protein reserves (as indexed by breast and leg muscle masses) of female Mallards arriving in North Dakota (Krapu 1981) were also substantially lower than similar muscle masses of females collected in the Mingo Basin in late spring (Heitmeyer 1985:167–168). Differences between the body, lipid, and protein masses of female Mallards in the Mingo Basin and North Dakota are probably mostly related to costs of spring migration between the two areas (for calculation of theoretical costs, see Heitmeyer 1985: 201). Female Mallards that nest in the prairie pothole region of North Dakota are from the same population that winter in the Mingo Basin (see extensive review of evidence from banded birds in Geis 1971, Munro and Kimball 1982, and Heitmeyer 1985:200); therefore, comparisons between the two areas are justified.

TIMING OF ANNUAL EVENTS

Variation between immature and adult Mallards and among years in this study was more marked in the chronology of undertaking events than in carcass composition masses within status groups. Adults became paired and molted into the basic plumage earlier than immatures (Heitmeyer 1987) and no immatures were collected that had completed the prebasic molt before migrating out of the Mingo Basin in spring. Additionally, both adults and immatures paired and molted (prebasic molt) earlier in the wet winter of 1982–1983 than in the drier winters of 1981–1982 or 1980–1981 (Heitmeyer 1987). These data suggest that certain annual events such as molt and pairing impose fairly precise nutritional requirements on individuals and that initiation and efficient completion of these events may be partly controlled by availability of nutrients and subsequent storage of reserves. Differences in the timing of molt and pairing between immatures and adults was probably partly related to when immatures hatched and their subsequent growth and plumage development during summer and early fall (Rhymer 1982) and to their ability to efficiently acquire nutrients during winter. It seems doubtful that immatures gained advantages by storing fewer reserves than adults in winter (suggested as a possibility by Delnicki and Reinecke 1986:48) because data presented herein demonstrated that body and lipid masses were similar between adults and immatures during almost all status periods even though immatures were slightly smaller in structure.

Survival (Anderson and Burnham 1976, Nichols and Hines 1987) and recruitment (Krapu and Doty 1979, Heitmeyer and Fredrickson 1981, Krapu 1981) of female Mallards are heterogeneous between ages and among years. This heterogeneity may be, at least partly, influenced by variable winter nutrient availability in lowland hardwood wetlands (Heitmeyer and Fredrickson 1981, Heitmeyer 1985, White 1985). When winter precipitation occurs early and is sufficient to cause widespread shallow flooding throughout the Mississippi Alluvial Valley (such as in 1982–1983), wintering female Mallards have more area and more resources to exploit than in dry years (Reinecke et al. 1988). Under these wetter conditions females proceed through annual events more rapidly and subsequently survive and reproduce at greater levels than during and following dry winters (Heitmeyer and Fredrickson 1981, Nichols and Hines 1987).

Mallards are among the earliest spring migrant and nesting waterfowl in North America. Within Mallards, historically, females that migrated and nested earliest may have gained survival and reproductive potential advantages (e.g., Dzubin and Gollop 1972). These early nesters were usually adults with large lipid reserves, produced larger clutches, had higher nest success, and their broods had greater survival than those produced by later nesters (Dzubin and Gollop 1972, Krapu and Doty 1979, Krapu 1981). Land use and predator population changes have possibly reduced the value of nesting early in midcontinent prairies in recent years (Greenwood et al. 1987). However, Mallards continue to nest in large numbers (>60% of the total North American population, calculated from Bellrose 1979) in parkland, boreal forest, taiga, arctic delta, and southern (e.g., in the White Mountains of Arizona and in the Central Valley of California) wetlands and strong selective forces such as the long-term seasonal availability of resources in wetlands used during both winter (Heitmeyer 1985) and in spring (Weller 1975, Krapu 1981:36) have continued to shape the adaptations of Mallards to undertake annual events earlier than for most other ducks.

ACKNOWLEDGMENTS

This study was funded by the Office of Migratory Bird Management, U.S. Fish and Wildlife Service Contract #USDI 14-16-009-801-029 and is a contribution from the Gaylord Memorial Laboratory (School of Forestry, Fisheries and Wildlife, University of Missouri–Columbia, and Missouri Department of Conservation cooperating), Missouri Cooperative Fish and Wildlife Research Unit (U.S. Fish and Wildlife Service, University of Missouri–Columbia, Missouri Department of Conservation, and Wildlife Management Institute cooperating), Edward K. Love Fellowship, and Missouri Agricultural Experiment Station, Project 183, Journal Series No. 10297. The staffs of the Mingo National Wildlife Refuge (U.S. Fish and Wildlife Service) and the Duck Creek Wildlife Management Area (Missouri Department of Conservation) graciously provided access and assistance. J. C. Ware assisted with all field and laboratory work, T. S. Taylor provided computer and data analyses advice, and M. S. Heitmeyer typed various drafts of the manuscript. C. R. Blem, R. D. Drobney, L. H. Fredrickson, D. E. Joyner, and D. G. Raveling provided very helpful reviews of earlier drafts of the manuscript.

LITERATURE CITED

Akesson, T. R., and D. G. Raveling. 1981. Endocrine and body weight changes of nesting and non-nesting Canada Geese. Biol. Reprod. 25:792–804.

Anderson, D. R., and K. P. Burnham. 1976. Population ecology of the Mallard. VI. The effect of exploitation on survival. U.S. Fish Wildl. Serv. Resour. Publ. 128.

Ankney, C. D., and C. D. MacInnes. 1978. Nutrient reserves and reproductive performance of female Lesser Snow Geese. Auk 95:459–471.

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.

Balthazart, J. 1983. Hormonal correlates of behavior, p. 221–365. *In* D. S. Farner, J. R. King, and K. C. Parkes [eds.], Avian biology. Vol. 7. Academic Press, New York.

Bellrose, F. C. 1959. Lead poisoning as a mortality factor in waterfowl populations. Ill. Nat. Hist. Surv. Bull. 27:235–288.

Bellrose, F. C. 1979. Species distribution, habitats, and characteristics of breeding dabbling ducks in North America, p. 1–15. *In* T. A. Bookhout [ed.], Waterfowl and wetlands—an integrated review. Proc. Symp. N. Cent. Sect., The Wildl. Soc., Madison, WI.

Bellrose, F. C., F. L. Paveglio, Jr., and D. W. Steffeck. 1979. Waterfowl populations and the changing environment of the Illinois river valley. Ill. Nat. Hist. Surv. Bull. 32:1–54.

Blackmore, F. H. 1969. The effect of temperature, photoperiod and molt on the energy requirements of the House Sparrow, *Passer domesticus*. Comp. Biochem. Physiol. 30:433–444.

Blem, C. R. 1980. The energetics of migration, p. 175–224. *In* S. A. Gauthreaux [ed.], Animal migration, orientation, and navigation. Academic Press, New York.

Brisbin, I. L., Jr. 1968. A determination of the caloric density and major body components of large birds. Ecology 49:792–794.

Chilgren, J. D. 1978. Effects of photoperiod and temperature on the postnuptial molt in captive White-crowned Sparrows. Condor 80:222–229.

Daly, M. 1978. The cost of mating. Am. Nat. 112: 771–774.

Davies, J. C., and F. Cooke. 1983. Annual nesting productivity in Snow Geese: prairie droughts and arctic springs. J. Wildl. Manage. 47:291–296.

Delnicki, D., and K. J. Reinecke. 1986. Mid-winter food use and body weights of Mallards and Wood Ducks in Mississippi. J. Wildl. Manage. 50:43–51.

Den Held, J. J. 1981. Population changes in the Purple Heron in relation to drought in the wintering area. Ardea 69:185–191.

Dittami, J. P. 1981. Seasonal changes in the behavior and plasma titers of various hormones in Barheaded Geese, *Anser indicus*. Z. Tierpsychol. 55: 289–324.

Donham, R. S. 1979. Annual cycle of plasma luteinizing hormone and sex hormones in male and female Mallards (*Anas platyrhynchos*). Biol. Reprod. 21:1273–1285.

Drobney, R. D. 1980. Reproductive energetics of Wood Ducks. Auk 97:480–490.

Drobney, R. D. 1982. Body weight and composition changes and adaptations for breeding in Wood Ducks. Condor 84:300–305.

Dzubin, A., and J. B. Gollop. 1972. Aspects of Mallard breeding ecology in Canadian parkland and grassland, p. 113–152. *In* Population ecology of migratory birds. U.S. Dept. Inter., Bur. Sport Fish. Wildl. Res. Rep. 2.

Ewald, P. W., and S. Rohwer. 1980. Age, coloration and dominance in nonbreeding hummingbirds: a test of the asymmetry hypothesis. Behav. Ecol. Sociobiol. 7:273–279.

Fretwell, S. D. 1972. Populations in a seasonal environment. Princeton Univ. Press, Princeton, NJ.

Gatti, R. C. 1983a. Spring and summer age separation techniques for the Mallard. J. Wildl. Manage. 47:1054–1062.

Gatti, R. C. 1983b. Incubation weight loss in the Mallard. Can. J. Zool. 61:565–569.

Gauthreaux, S. A., Jr. 1978. The ecological significance of behavioral dominance, p. 17–54. *In* P.P.G. Bateson and P. H. Klopfer [eds.], Perspectives in ethology. Plenum Press, New York.

Geis, A. D. 1971. Breeding and wintering areas of Mallards harvested in various states and provinces. U.S. Fish and Wildl. Serv. Spec. Sci. Rep. Wildl. 144.

Greenwood, H., R. G. Clark, and P. J. Weatherhead. 1986. Condition bias of hunter shot Mallards (*Anas platyrhynchos*). Can. J. Zool. 64:599–605.

Greenwood, R. J., A. B. Sargeant, D. H. Johnson, L. M. Cowardin, and T. L. Shaffer. 1987. Mallard nest success and recruitment in prairie Canada. Trans. N. Am. Wildl. Nat. Resour. Conf. 52: 298–309.

Haase, E. 1983. The annual reproductive cycle in Mallards. J. Steroid Biochem. 19:731–737.

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.

Harris, H. J., Jr. 1970. Evidence of stress response in breeding Blue-winged Teal. J. Wildl. Manage. 34:747–755.

Heitmeyer, M. E. 1985. Wintering strategies of female Mallards related to dynamics of lowland hardwood wetlands in the Upper Mississippi Delta. Ph.D.diss., Univ. of Missouri, Columbia.

Heitmeyer, M. E. 1987. The prebasic moult and basic plumage of female Mallards. Can. J. Zool. 65:2248–2261.

Heitmeyer, M. E. 1988. Protein costs of the prebasic molt of female Mallards. Condor 90:263–266.

Heitmeyer, M. E. In press. Changes in the visceral morphology of wintering female Mallards (*Anas platyrhynchos*). Can. J. Zool.

Heitmeyer, M. E., and P. A. Vohs, Jr. 1984. Characteristics of wetlands used by migrant dabbling ducks in Oklahoma, USA. Wildfowl 35:61–70.

Heitmeyer, M. E., and L. H. Fredrickson. 1981. Do wetland conditions in the Mississippi Delta hardwoods influence Mallard recruitment? Trans. N. Am. Wildl. Nat. Resour. Conf. 46:44–57.

Hepp, G. R. 1984. Dominance in wintering Anatidae: potential effects on clutch size and time of nesting. Wildfowl 35:132–134.

Hepp, G. R. 1986. Effects of body weight and age on the time of pairing of American Black Ducks. Auk 103:477–484.

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 vulnerability. J. Wildl. Manage. 50:177–183.

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

Horwitz, W. 1975. Official methods of analysis. 12th ed. Assoc. Off. Anal Chem., Washington, DC.

Johnsgard, P. A. 1965. Handbook of waterfowl behavior. Cornell Univ. Press, Ithaca, NY.

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.

Ketterson, E. D. 1979. Aggressive behavior in wintering Dark-eyed Juncos: determinants of dominance and their possible relation to geographic variation in sex ratio. Wilson Bull. 91:371–383.

King, J. R. 1974. Seasonal allocation of time and energy resources in birds, p. 4–70. *In* R. A. Paynter, Jr. [ed.], Avian energetics. Nuttall Ornithol. Club, Cambridge, MA.

KLINT, T. 1980. Influence of male nuptial plumage on mate selection in the female Mallard (*Anas platyrhynchos*). Anim. Behav. 28:1230–1238.

KRAPU, G. L. 1974. Feeding ecology of Pintail hens during reproduction. Auk 91:278–290.

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

KRAPU, G. L., AND H. A. DOTY. 1979. Age-related aspects of Mallard reproduction. Wildfowl 30:35–39.

KRAPU, G. L., D. H. JOHNSON, AND C. W. DANE. 1979. Age determination of Mallards. J. Wildl. Manage. 43:384–393.

LEBRET, T. 1961. The pair formation in the annual cycle of the Mallard, *Anas platyrhynchos* L. Ardea 49:97–158.

MCKINNEY, F. 1975. The evolution of duck displays, p. 331–357. *In* G. Baerends, C. Beer, and A. Manning [eds.], Function and evolution in behavior. Clarendon Press, Oxford.

MCKINNEY, F. 1986. Ecological factors influencing the social systems of migratory dabbling ducks, p. 153–171. *In* D. I. Rubenstein and R. W. Wrangham [eds.], Ecological aspects of social evolution. Princeton Univ. Press, Princeton, NJ.

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

MCLANDRESS, M. R., AND D. G. RAVELING. 1981b. Hyperphagia and social behavior of Canada Geese prior to spring migration. Wilson Bull. 93:310–321.

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

MITSCH, W. J., AND J. G. GOSSELINK. 1986. Wetlands. Van Nostrand Reinhold Co., New York.

MUNRO, R. E., AND C. F. KIMBALL. 1982. Population ecology of the Mallard. VII. Distribution and derivation of the harvest. U.S. Fish Wildl. Serv. Resour. Publ. 147.

MURPHY, M. E., AND J. R. KING. 1987. Dietary discrimination by molting White-crowned Sparrows given diets differing only in sulfur amino acid concentration. Physiol. Zool. 60:279–289.

NICHOLS, J. D., AND J. E. HINES. 1987. Population ecology of the Mallard. VIII. Winter distribution patterns and survival rates of winter-banded Mallards. U.S. Fish Wildl. Serv. Resour. Publ. 162.

NILSSON, L. 1979. Variation in the production of young of swans wintering in Sweden. Wildfowl 27: 141–142.

OTTINGER, M. A. 1983. Hormonal control of reproductive behavior in the avian male. Poultry Sci. 62:1690–1699.

OWEN, R. B., JR. 1970. The bioenergetics of captive Blue-winged Teal under controlled and outdoor conditions. Condor 72:153–163.

PALMER, R. S. 1976. Handbook of North American birds. Vol. 2. Yale Univ. Press, New Haven, CT.

PATTENDEN, R. K., AND D. A. BOAG. In press. Effects of body mass on courtship, pairing, and reproduction in captive Mallards. Can. J. Zool.

PATTERSON, I. J. 1982. The Shelduck, a study in behavioural ecology. Cambridge Univ. Press, New York.

PAULUS, S. L. 1983. Dominance relations, resource use, and pairing chronology of Gadwalls in winter. Auk 100:947–952.

PERRY, M. C., W. J. KUENZEL, B. K. WILLIAMS, AND J. A. SERAFIN. 1986. Influence of nutrients on feed intake and condition of captive Canvasbacks in winter. J. Wildl. Manage. 50:427–434.

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

RAVELING, D. G. 1981. Survival, experience, and age in relation to breeding success of Canada Geese. J. Wildl. Manage. 45:817–829.

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

REINECKE, K. J., R. C. BARKLEY, AND C. K. BAXTER. In press. Potential effects of changing water conditions on Mallards wintering in the Mississippi Alluvial Valley. *In* M. W. Weller [ed.], Waterfowl in winter—a symposium and workshop. Univ. Minnesota Press, Minneapolis, MN.

RHYMER, J. M. 1982. Effect of egg weight and renesting on thermoregulatory ability and growth of Mallard ducklings. M.Sc.thesis, Univ. of Manitoba, Winnipeg.

RINGLEMAN, J. K., AND M. R. SZYMCZAK. 1985. A physiological condition index for wintering Mallards. J. Wildl. Manage. 49:564–568.

SCOTT, J. P. 1958. Aggression. Univ. Chicago Press, Chicago, IL.

SWANSON, G. A., G. L. KRAPU, AND J. R. SERIE. 1979. Foods of laying female dabbling ducks on the breeding grounds, p. 47–57. *In* T. A. Bookhout [ed.], Waterfowl and wetlands—an integrated review. Proc. Symp. N. Cent. Sect., The Wildl. Soc., Madison, WI.

THIESSEN, D. D. 1976. The evolution and chemistry of aggression. Charles C Thomas Publ. Co., Springfield, IL.

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

WELLER, M. W. 1975. Migratory waterfowl: a hemispheric perspective. Publ. Biol. Inst. De Invest. Cient. U.A.N.L. 1:89–130.

WEST, G. C. 1968. Bioenergetics of captive Willow Ptarmigan under natural conditions. Ecology 49: 1035–1045.

WHITE, D. C. 1985. Lowland hardwood wetland invertebrate community and production in Missouri. Arch. Hydrobiol. 103:509–533.

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.

WIELICKI, D. J. 1987. Aspects of Mallard nutrition during molt. M.Sc.thesis, Univ. of Manitoba, Winnipeg.

Wise, R. W. 1960. Food consumption and nutritive requirements of Mallard and Pintail ducks in captivity. M.A.thesis, Univ. of California, Davis.

Wishart, R. A. 1979. Indices of structural size and condition of American Wigeon (*Anas americana*). Can. J. Zool. 57:2369–2374.

Wishart, R. A. 1983. Pairing chronology and mate selection in the American Wigeon (*Anas americana*). Can. J. Zool. 61:1733–1743.

Woodall, P. F. 1978. Omental fat: a condition index for Red billed Teal. J. Wildl. Manage. 42:188–190.

Wypkema, R. C., and C. D. Ankney. 1979. Nutrient reserve dynamics of Lesser Snow Geese staging at James Bay, Ontario. Can. J. Zool. 57:213–219.

Young, D. A., and D. A. Boag. 1981. A description of moult in male Mallards. Can. J. Zool. 59:252–259.