The Condor 95:45–56

INTRASPECIFIC VARIATION IN THE USE OF NUTRIENT RESERVES BY BREEDING FEMALE MALLARDS[1]

ANDREW D. YOUNG[2]
Ecology and Evolution Group, Department of Zoology, University of Western Ontario, London, Ontario N6A 5B7, Canada

Abstract. Female Mallards (*Anas platyrhynchos*; $n = 249$) were collected from grassland and parkland habitats in western and eastern Saskatchewan to compare the use of stored nutrients by breeding birds in these two habitats. The use of nutrient reserves varied little between habitats. Fat and mineral use did differ between collection sites. Protein reserves were not used during laying and protein levels did not differ among sites. Body fat declined at a rate of −0.6 g per gram of clutch fat deposited at the western grassland (WG) site whereas fat declined −1.5 g for every gram invested in clutch fat in other females. Body fat contributed 8.2% of the energy needed by WG females during the formation of a 10 egg clutch and 20.7% of energy needs during clutch formation for females from all other sites. WG females did not rely upon stored minerals during egg formation; however, body ash contributed 11–13 g for a 10 egg clutch at other sites, enough for about 1 egg shell. Based on ovarian follicle development of late layers, WG females would lay similar sized clutches (11.1; $n = 14$) to females breeding at other sites (10.6; $n = 41$), despite using much less stored body fat. This result does not support food limitation hypotheses which predict that the amount of stored body fat limits clutch size in mallards.

Key words: Anas platyrhynchos; *breeding; egg formation; habitat; Mallard; nutrient reserves; nutrition.*

INTRODUCTION

Many waterfowl store nutrient reserves prior to nutritionally costly events such as migration, winter cold stress and reproduction (Whyte et al. 1986; Alisauskas and Ankney, in press). The nutritional costs of egg laying in waterfowl are substantial compared with those in other birds (Ricklefs 1974). Reliance on stored nutrients varies among waterfowl, and different tactics are used to meet the nutritional requirements of egg laying. For example, arctic-nesting geese rely entirely on stored fat and protein during laying that is accumulated prior to arrival at breeding areas (Alisauskas and Ankney, in press). Many dabbling and diving ducks use stored fat during clutch formation, whereas clutch protein requirements are met by consuming large quantities of aquatic invertebrates (Swanson et al. 1985).

Interspecific comparisons of exogenous and endogenous nutrient acquisition and allocation in waterfowl have provided much information about the role of nutrients in egg formation (Alisauskas and Ankney, in press). Few studies have examined intraspecific variation in nutritional tactics with respect to environmental factors (Gauthier et al. 1984, Morton et al. 1990). Deposition of fat by spring migratory Greater Snow Geese (*Chen caerulescens atlantica*) differs markedly between habitats varying in food quality (Gauthier et al. 1984). Interspecific variation in nutrient use can best be understood after there has been sufficient research on the extent and nature of intraspecific variation in these tactics (Alisauskas and Ankney, in press).

Prairie grassland and aspen parkland habitats in the mid-continent region of North America support high densities of breeding Mallards (*Anas platyrhynchos*) (Bellrose 1980). The aquatic invertebrate food base, used heavily by breeding Mallards (Swanson et al. 1985), likely shows greater annual variation in prairie grassland than in aspen parkland habitats, a reflection of annual wetland permanence (Lynch et al. 1963, Smith 1971, Nudds 1980). Consequently, given potential differences in food availability, Mallards breeding in these two habitats may differ in their reliance on endogenous reserves during egg formation.

[1] Received 23 April 1992. Accepted 28 September 1992.
[2] Present address: 373 Edgehill Dr., Barrie, Ontario L4M 4S4, Canada.

METHODS

STUDY AREA AND DATA COLLECTION

Topographical and vegetational features were the criteria used in choosing sampling areas. Grassland habitat areas were characterized by gently undulating topography with few trees. Parkland areas contain irregular knob and kettle topography with an abundance of aspen trees (*Populus* spp.). Both grassland and parkland habitats contain post-glacial wetlands that have been extensively modified through drainage for agricultural production (Johnson and Shaffer 1987).

Annual wetland conditions at the four sampling sites were determined from May pond counts collected by the United States Fish and Wildlife Service (USFWS) from 1961–1988 (Anonymous 1987). Ephemeral wetlands were not counted. I used data from four segments (29 km × 200 m sampling unit) at each sample site. These segments were located over the collection sites of ducks. Density of lone male Mallards was estimated using larger sampling segments (29 km × 400 m). These data were not corrected for visibility; consequently wetland numbers and male counts in wooded parkland areas may have been underestimated.

Mallards collected in this study were paired. All ducks were shot. In 1986, females were collected in prairie grassland habitat ($n = 68$) within a 45 km radius of Leader, Saskatchewan (51°N, 110°W) and from aspen parkland habitat (WP; $n = 70$) within a 15 km radius of Baldwinton, Saskatchewan (53°N, 109°W; Fig. 1). In 1987, 51 female Mallards were collected from a 20 km^2 area located just west of Weyburn, Saskatchewan (49°N, 104°W) in grassland habitat. Females ($n = 60$) were collected from a 15 km^2 area in parkland habitat just north of Melville, Saskatchewan (51°N, 103°W). Collection sites of birds in 1986 are hereafter called western grassland (WG) and western parkland (WP) and those in 1987 as eastern grassland (EG) and eastern parkland (EP). I chose new sampling locations in 1987 so that I was not sampling replacement birds (e.g., yearlings) that were not typical of the breeding population (after Ankney and Scott 1980). This sampling scheme tested for potential habitat differences at two sites so that site and habitat effects are not confounded.

Mallards were collected from each habitat alternately commencing with grassland sites immediately after arrival (Table 1) from 5 April to 8 May in 1986 (06:30–19:00) and from 7 April to 4 May in 1987 (06:30–20:00). Here I distinguish between collection region to refer to either western (1986) or eastern (1987) Saskatchewan, collection habitat as grassland or parkland, and collection site as one of the four areas collected from, e.g., WG collection site. The term "region" refers to year or regional effects synonymously. Region is used rather than year because greater variation in water availability is attributable to region than to year.

Ovaries were removed from females and placed in formalin within a few hours of collection. Oviducal eggs were removed, and if intact, were hard boiled for 6 min and frozen for chemical analysis. Broken oviducal eggs were noted and discarded. The remainder of the carcass was tagged, double bagged and frozen until subsequent lab analysis.

CARCASS ANALYSIS

Thawed body mass was weighed to the nearest 0.01 g in the lab. This mass minus reproductive tissue and ingesta was fresh body mass. All abdominal fat, including that adhering to digestive organs was removed, weighed and discarded. I recorded the presence or absence of the bursa of Fabricius; presence indicated that a bird was no greater than one year old (yearling) whereas absence suggested the bird was at least one year old (adult). The rest of the carcass was passed twice through a Hobart meat grinder. Approximately 400 g (roughly half) of the carcass was dried to constant mass at 90°C and ground once more. Proximate analysis of the carcass homogenate was performed as outlined by Alisauskas and Ankney (1985). Two subsamples of this dry homogenate from each bird (about 6 g) were placed into cellulose extraction thimbles, and fats were extracted for 6 hr in a modified Soxhlet apparatus using petroleum ether as a solvent. The mass of fat extracted from the sample was obtained by subtraction. The remaining lean dry sample was placed in a muffle furnace at 550°C for 6 hr and the residue (ash) was weighed. Ash free lean dry mass (AFLDM) was obtained by subtraction. The proportion of sample fat was multiplied by estimated dry body mass, and this total was added to abdominal fat to give total carcass fat. Total body ash was estimated by multiplying the ratio of sample ash by estimated dry body mass. Total body fat and ash were subtracted from dry body mass, leaving only AFLDM of the carcass, an index of protein, and hereafter referred to as pro-

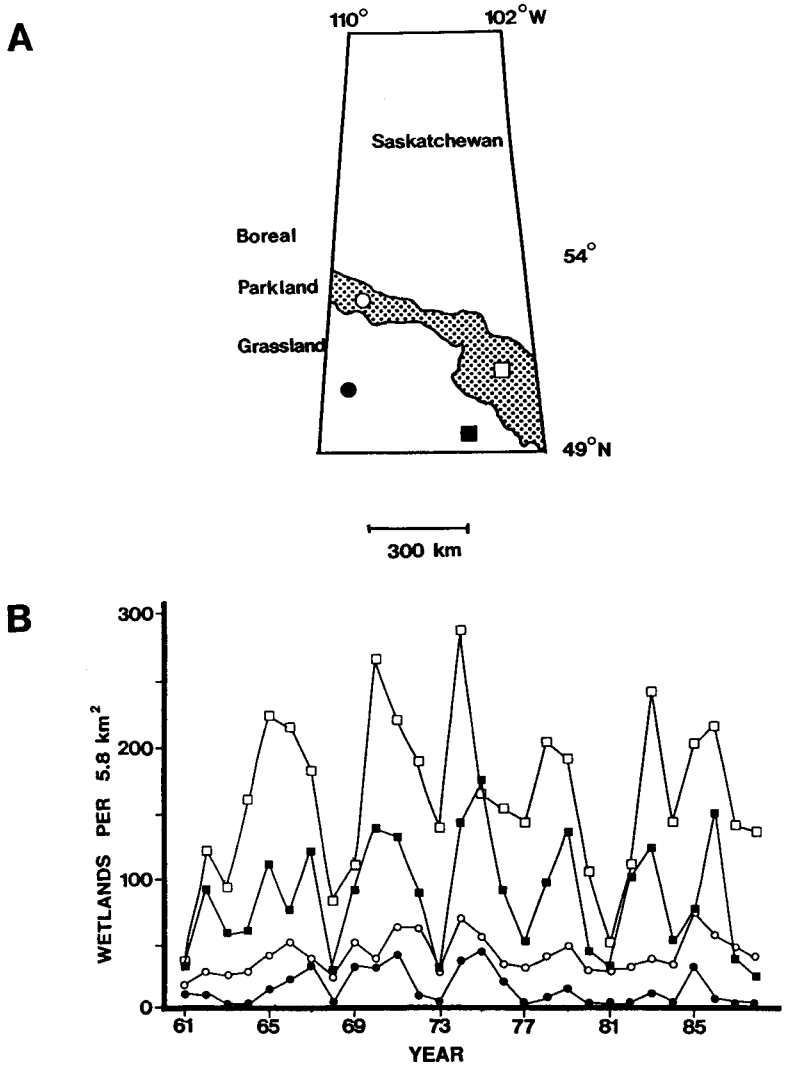

FIGURE 1. A. Location of sampling sites in western (circles) and eastern (squares) Saskatchewan in grassland (closed symbols) and parkland (open symbols) habitats. Habitat zones after Kiel et al. (1972). B. Annual May pond densities per 5.8 km² of Saskatchewan sample sites over a 28-year-period from 1961–1988. Densities represent the average of four transects per sample site. Plot symbols designate collection site and correspond with figure A, closed circles = western grassland (WG), open circles = western parkland (WP), closed squares = eastern grassland (EG), open squares = eastern parkland (EP).

TABLE 1. Timing and number of female Mallards collected in grassland and parkland habitats.

		April					May	
Year	Site[a]	5–10	11–15	16–20	21–25	26–30	1–5	6–8
1986	WG	13	9	0	20	0	16	10
	WP	15	0	10	18	0	14	13
1987	EG	15	9	0	25	0	5	0
	EP	10	0	20	0	19	11	0

[a] WG = western grassland, WP = western parkland, EG = eastern grassland, EP = eastern parkland.

tein. Total carcass fat, protein and ash were adjusted for differences due to structural size (see below) and are hereafter called body fat or fat, body protein or protein and body ash or ash.

REPRODUCTIVE TISSUE

For each female, I determined: (a) lipid content and lean dry mass of each yolky ovarian follicle (maximum $n = 6$), (b) lipid content and lean dry weight of the remainder of the ovary, (c) dry oviduct mass (assumed to be 100% protein, see Alisauskas and Ankney 1985), and (d) number of eggs laid by counting the number of post-ovulatory follicles (POF) on the ovary. Some developing ovulatory follicles (DOFs) were broken during collection; the fat and protein content of these follicles were estimated using average values of these nutrients for intact series of six developing follicles from laying females (Young 1991).

I determined the average amount of egg fat and protein for 27 shelled oviducal eggs following the procedure of Alisauskas and Ankney (1985). Mean egg fat was 6.54 ± 0.76 g (SD) and protein was 7.72 ± 0.94 g. Oviducal egg shells may not be complete so a published mean value for dry shell mass of 9.8 g was used (Birkhead 1985). These data were used to calculate total reproductive nutrients for each female as follows: *REPRODUCTIVE LIPID (R-FAT)* = DOF lipid + remaining ovarian lipid + lipid in eggs laid (i.e., average egg yolk lipid × number of POFs), *REPRODUCTIVE PROTEIN (R-PROTEIN)* = DOF lean dry mass + remaining ovarian follicular lean dry mass + oviduct dry mass + protein in eggs laid (i.e., average egg protein × number of POFs), and *REPRODUCTIVE ASH (R-ASH)* = ash in eggs laid (as indexed by the average dry shell × number of POFs).

Females were placed into one of five categories based on the development of the ovary as follows:

NON-RAPID FOLLICLE GROWTH (non-RFG): 0–1 DOFs, largest DOF had a dry mass of ≤0.39 g. These masses were based on the mean dry mass of the second smallest DOF in a hierarchy of six DOFs of laying females (Young 1991). This category contains all non-breeding and pre-breeding birds.

RAPID FOLLICLE GROWTH (RFG): 1–6 DOFs, largest DOF had a mean dry mass of >0.39 g and no POFs were present; only birds collected prior to or on 23 April (early RFG) were using in regression models.

LAYING: ovaries with at least one POF and at least one DOF or an egg in the oviduct.

Data from eight renesting females were discarded. Criteria were that the ovary contained a series (>5) of very small POF, at least one DOF, and a vascularized brood patch. Also, two females were discarded because they were collected during incubation as evidenced by a highly developed brood patch, no DOFs, and very small POFs.

I estimated clutch size of late laying (>4 POF) females by adding the number of DOFs that would have produced eggs and the number of eggs that had been laid as evidenced by POFs (Ankney and Afton 1988).

STATISTICAL ANALYSES

Statistical analyses were performed using either the SAS (1985) or SYSTAT (Wilkinson 1988) packages. Variation in body fat, protein and mineral components of all female Mallards were examined with respect to a number of independent variables including: mass of reproductive tissue, region (western or eastern), habitat (grassland or parkland), and age (yearling or adult). Non-significant ($P > 0.05$) interaction terms were excluded from the models.

I removed variation in body fat, protein and mineral due to differences in structural size using the following method. Eight linear measures were taken on Mallard carcasses (bones exposed) using either calipers (0.1 mm) or a ruler (1 mm). Measurements were, wing chord, keel length, tarsus length, neck length, body length, culmen length, skull length, and cranial height (see Young 1991 for further details). Principal component analysis (PCA) was performed on the correlation matrix of these eight morphological measures. PC_1 eigenvectors for the 8 structural measures were all positive, so PC_1 scores can be used to index structural size (Pimental 1979). Scores of greater magnitude indicate structurally larger birds than do scores of lesser magnitude. I used ordinary least squares regression analyses to determine whether fat, protein, and ash were positively correlated with PC_1 scores. Carcass components that showed a significant positive relationship to body size were adjusted to remove variation in component mass due to structural size. Residuals from the least squares regression of component masses on

PC_1 scores were retained and added to the means for all the Y observations using the following equation and the DO statement in SAS (1985).

$$^{Y}\text{adjusted} = {}^{Y}\text{observed} - [a + b(PC_1)] + \bar{}^{Y}\text{observed}$$

For breeding birds (RFG and LAYING), I used Alisauskas and Ankney's (1985) regression technique to estimate the contribution of nutrient reserves to clutch formation. The regression model used for these analyses took the form Y (body nutrient) = a + b(X), where X is the reproductive tissue corresponding to the body nutrient used as a dependent variable (Y; i.e., fat and R-FAT, protein and R-PROTEIN, ash and R-ASH). Only data from early RFG and LAYING birds were used in these analyses as body fat was significantly lower in late RFG birds. I wanted to estimate body fat use of initial nesting birds without including late or renesting birds in the sample.

I used analysis of covariance (ANCOVA) with reproductive tissue as the covariate to test for differences in the use of nutrient reserves between habitats. If models had common habitat slopes (interaction term $P > 0.05$), then intercepts were tested (P associated with main effect; Sokal and Rohlf 1981). Regression slope and intercept estimates were from pooled data if habitat and regional slopes and intercepts were not different ($P > 0.05$). The ANCOVA procedure was repeated testing for age differences in nutrient dynamics of breeding birds.

RESULTS

HABITAT CONDITIONS

Annual May wetland densities per 5.8 km^2 at the WG site were the lowest of all sites over a 28 year period averaging (±SE) 15 ± 3 ponds, compared to WP (42 ± 3), EG (86 ± 8) and EP (162 ± 12) sites (Fig. 1). In the years sampled, wetland densities per 5.8 km^2 were drier than long-term averages at the WG (7.0), EG (40) and EP (141) sites, and was wetter than normal at the WP (57.5) site. Average breeding density of lone males per 11.6 km^2 at the four sites were WG (4 ± 1), WP (12 ± 3), EG (9 ± 2) and EP (16 ± 4).

REPRODUCTIVE PARAMETERS

Breeding WG females, initiated laying later (27 April ± 1.3; $n = 26$) than did females from WP (21 ± 1.0; $n = 25$), EG (20 ± 1.3; $n = 20$) or EP (22 ± 0.8; $n = 27$) using collection date ($P = 0.0008$) as a covariate. Chi-square tests revealed that there was a greater percentage ($P < 0.01$) of *non-RFG* birds at the WG site (30%) compared with WP (16%), EG (20%) and EP (17%) sites. The percentage of yearling female Mallards collected was greater ($P < 0.001$) at WG (43%) and WP (39%) sites than at EG (23%) and EP (15%) sites. Predicted clutch sizes did not differ ($P = 0.31$) among the four sampling sites WG (11.1 ± 0.5; $n = 14$), WP (10.6 ± 0.6; $n = 13$), EG (10.5 ± 0.3; $n = 11$) or EP (10.8 ± 0.4; $n = 17$). Yearlings initiated laying later ($P < 0.01$) than adults at WG (3 May ± 1.7; $n = 16$), WP (28 April ± 1.7; $n = 21$), and EG (2 May ± 1.0; $n = 7$) sites, but not at the EP site (23 April ± 2.1; $n = 8$).

BODY SIZE

PC_1 eigenvectors for females ($n = 249$) were all positive ranging from 0.22–0.44 for the eight linear measures, had an eigenvalue of 3.1 and explained a cumulative total of 38.8% of the variation in body size. PC_1 scores were all positive and therefore the PC_1 axis can be used as a general size (rather than shape) component, with larger scores indicating structurally larger birds (Pimental 1979). Body fat was related to body size in EG females ($P < 0.05$), but not in other samples of females ($P > 0.05$). Body protein increased with body size in females with WG ($P < 0.05$), WP ($P < 0.01$), EG ($P < 0.001$) and EP ($P > 0.05$). Body ash increased with body size in females from WG ($P < 0.05$), EG ($P < 0.001$) and EP ($P < 0.05$) but not WP ($P > 0.05$) females.

NUTRIENT RESERVES

There was significant variation in body mass and composition of female Mallards (Tables 2, 3). WG and EG females had slightly less body fat and ash than did their parkland counterparts. Differences in fat and ash content of these females was also partly dependent on region as indicated by a significant region*habitat interaction term in both models. Eastern females from both habitats had slightly higher ash content than did western females. Most of the variation in body components was not explained by the predictor variables R-TISSUE, region, habitat, and age. Variation in body nutrients explained by the models ranged from 12% for protein to 35% for fat content (Table 3).

TABLE 2. Mean ± SE (g) body mass and composition of Mallards collected from Saskatchewan grassland and parkland habitats prior to and during egg formation.

Site[a]	Stage	Age	*n*	Body mass	Fat	Protein	Ash
WG	non-RFG	A	9	1046 ± 31	131 ± 21	265 ± 6	56 ± 2
		Y	12	1022 ± 20	106 ± 8	256 ± 6	54 ± 2
	RFG	A	9	1074 ± 24	122 ± 17	275 ± 5	54 ± 3
		Y	10	1024 ± 25	109 ± 9	267 ± 5	54 ± 2
	LAY	A	20	1010 ± 14	95 ± 6	277 ± 4	58 ± 2
		Y	6	1054 ± 33	100 ± 13	289 ± 9	59 ± 2
WP	non-RFG	A	8	1088 ± 45	158 ± 43	262 ± 7	60 ± 7
		Y	3	1016 ± 50	125 ± 40	241 ± 5	48 ± 4
	RFG	A	16	1072 ± 18	159 ± 13	265 ± 4	61 ± 2
		Y	13	1083 ± 16	125 ± 9	274 ± 3	57 ± 2
	LAY	A	16	1034 ± 20	103 ± 14	285 ± 5	53 ± 2
		Y	9	987 ± 21	72 ± 10	277 ± 6	49 ± 1
EG	non-RFG	A	7	1136 ± 16	180 ± 14	253 ± 11	63 ± 2
		Y	3	1104 ± 37	116 ± 12	264 ± 12	55 ∓ 3
	RFG	A	15	1160 ± 23	148 ± 12	165 ± 4	61 ± 2
		Y	6	1052 ± 34	91 ± 16	266 ± 5	48 ± 1
	LAY	A	17	1046 ± 19	102 ± 8	265 ± 5	53 ± 2
		Y	3	1109 ± 15	86 ± 6	263 ± 4	49 ± 5
EP	non-RFG	A	11	1145 ± 33	171 ± 20	257 ± 5	62 ± 4
		Y	2	1061 ± 38	131 ± 31	261 ± 6	61 ± 6
	RFG	A	16	1150 ± 25	160 ± 14	265 ± 5	65 ± 3
		Y	3	1099 ± 34	145 ± 23	249 ± 20	64 ± 4
	LAY	A	24	1105 ± 17	100 ± 8	266 ± 6	54 ± 2
		Y	3	1021 ± 27	116 ± 43	226 ± 19	56 ± 10

[a] Site—WG = western grassland, WP = western parkland, EG = eastern grassland, EP = eastern parkland; Stage—non-RFG = non-rapid follicle growth, RFG = rapid follicle growth, LAY = laying; AGE—A = adult >1 year old, Y = yearling ≤1 year old; Body mass—fresh body mass minus ingesta and reproductive tissue; Fat = total carcass fat; Protein = total carcass ash free lean dry mass; Ash = total carcass mineral.

TABLE 3. Analysis of variance of fat, protein and ash of all (n = 241) female Mallards collected in Saskatchewan.

	Fat	Protein	Ash
r^2	0.35	0.12	0.31
R-TISSUE[a] (R)	24.32[b] ****	1.73 ns	9.51 **
Region (RE)	1.01 ns	0.34 ns	3.93 *
Habitat (H)	6.28 *	0.54 ns	6.10 **
Age (A)	9.82 ***	0.10 ns	6.31 **
R•H	3.78 *	—[c]	6.38 *
R•RE•H•A	3.12 *	—	—

[a] R-TISSUE the predictor variable used corresponded to the Y variable body nutrient, that is R-FAT with body fat, R-PROTEIN with body protein, and R-ASH with body ash.

[b] F value (top) probability (bottom) associated with type III sums of squares, ns = $P > 0.05$, *$P < 0.05$, **$P < 0.01$, ***$P < 0.001$, ****$P < 0.0001$.

[c] Non-significant interaction terms ($P > 0.05$) were removed from the model.

An obvious trend was a reduction in body mass and fat of female Mallards with increasing commitment to reproduction (see below). Post-arrival body fat content (g) of non-RFG Mallards collected within the first 6 days after arrival averaged WG 129 ± 16, (WG, n = 10, 5–8 April), 191 ± 32 (WP, n = 5, 9 April), 147 ± 3 (EG, n = 8, 7–8 April), 201 ± 18 (EP, n = 5, 10 April).

BREEDERS

Regression analyses indicated that WG females used body fat at a slower rate than did females from other sites (ANCOVA $P = 0.043$). Body fat of WG females declined only 0.6 g per gram invested in R-FAT, whereas females from other sites expended 1.5 g body fat per gram of R-FAT (Table 4; Fig. 2). Using these slope estimates, and that an average ten egg clutch contains an estimated 65.4 g of R-FAT, WG females would expend 39.2 g and other females 98.1 g of body fat during egg formation. Assuming 1 g of fat yields 37.7 kJ of energy (Ricklefs 1974), and a 1,000 g female expends 17,835 kJ laying a 10

TABLE 4. Least squares regression models relating body nutrients (Y) of breeding female Mallards (early RFG and laying) to their corresponding reproductive tissue (X).

Nutrient	Sample[a]	n	r^2	Intercept ± SE	Slope ± SE	P
Fat	WG	36	0.25	131 ± 6	−0.6[b] ± 0.2	0.0181
	WP, EG, EP	121	0.38	175 ± 6	−1.5 ± 0.2	0.0001
Protein	ALL	158	−0.02	266 ± 2	0.1 ± 0.1	0.2110
Ash	WG	36	−0.01	56 ± 1	0.02[c] ± 0.03	0.4870
	WP, EG	80	0.23	58[d] ± 1	−0.11 ± 0.03	0.0009
	EP	40	0.17	64 ± 2	−0.13 ± 0.04	0.0011

[a] WG = western grassland, WP = western parkland, EG = eastern grassland, EP = eastern parkland, samples from these areas were pooled by habitat, then region if slopes (interaction term) and intercepts (main effect) were not significantly different ($P > 0.05$), see text for further details.
[b] ANCOVA test Habitat•R-FAT (slopes) of samples WG and WP, EG, EP, $P = 0.043$.
[c] ANCOVA test Habitat•R-ASH (slopes) of samples WG and WP, EG, WP, $P = 0.01$.
[d] ANCOVA test Habitat (intercepts) of samples WG and WP, EG, $P = 0.003$.

egg clutch (Arnold and Rohwer 1991), body fat contributed only 8.2% to the total energy needs of laying WG females and 20.7% to clutch needs of females from all other sites. On average, WG females laying a ten egg clutch initiated incubation with 92.3 g of body fat and other females started with 77.0 g of body fat.

Body protein of female Mallards did not change with respect to R-PROTEIN invested in a clutch (Table 4). Ash levels of WG females did not change during egg formation (Table 4), but ash declined significantly in samples of female Mallards from other sites (Fig. 3). WP and EG females initiated RFG with less ash (58.1 ± 1.3) than did EP females (63.8 ± 1.7), and females from both groups used ash at a similar rate during egg formation (Table 4).

Adult females had more body fat than yearlings (Tables 2, 3). Regression and ANCOVA analyses indicate this was especially true for adult females breeding in WP habitat that initiated RFG with substantially ($P = 0.023$) more fat

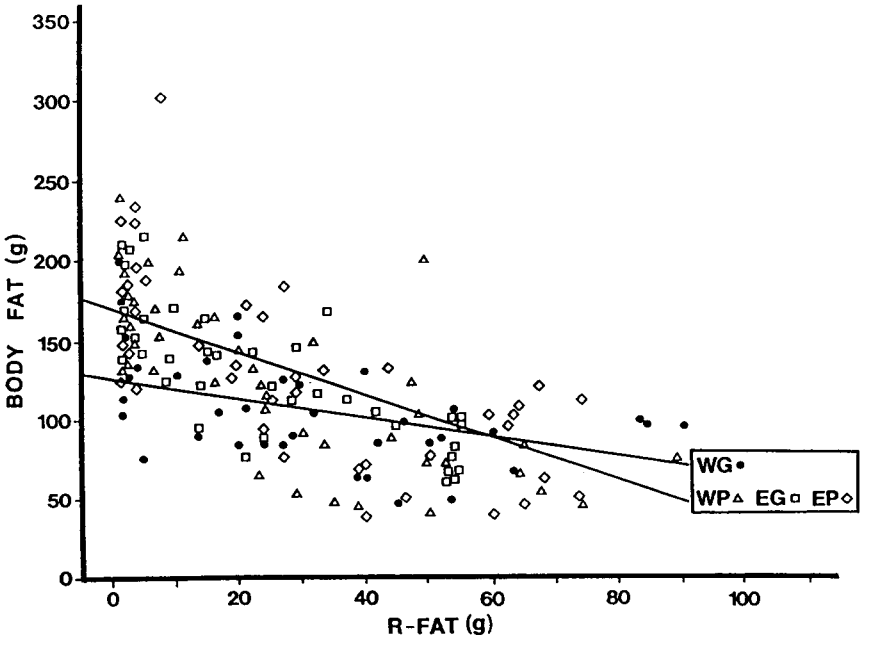

FIGURE 2. Body fat (Y) on R-FAT (X) scatter plot of breeding female Mallards collected in grassland and parkland habitats from western and eastern Saskatchewan regions. See Table 4 for regression model intercepts and slopes.

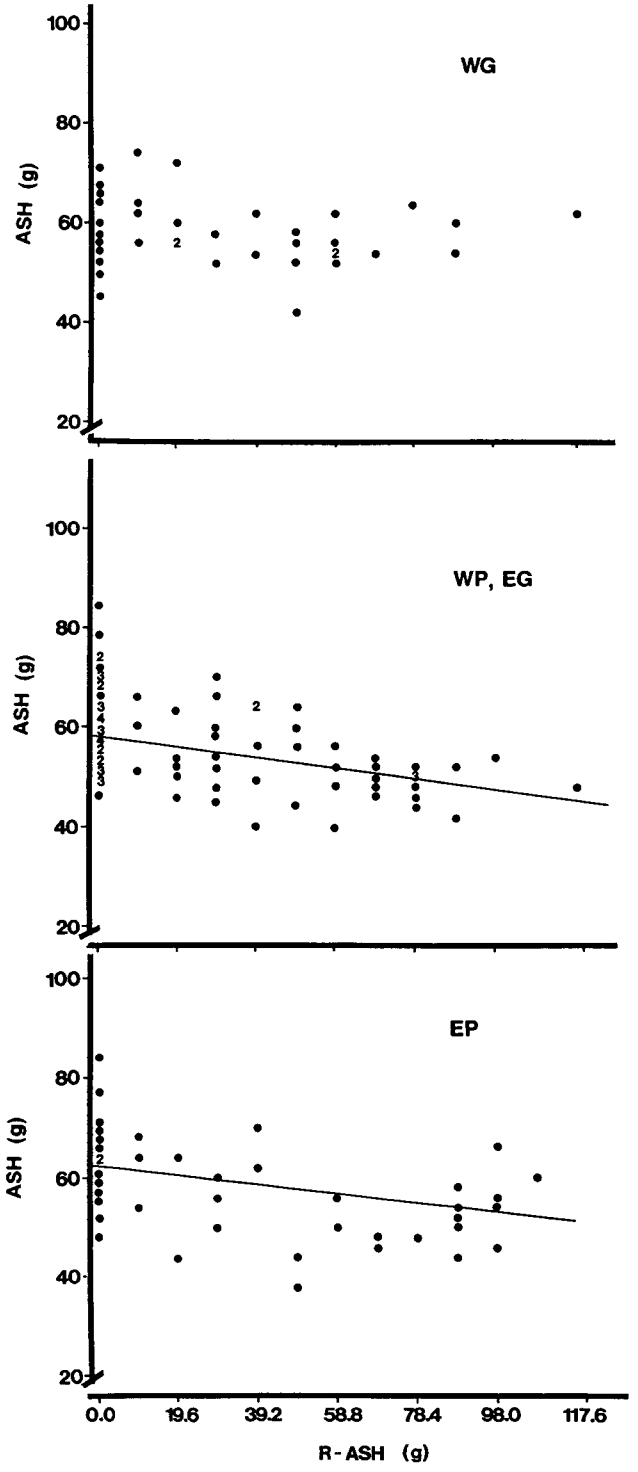

FIGURE 3. Body ash (Y) on R-ASH (X) scatter plot of breeding female Mallards collected from western grassland (WG), western parkland (WP) and eastern grassland (EG), and eastern parkland (EP) in Saskatchewan. See Table 4 for regression model intercepts and slopes.

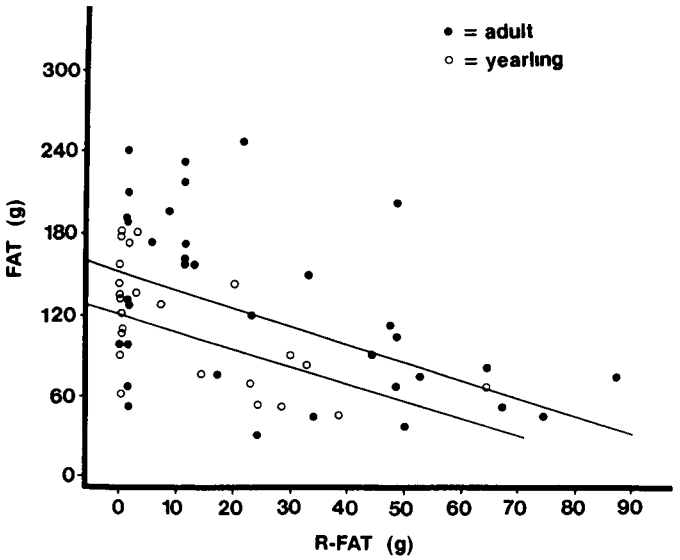

FIGURE 4. Body fat (Y) on R-FAT (X) of yearling (open circles) and adult (closed circles) female Mallards from western Saskatchewan parkland habitat.

(intercept = 161.3 g ± 12.1; $n = 34$) than yearlings (125.6 g ± 8.8; $n = 23$). Both groups used fat at the same rate ($P > 0.05$; Fig. 4). There was no difference detected in the fat use slope or intercepts of breeding adult and yearling WG females ($P < 0.05$) using ANCOVA. A small sample of yearlings (18.9% of females; 5.5% of males) at the eastern sites, compared with 40.6% yearlings at the western sites, resulted in little power to detect potential age differences.

DISCUSSION

The magnitude of intraspecific variation in the use of fat reserves by Mallards breeding in adjacent areas exceeds most interspecific comparisons of fat use (Alisauskas and Ankney, in press). The rate of body fat use by WG females (−0.6) was more similar to that of egg-laying Lesser Scaup (*Aythya affinis*), Ring-necked Ducks (*A. collaris*) and Blue-winged Teal than it was to Mallard females from other sites (−1.5). The use of body fat by Mallards breeding in WP, and both eastern sites is similar to fat use by egg laying Canvasbacks (*Aythya valisineria*; Barzen and Serie 1990). The rate of fat loss by breeding Mallards in North Dakota (−1.04) was intermediate between the two estimates produced in this study (see Alisauskas and Ankney, in press). Besides body fat, intraspecific differences have been noted in protein reserve dynamics of egg laying Ring-necked Ducks (Hohman 1986, Alisauskas et al. 1990) and ash dynamics of Mallards. Given the variation in reliance on nutrient reserves within one species, especially samples collected in relative proximity, it is not valid to generalize about species-specific patterns of nutrient reserve use based on data from one study site or year.

Intraspecific variation in the use of body fat was not attributable to differences in age structure between sites. Yearling female Mallards initiate egg formation with less fat than do adults (Krapu and Doty 1979; this study), and could potentially account for the low rate of fat use by WG females. However, this was not the case in this study for two reasons. First, WG and WP sites had a similar percentage of yearlings, yet WP females used fat at a much faster rate than did WG females. Secondly, potential age effects were accounted for in statistical models, in which site differences were still apparent.

There was also substantial among-site variation in body ash dynamics during egg formation. For example, WG females did not use stored mineral reserves. WP and EG females did use stored minerals but did not initiate RFG with as large a reserve as EP females. Published data on the use of mineral stores by breeding waterfowl suggests that arctic nesting geese (Alisauskas and Ankney, in press), Ruddy Ducks (*Oxyura jamaicensis*; Tome 1981) and Lesser Scaup (Afton

and Ankney 1991) use mineral stores during egg laying, while most other ducks do not (Alisauskas and Ankney, in press). Colmar and Driggers (1979) estimated that 25–40% of the calcium required for egg shell formation in domestic chickens (*Gallus domesticus*) comes from medullary bone. Krapu (1979) suggested that calcium is probably not a limiting food item for prairie ducks because of the abundance of snail shells available in semi-permanent and permanent wetlands. Crustaceans also are rich in calcium (Krapu 1979). Use of body calcium in this study would contribute enough calcium for about one egg in an average 10 egg clutch. Use of calcium stores during egg formation may suggest that conversion of dietary calcium to egg shells is rate limited, and females must rely on labile calcium available in medullary bone.

There has been much debate recently over the role of nutrient reserves during clutch formation in prairie ducks (e.g., Ankney et al. 1991, Arnold and Rohwer 1991). WG females laid similar-sized clutches to those from other sites, despite using much less stored body fat during egg formation. This does not support food limitation hypotheses which predict that egg production is constrained by the amount of stored body fat females can attain prior to laying (Krapu 1981, Ankney and Afton 1988). Mallards derive from 8–20% of their energy needs from stored reserves, a contribution which does not appear large enough to limit clutch size (Arnold and Rohwer 1991). In addition, variation in body fat of females near or at the end of laying was high but should be low if all excess fat is devoted to egg production. Also, Mallards spend 15% of their time on wetlands resting (Titman 1981), time that could be devoted to foraging if food is limiting. Data presented here support the conclusion that food is not a factor limiting clutch size in Mallards (Arnold and Rohwer 1991).

Apparently, WG females relied to a much greater extent upon dietary sources of food to form clutches. According to this reasoning, WG females should have larger digestive organ sizes than those of females from other sites reflecting greater food consumption. This was not the case (Young 1991), perhaps because estimates of food consumption using digestive organ size are too crude. Another possibility is that WG females may need to expend less energy on costly pursuit flights (Titman 1983) when breeding at extremely low densities.

Dzubin and Gollop (1972) found that Mallards breeding in grassland habitat (Kindersley, SK) bred earlier, laid larger clutches and contained a greater proportion of adults than did Mallards breeding in parkland habitat (Roseneath, MB). I found no difference in breeding chronology, predicted clutch size or in the proportion of yearlings between habitats. There were proportionately more yearlings at western than at eastern collection sites. Breeding chronology was delayed at the WG site and was similar among other sites. Dzubin and Gollop (1972) may have collected data during a much wetter period, which may have resulted in substantially different findings. Grassland habitats during wet years are likely very productive, and an abundant food source may result in earlier nesting and larger clutches.

I suggest that little of the fat used for breeding is obtained on the wintering grounds, but rather that most is acquired at staging areas. Pre-departure fat levels of adult female Mallards wintering on the southern high plains of Texas are 180 g and in the Mingo Basin (MO) are 190–220 g (Whyte et al. 1986, Heitmeyer 1988). Upon arrival in Saskatchewan, Mallards have 130–200 g of body fat. Female Mallards are expected to expend 72–84 g of fat during a 1,000 km flight (Whyte and Bolen 1988). Mallards wintering in the United States fly from 950 km (central Washington) to 2,500 km (southern Alabama and Mississippi). Therefore, Mallards wintering in central Washington should expend at least 72 g of fat for migration and those from southern Alabama and Mississippi should expend at least 180 g. Female Mallards arrive in Saskatchewan with 130, 190, 150 and 200 g of fat at the WG, WP, EG and EP sites, respectively. The only birds that may not have to replenish fat stores during migration and still have enough left over for breeding would be those departing from the closest wintering areas (e.g., Washington) with a maximum of 220 g of body fat. Fat reserves of females from all other wintering areas would have to be at least partially, if not totally, renewed during migration. This emphasizes the importance of spring staging areas as sources of energy for migration and to store fat for breeding.

ACKNOWLEDGMENTS

This study was funded through an NSERC operating grant and Canadian Wildlife Service University Research Support Fund to D. Ankney and an NSERC post-graduate scholarship to ADY. The Canadian Wildlife Service (Saskatoon) issued the permits re-

quired to collect the ducks. I am grateful to L. Kellaway and V. Young for field assistance and to R. Dewsnap and J. Amery for lab assistance. J. Bladen (USFWS) provided aerial census data. M. Heitmeyer, J. Morton and R. Gates provided comments on an earlier draft of this manuscript.

LITERATURE CITED

AFTON, A. D., AND C. D. ANKNEY. 1991. Nutrient-reserve dynamics of breeding Lesser Scaup: A test of competing hypotheses. Condor 93:89–97.

ALISAUSKAS, R. T., AND C. D. ANKNEY. 1985. Nutrient reserves and the energetics of reproduction in Coots. Auk 102:133–144.

ALISAUSKAS, R. T., R. T. EBERHARDT, AND C. D. ANKNEY. 1990. Nutrient reserves of breeding Ring-necked Ducks (*Aythya collaris*). Can. J. Zool. 68:2524–2530.

ALISAUSKAS, R. T., AND C. D. ANKNEY. In press. The cost of egg laying and its relation to nutrient reserves in waterfowl. *In* B. D. J. Batt et al. [eds.], The ecology and management of breeding waterfowl. Univ. of Minnesota Press, Minneapolis.

ANKNEY, C. D., AND D. M. SCOTT. 1980. Changes in the nutrient reserves and diet of breeding Brown-headed Cowbirds. Auk 97:684–696.

ANKNEY, C. D., AND A. D. AFTON. 1988. Bioenergetics of breeding Northern Shovelers: Diet, nutrient reserves, clutch size and incubation. Condor 90:459–472.

ANKNEY, C. D., A. D. AFTON, AND R. T. ALISAUSKAS. 1991. The role of nutrient reserves in limiting waterfowl reproduction. Condor 93:1029–1032.

ANONYMOUS. 1987. Standard operating procedures manual. Section III: Waterfowl breeding population and habitat survey. United States Fish and Wildlife Service. Laurel, MD. 20708.

ARNOLD, T. W., AND F. C. ROHWER. 1991. Do egg formation costs limit clutch size in waterfowl? A skeptical view. Condor 93:1032–1038.

BARZEN, J. A., AND J. R. SERIE. 1990. Nutrient reserve dynamics of breeding Canvasbacks. Auk 107:75–85.

BELLROSE, F. C. 1980. Ducks, geese and swans of North America. 2nd ed. Stackpole Books, Harrisburg, PA.

BIRKHEAD, M. 1985. Variation in egg quality and composition in the Mallard (*Anas platyrhynchos*). Ibis 127:467–475.

COLMAR, C. L., AND J. C. DRIGGERS. 1979. Secretion of radioactive calcium in the hen's egg. Science 109:282.

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. Fish and Wildl. Serv. Res. Rep. 2.

GAUTHIER, G., J. BEDARD, J. HUOT, AND Y. BEDARD. 1984. Spring accumulation of fat by Greater Snow Geese in two staging habitats. Condor 86:192–199.

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

HOHMAN, W. L. 1986. Changes in body weight and body composition of breeding Ring-necked Ducks (*Aythya collaris*). Auk 103:181–188.

JOHNSON, D. H., AND T. L. SHAFFER. 1987. Are Mallards declining in North America? Wildl. Soc. Bull. 15:340–345.

KIEL, W. H., A. S. HAWKINS, AND N. G. PERRET. 1972. Waterfowl habitat trends in the aspen parkland of Manitoba. Can. Wildl. Serv. Rep. 18.

KRAPU, G. L. 1979. Nutrition of female dabbling ducks during reproduction, p. 59–70. *In* T. A. Bookout [ed.], Waterfowl and wetlands—an integrated review. Proc. Symp. North Central Section, The Wildlife Soc. LaCrosse Printing, LaCrosse, WI.

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.

LYNCH, J. J., C. D. EVANS, AND V. C. CONOVER. 1963. Inventory of waterfowl environments of prairie Canada. Trans. N. Am. Wildl. and Nat. Res. Conf. 28:93–108.

MORTON, J. M., R. L. KIRKPATRICK, AND M. R. VAUGHAN. 1990. Changes in body composition of American Black Ducks wintering at Chincoteague, Virginia. Condor 92:598–605.

NUDDS, T. D. 1980. Resource variability, competition and the structure of waterfowl communities. Ph.D.diss., Univ. of Western Ontario, London, Ontario, Canada.

PIMENTAL, R. A. 1979. Morphometrics: the multivariate analysis of biological data. Kendall/Hunt Publ. Comp., Dubuque, IA.

RICKLEFS, R. E. 1974. Energetics of reproduction in birds, p. 152–292. *In* R. A. Paytner, Jr. [ed.], Avian energetics. Nuttall Ornithol. Club, Cambridge, MA.

SAS INSTITUTE. 1985. SAS users guide. SAS Institute, Cary, NC.

SMITH, A. G. 1971. Ecological factors affecting waterfowl production in the Albertan Parklands. U.S. Fish and Wildl. Serv. Res. Publ. 98.

SOKAL, R. R., AND F. J. ROHLF. 1981. Biometry, 2nd ed. W. H. Freeman. New York.

SWANSON, G. A., M. I. MEYER, AND V. A. ADOMAITIS. 1985. Foods consumed by breeding Mallards on wetlands of South-central North Dakota. J. Wildl. Manage. 49:197–203.

TITMAN, R. D. 1981. A time-activity budget for breeding Mallards in Manitoba (*Anas platyrhynchos*). Can. Field Nat. 95:266–271.

TITMAN, R. D. 1983. Spacing and three-bird flights of Mallards breeding in pothold habitat. Can. J. Zool. 61:839–847.

TOME, M. W. 1981. Reproductive bioenergetics of female Ruddy Ducks in Manitoba. M.Sc.thesis, Univ. of Maine, Orono, ME.

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. 1988. Flight ranges and lipid dynamics of Mallards on the southern high plains of Texas. J. Field Ornithol. 59:143–148.

WILKINSON, L. 1988. SYSTAT: The system for statistics. SYSTAT, Inc., Evanston, IL.

YOUNG, A. D. 1991. Nutrient reserves and diet of breeding Mallards and Blue-winged Teal. Ph.D.diss., Univ. of Western Ontario, London, Ontario, Canada.