

NUTRIENT-RESERVE DYNAMICS AND DIET OF BREEDING FEMALE GADWALLS¹

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Abstract. We analyzed food habits, digestive organs, and nutrient reserves (lipid, protein, and mineral; the latter two corrected for structural size) of yearling and adult female Gadwalls (*Anas strepera*) collected in southwestern Manitoba. Gadwalls are herbivores outside the breeding season and we predicted, therefore, that they would be relatively inefficient at foraging for invertebrates. Thus, they provided a test of our hypothesis that if female ducks normally encountered protein deficiencies during egg production, they would store and then use protein reserves, but would not use lipid reserves at a greater rate than do other ducks.

Predictably, we found that prelaying and laying females consumed a low proportion (50%) of animal matter relative to other *Anas* spp. Overall, lipid reserves declined by 0.78 g for every 1 g of lipid deposited in eggs, a rate similar to those reported for closely related species. Separate analyses suggested that yearlings began rapid follicle growth (RFG) with 15 g less lipid reserve than did adults and used these reserves at a lower rate (-0.62 g vs. -0.94 g per gram lipid committed to eggs). Protein reserves declined by 0.16 g for every 1 g protein deposited in eggs, but neither mass nor rate of use of these reserves differed between yearlings and adults. In females collected late in the laying cycle (≤ 5 developing follicles), number of developing follicles was positively related to protein reserves ($r = +0.52$). Females in early RFG (1 or 2 developing follicles) had significantly more lipid (27 g) and protein (8 g) reserves than did non-breeders (no developing follicles), suggesting a threshold amount of these reserves is reached before initiation of RFG. Mineral reserves were unrelated to eggshell production.

Female Gadwalls are exceptional among temperate-nesting ducks in use of protein reserves during egg production, yet are unexceptional in rate of use of lipid reserves. Thus, we conclude that data from them support the hypothesis that temperate-nesting ducks are generally lipid-, not protein-, limited. Finally, we hypothesize that among-female variation in size of reserves, especially lipid, at the end of egg laying reflects different tactics for successfully completing incubation.

Key words: Gadwalls; diet; digestive organs; nutrient reserves; clutch size; incubation.

INTRODUCTION

Use of lipid reserves during egg formation is common among waterfowl species that have been studied (Alisauskas and Ankney, in press). It is generally accepted that such use by Arctic geese (Ankney and MacInnes 1978, Raveling 1979, Ankney 1984) and Common Eiders (*Somateria mollissima*; Korschgen 1977) is a direct commitment to egg formation (as these birds feed little then) and that size of lipid reserves may limit their clutch size.

There is not general agreement, however, about the significance of lipid use by temperate-nesting ducks. Some authors have hypothesized that (1) females rely heavily on lipid reserves during egg formation to enable them to forage for protein-rich, but relatively scarce invertebrates (Drobney 1980, Krapu 1981, Hohman 1986, but see Alisauskas et al. 1990), and (2) a female's ability to acquire animal protein limits her clutch size (Drobney and Fredrickson 1985). Ankney and Afton (1988) evaluated this "protein limitation hypothesis" with data from Northern Shovelers (*Anas clypeata*), which are invertebrate specialists. They found that although lipid reserves of females declined during egg formation, protein reserves increased, i.e., protein ingestion was greater than that required for maintenance and

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egg production. Ankney and Afton (1988) therefore concluded that the protein limitation hypothesis did not apply to Northern Shovelers and that it likely did not apply to other duck species that had been studied.

Because waterfowl eggs and reproductive tissue contain approximately equal amounts of lipid and protein, Ankney and Afton (1988) argued that the protein limitation hypothesis overemphasized the importance of protein to egg-laying ducks. They suggested that if female ducks normally encountered protein deficiencies during laying they would store and then use protein reserves during breeding [as do Arctic geese, e.g., Ankney and MacInnes (1978)]. Ankney and Afton further hypothesized that, in the highly productive wetlands used by most temperate waterfowl, protein is easier to obtain than is lipid, and therefore the size of a female's lipid reserve is more likely to limit her clutch size than is her rate of protein ingestion [the "lipid limitation hypothesis," Afton and Ankney (1991)].

Herein, we evaluate the lipid and protein limitation hypotheses using data from breeding female Gadwalls (*A. strepera*). We chose to study Gadwalls because, with perhaps the exception of the American Wigeon (*A. americana*), they are the most herbivorous of North American *Anas* on an annual basis (Bellrose 1976, Paulus 1982). Thus, we assumed that they would be less efficient at foraging for invertebrates than are other ducks. Therefore, according to the protein limitation hypothesis, Gadwalls should utilize large amounts of lipid reserves during egg formation; according to the lipid limitation hypothesis, they should use lipid reserves similarly to other ducks, but should also use protein reserves.

METHODS

Data are from female Gadwalls shot in southwestern Manitoba (within a 30 km radius of Minnedosa) from 13 May–17 June, 1988. Each bird was weighed (± 10 g) immediately after it was killed and 70% ethanol was injected into its esophagus to prevent post-mortem digestion. Later that day, esophageal/proventricular contents were removed and stored in 70% ethanol until subsequent analysis. The ovary and oviduct then were removed and stored in 10% formalin.

Females were assigned to one of two age categories for analysis: *Yearling*—Bursa present

(range of lengths = 5–19 mm); and *Adult*—Bursa absent.

They were also assigned to various categories related to their reproductive condition: *Non-Rapid Follicle Growth* (non-RFG)—dry mass of largest developing ovarian follicle < 0.4 g, those with no developing follicles were designated as *Non-breeders*; and *Rapid Follicle Growth* (RFG)—dry mass of largest ovarian follicle ≥ 0.4 g.

For some analyses, birds in RFG were further categorized as: *Early-RFG*—1 or 2 developing follicles, but no post-ovulatory follicles (POFs); *Prelayers*—1–6 developing follicles, but no POFs; *Layers*—1 or more POFs; *Late-layers*—4 or more POFs but ≤ 5 developing follicles; and *Re-nesters*—several small, i.e., old, but no large POFs, or a large gap in sizes of POFs. Resting females ($n = 3$) and incubating females (determined by ovarian examination and presence of brood patch, $n = 3$) were excluded from analyses. The criterion for estimating initiation of RFG, i.e., dry mass of largest follicle ≥ 0.4 g, was based on dry mass of developing follicles from ovaries of laying females with a complete set of intact developing follicles: the minimum dry mass of the second smallest developing follicle from these ovaries ($n = 31$) was 0.4 g. We also used the \bar{x} dry mass of developing follicles in the ovarian hierarchy (F_1 = largest follicle, F_6 = smallest follicle) to estimate dry mass of individual follicles broken during collection.

DIET ANALYSIS

Food items from each bird were sorted by family (animals) or genus (plants) and dried (65°C) to constant mass. Diet of each bird was determined by calculating percentages of its total food mass accounted for by each taxon. Mean percentages were calculated for each taxon (aggregate percentage, Swanson et al. 1974) found in non-RFG, pre-laying, and laying females.

CARCASS ANALYSIS

Thawed carcasses were plucked and the following structural measurements were made: bill height at the base (0.1 mm), maximum bill width (0.1 mm), culmen (0.1 mm), wing chord (1.0 mm), mid-toe length (0.1 mm), tarsus length (0.1 mm), and keel length (1.0 mm).

Dissections and determinations of lipid and ash were done as detailed in Ankney and Afton (1988). Subsequently, we calculated for each bird:

ASH = total carcass ash

$$\text{PROTEIN} = \text{AFLDM}_{\text{carcass}} + \text{LDM}_{\text{leg}} \\ + \text{LDM}_{\text{breast}} + \text{LDM}_{\text{liver}}$$

$$\text{FAT} = \text{fat}_{\text{carcass}} + \text{fat}_{\text{leg}} + \text{fat}_{\text{breast}} \\ + \text{fat}_{\text{liver}}$$

where AFLDM is ash-free, lean dry mass and LDM is lean dry mass.

REPRODUCTIVE-TISSUE ANALYSIS

Ovaries, oviducts, and developing follicles were analysed as detailed in Ankney and Afton (1988). We were unable to obtain a sample of fresh Gadwall eggs for proximate analysis, but we did determine the mean fresh mass (44.9 g) of 32 eggs. Because there is little variation in proportional egg composition among North American *Anas* spp. (F. Rohwer, pers. comm.), we used the percentage composition of shoveler eggs (calculated from Table 1 of Ankney and Afton, 1988) to estimate the \bar{x} egg yolk lipid (=5.82 g), \bar{x} egg protein (= \bar{x} yolk LDW + \bar{x} dry albumen = 6.85 g) and \bar{x} dry shell (=3.28 g), for Gadwall eggs. These data and those from ovaries and oviducts were used to calculate each female's cumulative production of egg nutrients:

$$\text{Reproductive lipid (R-FAT)} \\ = \text{follicular lipid} + \text{ovarian lipid} \\ + (\bar{x} \text{ egg yolk lipid} \times \text{no. of POFs})$$

$$\text{Reproductive protein (R-PROTEIN)} \\ = \text{follicular LDM} + \text{ovarian LDM} \\ + \text{oviduct dry mass} \\ + (\bar{x} \text{ egg protein} \times \text{no. of POFs})$$

$$\text{Reproductive ash (R-ASH)} = \bar{x} \text{ dry shell} \\ \times \text{no. of POFs.}$$

STATISTICAL ANALYSES

We used two-way analysis of variance to determine effects of reproductive stage, female age, and their interaction, on size of digestive organs.

Structural size can be a significant source of variation in size of a bird's nutrient reserves (Alisauskas and Ankney 1987). To account for this variation, we did principal components analysis of the correlation matrix for the seven structural measurements taken on each bird (PROC PRINCOMP, SAS Institute Inc. 1985). The first principal component (PC_1) described

positive correlation in the seven variables with loadings ranging from 0.26 to 0.54. The corresponding eigenvalue was 2.06 and PC_1 accounted for 30% of the total original variance. We used PC_1 scores for each bird as a measure of body size and separately regressed PROTEIN, FAT, and ASH on PC_1 . FAT was unrelated to body size ($P > 0.9$) but

$$\text{PROTEIN} = 144.54 + 3.742 PC_1, \text{ df} = 110, \\ r^2 = 0.29, P < 0.0001$$

$$\text{ASH} = 26.48 + 1.105 PC_1, \text{ df} = 110, r^2 = \\ 0.18, P < 0.0001.$$

Residuals from these regressions were used to calculate a new value (y_i), corrected for structural size, for PROTEIN and ASH of each female:

$$y_i = y_{\text{obs}} - [a + b(PC_1)] + \bar{Y}_{\text{obs}}$$

These corrected values were used in subsequent analyses. (Note that in Ankney and Afton [1988: 462] the preceding equation contained a typographical error; the last term, as shown here, should have been *mean* of Y observations.)

To determine if, and how much, females used reserves during RFG, i.e., from initiation of RFG to end of egg-laying, we used a general linear model with type III (i.e., orthogonal) sums of squares (PROC GLM, SAS Institute Inc. 1985). The general form of the model was: Nutrient reserve = Age, Date, R-Nutrient, plus all interactions where, for Age, adult = 1 and yearling = 2, and, for Date, 13 May = 1. If interactions were non-significant when the overall model was significant ($P < 0.05$), the interaction terms were removed from the model and the data were reanalyzed. We followed the same protocol for removal of predictor variables. Herein, we report only significant predictors in each model. Further statistical procedures are described in the Results.

RESULTS

We analysed data from 112 female Gadwalls (65 adults, 47 yearlings), of which 33 were non-RFG (20 adults, 13 yearlings), 28 were pre-layers (16 adults, 12 yearlings), and 51 were layers (29 adults, 22 yearlings).

FOOD HABITS AND DIGESTIVE ORGANS

The proportion of females that contained food did not differ (G-test; $P > 0.2$) among non-RFG

TABLE 1. Aggregate percent dry mass of foods consumed by female Gadwalls collected in southern Manitoba during May–June, 1988.

Food type ^b	Reproductive Stage ^a					
	Non-RFG		Pre-laying		Laying	
	Adult (12) ^c	Yearling (8)	Adult (14)	Yearling (7)	Adult (21)	Yearling (18)
Insects	15	19	27	34	14	27
(Diptera)	(9)	(18)	(24)	(31)	(10)	(17)
Crustaceans ^d	15	4	15	5	39	24
Gastropods	tr ^e	tr	7	tr	5	5
Total animal	30	23	49	39	58	56
Seeds	tr	15	7	10	8	2
Vegetation	55	53	37	30	30	35
(<i>Lemna</i>)	(49)	(28)	(23)	(10)	(19)	(18)
Algae	14	9	7	21	4	7
Total plant	70	77	51	61	42	44

^a See Methods for definition of categories.

^b Taxonomic composition of foods (animals to family, plants to genus) is available from the senior author.

^c Sample size.

^d Primarily zooplankton (Cladocera).

^e <0.5%

(61%), pre-layers (75%), and layers (76%) (Table 1). Overall, diets of adults and yearlings were similar (Table 1) and age-combined data show that animal matter, on a dry-mass basis, was 27%, 46%, and 57% of diets of non-RFG, pre-laying, and laying females, respectively. Insects, primarily dipterans, and crustaceans were the dominant animal groups in the diets, and gastropods were remarkably uncommon, even in

laying females. The most important plant foods were duckweed (*Lemna* spp.) and algae (primarily Chlorophyceae).

Other than for liver lipid, relations between reproductive stage and mean size/composition of digestive organs did not differ between yearling and adult females (non-significant interactions; Table 2). Also, size/composition of digestive organs was not significantly related to age,

TABLE 2. The relation between size of digestive organs ($\bar{x} \pm 1$ SE), age, and stage in the reproductive cycle for female Gadwalls collected in southern Manitoba, May–June, 1988.

Variable	Age ^c	Reproductive stage ^a			Effect ^b		
		Non-RFG	Pre-laying	Laying	Stage	Age	S-A
Gizzard mass (g)	Ad	30.0 ± 1.29	28.3 ± 0.99	20.3 ± 0.72	0.0001	NS	NS
	Yr	30.9 ± 1.44	24.7 ± 1.27	20.1 ± 0.93			
Pancreas mass (g)	Ad	1.85 ± 0.122	1.65 ± 0.097	1.76 ± 0.100	NS	0.09	NS
	Yr	1.88 ± 0.125	2.05 ± 0.084	2.05 ± 1.88			
Liver lipid (g)	Ad	0.49 ± 0.048	1.04 ± 0.141	0.87 ± 0.080	0.0001	NS	0.035
	Yr	0.53 ± 0.101	0.67 ± 0.063	0.96 ± 0.090			
Liver LDM (g)	Ad	3.33 ± 0.151	3.87 ± 0.175	4.00 ± 0.156	0.0001	NS	NS
	Yr	3.39 ± 0.246	3.86 ± 0.164	4.49 ± 0.185			
Intestine length (cm)	Ad	199 ± 3.7	201 ± 4.8	201 ± 3.4	NS	NS	NS
	Yr	197 ± 7.8	210 ± 8.2	201 ± 5.3			
Intestine mass (g)	Ad	16.5 ± 0.68	17.1 ± 0.66	16.1 ± 0.58	NS	NS	NS
	Yr	17.6 ± 0.67	15.9 ± 0.67	17.6 ± 0.70			
Ceca length (cm)	Ad	45.5 ± 1.52	44.3 ± 1.78	41.6 ± 1.23	0.08	NS	NS
	Yr	46.1 ± 2.15	41.3 ± 1.37	43.5 ± 1.33			
Ceca mass (g)	Ad	2.39 ± 0.119	2.31 ± 0.110	2.07 ± 0.021	0.007	NS	NS
	Yr	2.41 ± 0.132	2.04 ± 0.089	2.07 ± 0.094			

^a See Methods for definitions.

^b Probability values from 2-Way Anovas; NS = $P > 0.10$.

^c Sample sizes were: Non-RFG = 20 Ad, 13 Yr; Pre-laying = 16 Ad, 12 Yr; Laying = 29 Ad, 22 Yr.

TABLE 3. Results from analyses of covariance, based on type III sums of squares, testing the relation between size of nutrient reserves (g) of female Gadwalls and nutrients committed to reproduction (g; R-NUTRIENT), age (adult = 1, yearling = 2), and date. All interactions were nonsignificant ($n = 45$ adults, 34 yearlings).

Dependent variable	Model			Intercept	Source	Estimate	F	P
	F	P	R ²					
FAT	15.58	0.0001	0.40	106.75	R-FAT	-0.78	29.51	0.0001
					Age	-9.54	4.59	0.0356
					Date	0.00001	0.19	0.6640
PROTEIN	7.12	0.0004	0.23	148.48	R-PROTEIN	-0.16	13.93	0.0004
					Age	0.43	0.06	0.8015
					Date	0.000004	0.16	0.6947
ASH	0.0003	0.99	0					

although mean pancreas mass of yearlings tended to be greater than that of adults ($P < 0.1$).

Gizzard mass and ceca length and mass were highest in non-RFG females and lowest in laying females (Table 2), liver lipid and LDM were lowest in non-RFG females and highest in laying females, and intestine length and mass did not differ by reproductive stage.

NUTRIENT RESERVES AND EGG PRODUCTION

No interaction term was significant in any model relating size of nutrient reserves to reproductive nutrients, age, and date (but see below). Furthermore, date was a nonsignificant predictor in all models (Table 3).

FAT was negatively related to amount of lipid deposited in ova and yearlings had less FAT than did adults (Table 3). Although the interaction between age and R-FAT was nonsignificant ($P = 0.18$), we described more precisely how adults and yearlings used lipids during egg production by doing separate regressions:

Adults: $FAT = 102.4 - 0.94 R-FAT$, $df = 44$, $r^2 = 0.47$, $P < 0.001$

Yearlings: $FAT = 87.0 - 0.62 R-FAT$, $df = 33$, $r^2 = 0.26$, $P < 0.01$.

For every gram of R-FAT produced, FAT declined 0.94 g in adults and 0.62 g in yearlings (Fig. 1).

PROTEIN was negatively related to R-PROTEIN ($P < 0.0001$; Fig. 2), but yearlings and adults did not differ in their mean amounts of PROTEIN (Table 3) or in rates of use (P for interaction > 0.8). Overall, for every g of PROTEIN committed to reproduction, protein reserves decreased by 0.16 g (Table 3).

ASH was unrelated to R-ASH, age, or date (P

> 0.9 ; Table 3), indicating no use of mineral reserves by egg-laying female Gadwalls.

To further investigate importance of lipid and protein reserves to egg-laying females, we determined if, in late-layers, number of developing follicles was related to either FAT or PROTEIN; 22 females met our criteria, ≥ 4 POFs and ≤ 5 developing follicles, for designation as late-layers. We limited our analysis to females with 5 or fewer developing follicles because females with

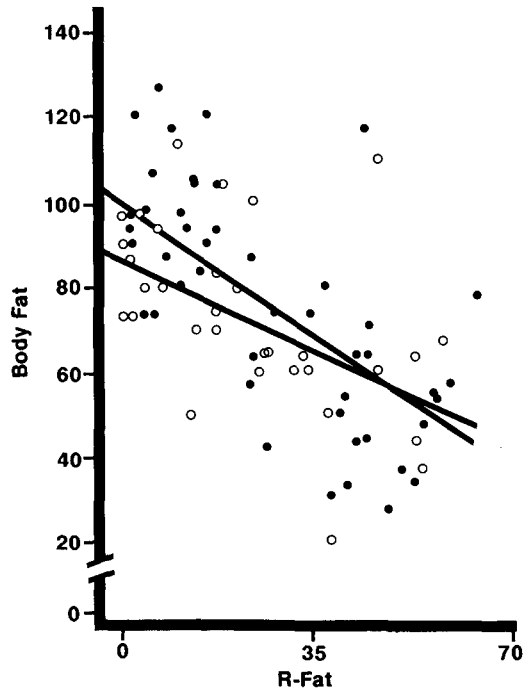


FIGURE 1. Relation between FAT reserves (Y-axis) of female Gadwalls and their corresponding commitment of FAT to egg production. Solid circles represent adults and open circles represent yearlings (see Table 3 and text for equations describing these data).

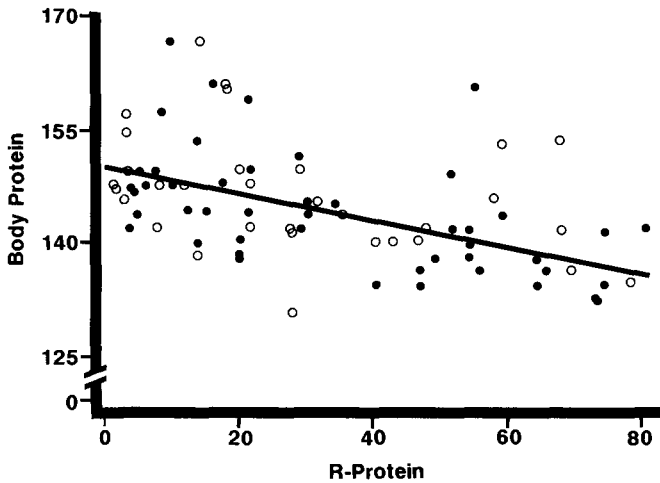


FIGURE 2. Relation between PROTEIN reserves (Y-axis) of female Gadwalls and their corresponding commitment of PROTEIN to reproduction. Solid circles represent adults and open circles represent yearlings (see Table 3 for equation describing these data).

only 1 or 2 POFs (i.e., early in laying) always had 6 developing follicles. Thus, only females with 5 or fewer developing follicles can be recognized as nearing the end of laying. Simple linear regressions of number of developing follicles (y) on nutrient reserve (x) showed that:

$$\text{No. Dev.} = -11.0 + 0.095 \text{ PROTEIN,} \\ r^2 = 0.27, P = 0.013.$$

Thus, late-laying females with more protein reserves had more developing follicles. The relation was nonsignificant for FAT ($r^2 = 0.03$, $P > 0.4$).

NON-BREEDERS VS. EARLY-RFG FEMALES

As shown by the foregoing analyses, female Gadwalls use protein and lipid reserves during egg-production. If these nutrient reserves are important limiting resources during that period, then, predictably, females should reach some "threshold" level of reserves before commencing RFG. Furthermore, because food availability, especially of invertebrates, probably increases with date, and/or because clutch size of waterfowl declines with date (Rohwer, in press), this "threshold" level could decline with date (Alisauskas and Ankney, in press). Fortunately, we collected 14 non-breeders (7 adults, 7 yearlings) that we compared with early-RFG females (9 adults, 9 yearlings) (see Methods for definitions of categories). We chose early-RFG females because, although their ovaries indicated that they

were going to attempt reproduction, their nutrient commitment to eggs was very slight. Thus, the mean size of their nutrient reserves should reflect the mean level at which female Gadwalls initiate RFG. We restricted our sample of non-breeders to those collected on or after the date on which we collected the first female in early-RFG.

We used a general linear model with type III sums of squares (PROC GLM, SAS Institute Inc. 1985) to assess if the two groups of females differed in nutrient reserves:

$$\text{Nutrient Reserve} = \text{Reproductive status (1 = non-breeder, 2 = early-RFG), Age (1 = adult, 2 = yearling), Date (1 = 18 May), plus all interactions,}$$

and used the protocol outlined in Methods for deleting non-significant terms. The model for ASH was non-significant (Table 4), but deleting all non-significant predictors,

$$\text{FAT} = 21.5 + 27.0 \text{ Reproductive status,} \\ r^2 = 0.36, P = 0.0003$$

$$\text{PROTEIN} = 130.7 + 8.1 \text{ Reproductive status,} \\ r^2 = 0.24, P = 0.006.$$

Thus, neither date nor age significantly affected the size of nutrient reserves in this sample of birds (Table 4), but non-breeders had 27 g less FAT and 8.1 g less PROTEIN than did early-RFG females (see Fig. 3).

FAT and PROTEIN were correlated in these

TABLE 4. Results from analyses of covariance based on Type III sums of squares, testing the relation between size of nutrient reserves (g) of female Gadwalls and reproductive status (non-breeder = 1, early-RFG = 2), age (adult = 1, yearling = 2) and date. All interactions were nonsignificant and are not shown ($n = 7$ adult and 7 yearling non-breeders; 9 adult and 9 yearling early-RFG females).

Dependent variable	Model			Intercept	Source	Estimate	F	P
	F	P	R ²					
FAT	7.36	0.0009	0.44	46.26	Reprod. status	+27.31	4.30	0.0002
					Age	-7.79	1.19	0.2451
					Date	-1.02	1.87	0.0723
PROTEIN	3.34	0.033	0.26	135.11	Reprod. status	+8.13	3.01	0.0055
					Age	-0.89	0.32	0.7509
					Date	-0.25	1.06	0.2989
ASH	0.75	0.6334	0.15					

females (Fig. 3). More importantly, most non-breeders were below median FAT and PROTEIN levels (86%, 79% respectively), whereas most (72%) early-RFG females were above both median levels. It is also noteworthy that mean lipid and protein reserves of three re-nesters were 69 g and 155 g, respectively, i.e., they also had above median lipid and protein levels. The two

adult non-breeders with high levels of FAT and PROTEIN (Fig. 3) appear anomalous and point out a limitation in our analysis. Although we are reasonably confident that females categorized as early RFG would have produced eggs, it is also likely that some females categorized as non-breeders would have been in early RFG if collected at a later date. We suspect that the two anomalous females soon would have entered RFG (whereas other non-breeders would have required more time) and therefore, the difference in FAT and PROTEIN between breeding and non-breeding Gadwalls may be even greater than indicated by our analysis.

DISCUSSION

DIET AND DIGESTIVE ORGANS

Animal matter (dry-mass basis) was about 50% of the diets of prelaying and laying females and this was about twice the proportion found in non-RFG females. The diet of breeding female Gadwalls contained only slightly more animal matter than did that of American Wigeon (41% animal matter during egg-laying; Wishart 1983). Thus, of ducks that have been studied, female Gadwalls are the second most herbivorous during breeding (reviewed by Krapu and Reinecke, in press), which is consistent with our prediction that they would be inefficient at foraging for invertebrates.

Low consumption of molluscs (5%) by egg laying Gadwalls was also reported by Swanson et al. (1979). Gadwalls are unusual among North American *Anas* species in this regard (Krapu 1979). However, as crustaceans, especially cladocerans, contain relatively high amounts of calcium (Krapu 1979), this apparently is how Gad-

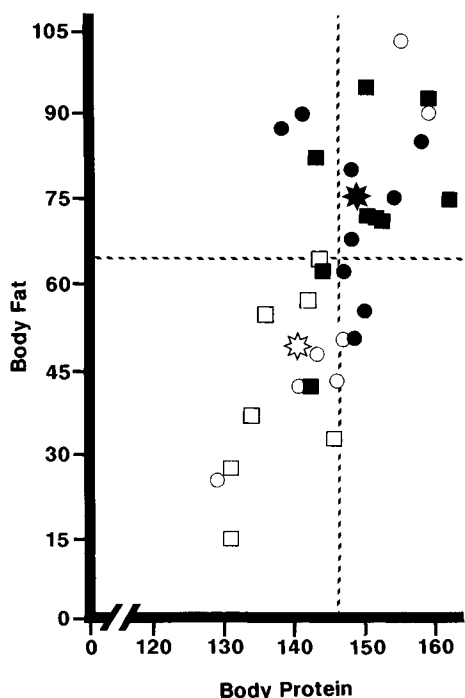


FIGURE 3. The relation between FAT and PROTEIN reserves of non-breeding (open symbols) and early-RFG (closed symbols) female Gadwalls. Circles represent adults and squares represent yearlings. Dashed lines are median values for each reserve and stars represent mean values.

walls obtain sufficient amounts of this mineral for egg shell production (Table 1; and see below).

Overall, diets of adult and yearling females were similar in composition and consequently their digestive organs did not differ either in size or in magnitude of changes relative to stage in the breeding season (Table 2). As reported for other waterfowl (Drobney 1984, Ankney and Afton 1988), lipid and nonlipid components of the liver increased during egg production; such increases are thought to be due to increased food consumption (Drobney 1984), the role of the liver in synthesis of egg lipids during laying (Drobney 1984) and diet change (Ankney and Afton 1988). These explanations all seem plausible and only experimental work can determine which is most important (e.g., Kehoe et al. 1988).

The lighter gizzards of egg laying Gadwalls may reflect atrophy due to decreased use resulting from a diet low in fiber (i.e., decreased plant material) or active catabolism (see Korschgen 1977, Drobney 1984). We favor the former hypothesis because the phenomenon occurs in Northern Shovelers (Ankney and Afton 1988) despite their positive protein balance during egg production. Regardless, freed amino acids would be available for egg protein synthesis. The 10 g decline in wet mass of gizzards (Table 2) equals a loss of about 2.5 g of protein as gizzard muscle averages 25% LDW (Ankney, unpubl. data); thus, gizzard muscle decline could contribute only about one third of the protein in one egg.

Ceca length and mass were about 10% lower in laying females than in non-RFG females, but intestine length and mass were not different between these groups. The reduced size of ceca likely reflects decreased dietary fiber, which, however, also results in smaller intestines in non-breeding waterfowl (Miller 1975, Kehoe et al. 1988). Thus, assuming that food consumption increases during egg laying, these data support the conclusions of Fenna and Boag (1974) and Ankney and Scott (1988) that increased food consumption and/or nutrient demand can be more important than diet quality in affecting intestine length.

USE OF RESERVES

Mineral. Female Gadwalls do not use mineral reserves for eggshell production, apparently deriving the necessary calcium from zooplankton and the relatively low proportion of snails in their diets. Use of mineral reserves appears un-

usual among North American waterfowl, except for Arctic geese (Ankney and Alisauskas 1991). Only female Lesser Scaup (*Aythya affinis*; Afton and Ankney 1991) and Ruddy Ducks (*Oxyura jamaicensis*; Alisauskas and Ankney, unpubl. data), of 10 duck species for which data are available, show a significant, albeit slight, decline in these reserves during egg laying. Molluscs comprise a small ($\leq 5\%$) proportion of the diets of Lesser Scaup (Afton and Hier, unpubl. ms.) but, unlike Gadwalls, they consume relatively little zooplankton.

Lipid. On average, 78% of the lipids that female Gadwalls deposited in eggs came from reserves (assuming that the conversion is 100% efficient). Of the five *Anas* species for which such analyses have been done, only Mallards (*A. platyrhynchos*) show a greater reliance on lipid reserves (slope of regression = -1.04 ; see Ankney and Alisauskas 1991).

Yearling females, on average, began RFG with smaller lipid reserves than did adults and separate regression analyses suggested that yearlings relied less on their reserves for egg production. Use of reserves was also more variable among yearlings than among adults (lower r^2 for yearlings). Perhaps yearling females have greater difficulty accumulating lipid reserves than do adults. If so, it would be consistent with their later nest initiation dates (Lokemoen et al. 1990) and lower clutch sizes (Blohm 1979). However, when we controlled for effects of age and lipid committed to reproduction, there was no relation between date and size of lipid reserves and no interaction between age and date (Table 3). This suggests that the seasonal decline in clutch size of Gadwalls (Lokemoen et al. 1990) does not result from females that initiate laying late having smaller lipid reserves (see beyond).

Protein. Our prediction that Gadwalls would use protein reserves for egg production was supported. The maximum proportion of egg proteins originating from protein reserves, 16%, is well below that reported for American Wigeon (44%, Alisauskas and Ankney in press) and Arctic-nesting geese (e.g., Ankney and MacInnes 1978, Raveling 1979, Ankney 1984). However, if this contribution translated into a concomitant 16% increase in clutch size (or a 16% increase in time to forage for other potentially limiting nutrients), then it is clearly important to female Gadwalls; this is strongly suggested by the positive correlation ($+0.52$) between size of protein

reserves and number of developing follicles in late layers (see below). Perhaps, without use of protein reserves, female Gadwalls could not maintain their laying rate of one egg per day. Remarkably, however, yearling and adult females did not differ either in amount or rate of use of protein reserves.

Nutrient-reserve threshold for clutch initiation. Alisauskas and Ankney (in press) argued that use of nutrient reserves for egg production implies that some minimum level of reserves must be stored before RFG is initiated. We found highly significant differences in lipid and protein reserves between non-breeders and early-RFG females (Table 4, Fig. 3). We conclude that, on average, female Gadwalls initiate RFG when they have attained a minimum, or threshold, level of these reserves. Alisauskas et al. (1990) found that non-breeding female Ring-necked Ducks (*Aythya collaris*) had significantly smaller protein reserves than did females that had initiated RFG. These two groups did not differ in size of lipid reserves, but, as argued by Alisauskas et al., such negative results do not necessarily mean that a lipid threshold does not exist; possibly, non-breeding females were able to surpass a lipid threshold before reaching a sufficient level of protein reserves. Regardless, the strong positive relation between lipid and protein reserves of non-breeders and early-RFG female Gadwalls suggests that they stored both reserves simultaneously.

Alisauskas and Ankney (in press) also predicted, based on Reynolds' (1972) model relating body mass, laying date, and clutch size of Mute Swans (*Cygnus olor*), that nutrient-reserve thresholds would decline seasonally. We found, however, no significant interaction between the effects of reproductive stage and date on either lipid or protein reserves ($P = 0.77$ and 0.34 , respectively), and no significant effect of date on reserves (although date had a nearly significant effect on lipid reserves, Table 4). Lokemoen et al. (1990) reported that 90% of Gadwall nests were initiated by about 21 June, in central North Dakota. Because our study area was about 400 km north of there and we completed our collection on 17 June (including one non-breeder), we probably missed collecting any of the last 20% or so of females that initiated nesting. Consequently, any relation between date and size of reserves in chronologically late-nesters was not fully evaluated.

Nutrient-reserve threshold for clutch termination. The importance of protein reserves to female Gadwalls is further emphasized by the positive correlation between those reserves and the number of developing follicles in late layers. In Northern Shovelers, there is a similar positive correlation between lipid reserves and number of developing follicles (Ankney and Afton 1988). This suggests a major difference in nutrient that limits egg production in these species and is consistent with their general food habits. Shovelers have no difficulty obtaining exogenous animal protein for eggs and store protein during laying (Ankney and Afton 1988). Gadwalls, however, are herbivores and apparently are even more constrained by their ability to supply protein to eggs than by ability to supply lipids.

CONCLUSIONS

Although female Gadwalls appear to be protein limited during egg laying, this, paradoxically, does not support the protein limitation hypothesis as a general explanation of clutch size determination in temperate-nesting ducks. Rather, we conclude that Gadwalls, like American Wigeon, are exceptions that support the general rule that temperate-nesting ducks are lipid limited and not protein limited during egg production. Two lines of evidence lead to this conclusion. First, as predicted by Ankney and Afton (1988), females of a species that normally encountered protein limitation should store protein reserves and use them to overcome such limitation (as noted for Arctic geese). We chose to study Gadwalls in this regard because, being herbivores for most of their annual cycle, they were more likely to be inefficient foragers for macro-invertebrates than are other duck species. Clearly, Gadwalls fulfilled both parts of this prediction as they consumed relatively little animal matter during laying and they used protein reserves. Second, according to the protein limitation hypothesis, females less efficient at procuring animal protein should use lipid reserves at a greater rate during egg production to meet maintenance costs associated with increased foraging. Gadwalls, however, used lipids at a lower rate than did Mallards and Canvasbacks (*Aythya valisineria*) and at only a slightly higher rate than did Northern Shovelers (see reviews by Ankney and Alisauskas 1991; Alisauskas and Ankney, in press). Further, American Wigeon, although clearly showing evidence of a dietary protein deficit during egg production,

showed no net decline in lipid reserves (Alisauskas and Ankney, in press). Thus, Gadwalls and American Wigeon appear protein limited during egg production, but neither use lipid reserves in the manner predicted by the protein limitation hypothesis. We believe that storage and use of a nutrient reserve reflects the normal inability of females of that species to acquire that nutrient exogenously. If so, nearly all temperate-nesting waterfowl species are unable to consume sufficient food appropriate for egg-lipid synthesis; few species are similarly constrained by inability to acquire protein.

Rohwer (1986; in press), based on a study of Blue-winged Teal (*Anas discors*), proposed that female waterfowl store lipids for energy during migration and as a hedge against poor weather upon arrival to breeding areas. This "migration-uncertainty hypothesis" concludes that because waterfowl generally breed shortly after arrival, females simply dispose of "unnecessary" lipid reserves into eggs. Our data, plus those for Canvasbacks (Barzen and Serie 1990), Ring-necked Ducks (Alisauskas et al. 1990) and lesser Scaup (Afton and Ankney 1991) show that this hypothesis, at the least, lacks generality and is likely specious. Canvasbacks store considerable lipid during prelaying, Ring-necked Ducks store lipid after arrival to breeding areas, Lesser Scaup maintain, or possibly store, lipid reserves after arrival, and Gadwalls with low lipid reserves do not initiate RFG.

Female Gadwalls at or near the end of laying show considerable variation in size of reserves (Figs. 1, 2), as do females of other duck species studied similarly (e.g., Rohwer 1986, Ankney and Afton 1988). This leads to the obvious question of, if reserves limit clutch size, "why do some females stop laying with considerably more reserves than carried by other females?" We hypothesize that the answer is related to genetic polymorphisms among females relative to their tactics for completing incubation.

Nur (1987) hypothesized that much intraspecific variation in clutch size of birds is due to genetic polymorphisms maintained by year-to-year fluctuations in environment and thus in selection pressures. That is, there is no "best" overall clutch size, but there is a best clutch size for a given year. This hypothesis does not explain variation in clutch size of waterfowl because (1) available evidence shows that, intraspecifically, large clutches produce more offspring than do

small ones (Rohwer 1985, Rockwell et al. 1987), and (2) limited evidence suggests very low heritability of clutch size (Findlay and Cooke 1987). However, Nur's arguments may apply to waterfowl if variation in size of reserves among females beginning incubation is genetically based and influences successful completion of incubation.

Use of reserves during incubation is prevalent among waterfowl (see review by Afton and Paulus, in press); all species use lipid reserves, but use of protein reserves is common. For some species, e.g., Common Eiders (Korschgen 1977) and Arctic-nesting geese (e.g., Ankney and MacInnes 1978, Raveling 1979), nutrient reserves are critically important to successful incubation. Even White-winged Scoters (*Melanitta fusca*), which do not use reserves for egg production, rely heavily on them during incubation (Dobush 1986). Recent evidence (Glutney 1989) suggests that reserves may also be critical to successful incubation by Mallards and Northern Shovelers because females that lost their nests late in incubation had significantly lighter body mass than did those that were successful. Thus, nutrient-reserve thresholds exist for initiation of clutches, termination of clutches, and for clutch abandonment (see also Ankney and MacInnes 1978).

If, as we think likely, there is annual variation in environmental factors that determine importance of reserves during incubation, e.g., temperature, food availability, predation pressure, then there will be variation in what constitutes the optimal trade off between allocation of reserves to eggs versus reserving them for use during incubation. Thus, in some years, females that invest heavily in eggs relative to size of their reserves (a "risky" strategy) will be favored; in other years, a "cautious" strategy of investing relatively less reserves will be favored. Consequently, in any year, there will be among-female variation in size of reserves at the start of incubation. One approach to evaluating this hypothesis would be to determine among-female variation in size of reserves at the start of incubation and to evaluate nest success and incubation behavior relative to body condition over several breeding seasons.

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