

BIOENERGETICS OF BREEDING NORTHERN SHOVELERS: DIET, NUTRIENT RESERVES, CLUTCH SIZE, AND INCUBATION¹

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Abstract. We analyzed food habits, digestive organs, and nutrient reserves (lipid, protein, and mineral) of male and female Northern Shovelers (*Anas clypeata*) nesting in southern Manitoba. We studied shovelers because, on an annual basis, they consume more animal matter than do other *Anas* spp. Thus, they are ideal subjects for testing the hypothesis that the inability of female ducks to obtain animal protein during egg laying limits clutch size. Predictably, we found that, during prelaying and laying, males and females primarily ate aquatic invertebrates. Despite this, the intestine lengths of breeding shovelers, particularly of females, are longer than those of many other waterfowl, which may be a response to an energy-deficient diet. Nutrient reserves of males changed little during prelaying and laying. Lipid reserves of females, on average, declined by 0.72 g for every 1 g of lipid that they deposited in eggs. Furthermore, in females that had laid \geq five eggs, there was a positive correlation (+0.60) between number of developing ovarian follicles and size of lipid reserves. Remarkably, however, the protein reserves of females increased by 0.1 g for every 1 g of protein committed to reproductive tissue. Mineral reserves were unrelated to eggshell production. The decline in lipid and protein reserves of incubating females could account for 26% of their energy requirements during that period.

The protein : lipid ratio in shoveler diets was about 14:1, whereas that in the reproductive tissue (eggs and oviduct) was near unity. Thus, we argue that lipid reserves, not protein acquisition, limit clutch size of shovelers and also that the importance of protein to temperate-nesting waterfowl has been overemphasized. We conclude that most intraspecific variation in clutch size of waterfowl is proximately caused and, thus, that few females lay the optimum clutch size, i.e., the average clutch size is not directly a product of natural selection, and probably reflects nutrients available to the average female.

Key words: Northern Shoveler; diet; digestive organs; nutrient reserves; clutch-size limitation; incubation.

INTRODUCTION

Recently, much research has been done to evaluate the relative importance of exogenous and endogenous nutrients to breeding waterfowl. These studies have revealed two major patterns by which females meet nutrient costs of reproduction: (1) Arctic- and temperate-nesting geese, and eiders, utilize large amounts of nutrient reserves (herein meaning lipid, protein, and mineral) during egg production and further rely heavily on lipid and protein reserves during incubation (Hanson 1962, Korschgen 1977, Ankney and MacInnes 1978, Raveling 1979, McLandress and Raveling 1981, Ankney 1984,

Mainguy and Thomas 1985), and (2) temperate-nesting ducks utilize lipid reserves during egg laying, obtain all or nearly all of their protein and mineral requirements exogenously, and then utilize most of any remaining lipid reserves during incubation (Drobney 1980, 1982; Krapu 1981; Reinecke et al. 1982; Tome 1984; Noyes and Jarvis 1985; Hohman 1986). Drobney (1980) and Krapu (1981) argued that female Wood Ducks (*Aix sponsa*) and Mallards (*Anas platyrhynchos*), respectively, were able to meet the protein requirement of egg production by feeding heavily on aquatic invertebrates. They further hypothesized that these normally granivorous/herbivorous species forage inefficiently for invertebrates and thus require lipid reserves (for egg production and/or maintenance) to ensure that they have sufficient time to forage for protein-rich invertebrates (we hereafter call this the "protein limitation hypothesis"). Drobney and

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Frederickson (1985) proposed that protein limitation may influence clutch size of prairie-nesting ducks, generally.

We tested the protein limitation hypothesis by determining the importance of endogenous nutrients to breeding Northern Shovelers (*Anas clypeata*, hereafter called shovelers). We chose shovelers because, on an annual basis, they consume far more animal matter than do other North American species of *Anas* (see Palmer 1976:514–515). Thus, they could be considered the invertebrate specialist of the genus, and therefore, based on the hypothesis, we predicted that females would require relatively little lipid reserves during egg laying. Breeding shovelers are the most territorial of prairie-nesting *Anas*, presumably to secure high-quality feeding sites for reproduction (McKinney 1973, Seymour 1974, Nudds and Ankney 1982). We therefore predicted that (1) prelaying females would have relatively small lipid reserves, (2) females would rely heavily on exogenous nutrients for egg production, and (3) males, because they are responsible for territory defense and show a marked decrease in time spent feeding during the egg-laying period (Afton 1979), would use endogenous lipids to meet maintenance costs then. This paper reports results of that research as well as previously unpublished data (see Afton 1979) concerning changes in body weight and carcass composition of incubating female shovelers.

METHODS

All data are from shovelers that were breeding in southern Manitoba. Data from incubating females were gathered in 1974 (body weights of nest-trapped and released females) and 1975 (females trapped and killed for carcass analysis); all data were from females whose stage of incubation was estimated, to the nearest day, by candling their eggs. Prelaying and laying birds were shot during 3 to 19 May 1985. This period corresponded to the peak of shoveler nest initiation and preceded the renesting period. Whenever possible, we shot the male of a pair immediately after we shot the female. Birds were weighed (± 5 g) immediately after they were trapped or collected. Females, collected in 1985, were categorized as *prelayers* (no postovulatory follicles) or as *layers* (one or more postovulatory follicles); males were categorized according to the category of their mate. For some analyses, we further subdivided prelaying females as pre-Rapid Follicle

Growth (pre-RFG; largest ovarian follicle with a dry weight < 0.1 g) or as Rapid Follicle Growth (largest follicle > 0.1 g).

FOOD-HABITS ANALYSIS

In 1985, 70% ethanol was injected into the esophagus of each bird after it was collected. Later that day, esophageal contents were removed from specimens and stored in 70% ethanol. Food items from each bird were sorted by family (animals) or genus (plants) and dried (65°C) to constant weight. Diet composition of each bird was determined by calculating percentages of its total food weight that were accounted for by each taxa. We then calculated mean percentages of each taxa (aggregate percentage, Swanson et al. 1974) found in males and females during prelaying and laying periods.

CARCASS ANALYSIS

Birds collected in 1975 were analyzed differently than those collected in 1985 and procedures were as follows:

1975 shovelers (incubation). Birds were reweighed in the laboratory after contents of the digestive tract were removed and the following structural measurements were made: body length (1.0 mm), wing length (1.0 mm), keel length (0.1 mm), length of middle tail feather (1.0 mm), culmen (0.1 mm), bill length (from rictus to nail edge) (0.1 mm), and maximum bill width (0.1 mm). All feathers were plucked from each bird and the liver, heart, gizzard, and right breast muscles were removed, cleaned of adhering fat, and weighed (0.1 g; gizzard was weighed minus contents). The entire carcass, including the above parts, was homogenized and a sample (ca. 3 g) was analyzed (Warf Institute, Madison, Wisconsin) for lipid proportion. We calculated total lipid content (FAT) for each duck by multiplying weight of the total homogenate by proportion of lipid in its sample.

1985 shovelers (prelaying and laying). On the day of collection, the ovary and oviduct were removed from each female and stored in 10% formalin; the carcass was frozen in double plastic bags. Thawed carcasses were plucked, and the following structural measurements were taken: culmen (0.1 mm), bill height at the base (0.1 mm), bill width at the nares (0.1 mm), keel length (1.0 mm), and plucked-wing length (1.0 cm). The right breast and leg muscles (defined in Ankney and MacInnes 1978), gizzard, liver, intestine,

TABLE 1. Composition (g) and energy content of Northern Shoveler eggs ($n = 32$).

Variable	\bar{x} (1 SE)
Egg weight	37.8 (0.61)
Yolk: dry	7.92 (0.15)
lipid	4.90 (0.12)
nonlipid dry	3.02 (0.06)
Albumen: dry	2.75 (0.09)
Shell: dry	2.76 (0.04)
Energy content (Kcal)	79.2 (1.1)

ceca, heart, and pancreas were removed; lengths of ceca (combined) and intestine were measured (1 cm) and the other parts were weighed wet (0.01 g). All organs, except the liver and breast and leg muscles, were combined with the rest of the carcass and this was ground twice in a Hobart meat grinder. A 100-g sample of this homogenate, the liver, and the breast and leg muscles from the right side were dried separately to constant weight at 90°C (Kerr et al. 1982). The dried carcass homogenate, liver, and breast and leg muscles were homogenized separately in an electric coffee-grinder. Proximate analysis of carcass homogenate, liver, and breast and leg muscle was done as detailed by Alisauskas and Ankney (1985). For each bird this involved: (a) removing lipids from a subsample (ca. 10 g) of each constituent using petroleum ether as a solvent (Dobush et al. 1985) in a modified Soxhlet apparatus, (b) multiplying dry weight of each constituent by proportion of lipid that it contained (derived from step a) to determine its total lipid weight, and (c) subtracting total lipid weight from dry weight of each constituent to determine its lean dry weight (LDW). The lean dry samples of carcass homogenate (ca. 6 to 9 g) were ashed in a muffle furnace at 550°C for 6 hr. The proportion of ash in each sample was used to calculate total ash (ASH) in the carcass of each bird. ASH was subtracted from LDW of each carcass to obtain ash-free lean dry weight (AFLDW), an index of protein. Thus, for each bird:

$$\text{PROTEIN} = \text{AFLDW}_{\text{carcass}} + \text{LDW}_{\text{leg}} + \text{LDW}_{\text{breast}} + \text{LDW}_{\text{liver}}$$

and

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

ASH, PROTEIN, and FAT are herein referred to as nutrient reserves as defined by Alisauskas

and Ankney (1985): "... the measure of a fraction (fat, protein, or mineral) of the whole bird (excluding feathers, ovary, oviduct, and testes) that may respond to nutritional demands of egg synthesis, or other changes in energy balance."

REPRODUCTIVE-TISSUE ANALYSIS

Testes were dried to constant weight, and discarded. For each female, we determined: (a) oviduct dry weight, (b) lipid content and LDW of each yolky ovarian follicle, (c) lipid content and LDW of the remainder of the ovary, and (d) number of eggs that had been laid by counting postovulatory follicles (POF) in the ovary. We collected 32 unincubated eggs from 16 shoveler nests and determined yolk lipid, yolk protein, dry albumen, and dry shell weight, following exactly the procedure in Alisauskas and Ankney (1985). We then calculated \bar{x} egg yolk lipid, \bar{x} egg protein (= \bar{x} yolk LDW + \bar{x} dry albumen) and \bar{x} dry shell, for shoveler eggs (see Table 1). These data, along with those for ovaries and oviducts, were used to calculate reproductive nutrients for each female:

Reproductive lipid (R-FAT)

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

Reproductive protein (R-PROTEIN)

$$= \text{follicular LDW} + \text{ovarian LDW} + \text{oviduct dry weight} + (\bar{x} \text{ egg protein} \times \text{no. of POFs})$$

Reproductive ash (R-ASH)

$$= \bar{x} \text{ dry shell} \times \text{no. of POFs}$$

STATISTICAL ANALYSES

Mean sizes of organs and of reserves, of prelaying males and females, were compared to those of laying males and females, using *t*-tests. To more precisely determine if, and how much, males and females utilized reserves during the egg-laying period, we used a regression model as outlined by Alisauskas and Ankney (1985). The general form of the equation was:

$$\text{Nutrient reserve} = a + b(\text{reproductive nutrient}).$$

For males, we used size of his mate's reproductive nutrients, i.e., how much R-PROTEIN, R-FAT, R-ASH she had committed to reproduction, in the equation; our rationale was that if a male used reserves during the egg-laying period, then this use should be a function of the female's stage in the cycle.

TABLE 2. Aggregate percent dry weight of foods consumed by breeding Northern Shovelers collected in southern Manitoba during May 1985.

Food item ^a	Females		Males	
	Pre-laying (14) ^b	Laying (23)	Pre-laying (9)	Laying (10)
Insects	14	10	3	19
Crustaceans ^c	13	21	24	14
Gastropods	59	55	41	32
Unidentified animal	tr ^d	4	11	tr
Nonsnail shell	4	4	11	2
Total animal	91	93	90	67
Seeds	6	2	6	11
Vegetation	3	5	4	23
Total plant	9	7	10	34

^a The taxonomic composition of these foods (animals to family, plants to genus) is available from the senior author.

^b Sample size.

^c Primarily zooplankton.

^d Less than 0.5%.

Structural size can be an important source of variation in the size of a bird's nutrient reserves, particularly of protein (e.g., Alisauskas and Ankney 1987). Thus, before analyzing use of reserves by breeding shovelers, we attempted to account for variation in reserves that was due to variation in structural size. First, we did a Principal Components Analysis (PCA; PROC PRINCOMP, SAS 1982) of the correlation matrix for the five morphometric variables for males and females combined. (Three females and one male could not be included in the PCA because, due to damage, they were each missing a structural measurement; data from them, uncorrected for body size, were used in subsequent analyses.) The first principal component (PC₁) described positive

correlation in the five variables, with loadings ranging from 0.33 to 0.51. We interpreted this covariation as variation in body size. The corresponding eigenvalue was 2.41, and PC₁ accounted for 48% of the total original variation. We used the PC₁ score for each bird as a measure of its body size and regressed PROTEIN, FAT, and ASH on PC₁, for males and females separately. The significant regressions were:

Females—

$$\text{PROTEIN} = 103.95 + 3.91\text{PC}_1,$$

$$\text{df} = 54, r^2 = 0.35, P < 0.001$$

$$\text{ASH} = 20.36 + 0.93\text{PC}_1,$$

$$\text{df} = 54, r^2 = 0.18, P < 0.01$$

Males—

$$\text{PROTEIN} = 95.37 + 3.20\text{PC}_1,$$

$$\text{df} = 35, r^2 = 0.21, P < 0.01$$

$$\text{ASH} = 18.34 + 0.84\text{PC}_1,$$

$$\text{df} = 35, r^2 = 0.13, P < 0.05.$$

FAT was not related to body size in either sex. Residuals from these regressions were used to calculate a new value (y_i), corrected for body size, for PROTEIN and for ASH of males and females:

$$y_i = y_{obs} - [a + b(\text{PC}_1)] + y_{obs}.$$

These corrected values were used in subsequent regression analyses. We used the same procedure to attempt to account for variation due to body size in the data for incubating females, but found that no variable (body weight, gizzard weight, heart weight, breast muscle, and FAT) was significantly related to PC₁ for these birds.

TABLE 3. Changes in digestive organs of breeding Northern Shovelers collected in southern Manitoba during May 1985.^a

Variable	Females			Males ^b		
	Pre-laying (22) ^c	P ^d	Laying (37)	Pre-laying (11)	P	Laying (27)
Gizzard weight ^e	10.2 ± 0.3	**	9.0 ± 0.2	9.0 ± 0.43	ns	8.9 ± 0.32
Pancreas weight	2.08 ± 0.24	ns	2.46 ± 0.18	1.83 ± 0.22	ns	1.88 ± 0.12
Liver weight	17.3 ± 0.5	***	19.7 ± 0.4	14.3 ± 0.9	ns	12.8 ± 0.4
Liver DW	4.77 ± 0.13	***	5.37 ± 0.11	3.90 ± 0.23	ns	3.49 ± 0.10
Liver lipid	0.62 ± 0.05	*	0.75 ± 0.04	0.33 ± 0.04	ns	0.32 ± 0.02
Liver LDW	4.15 ± 0.14	*	4.62 ± 0.11	3.57 ± 0.20	ns	3.17 ± 0.10
Intestine length ^f	292 ± 7	ns	294 ± 5	276 ± 6	ns	271 ± 7
Intestine weight	23.9 ± 1.1	ns	22.4 ± 0.7	20.1 ± 1.4	ns	17.5 ± 0.6
Ceca length	20.3 ± 0.7	ns	21.1 ± 0.5	19.8 ± 0.9	ns	20.0 ± 0.6
Ceca weight	1.40 ± 0.11	*	1.09 ± 0.05	1.17 ± 0.16	ns	1.05 ± 0.08

^a Weights are in g, lengths are in cm; values expressed as $\bar{x} \pm 1$ SE.

^b Males categorized on the basis of reproductive stage of their mate.

^c Sample size.

^d P is the probability that adjacent means differ by chance; * = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$, ns = $P > 0.05$.

^e Wet weights unless otherwise specified.

^f Combined length of large and small intestine.

TABLE 4. Body composition and reproductive characteristics of breeding Northern Shovelers collected in southern Manitoba during May 1985.

Variable	Females			Males ^a		
	Prelying (22) ^b	P ^c	Laying (37)	Prelying (11)	P	Laying (27)
Body composition^d						
Body weight (fresh)	630 ± 8	*	653 ± 7	585 ± 11	ns	584 ± 8
Body weight (corrected) ^e	536 ± 7	*	516 ± 6	511 ± 10	ns	509 ± 7
FAT	63.3 ± 4.5	***	41.9 ± 2.0	53.5 ± 7.2	ns	43.6 ± 3.8
ASH	18.5 ± 0.5	*	19.9 ± 0.3	18.5 ± 0.5	*	19.9 ± 0.4
PROTEIN	96.9 ± 1.5	*	100.9 ± 1.1	96.2 ± 1.8	*	100.7 ± 1.1
Breast LDW	15.1 ± 0.2	ns	15.6 ± 0.2	15.3 ± 0.3	ns	15.5 ± 0.2
Leg LDW	3.81 ± 0.06	**	4.10 ± 0.08	3.65 ± 0.10	**	4.03 ± 0.09
Heart weight (wet)	5.26 ± 0.09	ns	5.15 ± 0.08	5.83 ± 0.22	ns	5.79 ± 0.09
Reproductive characteristics^f						
Testes DW	—	—	—	0.53 ± 0.05	ns	0.57 ± 0.03
Developing follicles	2.6 (0-5)	—	4.4 (0-5)	—	—	—
Ovulated follicles	0	—	4.0 (1-10)	—	—	—
Oviduct DW	2.00 (0.3-4.7)	—	3.50 (2.3-4.9)	—	—	—
R-FAT	3.05 (0.2-9.52)	—	25.2 (10.2-52.2)	—	—	—
R-ASH	0	—	11.1 (2.8-27.6)	—	—	—
R-Protein	4.16 (0.48-11.16)	—	32.8 (13.5-69.4)	—	—	—

^{a,b,c} As in Table 3.

^d Weights in grams; values expressed as $\bar{x} \pm 1$ SE.

^e Corrected body weight is the weight of the bird minus feathers, ingesta, and reproductive tissue.

^f Testes data are combined dry weights ($\bar{x} \pm 1$ SE); data for females are \bar{x} (range).

RESULTS

PRELAYING AND LAYING

We collected 60 female and 38 male shovelers, none of which was reneesting. The reproductive organs of one female were undeveloped, so data from her were excluded from analysis.

Food habits and digestive organs. Most females (63%) and half the males contained food in their esophagi (Table 2). The proportion of females that contained food did not differ between prelaying and laying (14/22 vs. 23/37, $P > 0.5$), whereas that of males did (9/11 vs. 10/27, $P < 0.05$).

Diets of prelaying males and females contained about 90% animal matter, but females had consumed proportionally more snails than had males (Table 2). This difference was even more pronounced in laying birds, and also noteworthy was the increased consumption of plant material (34%) by laying males.

There were no significant changes in sizes of male digestive organs between prelaying and laying (Table 3). In females, gizzard and ceca weights declined, but liver weight increased, primarily due to an increase in water and in nonlipid material. Digestive organs of females were, on average, as large or larger than those of males; the

average intestine of females was about 7% longer than that of males.

Size of nutrient reserves and reproductive nutrients. Body weight of males did not change from prelaying to laying (Table 4); an average 10-g decline in FAT (nonsignificant) was balanced by a 4-g increase in PROTEIN ($P < 0.05$; note that a 4-g change in PROTEIN equals a 16-g change in body weight as muscle is ca. 75% water). ASH of males increased ($P < 0.05$) from prelaying to laying (Table 4).

The increase in fresh body weight of laying females ($P < 0.05$; Table 4) was due to increased size of their reproductive organs. The corrected body weight of laying females was lower ($P < 0.05$) than that of prelayers and most of this loss was FAT. PROTEIN and ASH of laying females was higher ($P < 0.05$) than that of prelaying females.

Leg muscle weight of males and females increased from prelaying to laying ($P < 0.01$), but weights of breast muscle and heart did not change ($P > 0.05$; Table 4).

No laying female had more than five rapidly developing follicles (Table 4) indicating that shovelers take 6 days to produce an egg, given that they lay one egg/day (Afton 1977). The average laying female in our sample had laid four

TABLE 5. Equations, from least squares regression, relating size of female nutrient reserves vs. her nutrient commitment to reproduction, and size of male nutrient reserves vs. the nutrient commitment to reproduction by his mate.^a

Y	X	n	Intercept	Slope	r ²	P ^b
Females						
FAT	R-FAT	55	63.0 (3.7) ^c	-0.72 (0.16)	0.27	0.001
ASH ^d	R-ASH	55	18.95 (0.36)	+0.07 (0.03)	0.06	0.064
PROTEIN ^d	R-PROTEIN	55	97.8 (1.1)	+0.10 (0.04)	0.11	0.014
Males						
FAT	R-FAT	37	54.9 (6.3)	-0.37 (0.26)	0.06	0.16
ASH ^d	R-ASH	37	19.15 (0.46)	+0.04 (0.04)	0.03	0.34
PROTEIN ^d	R-PROTEIN	37	99.2 (1.6)	+0.01 (0.05)	0	0.84

^a These analyses do not include four pre-RFG females and one male that was mated to one of those females.

^b Probability that $r = 0$.

^c 1 SE.

^d Corrected for variation due to body size—see Methods.

eggs and had invested 25.2 g of FAT, 11.1 g of ASH, and 32.8 g of PROTEIN in reproduction. These values are 40 to 50% of the investment required for a 10-egg clutch (based on data in Table 1), the average clutch size of shovelers (Bellrose 1976).

Use of reserves during egg production. Nutrient reserves of male shovelers did not change relative to the nutrient commitment to reproduction by their females (Table 5), i.e., although PROTEIN and ASH were higher in laying males than in prelayers (Table 4), these increases were independent of nutrient commitment by the paired female.

FAT of females was negatively related to amount of lipid that they had deposited in ova ($P < 0.001$; Fig. 1). For every gram of R-FAT produced, FAT declined by 0.72 g (Table 5). PROTEIN, however, was positively related to R-PROTEIN ($P < 0.05$; Fig. 1) and for every gram of protein committed to reproduction, protein reserves increased by 0.1 g (Table 5). Females showed no net loss of body minerals, over the course of laying, to produce eggshells ($P > 0.05$; Fig. 1), and the trend was toward an increase in ASH with increased R-ASH ($P < 0.1$; Table 5).

To further investigate the importance of lipid reserves to egg-laying females, we determined if, in females collected late in the laying cycle (hereafter called late-layers), there was a relation between number of developing follicles and FAT; we defined late-layers as those females which had five or more POFs. Such analysis is appropriate only for late-layers because (1) average clutch size of shovelers is 10 eggs, and (2) shovelers

never have more than five developing follicles. Thus, early-layers showed no variation in number of developing follicles, i.e., all had five. We found a positive correlation (+0.60, $P < 0.05$) between number of developing follicles and amount of FAT in late-laying females (Fig. 2). There is an important limitation to this analysis, i.e., actual clutch size of the shovelers, depicted in Figure 2, can only be known for certain for those birds with zero developing follicles. For birds with two, three, or four developing follicles, the sum of the number developing plus number of POFs equals their maximum potential clutch size because it is impossible to know if some (or all) developing follicles would have undergone atresia; the female with six POFs and zero developing follicles, in Figure 2, had four large atretics, but the other female with zero developing follicles had none (both of these females had an oviducal egg). Alternatively, it is impossible to determine the ultimate clutch of those females with five developing follicles—their clutch sizes could be less than (atresia), equal to, or greater than (more follicles develop) the sum of number of POFs plus number of developing follicles. Regardless, in those females with less than five, the number of developing follicles was clearly related to FAT.

It is remarkable that the absolute size of PROTEIN was the same in males and females (Table 4), given that male shovelers are structurally larger, on average, than females. So, we did an analysis of covariance (ANCOVA, Proc GLM, SAS 1982), using PC₁ as a measure of body size (see Methods), and found that females had relatively more PROTEIN than did males ($P < 0.001$; Ta-

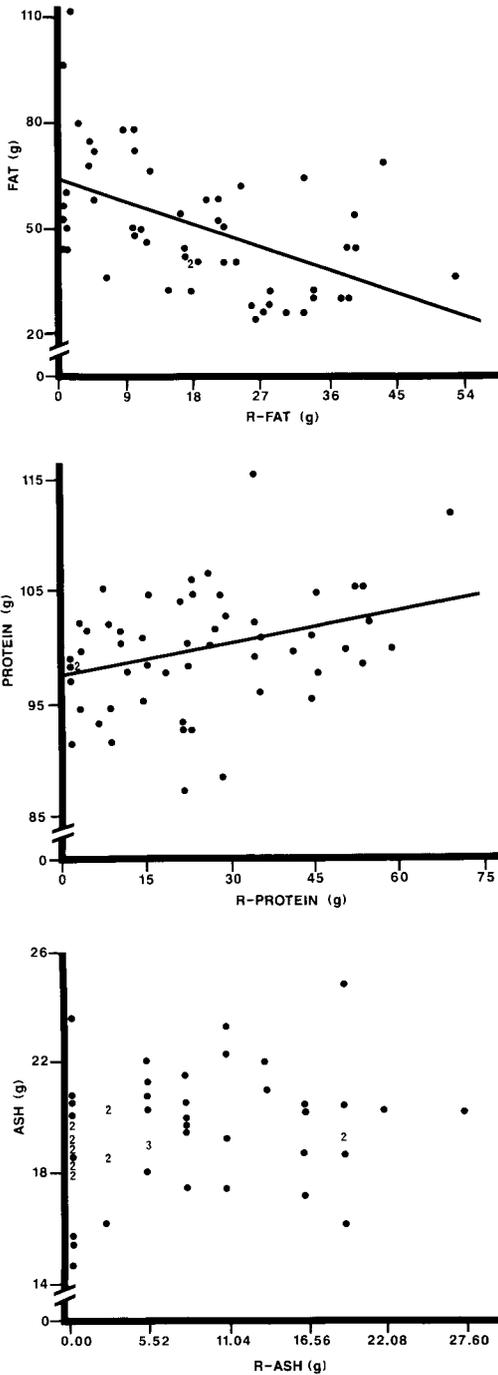


FIGURE 1. Relation between FAT, PROTEIN, and ASH reserves of female Northern Shovelers (Y-axes) and their corresponding commitment of those nutrients to egg production (X-axes). Equations describing these relationships are in Table 5; the relation between ASH and R-ASH was ns.

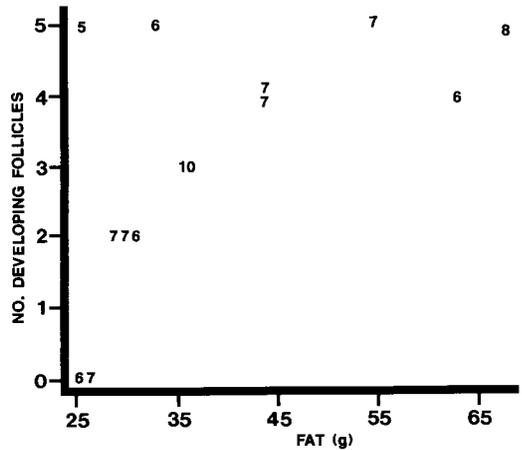


FIGURE 2. The correlation ($r = +0.60$) between number of developing ovarian follicles and FAT reserves of female Northern Shovelers late in the laying cycle (No. POF ≥ 5). Numbers represent individual females and depict the number of postovulatory follicles (POFs) in the ovary of each, e.g., of the three females with two developing follicles, two had seven POFs and one had six POFs. Both birds with zero developing follicles had an oviducal egg.

ble 6); slopes describing the relations of PROTEIN to body size did not differ by sex ($P > 0.2$ for the body size \times sex interaction; Table 6).

INCUBATION

In 1974, 17 incubating females were trapped, weighed, and released. The stages of these birds ranged from 1 to 23 days (incubation averages 23 days in shovelers, Afton 1977). Additionally, two of these females, initially trapped on days 1 and 2, respectively, were retrapped and weighed on days 22 and 23 (initial weights of these two birds were used in regression analysis of weight loss per day). In 1975, 16 females that had incubated from 1 to 23 days were trapped and killed for carcass analysis.

Using ANCOVA, we found that neither intercepts nor slopes of equations relating body weight to day of incubation differed between years ($P > 0.05$). Thus, we computed a single regression on the combined data (Table 7). Incubating females, on average, lost 4.46 g/day ($P < 0.001$), i.e., about 103 g or 18% of initial body weight. Two females, each weighed at the start and end of incubation, lost, on average, 4.02 and 5.26 g/day, respectively. Their average loss, 4.67 g/day (weighted by number of days incubated), was

TABLE 6. Linear regressions relating PROTEIN (Y) to body size (X, indexed by PC₁) in female and male Northern Shovelers, and an analysis of covariance in the PROTEIN of males and females with body size as the covariate.

	<i>n</i>	Intercept ^a	Slope	<i>r</i> ²
Linear regression				
Female	55	104.0	3.91	0.35
Male	37	95.4	3.20	0.21
Analysis of covariance				
Source	df	F ^b	<i>P</i>	<i>r</i> ^{2c}
Sex	1	15.3	<0.001	0.13
Body size	1	27.4	<0.001	0.22
Body size × sex	1	1.6	>0.2	0.01

^a Note that most female scores were negative, and male scores were positive; intercepts are at PC₁ = 0.

^b From partial sums of squares.

^c Partial sums of squares/total sums of squares.

close to the loss calculated by regression; their average body-weight loss was 24%.

FAT declined 1.68 g/day during incubation ($P < 0.001$, Table 7), i.e., about 39 g, which was 38% of total loss in body weight. Breast-muscle decline, 0.66 g/day ($P < 0.001$, Table 7), accounted for 30 g (29%) of the loss in body weight ($0.66 \times 23 = 15.2$ which is doubled to account for the other breast muscle); 30 g of breast muscle are equivalent to 7.5 g of PROTEIN as they average 25% LDW (Ankney, unpubl. data). Liver weight declined, on average, by 32% ($P < 0.05$) but gizzard weight did not change during incubation ($P > 0.05$, Table 7). Heart weight of females declined, on average, by 30% during incubation ($P < 0.001$, Table 7). In total, weight loss in variables that we measured accounted for 75% of loss in body weight of incubating females; we think it likely that the remainder was loss

from unanalyzed proteinaceous tissues, e.g., leg muscle and intestine.

DISCUSSION

FOOD HABITS AND DIGESTIVE ORGANS

Prelaying and laying female shovelers ate about 90% animal matter (dry weight basis) which agrees closely with data of Swanson et al. (1979) who reported that laying female shovelers in North Dakota consumed 99% animal matter (volumetric basis). Major types of animal foods eaten by females in their sample were gastropods (40%), crustaceans (54%), and insects (5%). These groups were also most important in our sample (55%, 21%, and 10%, respectively). Apparent differences in these percentages between the two samples likely are due to our use of dry weights, which emphasized the value for gastropods, and thus de-emphasized values for soft-bodied animals.

Male shovelers also consumed primarily animal foods, but they consumed a lower proportion of such foods during laying than did females. Differences in consumption of gastropods and "non-snail shell" by females (59%) vs. males (34%) during the laying period emphasizes the importance of calcareous foods to prairie-nesting ducks (see Krapu 1979), and further suggests there is a calcium appetite in egg-laying wild birds (Simkiss 1975, Ankney and Scott 1980). Paired shovelers feed close together (Afton, unpubl. data) and thus, diet difference must reflect choice. Dubowy (1985a) reported that postbreeding male shovelers ate 78% animal matter (aggregate percent wet weight), of which 90% was zooplankton. The latter percentage is far higher than that in diets of prelaying and laying shovelers. Thus, our data are inconsistent with Dubowy's (1985b) argument that shovelers time their arrival to breed-

TABLE 7. Linear regressions relating indices of body condition (Y) to day of incubation (X) for female Northern Shovelers. Data were obtained in southern Manitoba in 1974 (body weights only, $n = 17$) and 1975.

Variable	<i>n</i>	Intercept	Slope	<i>r</i> ²	<i>P</i> ^a
Body weight	33	569 (1.8) ^b	-4.46 (0.11)	0.61	<0.001
FAT	16	44.8 (1.2)	-1.68 (0.08)	0.66	<0.001
Breast muscle ^c	16	63.9 (1.6)	-0.66 (0.10)	0.75	<0.001
Gizzard ^c	16	9.62 (0.72)	-0.03 (0.05)	0.02	ns
Liver ^c	16	18.6 (1.5)	-0.26 (0.10)	0.34	<0.05
Heart ^c	16	4.87 (0.19)	-0.063 (0.013)	0.64	<0.001

^a Probability that $r = 0$.

^b 1 SE.

^c Wet weights.

ing areas so they can feed almost exclusively on zooplankton.

The decline in proportion of males with food in their gullets, from prelaying to laying, agrees with Afton's (1979) data showing that percentage of time spent feeding during daylight declined from 54% to 35% in prelaying and laying males, respectively. The proportion of females with food in their gullets did not change between prelaying and laying (64% vs. 62%) which agrees with values that Afton (1979) reported for percent time feeding by females in those two groups (58% vs. 57%, respectively). Note that Afton's (1979) time budgets and our diet analyses were only for males that were attending their female.

Nutrient reserves of males did not decline during laying (see below) which implies that males spend relatively more time feeding when their mates are on nests laying eggs. Indeed, observations ($n = 6$ hr) of paired males (Afton, unpubl.) indicate that males spent significantly (t -test, $P < 0.05$) more time feeding when alone (46.8%) than when with their mates (34.9%) during the laying period. Assuming a 10-egg clutch and adjusting for time that the average female spent on (25.2%) and off (74.8%) the nest (Afton 1979), the average male spent 37.9% of the total time feeding during laying, i.e., % total time = $[(0.468 \times 0.252) + (0.349 \times 0.748)] \times 100$. Adjusting for time spent on the nest, the average female spent 42.7% of the time feeding (% time = $(0.571 \times 0.748) \times 100$), or 1.2 hr more than her mate during daylight.

Both sexes spend less total time feeding during daylight hours during laying than during prelaying (males: $37.9 - 54.2 = -16.3\%$, females: $42.7 - 58.4 = -15.7\%$). Afton (1979) suggested that males reduced foraging time because of increasing food resources (Dwyer 1975), and/or by relying on stored nutrient reserves. Our results are inconsistent with the latter alternative.

Digestive organs of prelaying and laying males did not differ in size (Table 3), which further suggests that food consumption by males was not greatly reduced during the laying period. Decreased feeding is correlated with reduced size of digestive organs in some other waterfowl (Ankney 1977, Korschgen 1977, Drobney 1984).

The increase in liver weight (14%) of laying females, over that of prelayers, was much less than the increase (51%) that Drobney (1984) reported for Wood Ducks. Drobney argued that this increase was due to increased food con-

sumption and to the role of the liver in lipid metabolism during laying. Those factors probably explain some of the increase in Wood Ducks and perhaps all of it in shovelers. But, whereas there were no differences in diets of prelaying and laying shovelers, consumption of animal matter by laying Wood Ducks was 50% greater than that of prelayers (Drobney and Frederickson 1979). Kehoe et al. (unpubl.) found that liver weights of captive Mallards increased when their diet was changed from duck chow to either a high fiber, high animal protein, or high carbohydrate diet. Consequently, some of the increased liver weight of laying Wood Ducks may have been due to diet change.

Declines in gizzard weight of laying females have been attributed to reduced food consumption (Ankney 1977), use of gizzard protein for egg production (Korschgen 1977), and decreased dietary fiber (Drobney 1984). However, only the latter may explain the decline in gizzard weight of laying female shovelers; laying female shovelers do not show reduced food consumption (see above) and, overall, they show positive protein balance (see below). We speculate that, before RFG begins, female shovelers eat more fiber and thus, the decline in gizzard weight between prelaying and laying females reflected their continuing adjustment to foods that are easily macerated. Mean gizzard weight of the four pre-RFG females in our sample was 12.5 g, which is consistent with this speculation (see Table 3).

Intestine size of females did not change during prelaying and laying, but they were, on average, longer and heavier than those of males. This may be related to greater food consumption by females, which is thought to cause changes in gut size (Ankney 1977, Drobney 1984). Intestine lengths of breeding shovelers are longer than those reported for other waterfowl, e.g., *Aythya* spp. (Kehoe and Ankney 1985), Mallards (Miller 1975), Gadwalls, *Anas strepera* (Paulus 1982), White-winged Scoters, *Melanitta fusca* (Dobush 1986), and Snow Geese, *Chen caerulescens* (Ankney 1977). This is remarkable, given that (1) shovelers are smaller than the aforementioned species, and thus their guts are relatively far longer, and (2) shovelers are carnivores, which reportedly have shorter guts than do noncarnivorous birds (Sturkie 1976:187). Lipid digestion and absorption occurs in the small intestine of birds (Griminger 1976:253) and we hypothesize that the long intestine of a breeding shoveler is

an adaptation to a relatively energy-poor diet (see below).

IMPORTANCE OF RESERVES TO BREEDING SHOVELERS

Shoveler territories are aggressively defended by males, particularly during the laying period (McKinney 1973). Despite this, our prediction (and see Afton 1979:47) that breeding males would utilize endogenous lipids was not supported (Tables 4, 5). The territorial system of shovelers may put greater demands on time budgets of the males, compared to males of other *Anas* species. But, if these territories function primarily to secure a high-quality food supply for the female (McKinney 1973, Seymour 1974), benefits to the male (access to food) apparently balance the costs.

Protein reserves of laying males were heavier than those of prelaying males (Table 4), but this increase was unrelated to egg-laying schedules of their mates; this was also true for higher ash content of laying males. We cannot explain the apparent protein (and ash) storage of breeding males. Male shovelers, unlike males of most other *Anas* spp., remain paired with the female throughout incubation (Afton 1979), but their food habits and behavior during this period are unknown. However, as females spend <4 hr/day off the nest during incubation (Afton 1979), males should have sufficient time for foraging. Thus, we doubt that males, unlike females (see below), store protein to use as an energy source while females are incubating.

Lipid reserves of prelaying female shovelers (10% of fresh body weight, Table 4) were proportional to those of prelaying female Mallards (10%, Krapu 1981:table 3), but proportionally smaller than those of female Wood Ducks (20%, Drobney 1982:303). Thus, our prediction that female shovelers would have relatively small lipid reserves was not supported. Similarly, our prediction that female shovelers would rely exclusively on exogenous nutrients for egg production was not supported. Although these birds obtained sufficient exogenous minerals and protein to form eggs (Table 5, Fig. 1), they relied heavily on lipid reserves during egg laying. If conversion efficiency of lipid reserves to egg lipids approaches 100% (see Alisaukas and Ankney 1985) then about 70% of lipids required for egg formation in shovelers comes from reserves.

The protein limitation hypothesis does not ap-

ply to shovelers. Despite the ability of female shovelers to obtain more protein than needed for egg formation, they utilized lipid reserves, i.e., their utilization of lipid reserves must have involved factors other than difficulty obtaining aquatic invertebrates. Rather, our data on shovelers are consistent with those of Hails and Turner (1985) that showed that a diet of invertebrates is deficient in lipids for an egg-laying bird. Hails and Turner found that breeding White-bellied Swiftlets (*Collocalia esculenta*) fed solely on flying insects that contained, on average, 9% lipid and 64% protein by dry weight. Thus, Hails and Turner concluded that use of lipid reserves by egg-laying females was directly related to the inability to obtain sufficient lipids exogenously.

Diets of prelaying and laying shovelers were similarly deficient in lipids. Based on data summarized by Krapu (1979:table 2), major foods of breeding shovelers (i.e., Diptera, zooplankton, and snails) averaged 6%, 2%, and 1% lipid by dry weight, respectively; corresponding values for protein were 66%, 32%, and 17%. Based on those data, and the liberal assumption that all vegetation in diets of breeding females (Table 1) was seeds of aquatic vegetation, which average 10% protein and 3% lipid (Krapu 1979), we calculated that the ratio of protein : lipid in diets of these females was 14:1, approximately. To lay a 10-egg clutch, a female shoveler, on average, must produce 3.5 g of oviduct (Table 4), and 58 g of egg protein plus 49 g of egg lipids (Table 1), i.e., a protein : lipid ratio of 1.3:1, approximately. Thus, the diet of breeding shovelers contains about 10 times too much protein relative to lipid. Diets of Mallards (Krapu 1981) and Wood Ducks (Drobney and Frederickson 1979) contained more plant material, primarily seeds, than did that of shovelers, but they still had a protein : lipid ratio far higher than that of eggs. We conclude that the protein limitation hypothesis over-emphasized the importance of protein to egg-laying ducks.

Our data strongly suggest that lipid reserves, not protein availability, limit clutch size in shovelers (Fig. 1, and particularly, Fig. 2). Furthermore, we think that data for Wood Ducks and Mallards support a similar conclusion for those species. Drobney and Frederickson (1985) hypothesized that protein acquisition limits clutch size of Wood Ducks, but that hypothesis was based on an unlikely assumption. Drobney and Frederickson (1985:124) stated "... our studies

indicate that fat depletion is more likely to terminate laying in Wood Ducks because females do not use significant amounts of endogenous protein during laying." They further stated that "females with depleted fat reserves cease laying prematurely (after 3 to 4 eggs)" (we suggest that any female which lays fewer than the optimum number of eggs, surely far more than three or four, has ceased laying prematurely, e.g., those females in our Fig. 2, which have, or would have, laid 6 to 9 eggs). They then argued, however, that protein requirements during egg formation limit the number of eggs produced because females vary in their ability to obtain invertebrates (due to variability in foraging experience or invertebrate availability) which thus influences their rate of utilization of fat reserves. But, given that depletion of fat reserves causes termination of laying, this variability could only determine clutch size if those females with the greatest fat reserves at the start of egg formation had the most trouble finding invertebrates and vice versa. We think that this is unlikely to be valid. Instead, we suggest that the fat reserve with which a female begins RFG is much more important in affecting her clutch size than is her rate of protein acquisition.

Krapu (1981) suggested that the seasonal decline in clutch size of Mallards was related to exhaustion of lipid reserves. He argued, however, that this effect was indirect, i.e., that lower lipid levels reduced the capacity of females to secure protein. This argument does not consider that the female needs nearly as much lipid as protein for egg formation. Given that invertebrate populations will generally be higher later in spring, when females are reneating, lower lipid levels may directly limit clutch size in Mallards also.

Finally, the pattern of nutrient storage and acquisition by female shovelers, Wood Ducks, and Mallards indicates that lipids, not protein, directly limit clutch size in these species. Females store lipid reserves before egg formation and use them to form eggs. Data for all three species suggest that exhaustion of lipid reserves terminates laying, but there is no evidence that females of these species are ever short of exogenous protein; indeed, shovelers store protein during egg formation. We suggest that if female Wood Ducks or Mallards encountered protein shortages during laying, they would store and then use protein reserves during breeding. This phenomenon occurs in other waterfowl, e.g., Ring-necked Ducks,

Aythya collaris (Hohman 1986), several goose species (Ankney and MacInnes 1978, Raveling 1979, Ankney 1984, Mainguy and Thomas 1985), and Common Eiders, *Somateria mollissima* (Korschgen 1977). We do not imply that sources of protein are unimportant to prairie-nesting waterfowl and Wood Ducks. Rather, we think that during spring, in the highly productive wetlands used by these birds, protein is easier to obtain than lipid. We note that ingested protein could be converted to ovarian lipids, but the process is energetically inefficient and perhaps rate-limiting. This tactic apparently is used by female White-winged Scoters which use neither lipid nor protein reserves during egg formation (Dobush 1986) and feed exclusively on invertebrates then (Brown 1981). Scoters, however, have a laying rate of only 0.7 egg/day (Brown 1981), which is unlikely due to insufficient protein. In that context, we predict that laying rates of reneating shovelers (and other ducks that use stored lipids for first clutches) are lower than those of first nesters. Nothing is known about interfemale variation in laying rates even among first nesters, but laying rates could vary inversely with size of a female's lipid reserves.

If fat reserves limit clutch size of shovelers, then it is important to ask why these birds, on average, do not begin laying with larger reserves. Although food habits of shovelers during spring migration and immediately after arrival to breeding areas are unknown, we speculate that their diet contains relatively little carbohydrate and lipid then. Seeds of aquatic plants are at low levels in early spring and shovelers are not known to feed on waste grain. Protein reserves of pre-laying females were relatively larger than those of males, suggesting that their previous diets were high in protein. That female shovelers continue to store protein during egg formation indicates a tactic to make the best of an energy-poor diet; these protein reserves are used extensively during incubation (see below).

Incubating female shovelers meet metabolic requirements through periodic foraging and by utilizing lipid and protein reserves. The average female lost 103 g during incubation, of which 39 g was fat. We did not measure changes in total protein reserves, but declines in certain organs (breast muscle, heart) suggest that the remainder was loss of proteinaceous tissues, as occurs in some geese (see Ankney 1984). Consequently, of the 64 g of nonlipid loss, we estimate that 25%,

or 16 g, was protein and that the remainder (75%, 48 g) was water.

Afton and Paulus (unpubl.) estimated that the total energy requirement for incubating shovelers was 1,613 Kcal. Catabolism of lipids and protein yields 9.0 Kcal/g and 4.3 Kcal/g (Ricklefs 1974), respectively. Thus endogenous reserves provide, on average, 26% of the total kilocalories required during incubation. These calculations support Afton's (1979) argument that food resources in the territory are critical to successful incubation in shovelers. By hatch, females were virtually devoid of fat reserves (Table 7; equation for FAT).

Afton and Paulus (unpubl.) estimated that the percent of total energy requirements during incubation that was met from catabolism of endogenous reserves ranged from 4 to 79% (\bar{x} = 29%, SE = 5.5) in 17 studies of 14 waterfowl species. This percentage was related to female body weight at start of incubation (% from reserves = $2.42 + 0.0231$ (body weight); $r^2 = 0.61$, $P < 0.001$, $n = 17$). The estimated percentage from our results (26%) is 1.63 times higher than that predicted from female body weight (16%), i.e., use of endogenous reserves by incubating female shovelers is relatively higher than by other waterfowl of similar size. They accomplish this, in part, by using protein stores.

Average female body weight at start of incubation did not differ between 1974 and 1975. Furthermore, our estimate (569 g, Table 7), for both years combined, is similar to that from a more recent sample (1981 to 1983) of shovelers collected during early (days 1 to 3) incubation in southern Manitoba: \bar{x} = 563 g, n = 53 (Rohwer, pers. comm.). This similarity supports our arguments (see above) that clutch size in shovelers is dependent on lipid reserves, i.e., females terminate laying when they reach a minimum threshold level. Thus, our results are very similar to those reported for Snow Geese (Ankney and MacInnes 1978).

CONCLUSIONS

Lack (1967) hypothesized that average clutch sizes of waterfowl have evolved in relation to average availability of food for the laying female, modified by relative egg size. For clutch size to evolve, it must be genetically controlled; Lack assumed that interspecific differences in clutch size were hereditary but did not comment on intraspecific differences. Ankney and MacInnes (1978) thought

that most clutch-size variation in Snow Geese was due to a proximate cause (variation in nutrient reserves of females). Findlay and Cooke (1987), have now concluded that 80% of the variation in clutch size of Snow Geese is not genetically determined. Unfortunately, there are no such data for other waterfowl species in the wild (data from captive birds provide inflated heritability estimates because most environmental variation has been removed [Duncan 1987]). We predict that future studies of waterfowl will show that most intraspecific variation in clutch size is not genetically determined.

We doubt that average clutch size in waterfowl is an evolved trait. There is no evidence of selection against females laying clutches larger than average. Further, Rohwer (1985) showed that female Blue-winged Teal (*Anas discors*) successfully incubated experimentally-enlarged clutches of 16 and that those females fledged significantly more young than did those with (average) clutches of 10. Apparently, the optimum, i.e., the most productive, clutch size at least in Blue-winged Teal, is considerably larger than the average. This should not be so if the average was the product of natural selection. Possibly, the average clutch simply reflects inability of the average female to lay as many eggs as the most productive clutch size would dictate (see Murphy and Haukioja [1986] for a similar argument applied to clutch size of nidicolous birds). In that case, intraspecific variability in clutch size is more interesting than the mean.

Arnold et al. (1987) concluded that, for prairie-nesting ducks, there is no net gain to females laying more than about 13 eggs because of loss of viability and extended risk of predation to first-laid eggs. This, in conjunction with Rohwer's (1985) results, suggests that the maximum clutch size, set by selection, is also the most productive. Interestingly, about 13 eggs is the maximum number of eggs laid by prairie-nesting waterfowl (Bellrose 1976).

So, why do most female ducks lay fewer than the optimum clutch size? We think that Lack's (1967) hypothesis, that clutch size is related to food availability for the female, has great explanatory power when applied to intraspecific variation in clutch size, i.e., clutch size of individual females reflects the amount of nutrients available to them. In that context, Lack's hypothesis has not been adequately tested. Our data for shovelers suggest that lipid reserves of fe-

males are an important component of the nutrients available to females that may limit clutch size, but that provides only limited support for the hypothesis. Clearly, to more fully test Lack's ideas, simultaneous monitoring of nutrient reserves, food resources, and egg production of individual females must be done. That is presently logistically and technologically impossible, but until it has been done, any claims that food does not limit clutch size of ducks (e.g., Duncan 1986) are premature at best.

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