

CHANGES IN NUTRIENT RESERVES AND ORGAN SIZE OF FEMALE RUDDY DUCKS BREEDING IN MANITOBA

MICHAEL W. TOME¹

School of Forest Resources, University of Maine, Orono, Maine 04469 USA

ABSTRACT.—Female Ruddy Ducks (*Oxyura jamaicensis*) were collected at specific stages of reproduction to investigate the role of endogenous nutrients in breeding. Pectoral muscle weight decreased between prelaying and laying, suggesting the transfer of labile protein to the developing reproductive organs. Liver weights peaked during laying, reflecting increased metabolic activity associated with hyperphagia. Body weights increased 123 g (21%) between arrival and prelaying, primarily as a result of the deposition of stored lipids. Between laying and early incubation, body weights declined 145 g (20%), primarily as a result of the regression of the oviduct and lipid loss associated with egg formation. Body weights declined approximately 111 g (18%) during incubation, reflecting the catabolism of lipid reserves to supplement energy requirements not met by foraging during incubation recesses. Dietary intake provides the majority of the energy necessary for incubation, because lipid catabolism supplies only one-fifth of the basal metabolic requirements. Female Ruddy Ducks, therefore, depend almost exclusively upon dietary intake to meet the energy and nutrient requirements of reproduction. This pattern of energy acquisition for and allocation to reproduction differs markedly from that of other small-bodied anatids studied thus far. *Received 17 May 1982, resubmitted 31 October 1983, accepted 1 March 1984.*

RECENTLY, the reproductive energetics of waterfowl have been intensively investigated. Owen and Reinecke (1979) summarized four general patterns of energy acquisition for and allocation to reproduction. Waterfowl species studied thus far have exhibited patterns of energy acquisition and allocation that range from utilizing exclusively endogenous energy accumulated either on or away from the breeding grounds to depending upon dietary intake plus a small but significant energy component accumulated either on or away from the breeding area.

The breeding biology of the Ruddy Duck (*Oxyura jamaicensis*), the only oxyurid to nest regularly in North America north of Mexico, differs markedly from that of other North American Anatidae. Ruddy Ducks arrive unpaired on the southwestern Manitoba breeding grounds in late April. Monogamous pair bonding and other male-female associations, including promiscuous and polygynous behavior (Gray 1980), are exhibited, although Siegfried (1976a) reported that most Ruddy Duck pair bonds in Manitoba are monogamous. Egg lay-

ing begins approximately 4 weeks after the arrival on the breeding grounds (Siegfried 1976b). Oxyurids produce eggs that are the largest (proportional to body size) of any produced by Anatidae (Lack 1968), and a completed clutch may weigh more than the female. Furthermore, female Ruddy Ducks do not insulate their nests with down (Low 1941), and they take frequent, short, incubation recesses (Siegfried et al. 1976a, Tome 1981).

Although several aspects of the breeding biology of the Ruddy Duck have been described (Low 1941; Misterek 1974; Siegfried 1973, 1976a; Siegfried et al. 1976a; Joyner 1977, 1983; Gray 1980), no one has determined the significance of stored nutrients for reproduction in this species. The objective of this paper is to discuss the significance of nutrient reserves to reproduction in female Ruddy Ducks by examining changes in carcass composition and selected organ weights.

STUDY AREA AND METHODS

I collected female Ruddy Ducks in the prairie-pot-hole region of southwestern Manitoba approximately 16 km southeast of Minnedosa. Birds were collected from 1979 through 1981 from early May through the first 10 days of brood rearing in late July. Using the following criteria, I assigned each specimen to 1

¹ Present address: School of Natural Resources, Samuel Trask Dana Building, The University of Michigan, Ann Arbor, Michigan 48109 USA.

of 6 reproductive categories on the basis of ovarian development or stage of incubation.

Arrival.—No follicles in the rapid development stage, which is characterized by yolk deposition; largest follicle <8 mm ($n = 15$).

Prelaying.—Follicles yolky in appearance and ≥ 8 mm; no ruptured or regressing follicles present ($n = 9$).

Laying.—An egg present in the oviduct or ruptured follicles and large, developing follicles in the ovary; no regressing follicles present ($n = 6$).

Early incubation.—Females in the first 12 days of incubation as determined by comparing an embryo from the clutch with preserved embryos of known age ($n = 9$).

Late incubation.—Females in the last 12 days of incubation determined as above ($n = 8$).

Brood rearing.—Females accompanying broods <10 days old ($n = 5$).

Female Ruddy Ducks normally fed within the pot-hole on which their nest was located; consequently, I was able to locate a nest, determine the status of the female associated with that nest, and collect the bird at a known reproductive stage. I attempted to sample all reproductive categories equally.

Immediately after collection, the bird was weighed to the nearest 5 g on a 1,000-g Pesola spring scale, and the status of the bird was verified through examination of the ovary. For necropsy, the body feathers were sheared off, and wing feathers (remiges, tertaries, and coverts) and rectrices were plucked. The carcass was subsequently reweighed. I then removed the alimentary canal and emptied its contents. Small and large intestine lengths were measured to the nearest 1 mm. The gizzard, liver, right pectoral muscle (pectoralis major, supracoracoideus, and coracobrachialis), muscles of the right thigh and crus, ovary, and oviduct were excised, weighed, placed in a convection oven, dried to constant weight at 55°C, and reweighed.

In preparation for proximate analysis, each carcass was thawed for approximately 30 min and then cut into small pieces. These pieces and all organs previously removed were combined and homogenized in a commercial food grinder. The homogenate was spread onto flat enamel pans and dried to constant weight at 55°C.

Subsamples of the dried homogenate were ground in a Wiley mill. Two 3-g samples from each bird were ashed at 500°C. The remainder of the homogenate was sent to the Maine Agricultural Experiment Station to measure lipid content by means of petroleum ether Soxhlet extraction and nitrogen content by means of the Kjeldahl procedure (A.O.A.C. 1975). Lipid and protein content of the body, minus reproductive organs, was determined by subtracting lipid and protein content of the reproductive organs from the total body lipid and protein content. I derived lipid and protein content of the ovary and oviduct

by using dry weights of these organs and estimates of the composition of the ovary (64% protein, 32% lipid) from Romanoff and Romanoff (1949) and of the oviduct (5% lipid, 95% protein) from Ricklefs (1976).

I examined body weight as a function of day of incubation by weighing females ($n = 19$) that were captured once with a modified Weller (1959) nest trap and that were at known stages of incubation. These data were supplemented with the sample of females collected at known stages of incubation ($n = 17$). All birds were weighed to the nearest 5 g on a Pesola spring scale.

I found each data set either to deviate significantly from a normal distribution at $\alpha = 0.05$, when I used Lilliefors's test for normality (Conover 1980), or to violate the assumptions of equal variances ($P < 0.05$), when I used Box's modification of Bartlett's test (Box 1949). Consequently, differences between reproductive periods were investigated with the Kruskal-Wallis test (Conover 1980). If significant differences were detected, the nonparametric analog to a Least-Significant Difference multiple comparison test (Conover 1980) was employed to determine where the differences occurred. The relationship between day of incubation and fresh body weight and lipid content was determined with a regression analysis. The level of significance for all tests was $\alpha = 0.05$, unless otherwise noted.

RESULTS AND DISCUSSION

Organ and tissue changes.—Pectoral muscle weights (Table 1) remained constant between arrival and prelaying but decreased by 3.1 g (26%) ($P < 0.05$) between prelaying and laying and then remained unchanged. Ankney and MacInnes (1978) observed decreases in the pectoral and leg muscle weights of Lesser Snow Geese (*Chen caerulescens*) during laying, and Raveling (1979) observed decreases in the pectoral muscle weight of Canada Geese (*Branta canadensis*) during the same reproductive period. They hypothesized that, because the pectoral muscles were used little during incubation, it would be adaptive to catabolize the protein of these muscles and transfer it to egg production. Ankney (1977) proposed an alternative hypothesis to explain decreases in organ-muscle mass before incubation, suggesting that the resultant savings in maintenance metabolism would be advantageous to incubating females that were in negative energy balance. The decrease in pectoral muscle mass observed in female Ruddy Ducks lends support to both of these hypotheses. Pectoral muscle proteins could be transferred either to the developing

TABLE 1. Changes in organ weight [breast, liver, ovary, oviduct, gizzard, and leg (g)] and length [small and large intestine (cm)] in female Ruddy Ducks breeding in Manitoba (means \pm SE).

Stage	Breast	Liver	Ovary	Oviduct	Gizzard	Leg	Small intestine	Large intestine
Arrival	11.3 \pm 0.3 (14) NS	6.2 \pm 0.3 (15) NS	0.20 \pm 0.02 (13) *	0.9 \pm 0.1 (15) *	3.5 \pm 0.2 (15) NS	6.3 \pm 0.2 (15) NS	176.6 \pm 4.7 (15) NS	6.2 \pm 0.3 (15) NS
Pre-lay	12.0 \pm 0.5 (9) *	6.8 \pm 0.7 (9) NS	1.18 \pm 0.56 (8) *	2.4 \pm 0.6 (9) *	3.8 \pm 0.3 (9) NS	7.0 \pm 0.3 (9) NS	184.3 \pm 3.4 (9) NS	7.5 \pm 0.8 (9) NS
Lay	8.9 \pm 0.7 (6) NS	7.6 \pm 1.1 (6) *	15.04 \pm 6.20 (6) *	7.7 \pm 1.1 (6) *	3.8 \pm 0.3 (6) NS	6.9 \pm 0.3 (6) NS	195.5 \pm 7.1 (6) NS	8.2 \pm 1.3 (6) NS
Early incubation	8.7 \pm 0.4 (9) NS	5.2 \pm 0.4 (9) NS	0.31 \pm 0.04 (8) *	2.2 \pm 0.3 (9) *	3.9 \pm 0.3 (9) NS	7.3 \pm 0.2 (8) NS	172.4 \pm 5.5 (9) NS	8.8 \pm 1.5 (9) NS
Late incubation	7.9 \pm 0.3 (7) NS	4.5 \pm 0.2 (7) NS	0.19 \pm 0.03 (7) NS	0.7 \pm 0.1 (7) *	3.4 \pm 0.2 (7) NS	7.2 \pm 0.3 (7) NS	170.1 \pm 6.4 (8) NS	6.6 \pm 0.5 (8) NS
Brood	8.9 \pm 0.3 (5)	5.4 \pm 1.0 (5)	0.26 \pm 0.15 (5)	0.5 \pm 0.1 (4)	3.7 \pm 0.5 (5)	6.8 \pm 0.7 (5)	177.8 \pm 10.3 (5)	7.0 \pm 0.6 (5)

* * indicates significant difference between adjacent stages within a column: $P < 0.05$. NS indicates no significant difference between adjacent stages within a column: $P > 0.05$.

reproductive organs or to the production of eggs during laying. Incubating Ruddy Ducks are partially dependent on endogenous energy (Tome 1981) and would benefit from the decreased metabolism resulting from a smaller pectoral muscle mass.

Liver weights (Table 1) peaked during laying and subsequently decreased ($P < 0.05$) 2.4 g (32%) by early incubation. This pattern has been observed in many other waterfowl species, including Lesser Snow Geese (Ankney 1977), Common Eiders (*Somateria mollissima*; Korschgen 1977), Canada Geese (Raveling 1979), Wood Ducks (*Aix sponsa*; Drobney 1982), and Ruddy Ducks breeding in California (Gray 1980). The liver functions during the intermediary metabolism of an organism and enlarges as food consumption increases (Hanson 1962, Pendergast and Boag 1973), a condition observed during laying in Ruddy Ducks (Tome 1981).

The ovary and oviduct (Table 1) had the greatest relative changes in weight of all organs measured. Ovary weights increased 13.9 g (1,174%) and oviduct weights 5.3 g (221%) between prelaying and laying ($P < 0.05$). Even so, ovary weights of the laying hens in this study are underestimated, because 5 of 6 birds had laid at least four eggs before collection. The female with the heaviest ovary (34.8 g) in this study had laid three eggs, and I believe that this weight better approximates the peak ovary weights. Average ovary weights declined ($P < 0.05$) 14.7 g (98%) between laying and early incubation from release of ova and reabsorption of follicles. Oviduct weights decreased ($P < 0.05$) 5.5 g (71%) between laying and early incubation. The regression of these organs decreases metabolic requirements and provides a source of energy during early incubation.

Female Ruddy Ducks do not catabolize gizzard protein for use in egg synthesis as Korschgen (1977) reported for female Common Eiders. Gizzard weights of female Ruddy Ducks (Table 1) did not vary during the reproductive season, probably because Ruddy Ducks feed primarily on soft-bodied aquatic invertebrates (Siegfried 1973, Gray 1980, Tome 1981) throughout the reproductive period. Consequently, a diet shift that might cause a change in gizzard size, as observed in other waterfowl species [e.g. Wood Ducks (Drobney 1977) and Mallards (*Anas platyrhynchos*; Krapu 1981)] does not occur.

The second largest potential source of endogenous protein for use in egg synthesis is the leg muscle mass. Leg weights (Table 1), however, did not vary among reproductive periods. The Ruddy Duck relies on leg muscles for underwater feeding activities and to escape danger; thus, it would be advantageous to maintain muscle in the legs.

Gray (1980) reported that large and small intestine lengths of female Ruddy Ducks peaked during the laying period, and other investigators have shown the lengths or weights of these organs to increase during periods of hyperphagia (Ankney 1977, Drobney 1977, Breitenbach et al. 1963). Although there was a trend for small and large intestine lengths to peak during laying in this study (Table 1), no significant differences between reproductive periods were detected.

Body-weight changes.—Mean body weights (Table 2) increased ($P < 0.05$) 123 g (21%) between arrival and prelaying. Maximum weights were observed during laying. Body weights declined ($P < 0.05$) 145 g (20%) between laying and early incubation, primarily as a result of the regression of the reproductive organs and loss of ova from the ovary. This pattern of weight change over the reproductive cycle is similar to trends in carcass weight observed in other breeding waterfowl [e.g. Redheads (*Aythya americana*; Weller 1957), Blue-winged Teal (*Anas discors*; Harris 1970), Northern Pintails (*Anas acutas*; Krapu 1974), Mallards (Krapu 1981), Wood Ducks (Drobney 1982), American Black Ducks (*Anas rubripes*; Reinecke et al. 1982), and Ruddy Ducks breeding in California (Gray 1980)].

The results of the regression of fresh body weight on day of incubation indicate that female Ruddy Ducks begin incubation when they weigh an average of 619 g ($Y = 618.5 - 4.61X$; $r^2 = 0.38$; $P < 0.001$; $n = 36$). By the end of the 24-day incubation period, the average total body weight has declined by 111 g (18%). In comparison, Mallards were reported to lose approximately 13% and 18% of their total body weight during incubation by Krapu (1981) and Gatti (1983), respectively.

Carcass composition changes.—Female Ruddy Ducks arrived on the breeding grounds with an average lipid content of 62 g (Table 2), about 11% of the total body weight and similar to levels observed by Drobney (1982) in pre-breeding female Wood Ducks. This reserve in-

TABLE 2. Body weights and carcass lipid, protein, and ash content of female Ruddy Ducks breeding in Manitoba (means \pm SE).

Stage	Body weight (g)	Lipid (g)	Protein (g)	Ash (g)
Arrival	582 \pm 15	62.0 \pm 8.6	94.1 \pm 2.3	19.2 \pm 0.4
<i>n</i>	(15)	(15)	(15)	(15)
<i>P</i> ^a	*	*	NS	*
Pre-lay	705 \pm 34	99.5 \pm 12.3	99.4 \pm 2.8	22.3 \pm 1.0
<i>n</i>	(9)	(9)	(9)	(9)
<i>P</i>	NS	NS	NS	NS
Lay	739 \pm 34	89.1 \pm 19.1	91.5 \pm 1.4	21.4 \pm 1.0
<i>n</i>	(6)	(6)	(6)	(6)
<i>P</i>	*	NS	NS	*
Early incubation	594 \pm 15	72.2 \pm 8.7	88.1 \pm 2.0	19.6 \pm 0.5
<i>n</i>	(9)	(9)	(9)	(9)
<i>P</i>	*	*	NS	NS
Late incubation	509 \pm 14	42.0 \pm 7.9	88.1 \pm 2.1	18.3 \pm 0.5
<i>n</i>	(8)	(8)	(8)	(8)
<i>P</i>	NS	NS	NS	NS
Brood	546 \pm 40	19.9 \pm 5.3	87.8 \pm 3.7	19.4 \pm 0.5
<i>n</i>	(5)	(5)	(5)	(5)

^a * indicates significant difference between adjacent stages within a column: $P < 0.05$. NS indicates no significant difference between adjacent stages within a column: $P > 0.05$.

creased ($P < 0.05$) 38 g (60%) between arrival and pre-laying. Visual inspection indicated that this increase was largely the result of deposition of subcutaneous fat, primarily in the neck region, as was also observed by Gray (1980). Lipid stores did not change significantly ($P > 0.05$) between pre-laying and laying, between laying and early incubation, or between pre-laying and early incubation, although there was a trend for lipid stores to decrease during these periods. Most of the laying females I collected had laid at least half of their total clutch and, consequently, had depleted at least half of the lipid reserve that could have been used for egg formation. It is appropriate, therefore, to compare pre-laying birds that have not yet utilized stored lipid for follicle growth (average lipid content: 98.2 ± 7.9 g, $n = 7$) with females that have laid the final egg or are in the early stages of incubation (average lipid content: 67.2 ± 5.9 g, $n = 6$). The difference in average lipid content of these two groups is 31.0 g, which represents only enough endogenous material to meet the lipid requirements of 35% of an eight-egg clutch (clutch size in this study, $\bar{x} = 7.6 \pm 0.2$, $n = 43$), if one uses Gray's (1980) value for the lipid content of Ruddy Duck eggs (8.5 g) and assumes an egg production efficiency of 77% (Brody 1945). A regression of carcass lipid

content as a function of incubation date indicates a decrease of 36 g during the 24-day incubation period ($Y = 76.5 - 1.49X$; $r^2 = 0.25$; $P < 0.05$; $n = 17$), which suggests that female Ruddy Ducks supplement dietary intake procured during incubation recesses with endogenous energy.

Carcass protein content (Table 2) did not vary significantly ($P > 0.05$) between any consecutive reproductive periods. On the basis of these data, the contribution of endogenous protein to egg production in female Ruddy Ducks is minimal, possibly limited to the 6.2 g of protein mobilized from the breast tissue between pre-laying and laying.

Average ash weights (Table 2) increased ($P < 0.05$) 3 g between arrival and pre-laying, then decreased ($P < 0.05$) 2 g between laying and early incubation. Ash was presumably deposited as medullary bone before egg laying and was used to supplement egg-shell formation. Drobney (1982) observed similar increases in the ash content of pre-laying and laying Wood Ducks.

Adaptations for reproduction.—Females of waterfowl species studied thus far [e.g. Pintails (Krapu 1974), Lesser Snow Geese (Ankney 1977), Common Eiders (Korschgen 1977), Canada Geese (Raveling 1979), Wood Ducks (Drob-

ney 1980, 1982), Mallards (Krapu 1981), Maccoa Ducks (*Oxyura maccoa*; Siegfried et al. 1976b)] have been shown to reduce reproduction costs by utilizing stored energy to supplement dietary intake. The female Ruddy Duck, however, differs from these species by accumulating a small nutrient store (38 g of lipid) 3-4 weeks before egg laying, which could only partially offset the costs of egg production. Arctic-nesting Lesser Snow Geese (Ankney and MacInnes 1978) and Common Eiders (Korschgen 1977) are two species that utilize primarily endogenous nutrients to meet the requirements of egg production. Female Pintails (Krapu 1974), Wood Ducks (Drobney 1980, 1982), and Mallards (Krapu 1981) meet protein requirements of egg production by feeding on protein-rich invertebrates. The lipid requirements of these species, however, are met mostly from endogenous sources.

Because exogenous energy is so important in meeting reproductive costs, Ruddy Ducks have two alternatives for reducing the daily dietary intake necessary for egg formation: they could (1) increase the laying interval and/or (2) increase the rapid development period of the ovary (Ricklefs 1974). Ruddy Ducks lay one egg per day (Siegfried 1976a, Tome unpubl. data). Gray (1980), however, reports the rapid development period of the ovary to be 11 days, or 3 days longer than the average laying period. This decreases the maximum daily energy requirement of egg formation by 15% of the energy cost if the development period is 8 days (Tome 1981).

During incubation, female Ruddy Ducks catabolize approximately 36 g (6% of body weight at the start of incubation) of lipid. This decrease is closer to lipid changes observed in Wood Ducks (17 g or 3% of body weight at start of incubation; Drobney 1982), which forage during incubation (Drobney and Fredrickson 1979), than to those in Common Eiders (300 g or 32% of wet body weight at start of incubation), which feed little during incubation (Korschgen 1977). The amount of lipid expended during incubation by female Ruddy Ducks is also less than the 104 g reportedly utilized by Maccoa Ducks (Siegfried et al. 1976b) during this reproductive period. At a basal metabolic rate of 275.5 kJ/day (Tome 1981), the 36 g of fat catabolized by female Ruddy Ducks would provide only 5 days of basal metabolic energy. If the entire 71 g of fat present at the

initiation of incubation were catabolized, this store would provide approximately 10 days of basal metabolic energy. Clearly, the majority of the energy requirements for incubation is met by foraging during incubation recesses.

Because female Ruddy Ducks lay such a large egg and total clutch mass relative to body mass, one has to wonder what factor, or combination of factors, has caused the Ruddy Duck to evolve a pattern of energy acquisition for and allocation to reproduction that is almost entirely dependent upon exogenous energy. I suggest that one factor is the effect of wing area relative to body weight on the ability of the Ruddy Duck to fly. Raikow (1973) reports that Ruddy Ducks have the smallest Buoyancy Index [square root of wing area divided by cube root of body weight as defined by Hartman (1961)] of the 15 waterfowl species (encompassing four tribes) that he measured. Raikow (1973) describes the shape of the Ruddy Duck wing as being "small, pointed and minimally slotted," which conforms to Savile's (1957) description of a "high-speed wing." A high-speed wing is adapted for direct, rapid flight and does not provide the lift necessary for rapid take-offs in restricted areas (Savile 1957). Ruddy Ducks have a very rapid wing beat and must "patter" long distances before flight is attained, "with seeming difficulty," as Palmer (1976) notes. Because of these flight restrictions, Ruddy Ducks do not accumulate large nutrient reserves, which would drastically increase body weight on wintering or spring migration staging grounds, as Pintails (Krapu 1974), Snow Geese (Ankney and MacInnes 1978), and Mallards (Krapu 1981) do. These nutrient reserves would be more likely to be accumulated on the breeding grounds during the mid- to latter portion of the arrival period, as has been observed in Wood Ducks (Drobney 1982). At this time, however, female Ruddy Ducks are searching for potential mates and nest sites (pers. obs.) and are flying between wetlands. If female Ruddy Ducks were to accumulate sufficient endogenous nutrients before egg laying to decrease daily energy requirements significantly during this period, the body weight of the bird would be increased so that flight would be difficult or impossible. The selection of mates and nest sites is an important reproductive activity, and the reproductive fitness of a female could be reduced if the hen were unable to fly at this time, especially to select an adequate wetland on which to nest.

Nest-site selection is especially important, because, once a female begins laying, she rarely leaves the wetland where the nest is located until she abandons the brood (Tome unpubl. data). It is important, therefore, that the female select a wetland that contains adequate food resources for providing nutrients for egg formation and for the developing ducklings during the entire brood-rearing period. Thus, for a female's reproductive fitness to be maximized, it is important that she be able to fly during the arrival period and to select a wetland with adequate food resources. This could also account for the observed delay between arrival on the breeding grounds and the initiation of egg laying. Females could be spending this time assessing the chironomid larvae densities in wetlands that are to be used as nest sites and brood-rearing areas.

ACKNOWLEDGMENTS

I thank P. Billeci, J. Lightbody, J. Nelson, and K. Savage for assistance in the field and lab. I am also grateful to J. Longcore, T. May, R. Owen, Jr., and M. Stokes for advice and support through all phases of the study. R. Drobney, G. Krapu, R. Owen, Jr., K. Reinecke, and two anonymous reviewers made recommendations on an earlier draft of this manuscript. Finally, special thanks are due P. Ward, B. Batt, and the students and staff of the Delta Waterfowl Research Station for advice and assistance throughout the study. Financial support was provided by the North American Wildlife Foundation through the Delta Waterfowl Research Station; the School of Forest Resources, University of Maine, Orono; and the School of Natural Resources, The University of Michigan, Ann Arbor.

LITERATURE CITED

- ANKNEY, C. D. 1977. Feeding and digestive organ size in breeding Lesser Snow Geese. *Auk* 94: 275-282.
- , & C. D. MACINNES. 1978. Nutrient reserves and reproductive performance of female Lesser Snow Geese. *Auk* 95: 459-471.
- A.O.A.C. 1975. Official methods of analysis of the Association of Official Analytical Chemists, twelfth ed. Washington, D.C., A.O.A.C.
- BOX, G. E. P. 1949. A general distribution theory for a class of likelihood criteria. *Biometrika* 36: 317-346.
- BREITENBACH, R. P., C. L. NAGREN, & R. K. MEYER. 1963. Effects of limited food intake on cyclic annual changes in Ring-necked Pheasant hens. *J. Wildl. Mgmt.* 27: 24-36.
- BRODY, S. 1945. *Bioenergetics and growth*. New York, Reinhold.
- CONOVER, W. J. 1980. *Practical nonparametric statistics*, second ed. New York, John Wiley and Sons.
- DROBNEY, R. D. 1977. The feeding ecology, nutrition, and reproductive bioenergetics of Wood Ducks. Unpublished Ph.D. dissertation. Columbia, Missouri, Univ. Missouri.
- . 1980. Reproductive bioenergetics of Wood Ducks. *Auk* 97: 480-490.
- . 1982. Body weight and composition changes and adaptations for breeding in Wood Ducks. *Condor* 84: 300-305.
- , & L. H. FREDRICKSON. 1979. Food selection by Wood Ducks in relation to breeding status. *J. Wildl. Mgmt.* 43: 109-120.
- GATTL, R. C. 1983. Incubation weight loss in the Mallard. *Can. J. Zool.* 61: 565-569.
- GRAY, B. J. 1980. Reproduction, energetics and social structure of the Ruddy Duck. Unpublished Ph.D. dissertation. Davis, California, Univ. California.
- HANSON, H. C. 1962. The dynamics of condition factors in Canada Geese and their relation to seasonal stresses. *Arct. Inst. North Amer. Tech. Paper No. 12*.
- HARRIS, H. J., JR. 1970. Evidence of stress response in breeding Blue-winged Teal. *J. Wildl. Mgmt.* 34: 747-755.
- HARTMAN, F. A. 1961. Locomotor mechanisms of birds. *Smithsonian Misc. Coll.* 143: 1-91.
- JOYNER, D. E. 1977. Behavior of Ruddy Duck broods in Utah. *Auk* 94: 343-349.
- . 1983. Parasitic egg laying in Redheads and Ruddy Ducks in Utah: incidence and success. *Auk* 100: 717-725.
- KORSCHGEN, C. E. 1977. Breeding stress of female Eiders in Maine. *J. Wildl. Mgmt.* 41: 360-373.
- KRAPU, G. L. 1974. Feeding ecology of Pintail hens during reproduction. *Auk* 91: 278-290.
- . 1981. The role of nutrient reserves in Mallard reproduction. *Auk* 98: 29-38.
- LACK, D. 1968. *Ecological adaptations for breeding in birds*. London, Chapman and Hall.
- LOW, J. P. 1941. Nesting of the Ruddy Duck in Iowa. *Auk* 58: 506-517.
- MISTEREK, D. 1974. The breeding ecology of the Ruddy Duck (*Oxyura jamaicensis*) on Rush Lake, Winnebago County, Wisconsin. Unpublished M.S. thesis. Oshkosh, Wisconsin, Univ. Wisconsin.
- OWEN, R. B., JR., & K. J. REINECKE. 1979. Bioenergetics of breeding dabbling ducks. Pp. 71-93 in *Waterfowl and wetlands—an integrated review* (T. A. Bookhout, Ed.). Proc. North Central Section, Wildl. Soc.
- PALMER, R. 1976. *Handbook of North American*

- birds, vol. 3. New Haven, Connecticut, Yale Univ. Press.
- PENDERGAST, B. A., & D. A. BOAG. 1973. Seasonal changes in the internal anatomy of Spruce Grouse in Alberta. *Auk* 90: 307-317.
- RAIKOW, R. J. 1973. Locomotor mechanisms in North American Ducks. *Wilson Bull.* 85: 295-307.
- RAVELING, D. G. 1979. The annual cycle of body composition of Canada Geese with special reference to control of reproduction. *Auk* 96: 234-252.
- REINECKE, K. J., T. L. STONE, & R. B. OWEN, JR. 1982. Seasonal carcass composition and energy balance of female Black Ducks in Maine. *Condor* 84: 420-426.
- RICKLEFS, R. E. 1974. Energetics of reproduction in birds. Pp. 152-292 in *Avian energetics* (R. A. Paynter, Jr., Ed.). Nuttall Ornithol. Club Publ. No. 15.
- . 1976. The chemical composition of the ovary, oviduct, and follicles of the Starling. *Auk* 93: 184-187.
- ROMANOFF, A. L., & A. J. ROMANOFF. 1949. *The avian egg*. New York, Wiley and Sons.
- SAVILE, D. B. O. 1957. Adaptive evolution in the avian wing. *Evolution* 11: 212-224.
- SIEGFRIED, W. R. 1973. Summer food and feeding of the Ruddy Duck in Manitoba. *Can. J. Zool.* 51: 1293-1297.
- . 1976a. Social organization in Ruddy and Maccoa ducks. *Auk* 93: 560-570.
- . 1976b. Breeding biology and parasitism in the Ruddy Duck. *Wilson Bull.* 88: 566-574.
- , A. E. BURGER, & P. J. CALDWELL. 1976a. Incubation behavior of Ruddy and Maccoa ducks. *Condor* 78: 512-517.
- , ———, & P. G. H. FROST. 1976b. Energy requirements for breeding in the Maccoa Duck. *Ardea* 64: 171-191.
- TOME, M. W. 1981. Reproductive bioenergetics of female Ruddy Ducks in Manitoba. Unpublished M.S. thesis. Orono, Maine, Univ. Maine.
- WELLER, M. W. 1957. Growth, weights, and plumages of the Redhead (*Aythya americana*). *Wilson Bull.* 69: 5-38.
- . 1959. An automatic nest trap for waterfowl. *J. Wildl. Mgmt.* 21: 456-458.