CHANGES IN BODY WEIGHT AND BODY COMPOSITION OF BREEDING RING-NECKED DUCKS (*AYTHYA COLLARIS*)

WILLIAM L. HOHMAN[1]

Department of Fisheries and Wildlife, University of Minnesota, St. Paul, Minnesota 55110 USA

ABSTRACT.—Body composition of male and female Ring-necked Ducks (*Aythya collaris*) changed substantially over the course of reproduction, with the largest nutrient reserves occurring before the onset of laying. Ring-necked Ducks used lipid reserves acquired before occupancy of nesting areas to meet subsequent reproductive requirements. Paired males reduced feeding and expended lipid reserves while attending prelaying and laying mates. Females depleted lipid reserves during ovarian follicle growth; after ovulation they were highly dependent on ambient food resources. Female Ring-necked Ducks obtain protein required for egg production from the diet during ovarian follicle growth. This conclusion was supported by (1) the limited extent of body protein fluctuation; (2) the absence of a relationship between body protein and protein contained in recrudesced reproductive tissues and expended in eggs; and (3) similarities in the rate of change in body protein by date between males and females, and among females before and after laying. Female energy expenditures during ovarian follicle growth are influenced by costs associated with obtaining nutrients needed for egg production. The level of lipid reserve needed for reproduction, therefore, changes with food availability. Deficiencies in female lipid reserve at the initiation of ovarian follicle growth further increase exogenous requirements for reproduction and may result in adjusted breeding patterns or deferred breeding. The contribution of body reserves to reproduction was partially a function of nutrient levels attained during the arrival period. Variations in Ring-necked Duck body-weight change, by year and by female age, suggest that nutrient acquisition and allocation for waterfowl nesting in temperate regions may be more indeterminant than has been implied previously. *Received 18 March 1985, accepted 20 September 1985.*

ENERGETIC costs of reproduction for ducks and geese are large relative to those of other major bird groups (King 1973, Ricklefs 1974). In general, birds have a substantial capability for storage and utilization of energy reserves, primarily in the form of lipids (Blem 1976). Such reserves play a prominent role in waterfowl reproduction (Barry 1962; Ryder 1967, 1970; Harvey 1971; Korschgen 1977; Ankney and MacInnes 1978; Raveling 1979; Krapu 1981; Drobney 1982; Reinecke et al. 1982; Ankney 1984; Tome 1984).

Ring-necked Ducks (*Aythya collaris*) are small-bodied (500–900 g), inland diving ducks (Tribe Aythyini), which have been studied principally in the northeast (Mendall 1958). They commonly nest in northern bog marshes, permanent wetlands characterized by low primary production (Reader 1978). I examined changes in body weight and body composition of breeding Ring-necked Ducks by sex and age. Attention was focused on body condition of returning birds, with the prediction that endogenous reserves accumulated before occupancy of wetlands used for nesting were critical to successful reproduction by this species.

METHODS

Breeding Ring-necked Ducks were studied from April to August 1978–1980 on Roseau River Wildlife Management Area (WMA) in northwestern Minnesota. Birds were collected by shooting, decoy trapping (Anderson et al. 1979), nest trapping (Weller 1957), or night-lighting (Lindmeier and Jessen 1961). Body weights (±5 g) were taken immediately after collection. Feathers (5th primary, 5th secondary, 12th and 13th greater upper secondary coverts) were removed in 1979 and 1980, and age (yearling = first-year bird, before prebasic II molt; adult = after-first-year bird, after prebasic II molt) was assigned on the basis of discriminant function analysis of feather measurements (Hohman 1984). Live-trapped birds were marked individually with a plastic nasal-saddle

---

[1] Present address: Delta Waterfowl Research Station, Rural Route 1, Portage la Prairie, Manitoba R1N 3A1, Canada.

(Doty and Greenwood 1974). Birds collected by shotgun were frozen in sealed plastic bags for later dissection.

Females and their mates were assigned to the following reproductive categories, based in part on Krapu (1974):

Arrival.—Females returning to the breeding grounds with ovary weight <3 g.

Prelaying.—Preovulating females with ovary weight ≥3 g.

Laying.—Ovulating females.

Early incubation.—Postovulating hens captured on nest, estimated days of incubation ≤9 days as determined by field candling (Weller 1956) or embryonic inspection (Caldwell and Snart 1974).

Middle incubation.—Eggs incubated 10–18 days.

Late incubation.—Eggs incubated >18 days.

Early brood.—Hens attending age class I ducklings (Gollop and Marshall 1954).

Late brood.—Hens attending age class II ducklings.

Postbreeding.—Birds collected in July and August on molting areas before remigial feather molt.

Females initiated ovarian follicle growth after 6 May, as verified by back-dating on hens of known reproductive status. Consequently, all birds handled before 6 May were placed in the arrival category. Pairing status was assigned to marked males on the basis of behavioral observations made following capture. Paired individuals were birds showing active association, i.e. copulation, mutual display, female tolerance of male, or nonrandom spacing. Unmarked males were considered unpaired if observed on collection before 6 May without a mate.

Predictive indices were used to estimate ash-free, lean dry weight ("protein"), and lipid composition of whole carcasses less reproductive tissues (Hohman and Taylor 1986). Body lipid was regressed on wet weights of abdominal fat and skin tissues. Protein was estimated from eviscerated carcass, right breast muscle and right leg muscle weights, and bill length measurement. Lipid and protein content of ovary and oviduct tissues were derived using wet weights of these organs and estimates of composition of the ovary (35.2% lipid, 17.7% protein; Romanoff and Romanoff 1949) and of the oviduct (22.4% protein; Drobney 1980). To monitor change in mineral composition, ashed (550°C, 48 h) weights were taken on female femurs and tibiotarsi.

Statistical comparisons of body weight, body lipid and protein composition, and weight of ashed leg bones by reproductive status and 10-day Julian date interval were made using one-way analysis of variance. Multivariate (factors = age, year, date, and reproductive status) analysis of variance was performed on body-weight data using BMDP-4V statistical software (Dixon and Brown 1981). The maximum extent of seasonal body-weight change was expressed as a percentage of maximum mean body weight (Reinecke 1977). Mean body weights by reproductive status and 10-day interval were compared between 1979 and 1980 using sign tests (Conover 1980). Regression procedures followed Weisberg (1981). Significance level was set at $P < 0.05$.

RESULTS

BREEDING PHENOLOGY

Paired Ring-necked Ducks began to arrive in the vicinity of Roseau River WMA in early April, soon after snowmelt. Sheet water on agricultural fields adjacent to the management area was used by birds initially. Birds remained on seasonal wetlands until about late April, when the study area became ice-free. Laying was initiated from mid-May to early June, and broods usually were evident by the fourth week of June. Males left Roseau River WMA by early July; females departed 4–6 weeks later, after their broods had attained class II stage of plumage development.

Breeding phenology for Ring-necked Ducks in northwestern Minnesota was similar to that observed by Sarvis (1972) in Michigan, but somewhat later than that recorded in Maine (Mendall 1958). Breeding phenology in northwestern Minnesota did not vary appreciably among years.

BODY WEIGHTS

Female.—Body weights were obtained from 263 breeding female Ring-necked Ducks. Female body weight changed substantially through reproduction (Table 1). Weight increased significantly from arrival to maximum seasonal levels at the initiation of ovarian follicle growth. Body weight declined after the onset of laying. Body weight recovered significantly in hens with class II ducklings after late July from seasonal minima observed in early brood rearing. The maximum body-weight change amounted to 29% (229 g) for breeding females.

The pattern of body-weight change differed for yearling and adult females, and varied among years. Adult females collected early in the arrival period were significantly heavier than yearlings in both 1979 and 1980 (Table 2). Mean body weights for adult and yearling birds, however, did not differ by reproductive status

TABLE 1.   Body weight and body composition of breeding female Ring-necked Ducks collected in northwestern Minnesota, 1978–1980.

Stage of reproduction	Body weight	Lipid	Protein
Arrival	703 ± 8[a]	88.0 ± 7.0	119.7 ± 1.1
n	69	35	35
P[b]	***	NS	NS
Prelaying	803 ± 35	118.2 ± 24.1	123.8 ± 3.2
n	8	4	4
P	NS	**	***
Laying	782 ± 12	51.0 ± 4.0	116.1 ± 1.2
n	16	14	14
P	***	NS	NS
Early incubation	666 ± 14	35.5 ± 4.1	111.9 ± 0.9
n	5	4	4
P	NS	NS	NS
Midincubation	653 ± 15	37.8 ± 5.7	111.9 ± 2.5
n	9	2	2
P	**	NS	NS
Late incubation	594 ± 8	27.9 ± 3.2	106.9 ± 7.9
n	23	2	2
P	NS	NS	NS
Early brood rearing	574 ± 7	28.1 ± 3.5	103.3 ± 2.9
n	54	3	3
P	NS	NS	NS
Late brood rearing	588 ± 7	40.1 ± 4.2	101.3 ±1.4
n	42	5	5

[a] Mean ± SE (g).
[b] P = probability (from one-way ANOVA) that adjacent means within a column are significantly different.
** = $P < 0.01$; *** = $P < 0.001$; NS = $P > 0.05$, not significant.

within years, suggesting that adult females returned heavier or gained weight more rapidly, or both, compared with yearlings.

Mean body weight by 10-day interval fluctuated more widely in 1979 than in 1978 and 1980 (Fig. 1). Differences among years were greatest early in the reproductive cycle. Before 6 May, adults and yearlings were significantly lighter in 1980 than early-arrival birds collect-

ed in the previous years (Table 2). Females by reproductive status (sign test, $T = 5$, df $= 5$, $P < 0.05$) and by 10-day interval (sign test, $T = 9$, df $= 10$, $P < 0.01$) were generally heavier in 1979 than in 1980. Outside of the arrival period, however, mean female body weight by 10-day interval or by reproductive status did not differ significantly between years.

Male.—Body weights were taken on 334

TABLE 2.   Body weights of breeding Ring-necked Ducks collected in northwestern Minnesota early in the arrival period (before 6 May).

	Female				Male			
Year	Yearling	P[a]	Adult	All	Yearling	P	Adult	All
1978[b]				700 ± 13[c]				731 ± 8
n				15				44
1979	715 ± 20	*	777 ± 18	742 ± 16	772 ± 21	NS	793 ± 15	787 ± 12
n	9		7	16	6		16	22
P	**		**	NT	NT		NT	***
1980	632 ± 12	***	705 ± 9	670 ± 11	700 ± 12	NS	726 ± 7	718 ± 6
n	12		13	25	20		50	70

[a] P = probability that adjacent means within a column or row are significantly different. * = $P < 0.05$;
** = $P < 0.01$; *** = $P < 0.001$; NS = $P > 0.05$, not significant; NT = no test.
[b] Age was not determined.
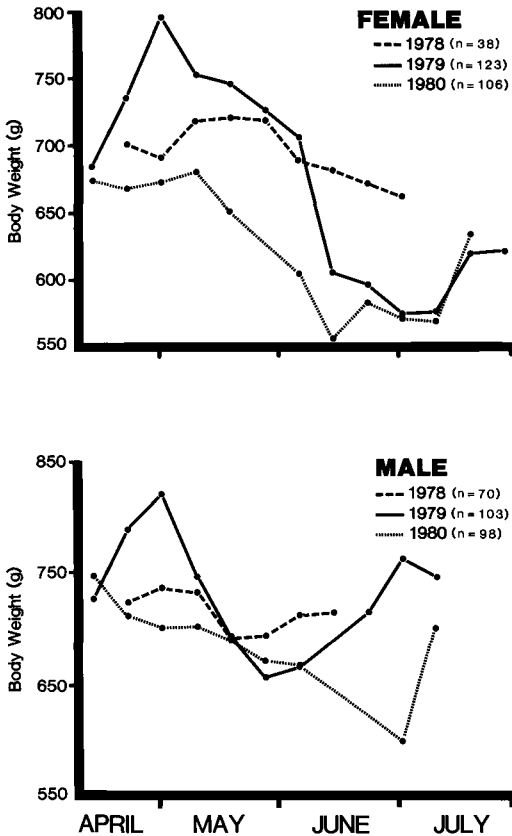[c] Mean ± SE (g).

Fig. 1. Mean body weights of breeding female and male Ring-necked Ducks by 10-day interval and year, 1978–1980.

breeding males. Male body weight changed significantly with their mates' reproductive status and by 10-day interval (Table 3). Birds were heaviest during their mates' arrival and prelaying reproductive periods. A significant decrease in body weight corresponding to the period of ovarian follicular growth occurred in mid- and late May. Seasonal minima in male body weight were recorded after their females began incubation. The maximum extent of change in male body weight amounted to 10% (73 g).

No significant age-related differences in male body-weight change were detected, but male body weight by 10-day interval changed differently in 1979 and 1980 (Fig. 1). Seasonal fluctuation in mean body weight by 10-day interval was greater in 1979 than in either 1978 or 1980. Males collected early in the arrival period were significantly heavier in 1979 than in 1978 and 1980 (Table 2). Weight was gained

between mid-April and early May 1979, and similar gains were shown by recaptured individuals. Similar increases were not observed before the onset of ovarian follicle growth in other years. Outside of the arrival period the patterns of seasonal weight change for all years were alike.

BODY COMPOSITION

Female.—Lipid and protein composition was estimated for 72 breeding females. Lipid stores were largest in arrival and prelaying birds before mid-May (Table 1). Body lipid declined significantly when females began laying. Seasonal minima occurred during late incubation and early brood rearing, mid-June to late July. No significant differences between adult and yearling females, or among years, were apparent in body lipid by reproductive status or by 10-day interval, although small sample sizes in some categories may have prevented the detection of differences.

Body protein declined 19% (23 g) from prelaying to late brood rearing (Table 1). Seasonal decline in body protein was approximately constant (Fig. 2) and unrelated to changes in reproductive protein, i.e. protein contained in recrudesced reproductive tissues and expended in eggs ($r = -0.3467$, df = 15, $P > 0.05$).

Minerals required for eggshell formation apparently were deposited in the skeleton during the period of ovarian follicle growth. Femoral and tibiotarsal mineral content increased significantly from arrival to prelaying and laying. Ashed leg-bone weights before and after the period of ovarian follicle growth did not differ, and were equivalent in adult and yearling females.

Male.—Lipid and protein composition was estimated for 78 breeding males. Body lipid in males decreased significantly between their mates' arrival and laying reproductive stages (Table 3). Lipid level in males was greatest before mid-May, when some females initiated laying. Seasonal minima were recorded in mid-June at the termination of the laying period. Body lipid remained at low levels while birds were on the study area. Changes in male lipid and protein composition were not significantly influenced by age, year, or pairing status.

Body protein declined in males from May to July (11%, 14 g) at the same rate observed in females (Fig. 2).

TABLE 3. Body weight and body composition of breeding male Ring-necked Ducks collected in northwestern Minnesota, 1978–1980.

Stage of mate's reproduction	Body weight	Lipid	Protein
Arrival	735 ± 5[a]	102.5 ± 6.8	125.6 ± 1.0
n	144	38	38
P[b]	NS	NS	NS
Prelaying	752 ± 22	93.0 ± 44.3	126.6 ± 2.1
n	6	3	3
P	NS	NS	**
Laying	707 ± 11	54.6 ± 4.5	117.8 ± 1.8
n	13	12	12
P	NS	NS	NS
Incubation	679 ± 19	49.6 ± 4.6	117.2 ± 2.2
n	12	5	5
P	**	NS	NS
Postbreeding	735 ± 22	65.4 ± 11.1	121.2 ± 2.0
n	9	9	9

[a] Mean ± SE (g).
[b] P = probability (from one-way ANOVA) that adjacent means within a column are significantly different. ** = P < 0.01; NS = P > 0.05, not significant.

DISCUSSION

Body composition of male and female Ring-necked Ducks changed substantially over the course of reproduction, with the largest nutrient reserves occurring before the onset of laying. Ring-necked Ducks use lipid reserves acquired before occupancy of nesting areas to meet subsequent reproductive requirements. Females incur substantial costs from egg production. Lipid reserves are depleted during ovarian follicle growth; after laying, females are highly dependent on ambient food resources. Paired males reduce feeding (Hohman unpubl. data) and expend lipid reserves while attending prelaying and laying mates. Close attendance of the female minimizes the chances of a male being displaced by another male, or having his mate inseminated by other males. Moreover, male defense of the female against intrusions by other birds and vigilance against potential predators probably facilitate female feeding (Ashcroft 1976). This may be especially important during ovarian follicle growth, when female nutrient demands are greatest.

Protein stored in muscle sarcoplasm (Kendall et al. 1973) is used by Common Eiders (*Somateria mollissima*; Korschgen 1977) and some arctic-nesting geese (Ankney and MacInnes 1978, Raveling 1979) to produce eggs. Over 80 g of protein are required for production of an average clutch and biosynthesis of oviduct tissue by Ring-necked Ducks (Hohman 1984). This is equivalent to about 67% of the protein content of female carcasses before ovarian follicle growth. Female Ring-necked Ducks obtain protein required for production of eggs almost exclusively from the diet during ovarian follicle growth. This conclusion is supported by (1) the limited extent of body protein fluctuation; (2) the absence of a relationship between body protein and protein contained in recrudesced reproductive tissues and expended in eggs; and (3) similarities in the rate of change in body protein by date between males and females, and among females before and after laying. Other small-bodied waterfowl, such as Wood Ducks (*Aix sponsa*; Drobney 1982), American Black Ducks (*Anas rubripes*; Reinecke et al. 1982), Mallards (*Anas platyrhynchos*; Krapu 1981), and Ruddy Ducks (*Oxyura jamaicensis*; Tome 1984), also obtain protein required for egg production from the diet during prelaying and laying.

Female energy expenditures during ovarian follicle growth are influenced by costs associated with obtaining nutrients for egg production. Depletion of body lipid by prelaying/laying Mallard and Wood Duck hens may exceed the amount contained in a completed clutch of eggs (Krapu 1981, Drobney 1982). This difference was attributed to additional foraging costs incurred by females specializing on invertebrate foods. Hohman (1985) suggested that selecting food on a noncaloric basis (e.g. protein, balanced amino acid composition, minerals) may reduce net foraging gains and result in
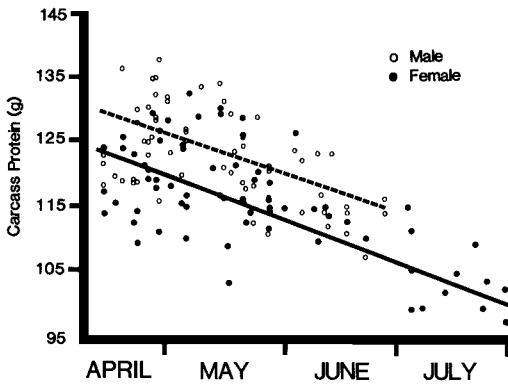
Fig. 2. Body protein composition by date for breeding male and female Ring-necked Ducks. Regressions significant at $P < 0.0001$.

expenditure of stored lipids, as noted in Mallard (Krapu 1981) and Wood Duck (Drobney 1982) hens. Birds may minimize the costs of obtaining reproductive protein requirements by timing laying to coincide with peak invertebrate abundance. This was suggested by a significant positive correlation between nonmollusc invertebrate biomass and the weight of female reproductive tissues (Hohman 1984).

Body weights are a useful index for examining nutrient changes in waterfowl (Bailey 1979, Raveling 1979, Wishart 1979, Ankney 1982, Drobney 1982). Body-weight data suggest that nutrient levels in Ring-necked Ducks entering reproduction may vary by year and by female age. Reduced reserves in females at the initiation of ovarian follicle growth increases reliance on exogenous sources for reproductive nutritional requirements. Deficiencies in female lipid reserve (i.e. lipid needed for egg production and energy costs associated with obtaining protein requirements) increase further the exogenous requirements for reproduction and may result in breeding adjustments such as altered time-activity patterns, delayed laying, or clutch-size reduction. Inadequate reserves coupled with reduced food availability could cause deferred breeding. Yearling females are lighter than adults early in the arrival period, and probably are more dependent than adults on food resources in wetlands used for nesting. Biomass and density of foods in these wetlands change seasonally and vary among years (Hohman 1984). Adult and yearling females entered reproduction in 1980 at reduced body weights, but available nutrients

(reserve + ambient food resources) apparently were inadequate for yearlings, most of which did not nest in 1980 (Hohman 1984).

The contribution of body reserves to reproduction was partially a function of nutrient levels attained during the arrival period. Whereas body weight during the arrival period was constant in 1980, weight gained before early May constituted over 50% (50% female, 62% male) of the total body-weight fluctuation observed in 1979. Before occupancy of the wetlands used for nesting, male and female diets consisted mostly of plant material, including seeds of native grasses and sedges, annual plants, and waste grain that birds gathered on temporally flooded wetlands (Hohman 1985). The rate of caloric intake by feeding Ring-necked Ducks was greater in temporary wetlands than in the semipermanent and permanent wetlands used for nesting. Deposition of lipids undoubtedly was facilitated by the use of high-carbohydrate plant foods, which were readily available in temporary wetlands. The lower body weights observed in 1980 were probably a consequence of drought, which reduced the area of temporary wetlands and, thereby, prevented access to seeds of wetmeadow vegetation.

Events occurring over winter and during migration also may influence the reserve status of returning birds. Ring-necked Ducks in southern Florida put on body fat and showed a constant weight gain through the wintering period (Hohman et al. 1986). The rate of increase was significantly greater in yearlings than adults, but varied annually. Yearlings in fall were initially lighter than adults, but body weights were equivalent by late winter. Ring-necked Ducks defer pairing until spring migration (Weller 1965) and, thus, simultaneously incur energetic costs of migration and courtship in March/April. Reductions in the body weight of returning birds from winter maxima presumably reflect these costs.

Similarities in the arrival body weights of males by age, and differences in adult and yearling female body weight (adult > yearling) early in the arrival period, suggest sex- and age-related differences in prearrival and arrival costs. Familiarity with food resources on staging and breeding areas may enable adult females to feed more efficiently than inexperienced yearling hens. Adult and yearling males following mates to their mates' natal areas were

presumably also naive regarding food resource availability in nesting wetlands and showed similar body weight changes. Krapu (1981) suggested that age-related differences in lipid reserve carried by Mallard females during the nesting season may result because inexperienced yearlings are less efficient at capturing invertebrates than adult females (i.e. incur greater energy costs). Differences in body weights of yearling and adult female Ring-necked Ducks, however, appeared before birds shifted to invertebrate foods.

Variation in the chronology of pairing also might account for initial differences in adult and yearling female body weight. Pair-bond formation entails costs and benefits that differ between the sexes. Males incur considerable energy costs during courtship and while attending mates. The advantages of early pair formation to the male, therefore, must be weighed against the risks of subsequent displacement by a bird in superior condition. Females benefit from mate attendance and may be ready to pair before males (Afton and Sayler 1982). Male investment probably is influenced by female quality. Thus, experienced females may obtain mates, and begin to accrue pairing benefits, before yearlings. Indeed, intensive courtship activity on nesting areas appears to involve primarily yearling individuals (Hohman unpubl. data). Extended courtship costs, or intrusions by unpaired males testing weak pair bonds and disrupting feeding, probably impair yearling female ability to accumulate nutrient reserves after their return to breeding areas.

Patterns of nutrient acquisition and allocation for ducks nesting in temperate regions, as evident in this study, may be more indeterminant than previously implied (Owen and Reinecke 1979). Waterfowl are long-lived occupants of variable environments and exhibit temporally dynamic reproductive strategies (Nichols et al. 1976). While ultimate control of factors such as clutch size and time of laying probably are genetically based (Batt and Prince 1979), expressed breeding patterns are the result of interplay between local environmental conditions (e.g. food availability) and the nutrient-reserve status of the parent. Changes in local environmental conditions or reserve status of the parent may result in altered, suboptimal breeding patterns. Studies that link the reproductive performance of individuals with

their environment are a necessary first step toward the interpretation of the broad pattern exhibited by the species (Drent and Daan 1980). Future research examining the bioenergetics of temperate-breeding waterfowl must consider the individual variation, as well as behavioral plasticity, in birds that enables individuals to adjust breeding patterns to changing environmental conditions.

LITERATURE CITED

AFTON, A. D., & R. D. SAYLER. 1982. Social courtship and pair bonding of Common Goldeneyes (*Bucephala clangula*) wintering in Minnesota. Can. Field-Natur. 96: 295–300.

ANDERSON, M. G., R. D. SAYLER, & A. D. AFTON. 1979. A decoy trap for diving ducks. J. Wildl. Mgmt. 44: 217–219.

ANKNEY, C. D. 1982. Annual cycle of body weight change in Lesser Snow Geese. Wildl. Soc. Bull. 10: 60–64.

———. 1984. Nutrient reserve dynamics of breeding and molting Brant. Auk 101: 361–370.

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

ASHCROFT, R. E. 1976. A function of the pair bond in the Common Eider. Wildfowl 27: 101–105.

BAILEY, R. O. 1979. Methods of estimating total lipid content in the Redhead Duck (*Aythya americana*) and an evaluation of condition indices. Can. J. Zool. 57: 1830–1833.

BARRY, T. W. 1962. Effect of late seasons on Atlantic Brant reproduction. J. Wildl. Mgmt. 26: 19–26.

BATT, B. D. J., & H. H. PRINCE. 1979. Laying dates, clutch size, and egg weight of captive Mallards. Condor 81: 35–41.

BLEM, C. R. 1976. Patterns of lipid storage and utilization in birds. Amer. Zool. 16: 671–684.

CALDWELL, P. J., & A. E. SNART. 1974. A photographic index for aging Mallard embryos. J. Wildl. Mgmt. 38: 298–301.

CONOVER, W. J. 1980. Practical nonparametric statistics. New York, John Wiley & Sons.

DIXON, W. J., & M. B. BROWN (Eds.). 1981. BMDP statistical software, P-series. Berkeley, Univ. California Press.

DOTY, H. G., & R. J. GREENWOOD. 1974. Improved nasal-saddle marker for Mallards. J. Wildl. Mgmt. 38: 938.

DRENT, R. H., & S. DAAN. 1980. The prudent parent: energetic adjustments in avian breeding. Ardea 68: 223–252.

DROBNEY, R. D. 1980. Reproductive bioenergetics of Wood Ducks. Auk 97: 480–490.

———. 1982. Body weight and composition changes and adaptations for breeding Wood Ducks. Condor 84: 300–305.

GOLLOP, J. B., & W. H. MARSHALL. 1954. A guide for aging duck broods in the field. St. Paul, Mississippi Flyway Council Tech. Sect. Rept.

HARVEY, J. M. 1971. Factors affecting Blue Goose nesting success. Can. J. Zool. 49: 223–234.

HOHMAN, W. L. 1984. Aspects of the breeding biology of Ring-necked Ducks (*Aythya collaris*). Unpublished Ph.D. dissertation, St. Paul, Univ. Minnesota.

———. 1985. Feeding ecology of Ring-necked Ducks in northwestern Minnesota. J. Wildl. Mgmt. 49: 546–557.

———, & T. S. TAYLOR. 1986. Indices of fat and protein for Ring-necked Ducks (*Aythya collaris*). J. Wildl. Mgmt. in press.

———, ———, & M. W. WELLER. 1986. Annual body weight change in Ring-necked Ducks (*Aythya collaris*). *In* Proc. Waterfowl in Winter Symp. (M. W. Weller, Ed.). Galveston, Texas.

KENDALL, M. D., P. WARD, & S. BACCHUS. 1973. A protein reserve in the pectoralis major flight muscle of *Quelea quelea*. Ibis 115: 600–601.

KING, J. R. 1973. Energetics of reproduction in birds. Pp. 78–107 *in* Breeding biology of birds (D. S. Farner, Ed.). Washington, D.C., Natl. Acad. Sci.

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.

LINDMEIER, J. P., & R. L. JESSEN. 1961. Results of capturing waterfowl in Minnesota by spotlighting. J. Wildl. Mgmt. 25: 430–431.

MENDALL, H. L. 1958. The Ring-necked Duck in the northeast. Orono, Univ. Maine Stud., 2nd Series No. 73.

NICHOLS, J. S., W. CONLEY, B. BATT, & A. R. TIPTON. 1976. Temporally dynamic reproductive strategies and the concept of r- and k-selection. Amer. Natur. 110: 995–1005.

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. Bookhut, Ed.). Madison, Wisconsin, Proc. Symp. North Central Section, The Wildlife Soc.

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

READER, R. J. 1978. Primary production in northern bog marshes. Pp. 53–62 *in* Freshwater wetlands: ecological processes and management potential (R. E. Good, D. F. Whigham, and R. L. Simpson, Eds.). New York, Academic Press.

REINECKE, K. J. 1977. The importance of freshwater invertebrates and female energy reserves for Black Ducks breeding in Maine. Unpublished Ph.D. dissertation, Orono, Univ. Maine.

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

RICKLEFS, R. F. 1974. Energetics of reproduction in birds. Pp. 152–292 *in* Avian energetics (R. A. Paynter, Jr., Ed.). Publ. Nuttall Ornithol. Club No. 15.

ROMANOFF, A. L., & A. J. ROMANOFF. 1949. The avian egg. New York, John Wiley & Sons.

RYDER, J. P. 1967. The breeding biology of Ross' Goose in the Perry River region, Northwest Territories. Can. Wildl. Serv. Rept. Ser. No. 3.

———. 1970. A possible factor in the evolution of clutch size in Ross' Goose. Wilson Bull. 82: 5–13.

SARVIS, J. E. 1972. The breeding biology and ecology of Ring-necked Ducks in northern Michigan. Unpublished M.S. thesis, Logan, Utah State Univ.

TOME, M. W. 1984. Changes in nutrient reserves and organ size in female Ruddy Ducks breeding in Manitoba. Auk 101: 830–837.

WEISBERG, S. 1981. Applied linear regression. New York, John Wiley & Sons.

WELLER, M. W. 1956. A simple field candler for waterfowl eggs. J. Wildl. Mgmt. 20: 111–113.

———. 1957. An automatic nest-trap for waterfowl. J. Wildl. Mgmt. 21: 456–458.

———. 1965. Chronology of pair formation in some nearctic *Aythya* (Anatidae). Auk 82: 227–235.

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