The Condor 88:290–296

INCUBATION RHYTHMS OF RING-NECKED DUCKS[1]

WILLIAM L. HOHMAN[2]
Delta Waterfowl and Wetland Research Station, Rural Route 1, Portage la Prairie, MB R1N 3A1, Canada

Abstract. Incubation behavior of Ring-necked Ducks (*Aythya collaris*) was studied in northwestern Minnesota from 1978 to 1980. Incubation constancy was similar for all birds (85%), but recess duration and frequency differed for females nesting along cattail/open water edges ($\bar{x}$ = 47 min, 5.1 recesses/day) and in flooded sedge meadow ($\bar{x}$ = 73 min, 2.7 recesses/day) away from open-water feeding areas. Timing of recesses also was influenced by nest site location. Nest attentiveness of Ring-necked Ducks apparently is influenced by nutrient reserve levels in females at the onset of incubation and food availability in wetlands used by breeding birds. My findings are consistent with Afton's (1979, 1980) prediction that in smaller species, environmental factors increasingly affect anatid incubation rhythms, and they generally support his conclusion that the relationship of fasting endurance to body size has been very important in the evolution of avian incubation behavior.

Key words: Ring-necked Ducks; Aythya collaris; *ecology, behavior; reproductive biology; incubation.*

INTRODUCTION

The behavior of birds during incubation is an important aspect of their subsequent reproductive performance and success. Individuals may improve hatching success by increasing nest attentiveness; however, investment by the parent(s) to meet the needs of developing embryos and to enhance hatching success must be weighed against risks (e.g., predation, dehabilitation, or starvation) to future reproductive performance.

Ducks, geese, and swans (Anseriformes) exhibit a wide range of incubation strategies (Kear 1970). Eggs laid parasitically by some anatids (e.g., Black-headed Ducks, *Heteronetta atricapilla*; Ruddy Ducks, *Oxyura jamaicensis*; and Redheads, *Aythya americana* are incubated by host species. Males and females share incubation in Magpie Geese (*Anseranas semipalmata*), Whistling-Ducks (Dendrocygnini) and some swans (Anserini), but females incubate without male assistance in 133 of 144 extant waterfowl species (Kear 1970). Whereas large waterfowl species such as the Canada Goose (*Branta canadensis*) utilize endogenous nutrient reserves and incubate at high constancy (Cooper 1978, Raveling 1979, Aldrich and Raveling 1983), nest attentiveness of small waterfowl species is generally lower because they have reduced capabilities for storage of nutrient reserves and must recess to feed. Limited fasting endurance led Afton (1980) to predict that in smaller, as compared with larger, anatids environmental factors should have more effect on incubation rhythms.

Ring-necked Ducks (*Aythya collaris*) are small-bodied (500 to 900 g) inland diving ducks. They commonly nest in northern bog marshes, wetlands characterized by low primary production (Reader 1978). This paper examines the behavior of incubating Ring-necked Ducks and relates incubation behavior to the breeding biology of the species.

STUDY AREA AND METHODS

Breeding Ring-necked Ducks were studied from 1978 to 1980 on Roseau River Wildlife Management Area (WMA) in northwestern Minnesota. Roseau River WMA is an impoundment situated on the bed of glacial Lake Agassiz in the prairie/boreal-forest transition. The management unit was described in detail by Hansen et al. (1980).

The return of Ring-necked Ducks to northwestern Minnesota in early April coincides with rapid snow melt and sheet-water formation on agricultural fields (Hohman 1984). Laying is initiated from mid-May to mid-June with broods usually appearing by the fourth week of June. Nests are constructed over water along cattail/open water edges and in flooded sedge meadow away (0.5 to 2 km) from open water feeding areas.

Nests were located by watching females fly to their nests or by flushing hens during systematic searches of the study area. Ring-necked Duck eggs require, on average, 26 days incubation to hatch, with hen and brood usually departing from the nest on the day after hatch (Mendall 1958). Day of incubation was estimated by back-dating from hatching date. Terminology (i.e., incubation constancy, nest attentiveness, recess frequency and length,

[1] Received 20 May 1985. Final acceptance 25 October 1985.
[2] Present address: Department of Fisheries and Wildlife, University of Minnesota, 1980 Folwell Ave., St. Paul, MN 55108, USA.

TABLE 1. Incubation rhythm components of nine Ring-necked Duck females recorded in northwestern Minnesota, 1978 to 1980. Components given are for all nests combined, and by two habitat types.

Component	Mean	SE	Median	*n*	Range
Incubation constancy (% of day)	85.2	0.4	85.4	197	68.7–100
Sedge meadow	86.1	0.4	86.7	142	69.8–98.6
Open-water edge	83.1	0.9	84.0	55	68.7–100
Total time off nest per day (min)	212.7	6.0	210	197	0–450
Sedge meadow	200.6	6.0	192	142	20–435
Open-water edge	244.0	12.8	230	55	0–450
Recess frequency per day	3.4	0.1	3	197	0–9
Sedge meadow	2.7	0.1	3	142	1–7
Open-water edge	5.1	0.2	5	55	0–9
Duration of all recesses (min)	62.4	1.2	60	716	5–315
Sedge meadow	73.1	1.7	70	421	5–315
Open-water edge	47.1	1.2	45	295	10–120
Duration of AM recesses (min)	52.5	1.4	55	307	5–170
Sedge meadow	57.1	2.1	60	163	5–170
Open-water edge	47.3	1.6	45	144	10–120
Duration of PM recesses (min)	69.8	1.8	65	409	5–315
Sedge meadow	83.2	2.3	78	258	5–315
Open-water edge	46.9	1.6	45	151	10–115
Session duration (min)	365.0	11.2	267	708	10–2,095
Sedge meadow	459.8	15.1	395	414	15–1,560
Open-water edge	231.5	13.1	155	294	10–2,095

session length) used in this paper follows that of Afton (1980).

Presence or absence at the nest was detected and recorded using a remote infrared thermistor sensor system (Cooper and Afton 1981). Only data from complete day records were used to calculate constancy and frequency of recesses/day. The relationship between day of incubation and incubation rhythm components (nest attentiveness, recess frequency, recess length, and session length) was examined for the complete data set by using simple correlation analysis. The distribution of recess initiation times by habitat or year was compared using a two-sided k-sample Smirnov test (Conover 1980). Multiple and pair-wise statistical comparisons were performed using Kruskal-Wallis rank sums multiple comparisons tests and Mann-Whitney U-tests, respectively (Conover 1980).

RESULTS

Eleven nest records were obtained from nine Ring-necked Duck females. Nest attentiveness of one hen was monitored in three consecutive years. An average of 18 complete day records (median = 20; range, 8 to 22 complete day records) were obtained per female. All monitored nests were successful first-nest attempts initiated between 18 May and 22 June.

Incubation constancy averaged 85%, but frequency, timing, and duration of recesses varied greatly among individual hens (Table 1). No significant correlations were found between the day of incubation and incubation rhythm components: nest attentiveness, recess frequency, recess length and session length ($P > 0.05$).

Ring-necked Duck incubation rhythms appeared to be influenced by nest site location. Birds incubated at similar constancy at cattail/open-water edge and sedge-meadow nest sites ($P > 0.05$), but females nesting at cattail/open-water edge sites adjacent to feeding areas recessed more frequently ($P < 0.05$) for shorter durations ($P < 0.05$) than did females nesting in sedge meadow (Table 1). Timing of recesses was also influenced by nest site location ($P < 0.01$). Females nesting at cattail/open-water edge sites tended to recess during daylight hours, while sedge-meadow nesters generally took a predawn recess and one or two recesses from 1200 to 2200 (Fig. 1). Morning recesses were shorter than those taken in the afternoon for sedge-meadow-nesting birds ($P < 0.001$).

Incubation rhythms for a single individual nesting in sedge meadow (1978, 1979, and 1980) varied from year to year (Table 2, Fig. 2). Incubation constancy was lower in 1980 than that recorded in the two previous years ($P < 0.05$). Whereas frequency of recesses/day was similar in all years ($P < 0.05$), recess length increased significantly in 1980 ($P < 0.001$). Timing of recesses also changed annually ($P < 0.02$). This female took predawn recesses during 1979 and 1980, but only diurnal recesses in 1978 (Fig. 2).

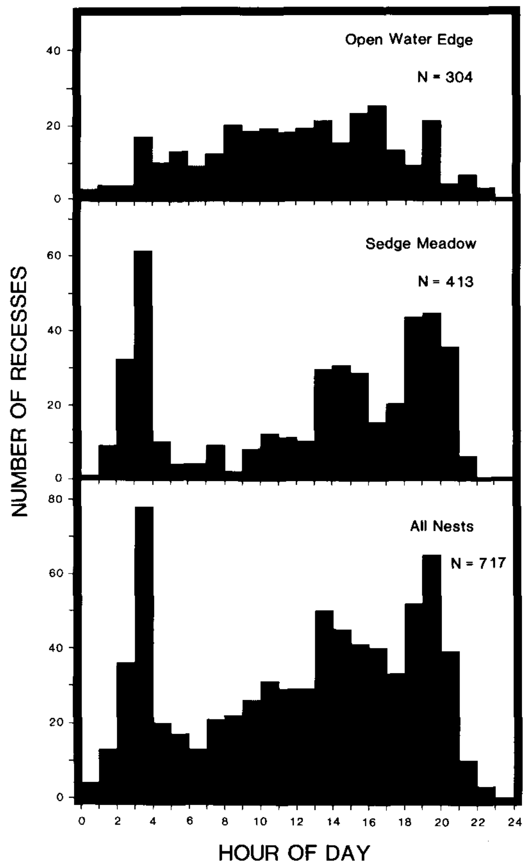

FIGURE 1. Distribution of recess initiation times for Ring-necked Duck females nesting in cattail/open-water edge and sedge-meadow sites.

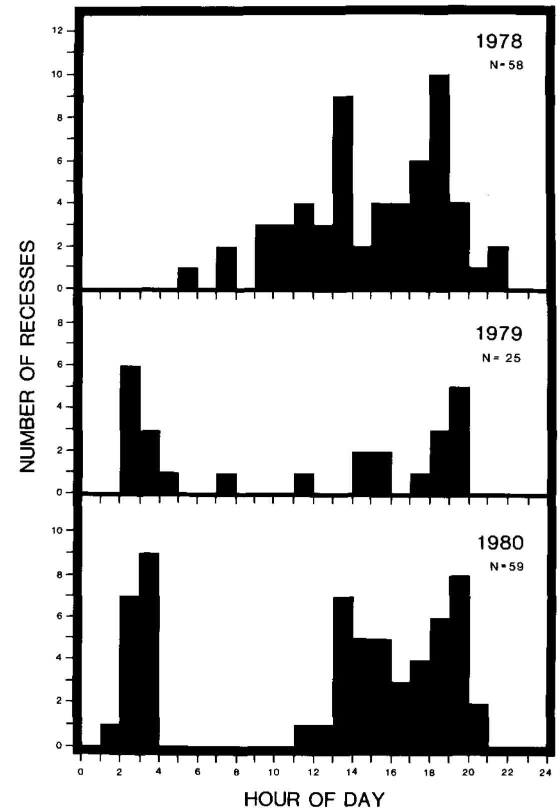

FIGURE 2. Distribution of recess initiation times for an individual Ring-necked duck female monitored in three consecutive years, 1978 to 1980.

DISCUSSION

Incubation constancy for Ring-necked Ducks (this study) is similar to that reported (Afton 1980, Ringelman et al. 1982) for Northern Shovelers (*Anas clypeata*) and American Black Ducks (*A. rubripes*). Captive Trumpeter Swans (*Cygnus buccinator*), Canada Geese, Wood Ducks (*Aix sponsa*), and captive Mallard Ducks (*Anas platyrhynchos*) incubate at greater than 90% constancy (Stewart 1962; Caldwell and Cornwell 1975; Cooper 1978, 1979). Lesser Snow Geese (*Chen caerulescens*) and Common Eider (*Somateria mollisima*), which fast during incubation (Milne 1976, Ankney and MacInnes 1978), also probably incubate at high constancy (>90%); however, Green-winged Teal (*Anas crecca carolinensis*), Blue-winged Teal (*Anas discors*), Redheads, Ruddy Ducks, and Maccoa Ducks (*Oxyura maccoa*) incubate at less than 82% constancy (Low 1945, Miller 1976, Siegfried et al. 1976, Afton 1978). Estimates of incubation constancy for Common Goldeneyes (*Bucephala clangula*) range from 75% (Siren 1952) to 85 to 89% (Semenov-Tyan-Shanski and Bragin 1969).

Except for Black Ducks, Redheads, and cavity nesters such as Wood Ducks and Common Goldeneyes, nest attentiveness of anatids increases with body size, as observed by Afton (1980). In general, birds have a substantial capability for storage and utilization of energy reserves, primarily in the form of fat (Blem 1976). Large waterfowl species have a proportionately greater capacity for fat storage and retain sufficient reserves after laying to maintain body metabolism throughout incubation (Ankney 1984). Perhaps equally important, large body size may enable individuals to defend themselves and their eggs against potential predators. Other factors, especially availability of food to females during incubation, influence incubation behavior as well. Continuous incubation is important in tundra-nesting waterfowl in preventing nest loss to avian predators (Ryder 1970, Harvey 1971, MacInnes et al. 1974). Body reserves of Brant (*Branta bernicla*) at the onset of incubation are insufficient to permit constant incubation (Ankney 1984). Brant delay reproduction and nest in areas that provide new green vegetation. This enables recessing females to feed near the nest while remaining vigilant against potential nest predators (Ankney 1984). Fa-

TABLE 2. Incubation rhythm components of an individual Ring-necked Duck hen monitored in three consecutive years (1978–1980) in northwestern Minnesota.

Component	Mean ± SE 1978	1979	1980
Incubation constancy (% of day)	87.6 ± 0.9	86.7 ± 1.1	82.5 ± 0.9
n	22	8	22
Recess frequency per day	2.3 ± 0.2	2.6 ± 0.2	2.6 ± 0.1
n	22	8	22
Duration of all recesses (min)	76.3 ± 3.0	72.0 ± 3.7	97.7 ± 3.3
n	58	25	59
Session duration (min)	534.7 ± 54	515.2 ± 58	459.6 ± 37
n	55	24	59

vorable nest microhabitat (i.e., lower rate of egg cooling) and reduced predation risks presumably allow cavity nesters to spend more time away from the nest, but high nest attentiveness (93%) relative to body size in Wood Ducks may shorten the incubation period (Breckenridge 1956) and also may be important in repelling parasitic laying attempts by other hens (Clawson et al. 1979). Food resources consumed by recessing Wood Duck hens must be abundant and of high quality to permit constancy at such high levels because, in spite of high nest attentiveness, weight loss by Wood Duck hens during incubation (11%) is less than that reported for other anatids (Drobney 1982, Gatti 1983). Ringelman et al. (1982) attributed low constancy (86%) in Black Ducks to small endogenous energy reserves and the increased foraging time required by females nesting in wetlands with low food density. Because of limited metabolic reserve capacity and specialized feeding habits, Northern Shovelers incubate at only 85% constancy (McKinney 1970, Afton 1980). Redheads are semiparasitic egg-layers; lower constancy (73%) in this species may be related to high levels of disturbance at the nest and reduced maternal investment in the incubated clutch, as well as environmental factors (Low 1945).

I believe that incubation constancy of Ring-necked Ducks is strongly influenced by nutrient reserve levels at the onset of incubation and food availability in the wetlands used during recesses. Ring-necked Duck females deplete nutrient reserves during laying and thus are almost entirely dependent during incubation on ambient food resources for their metabolic requirements (Hohman 1986). Ring-necked Duck females feed intensively during incubation recesses, as do other small-bodied waterfowl. The proportion of time spent feeding by recessing Black Duck (Seymour and Titman 1981), Mallard (Titman 1981), Blue-winged Teal (Miller 1976), and Northern Shoveler (Afton 1979) hens averaged from 60% to 90%, whereas Ring-necked Duck females fed 57% of the time they were off the nest (W. L. Hohman, unpubl.). The diet of Ring-necked Duck females during incubation consisted mostly of invertebrate foods, especially caddisflies (Trichoptera), whose density and biomass changed seasonally and annually (Hohman 1984, 1985). My hypothesis that environmental food resources and body condition of Ring-necked Duck females influence incubation constancy is supported by annual variation in nest attentiveness of an individual female. Nest attentiveness for this female was significantly reduced in 1980, a year in which birds entered reproduction at reduced body weights and remained lighter throughout reproduction, and invertebrate biomass during the period birds were incubating (June) was depressed (Hohman 1984, 1986).

Evidence linking nutrient reserve levels in incubating females to their nest attentiveness is available for several other waterfowl species. Diurnal recess time of Redheads during drought years was 25% greater than that observed during a wet year (Sayler 1985). Sayler (1985) attributed lower nest attentiveness during drought to reduced food abundance and lower endogenous reserves in breeding Redhead females. Female Canada Geese nesting for the first time began incubation at a lighter body weight and were less attentive than experienced females (Aldrich and Raveling 1983). Renesting waterfowl have depleted energy reserves (Krapu 1974, Krapu 1981) and incubate at lower constancy than initial-nesting birds (Low 1945, Afton 1978, Afton 1980). Gatti (1983) found seasonal and annual variation in body weight loss by incubating Mallards and speculated that condition of females at the onset of incubation may be an important factor affecting nest attentiveness.

Ambient temperature was the most important factor affecting Mallard incubation rhythms (Caldwell and Cornwell 1975). Afton (1980) suggested that Northern Shoveler hens remained at the nest from 1000 to 1300 to protect the eggs from solar radiation and high midday temperatures, which could kill the embryos (Snart 1970). Heavy rainfall modified incubation rhythms of both Mallards and Northern Shovelers (Caldwell and Cornwell 1975, Afton 1980). These environmental factors (ambient temperature, solar radiation and rainfall) appear to have relatively little effect on Ring-necked Duck incubation rhythms. Ring-necked Duck females recessed at night (2200 to 0500) when ambient temperatures were lowest and at midday when solar radiation was most intense. Moreover, I have observed incubating females recessing during moderate rain showers.

Timing of recesses may be influenced by the behavior of their invertebrate prey. Northern Shovelers feed extensively on planktonic crustaceans, Cladocera (Swanson and Nelson 1970, Swanson and Sargeant 1972), many of which undergo diel vertical migrations within the water column (Cushing 1951). Recesses taken before sunrise and at sunset by Northern Shovelers may be a response to higher food availability (Afton 1980). Invertebrates eaten by incubating Ring-necked Ducks are not known to show diel migrations, but females recessing before sunrise and at sunset may feed opportunistically on emerging insects. Peak feeding activity of breeding ducks on a northern Swedish lake coincided with periods of chironomid emergence (Sjöberg and Danell 1982). Swanson and Sargeant (1972) noted that nighttime (2100 to 0400) feeding activity of ducks breeding in the prairies of North Dakota appeared to be correlated with time and intensity of chironomid and mayfly (Ephemeroptera) emergences.

Predation also may influence incubation behavior of Ring-necked Ducks. Low recess frequency and initiation of recesses when light is dim may be advantageous for Northern Shovelers in reducing the likelihood that a predator would discover the nest by sight (Afton 1980). Patterns of recess initiation times for Ring-necked Ducks nesting in the sedge-meadow and Northern Shovelers (Afton 1980) are similar. Ring-necked Ducks nesting in sedge-meadow must fly to and from feeding areas and may be subject to predator constraints similar to those of nesting Northern Shovelers. Females nesting at the cattail/open-water edge recess throughout daylight hours. They may be able to do so because they can swim to feeding areas and, therefore, may be less susceptible to predator detection.

Although birds incubated at similar constancy in both habitats, costs of incubation probably differ for cattail/open-water edge and sedge-meadow-nesting females. Because of rapid egg cooling and the inefficiency of rewarming eggs (Drent 1973), the incubation pattern followed by cattail/open-water nesting birds of frequent, short recesses is probably more energy costly than that of sedge-meadow nesters (i.e., infrequent, long recesses). Recessing during daylight hours when ambient temperatures are elevated and covering eggs with nest material may help reduce the rate of egg cooling (Caldwell and Cornwell 1975). Moreover, females nesting adjacent to open-water feeding sites may benefit through lower costs (time and energy) moving to and from feeding areas. Ringelman et al. (1982) found differences between the incubation rhythms of Black Ducks nesting near wetlands and at upland sites. Hens nesting at upland sites took less frequent but longer recesses than wetland nesters. The rate of energy expenditure by Black Ducks in flight is over ten times greater than the estimated cost of incubating and rewarming a clutch (42.7 vs. 3.8 kcal/hr). Ringelman et al. (1982) hypothesized that upland-nesting birds compensate for increased flight costs by taking fewer, longer recesses.

Ruddy Duck nests are constructed over water in stands of emergent vegetation in semipermanent/permanent wetlands (Gray 1980). Like cattail/open-water-edge nesting Ring-necked Ducks, incubation rhythms of Ruddy Duck females are characterized by frequent, short recesses (Siegfried et al. 1976, Cooper and Afton 1981). Siegfried et al. (1976) suggested that 30 to 60 min was adequate for Ruddy Ducks to feed to the capacity of the esophagus and proventriculus, but this probably is not true for Ring-necked Ducks. My estimates of food consumption rate for Ring-necked Ducks are one-third to one-half those reported for Ruddy Ducks (Gray 1980, Tome 1981, Hohman 1985). Nonetheless, because of their proximity to open water feeding areas, females nesting at edge sites probably are able to better assess changes in food availability and exploit temporal abundances of foods (e.g., emerging insects). Disturbance from other birds using the open water area (e.g., courting males) also may influence incubation patterns of edge nesters.

If hens nesting at the edge of open-water feeding areas are able to minimize behavioral costs and optimize foraging (and thereby reduce risks of dehabilitation or starvation) while maintaining incubation constancy, then why do birds nest in the sedge meadow? Unfortunately, I lack sufficient data to assess the relative success of birds nesting in the two habitats, but I speculate that nests located at the cattail/open-water edge are subject to greater risks of predation than nests dispersed in the sedge meadow. Gates and Gysel (1978), studying nest dispersion, clutch size and fledging success of 21 species of passerines in relation to field-forest ecotones, found increased predation rate with decreased distance from edge. This they attributed primarily to a functional response by predators to greater nest density and predator activity in the vicinity of habitat discontinuities. The raccoon (*Procyon lotor*) is an important predator on nests of Ring-necked Ducks (W. L. Hohman, unpubl.) as well as those of other over-water-nesting waterfowl species (Stoudt 1982). In upland habitats, raccoon foraging activity focuses on ecotonal areas (Bider 1968). Advantages associated with nesting away from ecotonal areas, however, may be offset by increased mortality of offspring after hatch, e.g., duckling mortality resulting from long distance brood movements (Ringelman et al. 1982). I propose that reserve levels of birds entering reproduction influence nest site selection and predispose some individuals (those with low metabolic reserves) to take greater risks (i.e., select nest sites close to open-water feeding areas). Female experience also may influence incubation rhythms (Aldrich and Raveling 1983) and settlement patterns.

In conclusion, environmental factors play an important role in shaping Ring-necked Duck incubation strategies. Because of body size constraints on nutrient storage capabilities, environmental factors impacting female nutrient reserve levels at the onset of incubation and female energy expenditure during incubation are especially influential on the incubation behavior of small waterfowl species (Afton 1980).

ACKNOWLEDGMENTS

I am grateful to R. D. Crawford, L. L. Hawkins and M. W. Weller for their helpful comments on earlier drafts of the manuscript. I was assisted in the field or laboratory by J. Barzen, D. Carlson and J. Dixon. J. A. Cooper generously shared his nest monitoring equipment with me. Financial support was provided by the North American Wildlife Foundation through the Delta Waterfowl and Wetlands Research Station, by the Minnesota Department of Natural Resources, by the University of Minnesota Department of Fisheries and Wildlife, Computing Center, Agricultural Experiment Station, and Graduate School, and by the Minnesota Waterfowl Association.

LITERATURE CITED

AFTON, A. D. 1978. Incubation rhythms and egg temperatures of an American Green-winged Teal and renesting Pintail. Prairie Nat. 10:115–119.

AFTON, A. D. 1979. Time budget of breeding Northern Shovelers. Wilson Bull. 91:42–49.

AFTON, A. D. 1980. Factors affecting incubation rhythms of Northern Shovelers. Condor 82:132–137.

ALDRICH, T. W., AND D. G. RAVELING. 1983. Effects of experience and body weight on incubation behavior of Canada Geese. Auk 100:670–679.

ANKNEY, C. D. 1984. Nutrient reserve dynamics of breeding and molting Brant. Auk 101:361–370.

ANKNEY, C. D., AND C. D. MACINNES. 1978. Nutrient reserves and reproductive performance of female Lesser Snow Geese. Auk 95:459–471.

BIDER, J. R. 1968. Animal activity in uncontrolled terrestrial communities as determined by sand transect technique. Ecol. Monogr. 38:269–308.

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

BRECKENRIDGE, W. J. 1956. Nesting study of Wood Ducks. J. Wildl. Manage. 20:16–21.

CALDWELL, P. J., AND G. W. CORNWELL. 1975. Incubation behavior and temperatures of the Mallard Duck. Auk 92:706–731.

CLAWSON, R. L., G. W. HARTMAN, AND L. H. FREDRICKSON. 1979. Dump nesting in a Missouri Wood Duck population. J. Wildl. Manage. 43:347–355.

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

COOPER, J. A. 1978. The history and breeding biology of Canada Geese of Marshy Point, Manitoba. Wildl. Monogr. No. 61.

COOPER, J. A. 1979. Trumpeter Swan nesting behaviour. Wildfowl 30:55–71.

COOPER, J. A., AND A. D. AFTON. 1981. A multiple sensor system for monitoring avian nesting behavior. Wilson Bull. 93:325–333.

CUSHING, D. H. 1951. The vertical migration of planktonic crustacea. Biol. Rev. 26:158–192.

DRENT, R. H. 1973. The natural history of incubation, p. 262–311. *In* D. S. Farner [ed.], Breeding biology of birds. National Academy of Sciences, Washington, DC.

DROBNEY, R. D. 1982. Body weight and composition changes and adaptations for breeding Wood Ducks. Condor 84:300–305.

GATES, J. C., AND L. W. GYSEL. 1978. Avian nest dispersion and fledging success in field-forest ecotones. Ecology 59:871–883.

GATTI, 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. Ph.D.diss., Univ. of California, Davis.

HANSEN, J. L., J. M. PARKER, AND K. R. HENNINGS. 1980. Roseau River Wildlife Management Area Master Plan, 1980–89. Minnesota Department of Natural Resources, St. Paul.

HARVEY, J. M. 1971. Factors affecting Blue Goose nesting success. Can. J. Zool. 61:565–569.

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

HOHMAN, W. L. 1985. Feeding ecology of Ring-necked Ducks in northwestern Minnesota. J. Wildl. Manage. 49:546–557.

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

KEAR, J. 1970. The adaptive radiation of parental care in waterfowl, p. 357–392. *In* J. H. Crook [ed.], Social behavior in birds and mammals. Academic Press, New York.

KRAPU, G. L. 1974. Feeding ecology of Pintail hens during reproduction. Auk 91:278–290.

KRAPU, G. L. 1981. The role of nutrient reserves in Mallard reproduction. Auk 98:29–38.

LOW, J. B. 1945. Ecology and management of the Redhead, *Nyroca americana,* in Iowa. Ecol. Monogr. 15: 35–69.

MACINNES, C. D., R. A. DAVIS, R. N. JONES, B. C. LIEFF, AND A. J. PAKULAK. 1974. Reproductive efficiency of McConnell River small Canada Geese. J. Wildl. Manage. 38:686–707.

McKinney, F. 1970. Displays of four species of blue-winged ducks. Living Bird 9:29–64.

Mendall, H. L. 1958. The Ring-necked Duck in the Northeast. Univ. of Maine Studies, Second Series 73.

Miller, K. J. 1976. Activity patterns, vocalizations, and site selection in nesting Blue-winged Teal. Wildfowl 27:33–43.

Milne, H. 1976. Body weights and body composition of the Common Eider. Wildfowl 27:115–122.

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, p. 53–62. *In* R. E. Good, D. F. Whigham, and R. L. Simpson [eds.], Freshwater wetlands: ecological processes and management potential. Academic Press, New York.

Ringelman, J. K., J. R. Longcore, and R. B. Owen, Jr. 1982. Nest and brood attentiveness in female Black Ducks. Condor 84:110–116.

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

Sayler, R. D. 1985. Brood parasitism and reproduction of Canvasbacks and Redheads on the Delta Marsh. Ph.D.diss., University of North Dakota, Grand Forks.

Semenov-Tyan-Shanski, O. I., and A. B. Bragin. 1969. Incubation conditions for some precocial birds in the subarctic. Byull. Mosk. O-Va. Ispyt. Prir. Otd. Biol. 74:50–66.

Seymour, N. R., and R. D. Titman. 1981. Changes in activity patterns, agonistic behavior and territoriality of Black Ducks (*Anas rubripes*) during the breeding season in a Nova Scotia tidal marsh. Can. J. Zool. 56:1773–1785.

Siegfried, W. R., A. E. Burger, and P. J. Caldwell. 1976. Incubation behavior of Ruddy and Maccoa ducks. Condor 78:512–517.

Siren, M. 1952. Undersökningar över knipans, *Bucephala clangula,* fortplantningbiologi, Riistatiet. Julkaisuja 8:101–111.

Sjöberg, K., and K. Danell. 1982. Feeding activity of ducks in relation to diel emergence of chironomids. Can. J. Zool. 1383–1387.

Snart, A. E. 1970. The effects of heat on Mallard embryos. M.S.thesis, Univ. of Florida, Gainesville.

Stewart, P. A. 1962. Nest attentiveness and incubation period of a Wood Duck, J. Field Ornithol. 33:85–89.

Stoudt, J. H. 1982. Habitat use and productivity of Canvasbacks in southwestern Manitoba, 1961–1972. U.S. Fish Wildl. Serv. Spec. Publ. No. 248.

Swanson, G. E., and H. K. Nelson. 1970. Potential influence of fish-rearing programs on waterfowl breeding habitat, p. 65–71. *In* E. Schneberger [ed.], A symposium on the management of midwestern winterkill lakes. Am. Fish. Soc., North Central Div., Spec. Publ.

Swanson, G. A., and A. B. Sargeant. 1972. Observation of nighttime feeding behavior of ducks. J. Wildl. Manage. 36:959–961.

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

Tome, M. W. 1981. The reproductive bioenergetics of female Ruddy Ducks in Manitoba. M.S.thesis, Univ. of Maine, Orono.