

DIURNAL ACTIVITY BUDGET OF FEMALE RUDDY DUCKS BREEDING IN MANITOBA

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ABSTRACT.—I observed activities of pre-laying, laying, and incubating female Ruddy Ducks (*Oxyura jamaicensis*). Foraging comprised 66.3% and 54.4% of diurnal activities during pre-laying and laying, respectively. Time spent resting increased from 11.0% during pre-laying to 73.5% during incubation, primarily because of time spent on the nest. Female Ruddy Ducks took 7.4 ± 3.2 incubation recesses during a 24-h period and recesses averaged 39 ± 4 min (mean \pm SD). Foraging comprised 76.4% of recesses and accounted for 185.0 min of foraging/day. Female Ruddy Ducks meet most of their energy needs exogenously. Their pattern of energy acquisition for and allocation to reproduction supports the general hypothesis that smaller-bodied waterfowl can store less nutrient reserve than large-bodied waterfowl and must rely more on exogenous energy during reproduction. Received 15 June 1990, accepted 3 Nov. 1990.

Comparative studies of waterfowl behavior and energetics during reproduction indicate that females of different waterfowl species have evolved various patterns of energy/nutrient acquisition and allocation which decrease daily dietary requirements for reproduction during peak periods of energy/nutrient demand (Ricklefs 1974). To meet energy/nutrient demands of egg laying and incubation, some species store lipid and/or protein before arrival on breeding areas (Korschgen 1977, Ankney and MacInnes 1978, Raveling 1979, Krapu 1981), whereas others acquire energy/nutrients after arrival on breeding areas (Drobney 1980, 1982; Tome 1984; Brown and Fredrickson 1987a; Ankney and Afton 1988; Hohman 1986) and catabolize these reserves during laying and incubating. Female waterfowl adjust their activities during reproduction to meet changes in energy demands (Afton 1979, Gray 1980, Hohman 1986, Brown and Fredrickson 1987b).

Female Ruddy Ducks (*Oxyura jamaicensis*) produce eggs that are among the largest proportional to body size of all waterfowl (Lack 1968). Nonetheless, they meet most of their energy needs through dietary intake on the breeding grounds (Tome 1984). In this paper, I describe diurnal activity budgets of female Ruddy Ducks during pre-laying, laying, and incubating and discuss how their behavior relates to their energy/nutrient acquisition for and allocation to reproduction.

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STUDY AREA AND METHODS

I derived activity-budgets of female Ruddy Ducks breeding in the prairie-pothole region of southwestern Manitoba, approximately 16 km southeast of Minnedosa, during the spring and summers of 1979–1980. Topography in this region is a knob and kettle land-type interspersed with numerous wetlands ranging in size from permanent (>4 ha) ponds to small (<10 m²) seasonal sloughs. This area was described in detail by Evans et al. (1952).

I used focal animal observations (Altmann 1974) to sample activities of female Ruddy Ducks during pre-laying, laying, and incubating. All birds observed (N = 12) were individually marked with impied (Wright 1939) colored tail feathers or were recognized by unique plumage characteristics. An electronic metronome (Wiens et al. 1970) was used to delineate sampling points at 15-sec intervals. I also measured the duration of the first dive and dive-pause during feeding bouts. I recorded the behavior of a bird chosen at random from among those available for observation during 2-h periods that I systematically scheduled three times each day. All daylight hours were sampled every five days. I determined each bird's reproductive status by locating its nest, determining the stage of incubation, and back-dating to each observation date.

I categorized behaviors of female Ruddy Ducks as (1) rest (sleep, loaf, incubate), (2) comfort (preen, wing stretch, etc.), (3) alert, (4) swim, (5) bathe, (6) dive, (7) dive-pause (time spent between dives), and (8) social (courtship displays, chases, agonistic behavior, etc.). A small (4–6 g) transmitter was attached to the central three rectrices of three birds. I monitored signal attenuation when birds dived and thus recorded nocturnal feeding. The transmitters fell off after 3–5 days, so I collected only limited nocturnal data.

I observed the behavior of three females on the nest during incubation and during recesses; I derived diurnal activity budgets during incubation from these females. I observed six other incubating females during recesses only. I used the observations of these and the previous three females to determine behavior during recesses. I measured nest attentiveness (amount of time spent incubating) and number, duration, and time of incubation recess (definitions after Afton 1980) of five females with a nest monitor that recorded presence or absence of the female on the nest (Cooper and Afton 1981). I obtained a complete 24 day record for one female; the other nests were monitored for 20, 17, 12, and 11 days, respectively. Incomplete records resulted because nests were depredated or found several days into incubation.

Percentage of time engaged in each activity was calculated by dividing the number of times an activity was observed by the total number of observations in an observation session. Only observation sessions of at least one h were included in the analysis except for the analysis of recesses which, because they were <one h, were all included in this calculation.

Differences in percent time engaged in each activity among pre-laying, laying, and incubating were detected with Kruskal-Wallis tests (Conover 1980). Behavior during recesses was not included in the analysis. If differences among behaviors were detected, the non-parametric analog to the Least-Significant Difference multiple comparison test was employed to determine where differences occurred (Conover 1980). Differences were considered significant at $P \leq 0.05$.

RESULTS

Percent time engaged in various activities differed among reproductive periods (Table 1). Dive and dive-pause (foraging) activities were dominant during pre-laying and laying. Time spent diving was greater during pre-laying than during laying ($P \leq 0.05$); however, the dive-pause activity

TABLE 1
DIURNAL TIME-ACTIVITY BUDGET (PERCENT TIME \pm SD) FOR BREEDING FEMALE RUDDY DUCKS

Behavior	Pre-laying N = 41 h	Laying N = 15 h	Incubating	
			N = 22 h	N = 42 recesses
Rest	11.0 \pm 2.4 A ^a	23.4 \pm 6.0 B	73.5 \pm 7.1 C	2.2 \pm 0.1
Preen	9.3 \pm 1.4 A	9.2 \pm 2.2 A	10.7 \pm 2.5 A	9.9 \pm 0.2
Alert	1.4 \pm 0.3 B	tr A	tr A	0.4 \pm 0.01
Swim	10.0 \pm 1.5 B	9.6 \pm 1.7 B	0.6 \pm 0.2 A	3.6 \pm 0.1
Bath	1.0 \pm 0.1 A	1.1 \pm 0.3 A	1.1 \pm 0.6 A	6.3 \pm 0.4
Dive	44.1 \pm 2.6 C	32.5 \pm 6.0 B	8.4 \pm 0.8 A	46.7 \pm 0.3
Dive Pause	22.2 \pm 1.4 B	21.9 \pm 3.1 B	5.4 \pm 0.1 A	29.7 \pm 0.2
Social	1.0 \pm 0.1 B	2.3 \pm 0.9 B	0.3 \pm 0.01 A	1.2 \pm 0.01

^a Within a row, means with different letters are significantly different ($P \leq 0.05$).

did not differ between these periods. Dive and dive-pause duration averaged 21.7 ± 2.9 sec and 9.7 ± 5.8 sec (mean \pm SD; $N = 140$), respectively, and did not differ among reproductive periods (ANOVA; $P > 0.05$). Percent time engaged in preen, alert, swim, bathe, and display activities was not different ($P > 0.05$) between pre-laying and laying. Frequencies of all behaviors, except rest, maintenance activities (i.e., bathe or preen), and alert were reduced ($P \leq 0.05$) during incubation because most behavior on the nest was either rest, preen, or alert.

Incubation recesses were taken at all times of the day and night (see fig. 5 in Cooper and Afton 1981). Incubation constancy (percent of time spent on the nest), calculated from nest monitors, was $83.1 \pm 2.9\%$ ($N = 5$ females; mean \pm SE). Female Ruddy Ducks left the nest 7.4 ± 3.2 times per day, and each recess averaged 39 ± 4 min (mean \pm SD). Most of the recess was spent foraging (dive and dive-pause activities combined) (Table 1).

Radiotelemetry showed that pre-laying female Ruddy Ducks fed at night. I was unable to radio-mark laying or incubating females, however, incubating females likely fed during night-time recesses.

DISCUSSION

Activity budgets of female Ruddy Ducks, particularly foraging behavior, reflect their need to acquire nutrients and energy on the breeding grounds for egg production and incubation. Pre-laying and laying females spent most daylight hours foraging, and limited data indicate that they also fed at night. Incubating Ruddy Ducks foraged for most of their recesses.

TABLE 2
INCUBATION RECESSES AND LENGTH OF FEEDING PERIOD FOR EIGHT ANATIDS

Species	Incubation period (days)	Average weight (g) ¹	Time off nest/day (min)	Mean proportion of time spent feeding	Feeding time/day (min)
<i>Branta canadensis</i> ^a	27	5034	20.2	0.38	7.6
<i>Melanitta fusca</i> ^b	25	1200	223.0	0.61	136.0
<i>Anas platyrhynchos</i> ^c	26	1100	78.0	0.67	52.6
<i>A. rubripes</i> ^b	26	1100	189.6	0.70	132.7
<i>A. clypeata</i> ^c	23	635	221.3	0.68	151.1
<i>Oxyura jamaicensis</i> ^f	24	511	243.4	0.76	185.0
<i>A. discors</i> ^g	23	376	289.0	0.60	173.4
<i>A. crecca</i> ^h	24	343	296.6	0.65	193.4

References: ^a Cooper (1978); ^b Brown and Fredrickson (1987b); ^c Caldwell and Cornwell (1975); ^d Ringelman and Owen (1980); ^e Afton (1979); ^f this study; ^g Miller (1976); ^h Afton (1978); ⁱ Palmer 1976.

Female Ruddy ducks do not accumulate large lipid or protein stores before laying to defray costs of egg production and incubation, as do many large-bodied anatids, for example, Mallards (*Anas platyrhynchos*) (Krapu 1981) and Lesser Snow Geese (*Chen c. caerulescens*) (Ankney and MacInnes 1978). Female Ruddy Ducks catabolize approximately 31 g of lipid during laying, which provides 35% of the lipids for clutch formation; the remainder of the lipid and all protein requirements of clutch formation are met exogenously (Tome 1984).

Afton (1980) hypothesized that smaller bodied waterfowl are not able to store large (relative to large-bodied waterfowl) lipid reserves and, thus, are more dependent upon exogenous energy during incubation. The activity budgets (this study) and pattern of endogenous/exogenous energy allocation for reproduction of the female Ruddy Duck (Tome 1984) support this hypothesis. During incubation, female Ruddy Ducks catabolize approximately 36 g of lipid, which provides about 21% of their basal metabolic energy (Tome 1984). Thus, they must take incubation recesses to obtain the remaining 79%.

In comparison with other North American waterfowl, incubating female Ruddy Ducks spent proportionately more time feeding during recesses (Table 2). Except for Green-winged Teal (*Anas crecca*) (Afton 1978), incubating Ruddy Ducks spend more time/day feeding than do other species of waterfowl examined thus far, again supporting Afton's (1980) body size/nutrient reserve hypothesis.

The pattern of incubation recesses exhibited by female Ruddy Ducks is unusual relative to that of other waterfowl studied. Female waterfowl typically take one to three incubation recesses of 1 to 2 h each per day.

Ruddy Ducks take shorter recesses (averaging 39 min) and take them at all times of night and day, as also reported by Siegfried et al. (1976) ($N = 2$ females). This appears typical of Oxyurini, as female Maccoa Ducks (*Oxyura maccoa*) and White-headed Ducks (*O. leucocephala*) take frequent, short, incubation recesses (Siegfried et al. 1976, Matthews and Evans 1974).

Siegfried et al. (1976) suggested that length of Ruddy Ducks' recesses was a trade-off between cooling and re-warming rates of eggs (e.g., Drent [1975] found that rewarming eggs takes longer than it does for them to cool) and time necessary for a female to fill her esophagus with food. However, length and timing of recesses is likely related to some factor other than the time necessary to fill the esophagus. Breeding Ruddy Ducks feed primarily on chironomid larvae (Siegfried 1973, Tome 1981, Woodin and Swanson 1989), and these invertebrates pass very quickly from esophagus to gizzard (Swanson and Bartonek 1970). Only rarely were Ruddy Ducks' esophagi filled with larvae, even though birds were often observed for >20 min before they were collected (Tome, unpubl. data).

Female Ruddy Ducks typically feed on the pothole where their nest is located (Tome 1984). The high levels of feeding observed in this study and the energy/nutrient demands that female Ruddy Ducks meet with dietary intake (Tome 1984) highlight the importance of wetland selection for adequate food resources by breeding female Ruddy Ducks.

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