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TIME BUDGET AND INCUBATION BEHAVIOR OF BREEDING WHITE-WINGED SCOTERS

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ABSTRACT.—We studied the behavior and incubation constancy of breeding White-winged Scoters (*Melanitta fusca deglandi*) at Redberry Lake, Saskatchewan, during 1977–1980. Females spent 59.6% of their time feeding during the prelaying period, 61.2% during laying, 60.7% during incubation recesses, and 37% during brood rearing. Prelaying and laying females consistently spent more time feeding than did their mates. Incubation constancy declined from 89.3% of daylight hours during the first third of incubation to 69.3% during the last third. Near the end of incubation, females were off the nest most often between 11:00 and 17:00. White-winged Scoter females probably rely mainly on resources at the nesting area to meet the needs of reproduction. *Received 17 Feb. 1986, accepted 11 July* 1986.

Time-budget studies of breeding dabbling ducks have shown that laying females spend a large amount of time feeding (e.g., Dwyer 1975, Miller 1976, Afton 1979a, Dwyer et al. 1979), and that they spend more time feeding than do males because costs of reproduction are higher in females (King 1973, Ricklefs 1974). Similar information for diving ducks is not available.

During incubation, female ducks must meet their own metabolic needs while simultaneously incubating eggs. Regular incubation recesses suggest a need to feed if feeding is the predominant activity during recesses, whereas more constant incubation implies reliance upon endogenous reserves. Here we describe the time apportionment of breeding White-winged Scoters and evaluate their time budget and nest attentiveness.

STUDY AREA AND METHODS

We studied scoters on Redberry Lake, Saskatchewan, a 6900-ha Federal Bird Sanctuary about 65 km northwest of Saskatoon. Redberry Lake lies in the aspen parkland, and is surrounded by moderately rolling hills. Small grain agriculture and grazing are the predominant land uses. The water is brackish (Rawson and Moore 1944), and the shore and bottom are free of emergent vegetation. All nests were found on islands in the lake.

We captured females on the nest and marked them with nasal saddles (Sugden and Poston 1968). Activity budgets during prelaying, laying, incubation, and brood rearing were estimated from observations of marked females (N = 66) and their unmarked mates. Reproductive status of females was determined by back-dating nests. Behavior was recorded every 60 seconds (1977–78), or every 30 seconds (1979–80). Observations of pairs and females were randomly chosen by site and 2-h interval. Only one marked female and her mate, if present, were observed in sample periods. Observations of females taking incubation recesses

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(i.e., females off the nest) were opportunistic, and individuals were observed for as long as possible. All brood-rearing females had hatched a clutch, and all but two females were with conglomerate broods. Only observations of at least 1 h in duration were included in the analysis. Behavioral activities included: diving, dive pause (time spent on surface between dives), dabbling (feeding with only the head submerged), resting (loafing, sleeping), maintenance (preening, bathing, comfort movements), swimming, alert, interaction (threats, chasing, inciting), courtship or copulation, walking, and flying. Scoters often assumed an alert posture during the dive pause; this behavior was categorized as alert if the head was held high in an alert posture. We recorded a dive pause only if the bird was in a normal resting posture and the bird dove within 30 sec.

We recorded diurnal incubation constancy (i.e., time spent on the nest) of incubating females by focusing time lapse (one frame/sec) Super 8 movie cameras on nests. Data from the day the camera was set up on the nest were not used, and only full days of incubation were included in the analysis. We estimated stage of incubation by candling the eggs (Weller 1956). We obtained daily maximum, minimum, and mean temperatures, and rainfall records from the Meteorological Branch of Environment Canada for the nearby town of Hafford (13 km west of Redberry Lake). Behavioral differences were evaluated statistically with one-way ANOVA's, and correlation measures were estimated using Spearman's rho.

RESULTS

General behavior.—White-winged Scoters did not defend a fixed territory (Brown 1977), but like Velvet Scoters (*M. f. fusca*) (Koskimies and Routamo 1953) maintained a mated-female distance (Conder 1949). Pairs were mobile and often swam more than 1 km away from their original point of observation. We rarely observed marked females more than three times each year.

Prelaying and laying behavior.—Diving (including dive pause) and resting on the water were the most common activities during the prelaying and laying period both for males and females (Table 1). Females spent more time diving ($P < 0.01$), and less time in the dive pause ($P < 0.05$), than did males during prelaying and laying periods. Males spent more time alert ($P < 0.05$) than did females. Females spent more time resting during the prelaying period than did males ($P < 0.05$).

Incubation and brood-rearing behavior.—Total time spent off the nest and recess length (Table 2) were not correlated with maximum, minimum, or mean daily ambient temperatures ($P > 0.40$). Females never left the nest during rainfall (N = 32 bouts of rainfall). Incubation constancy was negatively correlated with stage of incubation ($r = -0.62$, $P < 0.0001$, N = 10 females, 70 days of monitoring) (Table 2). Females were off the nest most frequently between 11:00 and 17:00, corresponding with the warmest part of the day. Mean recess duration was 210 ± 13.1 min [SE] (N = 72, Range = 60–592) and females averaged 223 ± 16.8 (N = 68 days, Range = 0–592) off the nest each day. Females usually took one or two long recesses each day rather than several short recesses (Table 2). During incubation recesses, females spent a greater proportion of their

TABLE 1
DIURNAL TIME-ACTIVITY BUDGET (PERCENT) FOR BREEDING WHITE-WINGED SCOTERS

Behavior	Prelaying		Laying		Incubation	Brood rearing
	Male (N = 98)[a]	Female (N = 107)	Male (N = 82)	Female (N = 93)	Female (N = 36)	Female (N = 18)
Diving	35.3	41.8	32.1	43.6	44.8	23.0
Dive pause	21.5	17.2	17.1	17.5	15.9	7.7
Resting	16.4	16.1	12.6	13.0	2.5	10.5
Maintenance	11.4	11.1	10.3	11.7	22.2	13.2
Swimming	8.4	8.3	9.5	9.5	9.3	7.7
Alert	3.7	1.6	16.0	2.4	4.0	23.2
Interaction	1.5	0.9	0.6	0.5	0.1	0.7
Courtship or copulation	0.8	0.6	0.9	0.9	0.0	0.0
Walking	0.0	0.1	0.1	0.1	0.0	0.7
Flying	0.1	0.1	0.0	0.0	0.3	0.0
Dabbling	0.1	0.6	0.0	0.1	0.0	6.1
Out of view	0.6	0.6	0.6	0.5	0.9	0.2

[a] Hours of observation.

time diving, more time in maintenance, and less time resting than during any other reproductive category ($P < 0.05$) (Table 1). During brood rearing, females spent proportionally less time feeding ($P < 0.01$) and more time in alert behavior than at any other time.

DISCUSSION

General behavior.—Defense of the female by the paired male during prelaying and laying may be necessary for females to acquire adequate nutrients for reproduction, as is the case in Common Eiders (*Somateria mollissima*) (Milne 1974, Ashcroft 1976). The mated-female distance behavior allows females to move over large areas while being protected by their mates from harassment by other males. Other studies of scoter feeding ecology and bioenergetics suggest that large feeding areas are required (Brown 1981), making defense of a fixed territory by a breeding female energetically infeasible.

Time-activity allocation.—Differential feeding rates between males and females probably result from their different needs during reproduction. Differences in foraging rates between sexes have been reported for other ducks (see Drobney and Fredrickson 1979, Afton 1979a). Male scoters may not require as much feeding time because their energy and nutrient needs are lower than those of females during reproduction (Brown 1981).

Incubation behavior.—Although nests were not monitored during the night, females were assumed to be incubating because they were always recorded on the nest at dawn or dusk and because marked incubating

TABLE 2
WHITE-WINGED SCOTER NEST ATTENTIVENESS PARTITIONED BY TIME OF DAY AND STAGE OF INCUBATION ON REDBERRY LAKE, SASKATCHEWAN, 1977–1980

Category	Day of incubation		
	1–9	10–18	19–hatch
Mean % time on nest between:			
05:01–11:00	94.9	87.2	82.3
11:01–17:00	79.4	71.0	47.9
17:01–dark	93.7	84.9	79.1
Mean % time on nest during daylight hours	89.3	81.0	69.3
Recesses/day	0.8	1.1	1.3
Mean time off nest (min)/day	116	207	328
Number of days sampled	17	28	25
Number of females sampled	6	9	8

females were never observed elsewhere on the lake during the early evening or morning. In previous studies at Jessie Lake, Alberta (Brown 1977), females consistently returned to their nests before dusk and were present at dawn. As incubation progressed, female scoters spent more of the day off the nest (Table 2).

Mean recess duration (210 min) was much greater than that reported for the Mallard (*Anas platyrhynchos*) (24 min, Caldwell and Cornwell 1975), Maccoa Duck (*Oxyura maccoa*) (35 min, Siegfried et al. 1976), American Black Ducks (*Anas rubripes*) nesting near water (82 min, Ringelman et al. 1982), and Northern Shovelers (*A. clypeata*) (94 min, Afton 1979b), but similar to American Black Ducks nesting at upland sites (183 min, Ringelman et al. 1982). Scoters spent more time (223 min) off the nest each day than did Mallards (78 min, Caldwell and Cornwell 1975), marsh-nesting American Black Ducks (201 min, calculated from Ringelman et al. 1982), and Northern Shovelers (221 min, Afton 1979a, b), but less than Blue-winged Teal (*A. discors*) (289 min, Miller 1976), and upland nesting American Black Ducks (310 min, calculated from Ringelman et al. 1982).

Afton (1979a) compared the incubation behavior of Northern Shovelers to that of several other anatids, and suggested that smaller female anatids rely more on breeding-ground resources than larger anatids because of their inability to store a large endogenous reserve. Scoters apparently do not fit this pattern (see also Ringelman et al. 1982). Species that rely on endogenous reserves to meet metabolic needs during incubation have higher rates of nest attentiveness than do species that must feed to meet their needs (Afton 1979a, 1980). Incubation constancy is probably more

closely linked with the strategy of energy allocation employed by a species than with body size, although body size is a good indicator of the energy strategy of the species.

The incubation behavior of female scoters might also be influenced by the long distances ($\bar{x}$ = 96 m) nests are from water (Brown and Brown 1981). The energy required to rewarm eggs following an incubation recess (per minute of recess) is lower for females that take long recesses; a single recess is the most efficient incubation rhythm (Drent 1973).

Several characteristics may allow scoters to spend less time on the nest as incubation progresses. They nest during the warmest part of the summer, select dense nest cover, and line their nest with down (Brown 1977, Brown and Brown 1981). Also, embryonic heat production may increase during the later stages of incubation as found in other species (Drent 1970, White and Kinney 1974).

Four reproductive strategies have been identified in temperate and arctic nesting anatids (Owen and Reinecke 1979). These strategies represent points on a continuum related to (1) reliance on either stored or environmental resources to provide most of the energy used for reproduction, and (2) the location from which endogenous reserves are accumulated, either on or away from the breeding areas. Carcass composition studies of breeding female scoters have shown that lipid content changes little during laying, and that it begins to decline only after the onset of incubation (Brown 1981). This finding, combined with the high proportion of time females fed (i.e., dove) during the prelaying and laying periods, and their declining incubation constancy as incubation progresses, suggests that they rely mainly on resources on the breeding ground to meet most of their needs for reproduction.

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