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FACTORS AFFECTING INCUBATION RHYTHMS OF NORTHERN SHOVELERS

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ABSTRACT.—Nesting behavior of wild Northern Shovelers (*Anas clypeata*) was studied in 1974 and 1975 near Delta, Manitoba, Canada. Laying and incubation rhythms are described and adaptive aspects of the incubation rhythm discussed. Factors affecting total time spent off the nest per day, recess frequency, and recess duration are investigated with simple correlation and multiple regression analysis. The data support my prediction that in smaller individuals, environmental factors increasingly affect anatid incubation rhythms. Small size and concomitant critical dependence on food resources during incubation have apparently been important in the evolution of the Northern Shoveler's incubation behavior. The relationship of fasting endurance to body size has probably been of fundamental importance in the evolution of avian incubation behavior.

Avian incubation behavior has probably evolved in relation to at least three major factors: (1) physical requirements of the embryos for development; (2) metabolic requirements of the parent(s); and (3) predation on eggs and the parent(s). The requirements of the embryos must be met through incubation behavior that compensates for fluctuating environmental conditions, allow the parent(s) to maintain and/or acquire sufficient energy to support body metabolism, and reduce the probability of predation.

Environmental variables have little or no effect on incubation rhythms of Canada Geese (*Branta canadensis*) or Trumpeter Swans (*Cygnus buccinator*) (Cooper 1978, 1979). These large waterfowl fast during incubation (MacInnes et al. 1974, Cooper 1978, 1979, Raveling 1979) and their large eggs cool relatively slowly; hence, these birds are able to incubate unaffected by brief environmental fluctuations. Fasting endurance, or the period of time an individual can survive on stored energy, decreases with body size (Calder 1974). Small species are probably unable to subsist exclusively on body reserves during incubation and therefore, must rely more on environmental food resources (Skutch 1962, White and Kinney 1974, Afton 1978, 1979a). Thus, I predict that in smaller anatids as compared with larger, environmental factors should have more effect on incubation rhythms. This paper describes laying and incubation rhythms of the Northern Shoveler (*Anas clypeata*). Factors affecting the incubation rhythm are examined in order to evaluate my prediction.

METHODS

The 777-ha study area was located 12 km east of Delta, Manitoba, Canada and has been described in detail by Caldwell (1976). Nesting behavior of wild Northern Shovelers was studied in 1974 and 1975 by direct observation and with strip chart, thermistor-event recorders (Rustrak 2133) that synchronously recorded hen attentiveness and incubation temperatures. The hen's presence at the nest was detected with an infrared photoelectric relay (Microswitch MLS-3). Detailed descriptions of the nest monitoring system and its operation are given in Cooper and Afton (in press).

Nests were found by watching females fly to their nests or by flushing hens from cover with a dog or a chain drag device (Higgins et al. 1969). Clutch size and relative amounts of nest down were recorded upon discovery and subsequent visits. In nests found with complete clutches, incubation stage was estimated by opening one egg to determine the age of the embryo. Embryos were aged by comparison with known-age photos as in Caldwell and Snart (1974).

Air temperature was continuously recorded on the area with a thermograph (Marshalltown 1000A) housed 1.2 m above ground in a standard meteorological shelter. Records of daily sunshine duration were obtained from the University of Manitoba Delta Marsh Field Station, 18.5 km west of the study area. Additional weather data were provided by the Canadian Forces Base at Portage la Prairie, 21 km to the south.

Although incubation actually begins before the clutch is completed (Afton 1979b), "day 1 of incubation" is defined as the day of clutch completion in order to allow comparisons with previously published information. Periods spent on the nest by the hen are termed "sessions," while periods off the nest are "recesses." "Incubation constancy" is the average percent of time spent on the nest per day (Skutch 1962).

Multiple regression analysis was used to investigate factors affecting the incubation rhythm. Data were analyzed using the backward elimination procedure (Draper and Smith 1966:167) with the MULTREG statistical program (Weisberg 1977). A regression model which included all independent variables was calculated as the first step of this procedure. Then, the least important variables, as judged by the reduction of sum of squares unexplained by regression, were individually excluded in subsequent models until all remain-

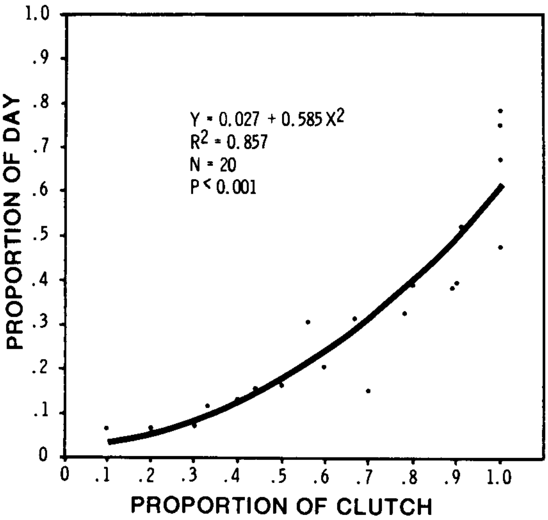

FIGURE 1. Relationship between the proportion of the day spent on the nest (Y) and the proportion of the clutch laid (X), for four female Northern Shovelers.

ing independent variables were judged to contribute significantly ($P < 0.05$) to the prediction of the dependent variable. Standard partial regression coefficients were calculated to determine the relative importance of the independent variables in the final model (Steel and Torrie 1960:299).

RESULTS

Data were collected on 4 laying and 12 incubating hens. Ten incubating hens were probably involved in initial nesting attempts, while two were probably renesting; based on nest initiation dates, clutch sizes, and relative amounts of nest down.

Hens arrived at their nests to lay between 03:29 and 07:54 ($\bar{x}$ = 06:05, SE = 27 min, N = 20 days). Arrival times on subsequent days by individual hens were random, showing no consistent pattern. Hens left their nests later each day after an egg was laid so that total time spent on the nest per day increased significantly as laying progressed (Fig. 1).

The onset of nocturnal incubation varied among five females. Three hens remained off their nests for one, two, and three nights after termination of laying, while two began

TABLE 2. Morning (AM) and afternoon (PM) recess frequency per day for 12 female Northern Shovelers.

Daily recess pattern	No. days	Percent of all days
No recesses taken	1	0.8
1 in AM	5	4.2
1 in PM	10	8.3
2 in PM	32	26.7
3 in PM	2	1.7
1 in AM and 1 in PM	23	19.2
1 in AM and 2 in PM	37	30.8
1 in AM and 3 in PM	8	6.7
2 in AM and 2 in PM	1	0.8
2 in AM and 3 in PM	1	0.8
Total	120	100.0

incubating at night on the day of clutch completion. Components of the incubation rhythm, after the onset of nocturnal incubation, are summarized in Table 1. The most common daily recess pattern was one in the morning and two in the afternoon (Table 2). Days with two recesses in the afternoon, or one in the morning and one in the afternoon were slightly less frequent. Other patterns were rare.

The distribution of recess initiation times was multimodal (Fig. 2). Morning recesses most frequently began about one hour before sunrise, but a secondary peak was evident from 06:00 to 07:00. Afternoon recesses most commonly began from 15:00 to 16:00, but were nearly as frequent at dusk (20:00–21:00). Females rarely left the nest during midday and never left late at night. The three recesses that started between 11:00 and 13:00 occurred on cool, cloudy days. Hens frequently left and returned to their nests about the same time on several consecutive days, and then changed to a different schedule.

Factors affecting total time spent off the nest per day, recess frequency, and recess duration were investigated with simple correlation and multiple regression analysis (Tables 3 and 4). I did not analyze factors affecting session duration because this rhythm component is a consequence of re-

TABLE 1. Incubation rhythm components of 12 female Northern Shovelers.

Component	Mean ± SE	Median	N	Range
Incubation constancy (% of day)	84.6 ± 0.48	84.6	120	74.7–100.0
Total time spent off nest per day (min)	221.3 ± 6.9	221.5	120	0–364
Recess frequency per day	2.3 ± 0.08	2.0	120	0–5
Duration of all recesses (min)	93.8 ± 2.9	79.0	283	31–265
Duration of morning recesses (min)	69.8 ± 2.8	67.0	77	31–156
Duration of afternoon recesses (min)	102.8 ± 3.7	88.0	206	31–265
Session duration (min)	519.2 ± 24.0	455.0	287	16–2,203

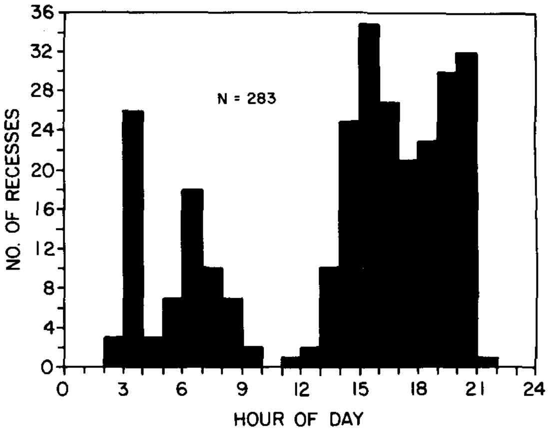

FIGURE 2. Distribution of recess initiation times for 12 female Northern Shovelers.

cess frequency and duration. The analysis included 81 days of incubation and 203 recesses of nine hens for which complete weather records were available. Only days 3 to 20 of incubation were analyzed because full constancy is not reached until day 3, and embryo and duckling movements and vocalizations affect hen behavior after day 20 (Afton 1977). Differences among females, investigated in the regression models with dummy variates, were not significant ($P > 0.05$) in any of the three analyses; therefore, the data were pooled.

Regression analysis suggested that days since arrival and rainfall were important factors affecting time off per day (Table 4, Model 1, $P < 0.001$, $R^2 = 0.655$). The biological significance of the most influential variable, days since arrival, was evident after examining the correlation matrix of the independent variables. Days since arrival was significantly correlated ($P < 0.01$) with stage of incubation ($r = 0.690$), air temperature ($r = 0.720$), and nest initiation date ($r = 0.708$). These three factors were significantly related to the dependent variable when I repeated the analysis without days since arrival (Table 4, Model 2, $P < 0.001$, $R^2 = 0.604$). However, model 2 explained 5.1% less of the variation in time off per day, indicating that days since arrival contained information in addition to these three factors. This additional information may have been increasing ground temperatures during the season which would have effected slower egg cooling rates (Afton 1979b).

Regression analysis indicated that recess frequency increased throughout days 3 to 20 of incubation and declined with increasing air temperature (Table 4, $P < 0.01$, $R^2 = 0.119$). Recess duration increased in the afternoon and with increasing air temperature (Table 4, $P < 0.001$, $R^2 = 0.334$). Air temperature was considerably more important than time of day in predicting recess duration (Table 4). Although not included in the analysis, rain affected recess duration. Hens promptly returned to the nest when heavy rainfall began (six observations).

DISCUSSION

Incubating hens maintained egg temperatures within a suitable range (Afton 1979b) by modifying their behavior in relation to varying weather conditions. Incubation constancy increased as ambient temperature declined and during rain, thereby reducing the risk of embryo injury from chilling. Many avian species respond to declining air temperatures with increased incubation constancy (see reviews in von Haartman 1956 and Drent 1970). Several open-nesting birds become more attentive during rain (Rittinghous 1961, Willis 1961, Skutch 1962, Drent 1970, Semenov-Tyan-

TABLE 3. Simple correlation coefficients (r) of selected independent variables and three components of the incubation rhythm.

Independent variables	Total time spent off nest per day (min)	Recess frequency per day	Recess duration (min)
Stage of incubation (days 3–20)	0.611**	0.240*	0.166*
Days elapsed since first arrival[a]	0.781**	0.116	0.353**
Air temperature (°C)[b]	0.591**	−0.088	0.566**
Total daily rainfall (mm)	−0.350**	−0.145	—[f]
Daily sunshine duration (h)	0.254*	0.091	—[f]
Wind speed (km/h)[c]	0.295**	0.136	0.210**
Nest initiation date (early/late)[d]	0.484**	−0.015	—[f]
Time recess initiated (AM/PM)[e]	—[f]	—[f]	0.358**

[a] Day 0 was the first day Northern Shoveler sighted on study area in spring.
[b] Mean of temperatures at start and end of recess used in analysis of recess duration; mean of hourly temperatures each day used in other analyses.
[c] Wind speed at start of recess used in analysis of recess duration; sum of hourly wind speeds each day used in other analyses.
[d] Nests initiated before (N = 7) and after (N = 2) 8 June were coded 0 and 1, respectively.
[e] Recesses initiated before (N = 58) and after (N = 145) 12:00 CST were coded 0 and 1, respectively.
[f] Independent variable not considered in analysis.
* $P < 0.05$; ** $P < 0.01$.

TABLE 4. Partial regression coefficients (and standard partial regression coefficients) and estimated constants resulting from multiple regression analyses of selected independent variables and three components of the incubation rhythm.

Independent variables[a]	Total time spent off nest per day (min) Model 1[b]	Model 2[b]	Recess frequency per day	Recess duration (min)
Stage of incubation (days 3–20)	—[c]	4.389 (0.364)	0.052 (0.389)	—[c]
Days elapsed since first arrival	4.699 (0.742)	—[d]	—[c]	—[c]
Air temperature (°C)	—[c]	5.342 (0.289)	−0.059 (−0.288)	5.537 (0.509)
Total daily rainfall (mm)	−8.248 (−0.214)	−11.555 (−0.300)	—[c]	—[d]
Daily sunshine duration (h)	—[c]	—[c]	—[c]	—[d]
Wind speed (km/h)	—[c]	—[c]	—[c]	—[c]
Nest initiation date (early/late)	—[c]	33.363 (0.218)	—[c]	—[d]
Time recess initiated (AM/PM)	—[d]	—[d]	—[d]	14.665 (0.128)
Constant (a)	−41.544	101.770	2.803	−9.064

[a] See Table 3 for explanation.
[b] See text for explanation.
[c] Variable excluded during stepdown multiple regression procedures (see Methods).
[d] Independent variables not considered in analysis.

Shanski 1970, Caldwell and Cornwell 1975). Shoveler females rarely left the nest from 10:00 to 13:00 and, therefore, protected the eggs from direct solar radiation and high midday temperatures in the vegetation (Whitman and Wolters 1967), which could kill the embryos (Snart 1970).

Although hens relied heavily on stored body reserves for nourishment during incubation (Afton, unpubl. data), food resources in the territory were apparently critical for successful incubation (Afton 1979a). Northern Shovelers maintained a lower incubation constancy than many anatids in order to obtain the needed food (Table 5). Females took advantage of warm afternoons by spending long periods feeding, with little risk to embryos from cooling. They were apparently able to spend more time in recesses as incubation progressed due to increasing embryonic heat production (White and Kinney 1974), and because the ground and air became warmer during the season, causing eggs to cool more slowly (Afton 1979b). The high frequencies of recesses prior to sunrise and at dusk may have been a response to a higher food availability. Breeding hens consume primarily crustaceans (Swanson and Nelson 1970), many of which migrate toward the water surface at these times (Cushing 1951, Pennack 1953). The low recess frequency and initiation of

TABLE 5. Incubation constancy reported for Anatidae.

Species	Constancy (%)	References
Branta canadensis maxima	98.5	Cooper (1978)
Anas superciliosa	98.4[a]	D'Ombrain (1944)
Cygnus buccinator	94.7–95.7[a]	Cooper (1979)
Anas platyrhynchos	94.6[a]	Caldwell and Cornwell (1975)
Aix sponsa	93.1	Stewart (1962)
Tadorna tadorna	87.4[b]	Hori (1964)
Bucephala clangula	86.3–89.0	Semenov-Tyan-Shanski and Bragin (1969)
Bucephala clangula	75.0	Siren (1952)
Anas acuta	86.3[c]	Afton (1978)
A. crecca crecca	85.1	Semenov-Tyan-Shanski and Bragin (1969)
A. clypeata	84.6	This study
Oxyura jamaicensis	81.5	Siegfried et al. (1976)
Anas discors	79.9	Miller (1976)
A. crecca carolinensis	79.4	Afton (1978)
Aythya americana	72.9	Low (1945)
Oxyura maccoa	72.6	Siegfried et al. (1976)

[a] Data from captive birds.
[b] Probably lower than normal due to disturbance.
[c] Data from a known renesting hen.

TABLE 6. Female body weights and simple correlation coefficients (r) of recess duration and air temperature reported for Anatidae.

Species[a]	Weight (g)[b]	r[c]	N[d]
Branta canadensis maxima	5,034.8	0.175	423
Anas platyrhynchos	1,106.8	0.459	67
A. clypeata	635.0	0.566	203
A. discors	376.5	0.660	258

[a] Data from Cooper (1978), Caldwell and Cornwell (1975), this study, and Miller (1976).
[b] Data from Bellrose (1976).
[c] Correlation coefficients are significantly different (Sokal and Rohlf 1969:520, $P < 0.001$).
[d] Sample size of correlation analysis.

recesses when light is dim would also be advantageous in reducing the likelihood that predators would discover the nest by sight.

The analysis of total time spent off the nest per day (Table 4, Model 2, see footnote) indicated that, considering the effects of air temperature, rain, and incubation stage, two late-nesting females spent more time off the nest than seven early-nesting hens. Although the two hens were unmarked, I believe they were attempting to renest. Perhaps they had depleted much of their body reserves during previous nesting attempts as Krapu (1974) showed for Pintails (*Anas acuta*) and thus had to rely even more on local food resources. Low (1945) found that initial-nesting Redheads (*Aythya americana*) were more attentive to their nests than was a renesting hen, but suggested the difference resulted only from warmer weather during the latter's incubation period. Further studies of the behavior and energetics of renesting anatids are needed.

Data presented here support my prediction that in a series of anatids from large to small, environmental factors increasingly affect incubation rhythms. I was able to explain considerably more of the variation in components of the Northern Shoveler's incubation rhythm with weather variables than could Cooper (1978, 1979) for the larger Canada Goose and Trumpeter Swan. In further support, simple correlations of recess duration and air temperature increase in a series of progressively smaller anatids for which data are available (Table 6). Notably the species reviewed by von Haartman (1956) and Drent (1970), which adjust their rhythms to air temperature, were mostly passerines (i.e., small birds).

In conclusion, I believe that small body size and concomitant critical dependence on environmental food resources during incubation have been important in the evolution of the Northern Shoveler's incubation behavior. Moreover, the relationship of fasting endurance to body size has probably been of fundamental importance in the evolution of avian incubation behavior.

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RECENT PUBLICATIONS

Birds of Prey.—Gareth Parry and Rory Putnam. 1979. Simon and Schuster, New York. 120 p. $25. A coffee table book on eagles, hawks, falcons, and owls, with text by Putnam (an "Oxford-educated biologist") and paintings by Parry (a 28-year-old Welsh bird artist). A section on general biology provides some information on classification, morphology, predatory habits, the history of falconry, impact of humans in recent time, and conservation. This section includes 12 black-and-white photographs, plus assorted drawings and figures. The focal point of the book is a section containing 35 full page, color plates of tight, detailed paintings. Each of the 35 species depicted is discussed in 300–1,000 words, plus there are 18 black-and-white photographs and various illustrations. There are 36 range maps showing worldwide distribution. The book is on good-quality paper and is well printed and bound.

Lambert's Birds of Shore and Estuary.—Paintings by Terence Lambert, text by Alan Mitchell. 1979. Charles Scribner's Sons, New York. 128 p. $15.95. Displayed here are 52 color plates of gulls, terns, alcids, ducks, shorebirds, and other birds of the seacoast. Lambert's skill justifies the book, for he paints with accuracy and a finely detailed, crisp manner. His birds are posed realistically, sometimes from unusual views, yet without calling attention to his artistic daring. Reproduction of the plates is first-rate, equal to the paintings themselves. Each plate is faced with short general text about the status and habits of the species in Britain (where the book was first published). The book will be admired by those who enjoy fine bird paintings.