Incubation temperatures of the northern shoveler

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Received August 23, 1978


Egg air cell and nest air temperatures, measured in nests of wild northern shovelers near Delta, Manitoba, Canada, averaged 36.1 and 32.0°C, respectively. Mean brood patch temperature of one captive incubating hen was 39.5°C. Body temperature of 16 wild incubating hens averaged 41.1°C. An egg cooling rate of 0.22°C/1°C h⁻¹ was calculated from temperature records of 170 incubation recesses. Factors affecting egg cooling during recesses were investigated using multiple regression analysis. Statements in the literature that incubation by Anatidae begins upon termination of laying are not supported by available data. Incubation by waterfowl, as in passerines, apparently begins gradually during the laying period. Air and ground temperatures, by influencing egg cooling rates during incubation, may have been important ultimate factors determining the breeding range and timing of the breeding season for the northern shoveler.


La température moyenne de la chambre à air de l’oeuf et celle de l’air dans le nid, telles que mesurées dans des nids de souchets du nord près de Delta, Manitoba, Canada, sont de 36.1 et 32°C respectivement. La température moyenne du couvoir d’une femelle couveuse en captivité est de 39.5°C. La température du corps mesurée chez 16 femelles couveuses en liberté est de 41.1°C en moyenne. Le taux de refroidissement des œufs a été évalué à 0.22°C/1°C h⁻¹ à partir des mesures de la température durant 170 périodes où des femelles ont quitté leur nid. Une analyse de régression multiple a permis de définir les facteurs qui affectent le refroidissement des œufs lorsque la femelle quitte le nid. Les affirmations trouvées dans la littérature à l’effet que, chez les Anatidae, l’incubation commence à la fin de la ponte ne sont pas corroborées par les données de cette étude. L’incubation chez les oiseaux aquatiques comme chez les passereaux semble commencer graduellement durant la période de ponte. En influençant le taux de refroidissement durant l’incubation, les températures de l’air et du sol peuvent être les facteurs déterminants de l’étendue de l’aire de reproduction de l’espèce et du déclenchement de la saison de reproduction chez le souchet du nord.

[Intaduit par le journal]

Introduction

In most birds, the heat required for embryonic development is supplied by the parent’s body warmth which is transferred to the eggs via the brood patch. Nest air temperature is important in determining the thermal gradient experienced by the embryo and the effectiveness of nest insulation (Kendeigh 1973). Drent’s (1975) compilation of reliable measurements of avian incubation temperatures indicated that insufficient comparative information is available for Anatidae. This paper reports egg, nest air, brood patch, and body temperatures for the northern shoveler (Anas clypeata). Factors affecting egg cooling during incubation recesses are also examined.

Methods

Egg and nest air temperatures were measured in nests of wild northern shovelers in 1974 and 1975 on a 777.3-ha study area, 12 km east of Delta, Manitoba, Canada. Egg temperatures were measured in 10 nests with a thermistor medical probe (Rustrak 1331) implanted in the egg air cell so that the sensitive junction was in contact with the inner cell membrane. Nest air temperature was measured in one nest with a thermistor air probe (Canlab T2620) mounted in the center of a plastic, perforated hollow ball (42.5 mm diameter), which was fixed in the center of the nest. Temperatures were continuously recorded with strip-chart, thermistor-event recorders (Rustrak 2133) which also recorded hen attentiveness (J. A. Cooper and A. D. Afton, unpublished data). Egg and nest air temperatures were taken for analysis at 6-min intervals (240 per day). Embryo fate and age at death were determined for all unhatched of incubated eggs so that only temperatures from eggs containing live embryos were analyzed. In nests found with complete clutches, stage of incubation 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).

Brood patch temperature of one captive hen at the Delta Waterfowl Research Station was measured with a flat-disc thermistor probe (Rustrak 1333). Measurements were made immediately after the hen was lifted from the nest on days 4, 8, 12, 16, and 20 of incubation. Body temperatures of wild incubating hens were measured immediately after being collected by shooting from the nest, by inserting a mercury thermometer 60 mm into the cloaca.

Air temperatures were continuously recorded on the study area with a thermograph (Marshalltown 1000A) housed 1.2 m aboveground in a standard meteorological shelter. Wind speed records were obtained from the Canadian Forces Base at Portage la Prairie, 21 km to the south.

Stepdown multiple regression procedures were used to investigate factors affecting the magnitude of egg cooling during incubation recesses. A regression model which included all indepen-
TABLE 1. Egg air cell temperatures, attentiveness, and air temperatures during the last 2 days of the laying cycle for two female northern shovellers

<table>
<thead>
<tr>
<th>Hen No.</th>
<th>Egg temperature, °C</th>
<th>% of day spent on nest</th>
<th>Air temperature, °C</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Mean&lt;sup&gt;a,b&lt;/sup&gt;</td>
<td>SE</td>
<td>Range</td>
</tr>
<tr>
<td>4-54</td>
<td>25.6</td>
<td>0.51</td>
<td>7.1–38.8</td>
</tr>
<tr>
<td>5-03</td>
<td>22.7</td>
<td>0.49</td>
<td>8.6–39.8</td>
</tr>
</tbody>
</table>

<sup>a</sup>Based on 480 measurements.
<sup>b</sup>Means are significantly different (t test, P < 0.001).
<sup>c</sup>Based on 48 hourly measurements.

Table 2. Summary of temperature measurements during the incubation period

<table>
<thead>
<tr>
<th>Temperatures</th>
<th>Mean, °C</th>
<th>SE</th>
<th>N</th>
<th>Range</th>
<th>No. of nests or females</th>
</tr>
</thead>
<tbody>
<tr>
<td>Nest air</td>
<td>32.0</td>
<td>0.03</td>
<td>5 040</td>
<td>22.2–37.7</td>
<td>1</td>
</tr>
<tr>
<td>Egg air cell</td>
<td>36.1</td>
<td>0.02</td>
<td>25 168</td>
<td>8.1–42.3</td>
<td>10</td>
</tr>
<tr>
<td>Brood patch</td>
<td>39.5</td>
<td>0.4</td>
<td>5</td>
<td>38.7–40.3</td>
<td>1</td>
</tr>
<tr>
<td>Body</td>
<td>41.1</td>
<td>0.2</td>
<td>16</td>
<td>39.5–42.5</td>
<td>16</td>
</tr>
</tbody>
</table>

<sup>a</sup>Includes measurements taken during recesses.

Results

Clutch size during the 2 years averaged 10.0 eggs (SE = 0.13, N = 79, R = 7–12). Mean fresh egg mass was 38.4 g (SE = 0.22, N = 150, R = 32.0–46.0) and mean standard linear dimensions were 51.8 mm (SE = 0.08, N = 486, R = 47.1–57.9) × 36.5 mm (SE = 0.04, N = 486, R = 31.4–39.1).

Incubation cycles are described in detail elsewhere (Afton 1977) and are only summarized here. Incubation constancy, recess frequency, recess duration, and session duration of 12 hens averaged 84.6%, 2.36 per day, 93.8 min, and 519.2 min, respectively.

Laying Period

Mean egg air cell temperatures measured in two nests were significantly different during the last 2 days of the laying cycle (Table 1). The difference was related to the higher attentiveness of hen 4-54 and the higher air temperatures during her laying cycle (Table 1).

Periodic heating of eggs by laying females resulted in significant embryonic development. I found differences of 1–2 days in embryo development within a clutch, when the eggs from two nests were opened 1 day after clutch completion.

Incubation Period

Temperature measurements during the incubation period are summarized in Table 2. Mean egg air cell temperatures varied significantly (P < 0.001, one-way ANOVA) between the 10 nests, but the differences were a function of the incubation stage recorded because air cell temperatures increased throughout incubation (Fig. 1). Mean daily nest air temperature in one nest also increased throughout incubation (Fig. 2). The difference between mean daily egg air cell and nest air temperature in the same nest decreased throughout incubation (Fig. 3). Brood patch and body temperatures showed no significant (P > 0.05) relationship to stage of incubation.

An egg cooling rate of 0.22°C/1°C h<sup>-1</sup> was calculated from temperature records of 170 incubation recesses. Hens averaged 101.2 min (SE = 4.1) off the nest during the recesses, and egg air cell temperatures declined an average of 7.6°C (SE = 0.2). Mean egg temperatures at the start and end of the recesses were 38.2°C (SE = 0.1) and 30.7°C (SE = 0.2), respectively. Air temperature averaged 18.2°C (SE = 0.4) during the recesses.
Fig. 1. Egg air cell temperatures by day of incubation, measured in 10 northern shoveler nests. Numbers at top are sample sizes. Regression of mean daily egg temperature (Y) on days 3–23 of incubation (X) was significant (Y = 34.763 + 0.110 X, P < 0.001, R² = 0.205).

Fig. 2. Nest air temperatures by day of incubation, measured in one northern shoveler nest. Regression of mean daily nest air temperature (Y) on days 3–23 of incubation (X) was significant (Y = 29.131 + 0.222 X, P < 0.001, R² = 0.745).

Multiple regression analysis suggested that recess duration, stage of incubation, air temperature, and days elapsed since first arrival of northern shoveler on the study area in spring, were important factors affecting the magnitude of egg cooling during recesses (Table 3, P < 0.001, R² = 0.318). Days since arrival was the most influential variable in the regression equation (Table 3). The small positive partial regression coefficient of incubation stage is difficult to interpret as it was negatively correlated with egg cooling (Table 3). An inverse relationship between incubation stage and egg cooling was predicted because embryonic heat production increases throughout incubation. The number of days since arrival was significantly correlated with incubation stage (r = 0.589, P < 0.01) and therefore contained some of the same information. However, the test to include incubation stage, given all other variables in the model was significant (P < 0.02). Incubation stage had a negative partial regression coefficient when I repeated the analysis without days since arrival, indicating that it apparently compensated for a slight underestimation of egg cooling by the latter variable in the full model.

Discussion

Incubation is defined as "the process by which the heat necessary for embryonic development is applied to an egg after it has been laid" (Beer 1964). Information on heat input to the egg or the resulting embryo development is needed to determine when incubation actually begins. Kendeigh (1952), Weller (1964), Kear (1970), Johnsgard (1975), Cramp and Simmons (1977), and others have stated that incubation by various Anatidae, including the northern shoveler, begins upon termination of laying. However, the only quantitative data available on egg temperatures and embryonic development during the laying period (Dement'ev and Gladkov 1967, pp. 372 and 454; Caldwell and Cornwell 1975; Cooper 1978; this study) indicate that laying female anatids do not transfer heat to the eggs and as a result embryo development occurs prior to clutch completion. Despite differential development in the beginning, eggs in a northern shoveler clutch hatch within 2–8 hours (Afton 1977), suggesting that a synchronizing mechanism is present (see Vince 1969). In conclusion, available waterfowl data indicate that incubation begins gradually during the laying period, which is a common feature among passerines (Haftorn 1978).

Mean egg air cell temperature of the northern shoveler was very similar to that reported for the mallard (Anas platyrhynchos) (Caldwell and
Cornwell 1975), but was approximately 2°C higher than temperatures reported for the ruddy duck (Oxyura jamaicensis), maccoa duck (O. maccoa) (Siegfried et al. 1976), and Canada goose (Branta canadensis) (Cooper 1978). The available waterfowl data further support Drent's (1975) observation that the range of variation in mean avian egg temperatures is small.

The marked increase in egg air cell temperature during days 1–3 of incubation corresponded with a rapid increase in incubation constancy (Afton 1977). Air cell temperature continued to increase slightly from days 3 to 20 of incubation despite slightly decreasing attentiveness by hens (Afton 1977). This temperature increase presumably was the result of embryonic heat production (Drent 1970) and increasing air and ground temperatures which would have effected slower egg cooling rates. Egg temperatures in the 40.0–42.3°C range were rarely recorded and probably occurred when the probed end of the egg was in close contact with the brood patch and because of embryonic activity and heat production (Caldwell and Cornwell 1975). Embryo temperatures were probably higher and less variable than egg air cell temperatures during early incubation, as Drent (1970) demonstrated for herring gulls (Larus argentatus). In early stages, the embryo floats freely on the yolk against the upper egg surface and thus is always in close contact with the brood patch. The constant brood patch temperature from days 4 to 20 of incubation suggests that the brood patch had reached full development by day 4 of incubation.

The egg cooling rate reported here is considerably lower than that predicted by interpolation from known cooling rates of other avian eggs (Drent 1975). The discrepancy is probably related to different conditions under which measurements were taken. Data summarized by Drent (1975) were apparently obtained from fully exposed, isolated eggs, while my measurements were made in nests during recesses. Northern shoveler hens always covered their eggs with down and nest materials prior to recess initiation (Afton 1977), which significantly decreases the cooling rate (Caldwell and Cornwell 1975). Also, individual eggs within a clutch may cool slower than isolated eggs (Kendegh 1973; Frost and Siegfried 1977).

In the analysis of factors affecting egg cooling, days since arrival and stage of incubation apparently jointly represented increasing embryonic heat production during incubation. Days since arrival may have also reflected increasing ground temperatures during the season which would result in less conductive heat loss because of a decreased temperature gradient between eggs and nest bottom. Some of the unexplained variability in egg cooling may have resulted from different surface to volume ratios of probed eggs and varying amounts of time in which females covered eggs with nest materials. Hens occasionally interrupted egg covering sequences and stood alert for up to 5 min (Afton

### TABLE 3. Results of simple correlation and multiple regression analysis of selected independent variables and the magnitude of egg air cell temperature cooling (°C) during 170 incubation recesses

<table>
<thead>
<tr>
<th>Variables</th>
<th>Coefficientsa</th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>r</td>
<td>b</td>
<td>Std b</td>
</tr>
<tr>
<td>Stage of incubation (days 1–23)</td>
<td>-0.158*</td>
<td>0.089</td>
<td>0.199</td>
</tr>
<tr>
<td>Days elapsed since first arrivalb</td>
<td>-0.444**</td>
<td>-0.152</td>
<td>-0.540</td>
</tr>
<tr>
<td>Mean air temperature during recess, °Cc</td>
<td>-0.204**</td>
<td>-0.108</td>
<td>-0.199</td>
</tr>
<tr>
<td>Wind speed at start of recess, km/h</td>
<td>0.067</td>
<td>Excludedd</td>
<td></td>
</tr>
<tr>
<td>Time of day recess initiated</td>
<td>0.102</td>
<td>Excludedd</td>
<td></td>
</tr>
<tr>
<td>Recess duration, min</td>
<td>0.180*</td>
<td>0.018</td>
<td>0.384</td>
</tr>
</tbody>
</table>

*a = simple correlation; b = partial regression; Std b = standard partial regression; a constant = 16.369.

bThe day the first northern shoveler was sighted on the study area in spring was day 0; days were numbered consecutively thereafter.

cCalculated by averaging air temperatures at the start and the end of the recess.

dVariable excluded during stepdown multiple regression analysis (P > 0.05).

* P < 0.05; ** P < 0.01.
1977), causing increased radiant heat losses from exposed eggs. In addition, probed eggs in the center of the nest probably cooled slower than did those on the edge.

Environmental food resources are apparently critically important to female northern shovelers during the incubation period (Afton 1979). Hens maintain a lower incubation constancy than many Anatidae in order to obtain the needed food (Afton 1977). Nesting is initiated later in spring (Sowls 1955), when air and ground temperatures are more favorable for leaving eggs unattended and perhaps food resources are more abundant. Thus, air and ground temperatures, by influencing egg cooling rates during incubation, may have been important ultimate factors determining the breeding range and timing of the breeding season for the northern shoveler.

Acknowledgements

This paper constitutes a portion of my M.S. thesis submitted to the Department of Entomology, Fisheries and Wildlife, University of Minnesota. I am grateful to B. Batt, J. Cooper, and P. Ward for advice and support during the study. I thank M. Afton for her assistance. B. Batt reviewed the manuscript. Financial support was provided by the University of Minnesota Agricultural Experiment Station, the R. Howard Webster Fellowship Fund, the James Ford Bell-Delta Scholarship Fund, the Canadian National Sportsmen’s Show, and the North American Wildlife Foundation through the Delta Waterfowl Research Station. The University of Minnesota Computer Center provided computer time. This is Paper No. 10476 of the Scientific Journal Series of the Minnesota Agricultural Experiment Station.


