

# INCUBATION BEHAVIOR AND TEMPERATURES OF THE MALLARD DUCK

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THE natural incubation environment of wild Mallards (*Anas platyrhynchos*) has received little deterministic study. Prince et al. (1969a) considered the general effect of temperature and humidity under artificial conditions upon Mallard embryos. Batt and Cornwell (1972) intensively investigated the effect of cold on Mallard embryos, while Snart (1970) studied the upper thermal limits of Mallard embryos. They found Mallard embryos much more tolerant of cold than of heat. The above research employed artificial incubation and environmental chamber treatments. The present study was undertaken to describe more adequately the natural incubation environment of Mallard eggs and the hen behavior that produces this environment.

Incubation behavior has been more thoroughly studied in avian species other than waterfowl. The incubation period is divided into attentive and inattentive periods which are related to species and clutch size (Skutch 1962). Incubation behavior and attentiveness are also affected by external stimuli (Kossack 1950, Kropivniui 1968, Barry 1962). Kendeigh (1952) reviewed the general daily rhythm of attentiveness to the nest by Anatids. Semenov-Tyan-Shanski and Bragin (1969) studying incubation behavior of Green-winged Teal (*Anas crecca*) and Common Goldeneye (*Bucephala clangula*) found the duck spent  $\frac{1}{4}$  to  $\frac{1}{8}$  of the incubation period off the nest. Cooper (1976) in an intensive study of Canada Goose (*Branta canadensis*) breeding behavior, found the female spent 98.5% of the incubation period on the nest. Kossack (1950) reported egg wetting in Canada Geese but the function of such behavior is unclear. McKinney (1952) described Mallard behavior patterns resulting in egg movements. Drent (1970) found Herring Gull (*Larus argentatus*) eggs maintained relatively constant orientation to gravitational forces, but they were frequently moved by the adult. Egg turning by the Wood Duck (*Aix sponsa*), a cavity nester, occurred about once a day (Stewart 1971).

Temperatures of naturally incubated bird eggs and nests have been investigated frequently, but little work has been done with waterfowl species. Egg temperatures were recorded for the Canada Goose (Kossack 1947, Cooper 1976) and Wood Duck (Breckenridge 1956).

## MATERIALS AND METHODS

Our research was conducted at the Delta Waterfowl Research Station, in south central Manitoba on the southern Lake Manitoba marshes, 88 km west of Winnipeg.

Hochbaum (1959) and Sowls (1955) describe the Delta Marsh, famous for anatic research.

A rectangular ( $38.7 \times 15.5 \times 4.9$  m) flight pen enclosing 0.06 ha was used. The pen walls were covered by a plywood and reed screen to a height of 2.4 m, reducing outside disturbance. Predominant plants that provided good nesting cover in the pen were several clumps of phragmites (*Phragmites communis*), extensive patches of nettles (*Urtica gracilis*), smartweed (*Polygonum natans*) in the lower damp spots, and clumps of sedges (*Carex*) along the walls. The rest of the pen was covered with grasses.

Five feeding pans were distributed in the pen, helping to assure dispersal of birds and lessening the frequency of conflicts. The birds were watched with little disturbance from an elevated blind. We searched the marsh within 152.4 m of this pen to locate nesting wild birds. The area incorporated several small ponds and was enclosed by a 1.5-m, woven wire fence with an electrified strand near the top.

We studied both penned and free-flying migratory Mallards. The penned Mallards were of wild stock more than two generations removed from the wild and of the "Delta-line" strain (Prince et al. 1969a). The age and background of each bird was known from station banding records. Eight females and eight males were placed in the pen on 7 April 1970. Individuals were identified by a combination of two colored 0.22-cm diameter discs held by washers and stainless steel pins placed through the nares.

A nest search was conducted every 5 to 7 days in both the flight pen and enclosure. Any nest containing six or more eggs with down present was visited each day after the initial discovery until incubation began or the nest was monitored. Only an infrequent check of the equipment at the nest was made after monitoring started, to cause as little disturbance as possible. All monitoring and photographic equipment was housed in weathertight boxes (Fig. 1A, 1B).

The following weather observations were recorded at the Delta Station during the study: maximum and minimum daily temperature, amount of rain or snow in a 12-hour period starting at 0800 and 2000 each day, relative humidity, and barometric pressure. Records of wind direction, wind speed, and continuous sky conditions were obtained from the University of Manitoba Field Station, 4.8 km west of the Delta Station.

Female nesting behavior was studied photographically and visually. Photographs were made by an automatically actuated, motor-driven Nikon F 35-mm camera powered by a 12-volt, 75-ampere automotive battery. The camera was timed and triggered by an intervalometer that maintained an exposure interval between 5 and 6 min. An electronic strobe eliminated all exposure control except the initial camera setting (Fig. 1B). A clock placed in the field of camera view recorded exposure time, permitting correlation with simultaneous temperature records. A bulk magazine, permitting about 24 h of continuous operation, held 11 m of film, which was developed and studied with a  $20\times$  microfilm reader.

On 15 April two camera boxes were positioned within 1.5 m and facing the feed pans. Two days later, a strobe was placed in operation in each box. The birds thus grew well accustomed to the strobe flash long before nesting began.

Visual observations were made on penned birds. Observation periods selected to sample all daylight hours generally lasted from 2 to  $2\frac{1}{2}$  h. Duck movements on the nest were described and related to their effect on egg movement.

To ascertain the effects of female behavior upon eggs, egg position and movement within the nest were studied. Eggs were numbered consecutively within each nest.

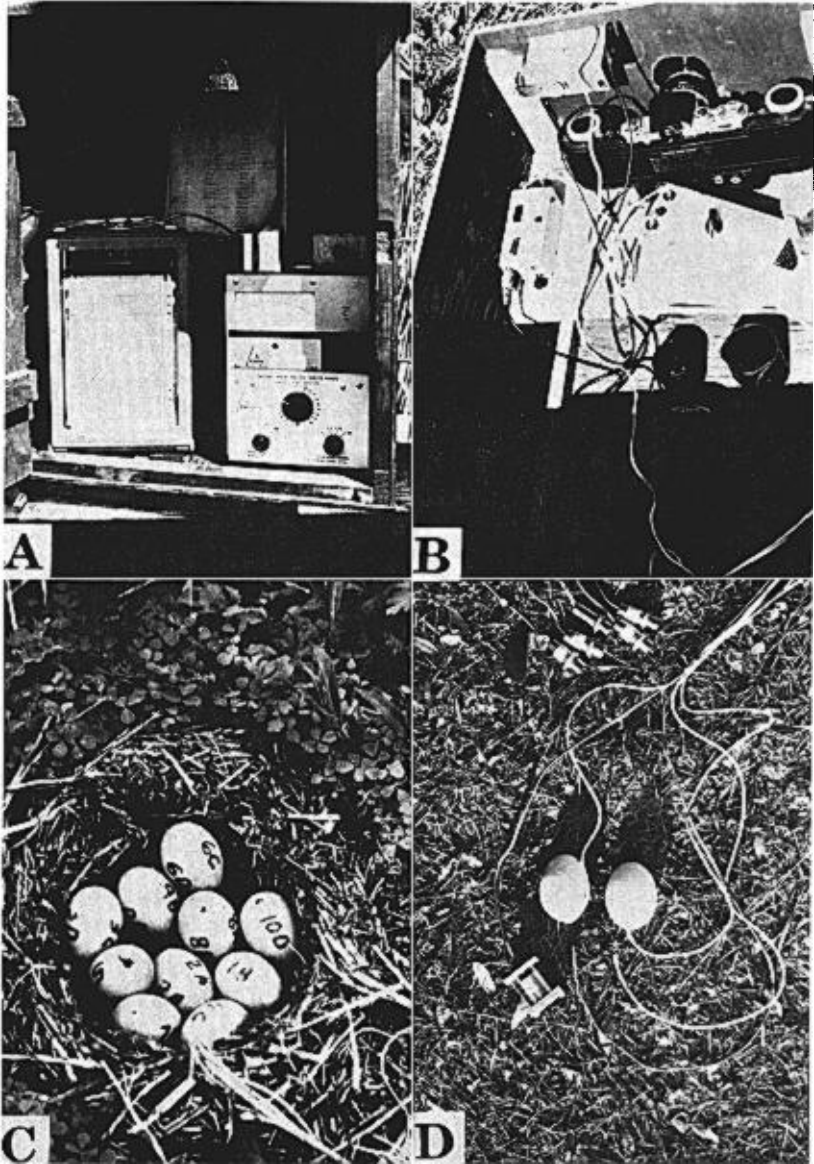


Fig. 1. A, box containing 20-channel switching and control equipment and spring driven recorder. B, box containing camera, intervalometer, relay, and electronic strobe. C, Mallard nest (hatching) with eggs marked to trace movements. D, probes and eggs; egg on left with wire taped to it is completed, egg probe in lower center right, steel tipped nest probe in center left, and metal ambient probe in left corner. Note connectors to main cable in upper portion of photo.

The numbers with a letter A through D in sequence were placed at 90° intervals around the egg's small perimeter. Each egg and about a 45° octant of that egg could thus be identified (Fig. 1C). Data were collected at approximately 6-day intervals until eggs hatched. The data collection lasted for 7 to 24 h and consisted of a nest photograph taken every hour. The female was lifted or coaxed from the nest before taking each photograph.

Egg temperature was monitored using a thermistor connected to one of two Atkins electronic monitoring devices and Esterline Angus potentiometer and chart recorders. The equipment used for most work consisted of a 20-channel automatic scanning switch and control box and a spring-driven variable speed recorder (Fig. 1A). The equipment was capable of measuring 20 temperatures in sequence, each for 30 sec, repeating the sequence every 10 min. Another unit used consisted of a six-channel automatic scanning switch and control box with identical recorder. This equipment was powered by two 12-volt, 75-ampere automotive batteries in series.

The 20-channel unit was placed in a permanent box along the pen wall and powered with 115 volts (A.C.). Three nests could be monitored simultaneously using seven conductor, six-channel cables to reach nests from this point. A total of 914.4 m of cable in four sections was available with color-coded conductors that monitored a specific parameter at a nest. Temperature was recorded in a sequence on Esterline Angus Inc. charts (No. 4309-D) running at 15.2 cm per hour. Each individual temperature was recorded six times per hour during the entire incubation period. Behavioral data from photographs were matched to these 10-min intervals.

Each nest was monitored soon after the sixth egg was laid with three egg probes, a nest probe, and an ambient temperature probe. The egg probe was a 1.5-mm diameter thermistor with rubber latex coated tip (Fig. 1D). The probes were placed in the air cell (blunt end) of the egg and nest in the following manner: (1) equipment and the air cell area of the shell were cleaned with soapy water and alcohol, and a wide spectrum antibiotic was applied to the air cell area; (2) a hole large enough to insert a probe was drilled in the eggshell over the center of the air cell, inserting the probe 6.3 mm into the air cell (in contact with air cell membrane) with a liberal amount of epoxy cement placed over the hole and wire; (3) the wire was taped to the long axis of the eggshell; (4) the egg was replaced in the nest and the probe wire drawn out through the nest bottom and covered with ground litter up to 1 m from the nest; (5) a metal tipped nest probe was placed on the nest bottom material; and (6) an ambient probe was placed within 0.3 m of the nest with an exposure to the sun similar to the incubating duck's.

Each nest was visited every evening until the last egg was laid. The day the last egg was deposited was designated as day 0 in the nesting cycle. During laying days were numbered negatively from day 0 (day last egg was laid) back to the day of nest discovery. Each nest, regardless of the calendar day incubation started, thus could be compared by matching days in the cycle.

The fate and age of an embryo at death was recorded for all probed eggs that failed to hatch. Only temperature data collected from eggs containing live embryos were used in the analysis. The embryo was aged by comparison to known age photos (Caldwell and Snart 1974).

Eggs warmed by the duck's presence during laying may reach temperatures high enough for development to occur. One day after clutch completion, the eggs were removed from the nest and the embryos aged to see if uneven ages were present.

Data from the three most complete Mallard nests were later transferred from

charts and photographs to computer cards. Analysis was carried out at the University of Florida and Kansas State University Computer Centers. All statistical tests were carried out at a 95% significance level.

## RESULTS AND DISCUSSION

### GENERAL NESTING CHRONOLOGY

Mallards remained in one large social group the first 2 weeks following their release, with little aggression shown even though pairing was evident. Two pairs, formed within 2 days of release were maintained into mid-June. Copulation occurred throughout this early period, but increased sharply in frequency when open water was available on 12 April. Persistent quacking (Dzubin 1957) or the going away call (Lorenz 1951-1953), an indicator of imminent nesting, was noted on 12 April, the same day several females were seen searching for nest sites. Although some wild Mallards arrived during the second week in April, large numbers were not present until the third week in April.

Breeding activity in the Mallard peaked during the last week in April and the first week in May when many rapes and chases occurred. The first nest within the pen was found on 19 April. Nest initiation by wild birds was later than normal, probably because of the late, cold spring. Vegetation growth on 1 June was about two-thirds complete providing good brood cover. Every Mallard female in the pen renested at least once, and one duck renested three times. A reduction in clutch size of renests as noted in previous studies (Sowls 1955) was evident. By mid-July only a few females remained on nests (Table 1).

### INCUBATION RHYTHM

Over 2200 h of temperature records and 500 h of film were combined and compared to piece together the daily incubation rhythm.

Incubation classically begins at the completion of the clutch in waterfowl (Hochbaum 1959). We found the Mallard's incubation period to vary from 24 to 26 days. When the duck is on the nest, temperatures high enough for development to occur are found as early as the sixth egg in the final clutch of 10 to 12. During this period, cycle days -4 to 0, the duck spends an average of 803 min ( $SD = 305$ ,  $N = 19$ ) on the nest mostly during daylight hours. With each added egg and day, the time on the nest generally increases. A regression of the proportion of the day spent on the nest on the proportion of the clutch completed was significant ( $t = 2.612$ ,  $P < 0.020$ ) (Fig. 2). The females usually initiated the bout at sunrise or soon after, and left the nest in late afternoon to early evening. Incubation, or duck attendance at the nest during darkness, generally did not take place until the last

TABLE 1  
MALLARD NEST INITIATION DATES AND CLUTCH SIZE OBSERVED  
AT DELTA, MANITOBA 1970

| Duck              | Date nest initiated |         |         | Number of eggs |    |   |
|-------------------|---------------------|---------|---------|----------------|----|---|
|                   | Renest              |         |         | Renest         |    |   |
|                   | 1                   | 2       | 3       | 1              | 2  | 3 |
| B-B <sup>1</sup>  | 26 Apr.             | 7 Jun.  | 22 Jun. | 12             | 9  | 8 |
| W-W               | 27 Apr.             | 8 Jun.  |         | 13             | 7  |   |
| G-G               | 25 Apr.             | 28 May  |         | 9              | 9  |   |
| R/T-R/T           | 23 Apr.             | 11 Jun. |         | 11             | 5  |   |
| B-R/T             | 21 Apr.             | 1 May   |         | 5 <sup>2</sup> | 10 |   |
| Av.               | 24 Apr.             | 14 Jun. | 22 Jun. | 11.2           | 8  | 8 |
| Av. 10 wild nests | 2 May               |         |         | 9.1            |    |   |

<sup>1</sup> Letters represent disc marker color; B, blue; R, red; T, turquoise; G, green; W, white; and Y, yellow.

<sup>2</sup> Not included in average; nest deserted.

egg was laid. On three occasions continuous incubation did not begin until after the last egg was laid (cycle days 1, 3, and 5). Two of these females (days 1 and 5) deserted after continuous incubation had started, while the other (3 days) successfully hatched all 10 eggs in the clutch, including 3 probed eggs. The time spent by five ducks on their nests during the last half of clutch laying and early incubation is summarized in Fig. 3. Other birds showing a similar inattentiveness during darkness are: Black-headed Gull (*Larus ridibundus*) (Beer 1962), Black-tailed Godwit (*Limosa limosa*) (Lind 1961), Pigeon Guil-

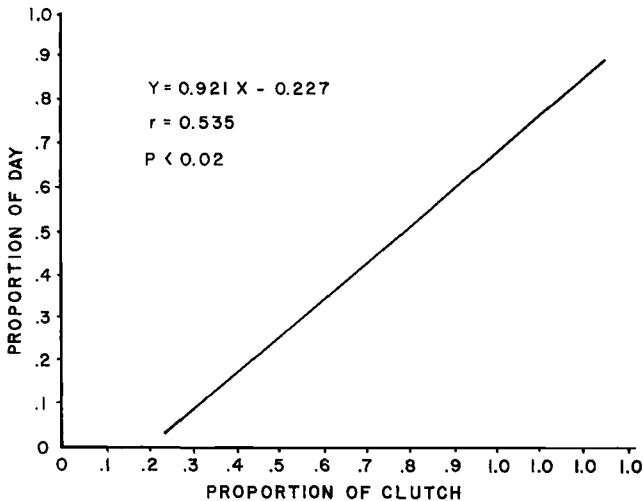


Fig. 2. Regression of the proportion of day spent on the nest as a function of the proportion of clutch layed.

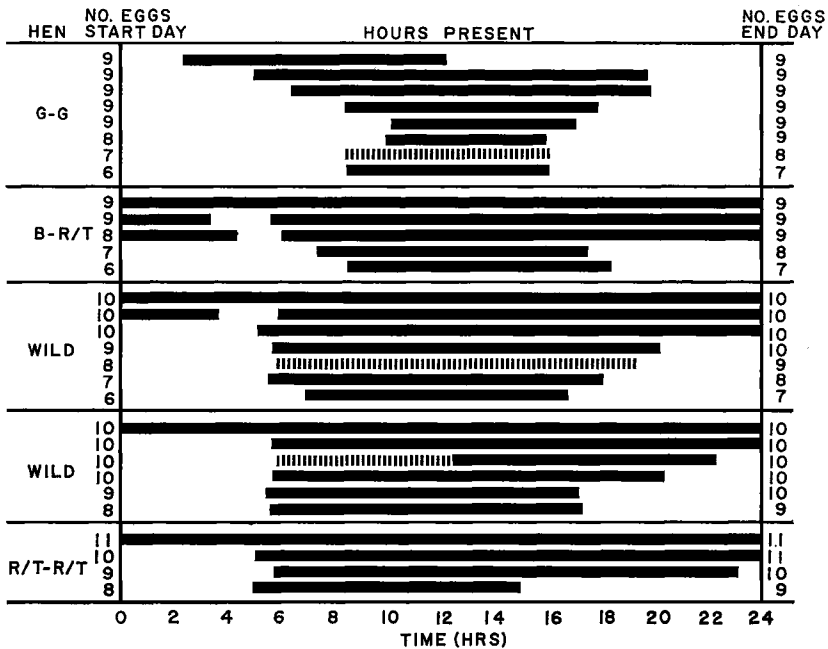


Fig. 3. The time spent on and off the nest as the clutch nears completion and incubation begins. Each line represents one day with the corresponding number of eggs at the beginning and end of the day. Earliest day appears on lower left for each hen. Dashed lines indicate missing data but probable attentiveness.

mot (*Cepphus columba*), and Herring Gull (Drent 1965, 1970). Cooper (1976) working with the much larger Canada Goose, found attentiveness similar for darkness and daylight hours during clutch formation.

Periodic heating of eggs by the female during clutch formation results in embryos varying in stages of development early in incubation as shown by eggs from three nests. When examined 1 day after clutch completion (cycle day 1), the embryos in each clutch differed 1-2 days in developmental age. This was also noted by Dane (pers. comm.). Prince et al. (1969b) found correlation between first-laid egg and hatching sequence that implies differential development during incubation, but Cooper and Hickin (1972) found no correlation between laying and emergence sequence in Canada Goose goslings. Although embryos are at different developmental stages as hatching time nears, Vince (1969) found communication between embryos synchronized the hatch.

Nest attentiveness must be quantified adequately to describe incubation. The bout, or attentive period, is that time spent on the nest or in the immediate vicinity of the nest. The bird may rise, preen, and

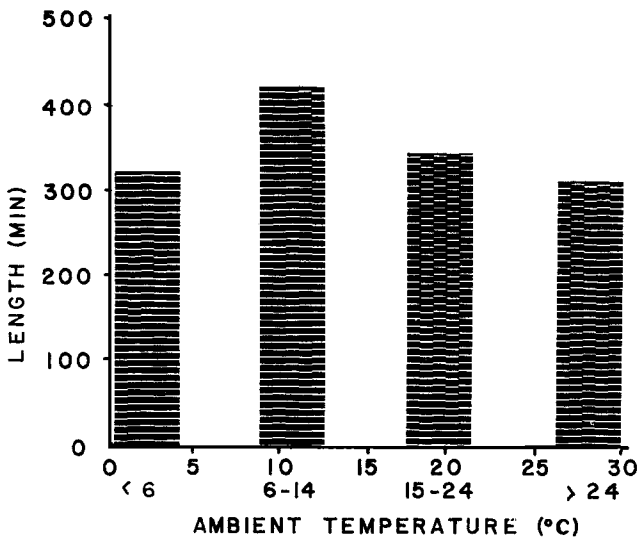


Fig. 4. Average bout length during four ambient temperature spans. There was no significant relationship.

turn eggs, but does not leave the nest. The usual bout during incubation lasts an average of 356 min (SD = 288.7, N = 56, R = 30 to 1360). At  $T_A$  below 6°C bout length averaged 324 min (SD = 204.4, N = 7), at  $T_A$  6-14°C 417 min (SD = 307.0, N = 17), at  $T_A$  15-24°C 338 min (SD = 317.0, N = 23), and at  $T_A$  above 24°C 313 min (SD = 255.0, N = 9).

Bout length did not increase with incubation. Mean bout length varied between two females monitored. Duck R/T-R/T, an adult, averaged 372 min (SD = 288.0, N = 32) per bout while duck B-R/T, a juvenile, averaged 336 min (SD = 300.0, N = 24). A *t*-test showed the means not significantly different. Cooler weather or previous experience may have tended to lengthen the bouts of R/T-R/T. No significant correlation was found between bout length and nine factors (ambient temperature ( $T_A$ ), day of incubation, wind speed, rain/no rain, sun/no sun, time of day,  $T_A$  squared, day of incubation squared, and time of day squared).

Rest periods averaged 24 min (SD = 17.5, N = 67) during incubation. Hen R/T-R/T averaged 17 min (SD = 8.6, N = 39) off the nest during rest periods while hen B-R/T averaged 34 min (SD = 21.7, N = 28). A *t*-test showed the difference was significant. The frequency and probable length of rest periods (time spent away from the nest) are affected by weather. At  $T_A$  below 6°C rest periods



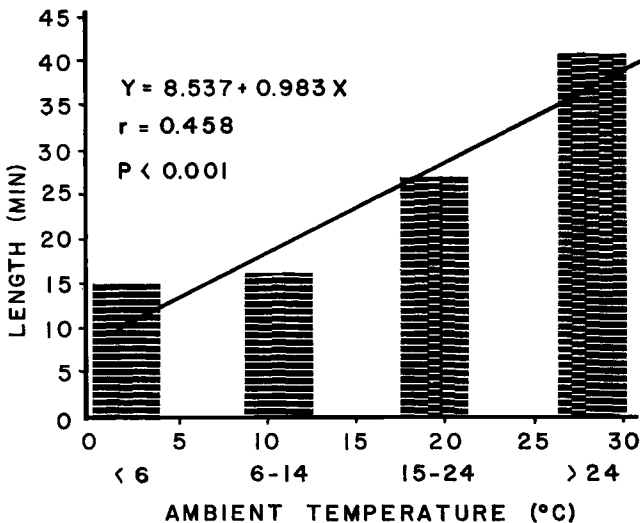


Fig. 5. Regression of rest period length on ambient temperature. Average rest period length during four ambient temperature spans.

lasted an average of 15 min (SD = 5.3, N = 10), at  $T_A$  6–14°C 16 min (SD = 7.5, N = 20), at  $T_A$  15–24°C 27 min (SD = 13.1, N = 25), and at  $T_A$  above 24°C 41 min (SD = 28.4, N = 12). The relationship between rest period length and increasing  $T_A$  was significant ( $t = 4.160$ ,  $P < 0.001$ ) (Fig. 5). A significant correlation was also found between rest period length and day, but ambient temperature was more significantly correlated ( $r = 0.459$ ,  $P < 0.001$ ) than day ( $r = 0.274$ ,  $P < 0.025$ ). Only once during the entire study was a duck absent when a nest was photographed during a rainy period.

During normal incubation an average 22.7 h (SD = 0.9, N = 18), or 94.6% of the 24 h, was spent in incubation. Attentiveness for a 24-h period averaged 23.2 h (SD = 0.2, N = 11) or 96.8% for hen R/T-R/T (average  $T_A$  12.5°C) and 21.9 h (SD = 1.1, N = 7) or 91.4% for hen B-R/T (average  $T_A$  21.3°C). Attentiveness was significantly different by  $t$ -test. Warm weather brought a significant decrease in attentiveness ( $t = 3.705$ ,  $P < 0.005$ ) (Fig. 6) as is also shown by increased rest period length (Fig. 5). Attentiveness during 24 h averaged 96.5% (SD = 1.3, N = 2)  $T_A$  below 6°C, 97.1% (SD = 1.2, N = 6)  $T_A$  6–14°C, 93.5% (SD = 3.8, N = 9)  $T_A$  15–24°C, and 85.4% (N = 1)  $T_A$  above 24°C. This did not affect average egg temperature. Breckenridge (1956) reported the same phenomenon in the Wood Duck. No significant correlation was found between nest attentiveness and the day of incubation.

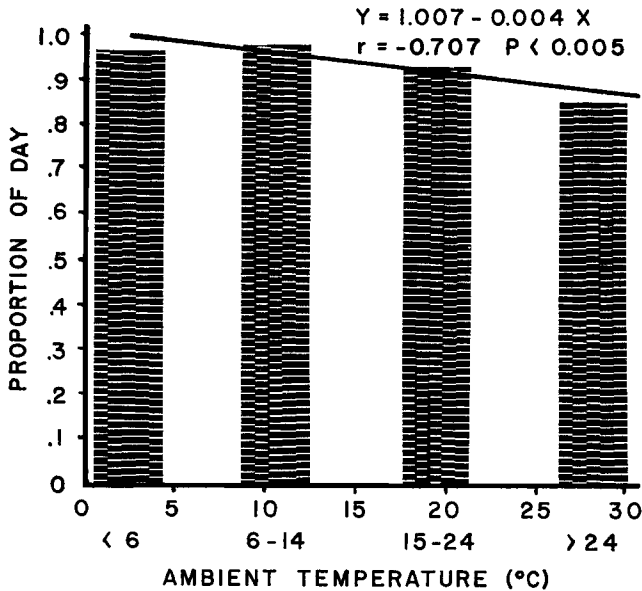


Fig. 6. Regression of attentiveness to the nest on ambient temperature. Average attentiveness during four ambient temperature spans. Incubation temperature average  $36.3^{\circ}\text{C}$ .

McKinney (1952) found the Mallard duck more active during hatching. Lind (1961) working with the Black-tailed Godwit and Drent (1970) working with the Herring Gull found these birds more active and less attentive during hatching. Our records show an increase in activity during hatching for the two ducks photographed, but attentiveness to the nest increased. Perhaps the female is responding to vocalizations and bill clapping by the embryos (Vince 1969). McKinney (1952) stated the duck oiled her breast feathers during this period, which helped waterproof the down of the young. Pipped eggs were found in nests 24-36 h before hatching, but once the first duckling left the shell, the rest of the brood hatched within 6-10 h.

#### INCUBATION BEHAVIOR

Incubation behavior was described and quantified from film records and 36 h of visual observations. Prior to nest initiation, nervous female Mallards persistently quacked and moved about the pen, usually along the walls. They apparently were searching out likely nesting sites, as they were seen performing nest-building movements. After selecting a nest site, the female rearranged and pulled up vegetation and ground

litter. She dropped forward on her breast and scraped or dug into the ground with her feet. Rotating around a pivot point under her mid-breast, she scraped out a bowl. After shaping and picking at and around the bowl, she pulled vegetation into it. At this point only one or two eggs were present in the nest bowl. Each day as an egg was added, usually between sunrise and noon, the duck shaped and worked the nest. Down generally appeared in the nest between the fourth and sixth egg. The duck plucked down from her breast and dropped it into or near the nest, eventually incorporating it into the nest bowl. The nest was built up around the female using material within reach of the nest. One duck stood within 1 m of the nest and threw material over her back from a more distant source.

During the bout the female may rise and resettle or preen, but she does not leave the immediate vicinity of the nest and remains on her feet only a very short time before settling again into the nest. We identified the periods between these movements as sitting spells. The duck may move her head about and perform certain nest-building and maintenance movements during the sitting spell, such as material pulling and patting as described by McKinney (1952). She may sleep or tuck the bill under her wing feathers. At the end of the spell the female may do one of three things: rise and resettle, turn without rising and resettling, or end the bout. Direction change without resettling occurred only once during visual observations. Just before rising at the end of a spell, the female usually is more alert, raising her head and looking about. This alertness may have a predator escape function. Then, standing, she may preen and pull down feathers for later inclusion in the nest, pull nest material toward the nest, or bill the eggs.

Resettling, which starts the new spell or bout, occurs when the duck lowers her breast to the eggs in a down and forward motion (Fig. 7A). Once on the eggs, her feet push back against the nest bowl shoving her forward. Slight movements backwards then cause her feathers to separate around the eggs. Standing and resettling, resulting in a direction change of the body, occurred an average of 1.6 (SD = 0.4, N = 295) times per hour in hen R/T-R/T and 2.1 (SD = 0.5, N = 165) times per hour in hen B-R/T. The difference, which was significant by *t*-test, may be due to warmer, fairer weather when data were collected for hen B-R/T. During rain, female R/T-R/T averaged 1.1 (SD = 0.9, N = 57) resettlings per hour. A regression of resettlings per hour on the occurrence of rain was significant ( $t = 7.749$ ,  $P < 0.001$ ) (Fig. 8). No data were available for duck B-R/T during rainy periods. Ducks resettled 1.1 (SD = 0.5, N = 52) times per hour ( $T_A$  below 6°C), 1.7 (SD = 0.6, N = 192) times per hour ( $T_A$  6–14°C), 1.8 (SD = 0.8,

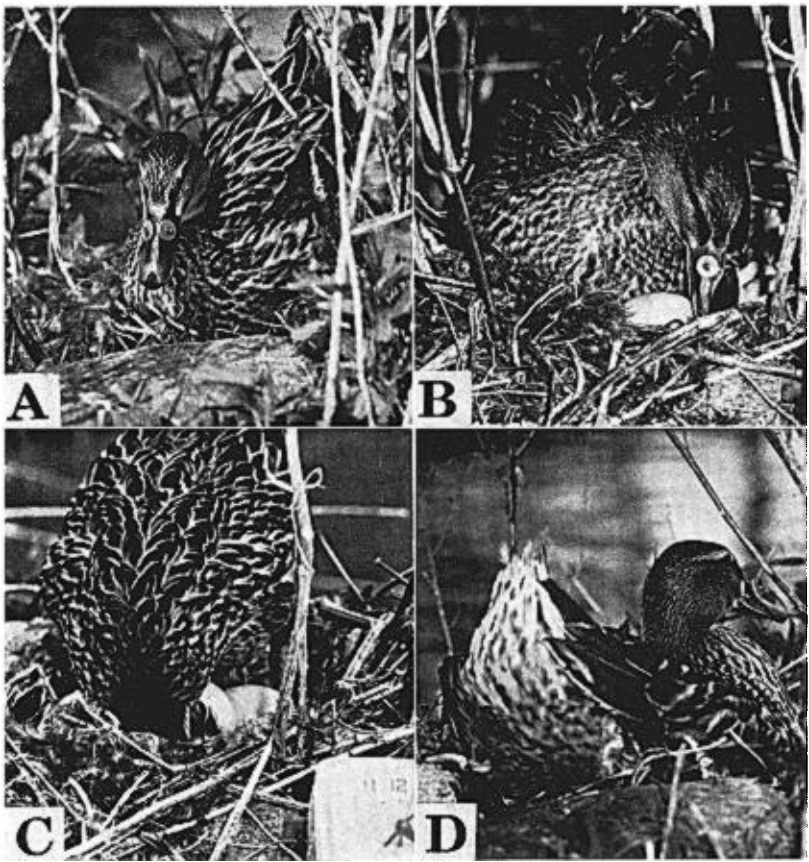


Fig. 7. A, female Mallard resettling upon the nest. B and C, female Mallards billing eggs. D, female Mallard treadle-wagging. All these movements serve to move the eggs.

$N = 136$ ) times per hour ( $T_A$  15–24°C), and 2.3 (SD = 0.7,  $N = 80$ ) times per hour ( $T_A$  above 24°C).

The relationship between resettlings per hour and ambient temperature was also significant ( $t = 6.610$ ,  $P < 0.001$ ). Excessive chilling of eggs could result at lower temperatures with frequent resettling. At high temperatures, perhaps as in the Common Nighthawk (*Chordeiles minor*) (Weller 1958), the Mallard continuously orients with respect to the sun. Resettling may also cool the duck as she exposes more body area and the feet to circulating air. Resettlings were more frequent during daylight. The average resettling rate per hour from 2200 to 0500 was 1.6 (SD = 0.5,  $N = 147$ ) compared to 2.0 (SD = 0.7,  $N$

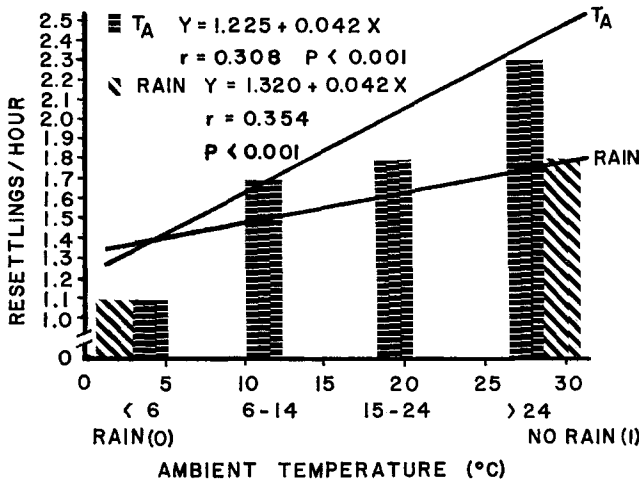


Fig. 8. Regression of average resettling rate per hour on ambient temperature and on occurrence of rain. Average resettling rate during four ambient temperature spans and during rain and no rain.

= 205) per hour from 0800 to 1800. The differences in these means, while not significant, probably reflect the differences in ambient temperatures during these periods. No consistent differences were found between different days within the incubation cycle. A significant relationship was also found between resettlings per hour and day of incubation ( $t = 2.845$ ,  $P < 0.005$ ). Ambient temperature ( $r = 0.308$ ,  $P < 0.000+$ ) and rain ( $r = 0.354$ ,  $P < 0.000+$ ) were more significant ( $r = 0.128$ ,  $P < 0.005$ ).

Between spells the female may bill the eggs (Figs. 7B, 7C). The standing duck pokes her bill between her eggs and the nest edge, while straddling the eggs or standing upon the edge of the nest bowl. She pulls her bill and one egg toward the middle of the nest, thus shifting the positions of the entire clutch of eggs relative to one another. Egg billing moves the presumably colder peripheral eggs to the center of the bowl and the center eggs to the cooler bowl edges, thus assuring more uniform heat distribution and uniform embryonic development.

McKinney (1952) reported that billing preceded resettling in 65% of the occurrences. Using this estimate, billing that resulted in egg shifting occurred 1.0 times per hour and 1.4 times per hour in the monitored nests. Egg turning rates of 0.7 times per hour have been recorded for Capercaillie (*Tetrao urogallus*) and 1.3 times for Willow Grouse (*Lagopus lagopus*) (Valanne 1966). Drent (1970) found billing frequency increased when an artificial egg was placed in the nest. The

temperature difference between live and artificial eggs might explain the billing increase as an attempt to heat all eggs equally. Drent et al. (1970) and Franks (1967) produced differences in female behavior by manipulating artificial egg temperatures. Thus attaching probes to eggs in a manner that permits free egg movement and a living embryo probably alters billing frequency or other hen behavior patterns only slightly.

When dropping the breast to the eggs in resettling, the female performs a movement called waggling (Drent 1970) or paddling (McKinney 1952). Waggling describes the side to side movement of the duck's body, while paddling describes foot action. As the female settles onto the eggs, she shifts her legs alternately forward and inward, the feet moving under the eggs (Fig. 7D). McKinney (1952) noted the action in 80–100% of all resettlings. The eggs probably are moved only slightly about the long axis relative to gravity rather than one another. Thus paddle-waggling and probably some egg movement occurred 1.7 to 2.1 times per hour for hen B-R/T and 1.1 to 1.6 times per hour for hen R/T-R/T. As this behavior pattern normally follows resettling, the same weather factors would affect both. This movement may occur without resettling, but only rarely. Paddle-waggling and other egg-moving behavior prevent sticking of embryonic membranes that results in embryonic death (Romanoff 1949, Robertson 1961). Drent (1970) indicates that quivering served to improve the contact of the egg and brood patch in the Herring Gull. The Mallard, which lacks a denuded brood patch, pushes the feathers down around the eggs. We saw quivering occur throughout the spell, while McKinney (1952) found these movements too variable to quantify.

Preening and sleeping are other major activities that take place during sitting spells, but they probably do not directly affect the eggs.

An egg that rots or breaks during incubation is removed by the female (Sowls 1955). While no ducks were seen removing broken or rotten eggs from the nest, none remained in the nest more than 8 h, including eggs with probe wires attached. Free shells were found in the pond while those with attached wires were ejected as far as possible.

#### EGG POSITION AND MOVEMENT

Fig. 9 summarizes 866 individual egg movements observed at embryo ages 5, 11, 15, 21, and 23 days. Each egg was considered separately to determine which  $\frac{1}{8}$  portion of the egg surface (octant) faced up in most photographs during an observation period. As all eggs had one or two adjacent octants facing up more than others, data were combined by summing all up-facing octants and the rest of the  $\frac{1}{8}$  surfaces correspondingly. Chi-square tests performed on data for each day indi-

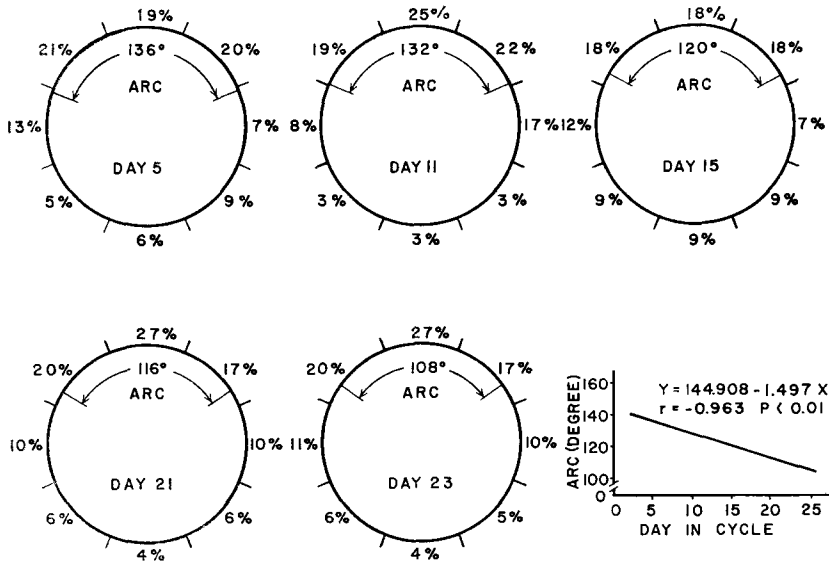


Fig. 9. Looking toward the combined blunt ends of the eggs in a nest on the indicated day of incubation. The percent in each 45° octant is the combined proportions of total observations that each surface faced up. The average arc through which eggs turned about their up octant is indicated for each day. Lower right, the regression of the arc of turning on the day of incubation.

cated significant differences between expected and observed values in each octant (day 5,  $\chi^2 = 46.988$ ,  $N = 178$ ; day 11,  $\chi^2 = 30.250$ ,  $N = 64$ ; day 15,  $\chi^2 = 27.066$ ,  $N = 240$ ; day 21,  $\chi^2 = 55.027$ ,  $N = 148$ ; day 23,  $\chi^2 = 85.423$ ,  $N = 236$ ). Only one nest was photographed on successive days (11, 15, and 21) and the same side of each egg remained up during each of the 3 days. A Chi-square test for differences between days found no significant difference between frequency of occurrence of up-facing octants during the 5 days. Thus egg position in relation to gravity was nonrandom during each of the 5 days observed. Similar data are reported by Drent (1970) for the Herring Gull and Lind (1961) for the Black-tailed Godwit. The female may cause uneven egg movement by her behavior (Holcomb 1969), or the egg may be asymmetrical in weight distribution (Oppenheim 1970, Drent 1970). Female behavior can be discounted, as her actions seemingly have a random effect on egg movement. Both Drent (1970) and Lind (1961) have shown eggs during the latter half of incubation to be asymmetrical in weight through flotation tests. The surface that floated up also appeared up most often during incubation. Drent applied a lead strip to eggs causing artificial weight asymmetry and found the strip remained

down during female incubation. We conducted no flotation tests such as Drent's, but our data suggest weight asymmetry at an early age.

The egg generally is tilted in relation to its long axis and a horizontal plane. The large, or blunt end, was tilted up in 77% (N = 866) of the observations. The degree of tilting was not measured, but probably varied up to 45°. Tilting in this manner can be important in assuring efficient transpiration between the air cell membrane and the chorio-allantois during early incubation. The embryo during this period floats to the uppermost portion of the egg, placing the two membranes and embryo in close proximity.

The angle of egg-turning about the long axis of the egg by the duck averaged 61.2° per hour. As each egg could turn either of two directions from its up position in the previous photograph, we doubled this angle obtaining the average arc through which an egg turned during day 5 (135.6°, SD = 116.8, N = 174), day 11 (132.4°, SD = 131.7, N = 36), day 15 (120.0°, SD = 109.4, N = 186), day 21 (116.0°, SD = 116.0, N = 121), and day 23 (108.2°, SD = 110.8, N = 193). The relationship between degrees an egg was turned and the day of incubation was significantly different from 0 ( $t = -6.189$ ,  $P < 0.01$ ) (Fig. 9). The suggested increase in weight asymmetry is similar to that found by Drent (1970).

Egg position relative to other eggs within the nest does not appear to be random. Some eggs were found in the center of the nest more often than others. A Chi-square test applied to data for each day indicated egg appearance in the middle of the nest was random during days 5 and 11, but was nonrandom during day 15 ( $\chi^2 = 27.481$ , N = 54), day 21 ( $\chi^2 = 27.923$ , N = 39), and day 23 ( $\chi^2 = 26.811$ , N = 53). Perhaps larger eggs remained in the bottom of the rounded nest bowl more often because of their heavier weight.

Only 5 times in 866 observations did an egg remain in the exact position as in the previous hour. Movement of eggs is extremely important in preventing the developing membranes from growing together, causing disruption of normal growth and early mortality (Romanoff 1949, Robertson 1961). Brody (1945) also found that egg movement during mid-incubation is important in preventing death near the end of incubation. Undoubtedly resettling after each photograph caused some egg movement. The female was watched until she reoccupied the nest, which usually took only 1 to 3 min and did not include billing, the major cause of egg position changes within the clutch.

Another important result of egg movement in birds that lay large clutches, including the Mallard, is the distribution of heat among eggs. Major differences in egg temperature occur within large clutches



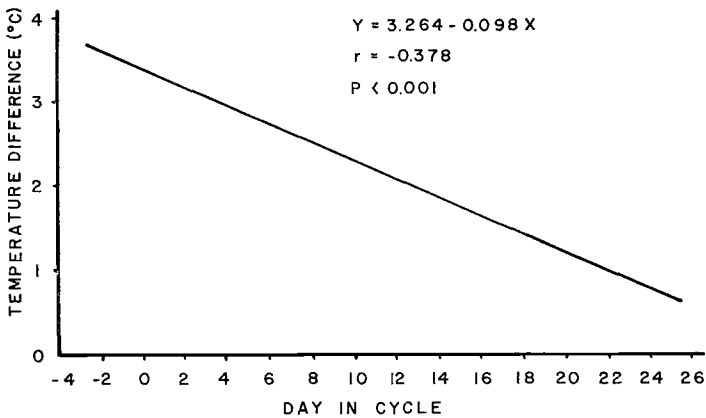


Fig. 10. Regression of the difference in egg temperatures within a nest on the day in cycle (age of embryo).

between centrally and peripherally located eggs. Huggins (1941) found an average difference in egg temperatures of  $5.6^{\circ}\text{C}$  within a Mallard nest. We found egg temperature differences ranging from an average of  $3.4^{\circ}\text{C}$  ( $\text{SD} = 1.9$ ,  $N = 122$ ) during early incubation (days 1–5) to  $0.8^{\circ}\text{C}$  ( $\text{SD} = 0.9$ ,  $N = 156$ ) during late incubation (days 21–25). A correlation between egg temperature differences and the day of incubation was significant ( $t = -6.062$ ,  $P < 0.001$ ) (Fig. 10). No embryo could remain long on the periphery of the clutch without retarding development.

#### NEST, EGG, AND EMBRYO TEMPERATURES

The internal body temperature of the female, plus the nest environment, produces the resulting egg temperatures needed for embryo development. Deep body temperatures for the domestic duck were  $41.5$  to  $42.5^{\circ}\text{C}$  (King and Farner 1961). For the Mallard, we found deep body temperatures of about  $41^{\circ}\text{C}$ . The brood patch temperature is somewhat lower, being measured at  $39.5^{\circ}\text{C}$  in the domestic duck (Tret'jakov 1953). No measurement of brood patch temperatures is available for the Mallard, but reasonable estimates can be made from the above data and our results.

Egg air cell temperatures reached  $41.5^{\circ}\text{C}$  several times during the study, probably because the probed portion of the egg was in close contact with the brood patch and perhaps because of embryonic activity and heat production (Caldwell 1971). Egg air cell temperature averaged  $36.3^{\circ}\text{C}$  ( $\text{SD} = 2.5$ ,  $N = 1655$ ) during the 24 days of incubation. During late incubation (cycle days 18–24), hourly egg air cell temperature

averaged  $38.0^{\circ}\text{C}$  ( $\text{SD} = 1.2$ ,  $\text{N} = 504$ ). Thus the brood area temperature reported for the domestic duck ( $39.5^{\circ}\text{C}$ ) probably approximates the Mallard. We estimated it at  $39.0^{\circ}\text{C}$  because the domestic duck body temperature is higher than that of the Mallard. Brood patch temperatures do not vary significantly throughout incubation in the Canada Goose (Kossack 1947), Ring-necked Pheasant (*Phasianus colchicus*) (Westerskov 1956), and Herring Gull (Drent 1970).

Our temperature measurements were all taken from probes placed within the egg air cell. As Drent (1970) points out, these readings do not represent the true embryonic temperature. As incubation proceeds, egg temperature rises slowly until near hatching the highest average daily egg temperature,  $38.7^{\circ}\text{C}$  ( $\text{SD} = 0.5$ ,  $\text{N} = 24$ ) approaches the  $39.0^{\circ}\text{C}$  we estimated for the brood patch. This increase is partly due to metabolic heat produced by the embryo. Regression analysis of egg temperature on day of incubation (cycle) indicated a significant correlation ( $t = 7.740$ ,  $P < 0.001$ ) (Fig. 11). We have previously described decreasing differences between individual egg temperatures within a clutch as incubation progresses. Development of the embryonic circulatory system transports and spreads heat more evenly throughout the yolk, and the embryo itself eventually fills most of the shell and provides direct metabolic heat.

We estimate embryo temperatures of about  $38.0^{\circ}\text{C}$  are more constant than indicated by our data throughout incubation. The embryo floats freely on the yolk against the upper egg surface and the air cell membrane, because of egg tilt and air cell position. This brings it close to the hen's brood patch. Free floating occurs in incubation up to day 14 and 15. At about 18 to 20 days, the embryo begins to orient itself lengthwise in the egg and no longer rests transversely to the long axis in the large end. Embryo position and development of thermogenesis are important in heat distribution, and these changes are suggested by the increase in average daily egg temperatures from three nests (Fig. 11).

A temperature gradient must occur within the egg, from that portion near the nest bottom to that near the brood patch. Nest bottom temperature averaged  $23.1^{\circ}\text{C}$  ( $\text{SD} = 5.8$ ,  $\text{N} = 235$ ) in early incubation (cycle days 2-7) and gradually increased as incubation advanced (days 19-24) to  $27.5^{\circ}\text{C}$  ( $\text{SD} = 8.4$ ,  $\text{N} = 248$ ) near hatching. From these data, the maximal egg gradient temperature between top and bottom of the egg decreased during incubation. The decrease in egg temperature gradient during incubation results from the increase in embryo size, circulation, and by the embryo itself producing metabolic heat.

Nest air temperature is important in determining the thermal gradient faced by the early embryo. It also is a useful indicator of the nest in-

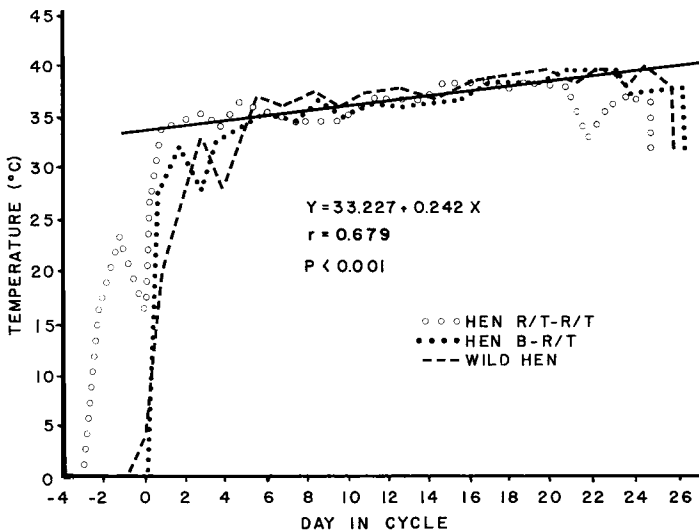


Fig. 11. Regression of daily average egg temperature on the day of incubation. Average egg temperatures are shown for three hens. Only eggs containing live embryos were considered.

sulative value. Various nest air temperatures have been recorded. Irving and Krog (1956) reported 35.9°C for the Pintail (*Anas acuta*) while Cooper (1976) found 32.2°C for the Canada Goose. To calculate average nest air temperature, we estimated upper air temperature near the top of the eggs of 37°C and an average nest bottom temperature of 25.3°C, yielding a nest air temperature of 31.2°C midway in the nest. Nest air temperature could be expected to rise gradually as incubation advances for the same reasons that egg gradient temperature decreases.

Weather apparently has no effect on egg temperatures while the eggs are incubated. No differences in egg temperature occurred in the dark hours between 2300 to 0500 and in the light hours between 0800 to 1800, whereas ambient temperatures fluctuated markedly. Egg temperatures vary during preincubation because of the females' prolonged absence at night; ambient temperature has a real effect on unattended eggs. Ducks averaged 24.4 min off the nest in 67 rest periods. During these rest periods ambient temperatures averaged 15.8°C, and egg temperatures dropped an average 5.4°C. Using these figures we calculated the rate of nest egg cooling to be 0.64°C/°C/h. During cold weather, temperatures of unattended eggs dropped by 11°C (SD = 3.1, N = 15, T<sub>A</sub> = 10°C) while during warm weather unattended egg temperatures dropped 4.3°C (SD = 1.9, N = 12, T<sub>A</sub> = 20°C). Regression analysis of unattended

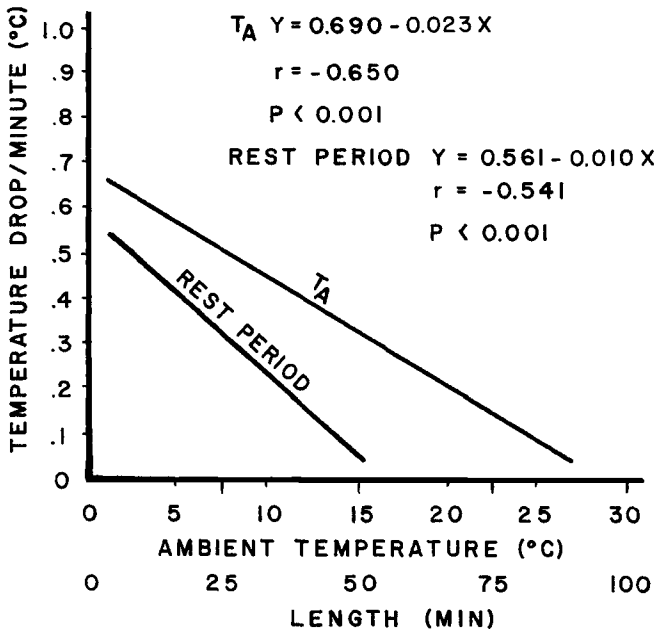


Fig. 12. Regression of egg temperature drop per minute on ambient temperature and length of rest period.

egg temperature drop per minute on  $T_A$ , rest period length, and day of incubation, indicated  $T_A$  and rest period length as significantly correlated factors ( $t = 6.934$ ,  $P < 0.001$  and  $t = -5.111$ ,  $P < 0.001$ ) (Fig. 12). The negative correlation of egg temperature loss on rest period length was caused by a positive correlation of rest period length on  $T_A$  (Fig. 5). Short rest periods at cold  $T_{As}$  allowed for greater egg temperature loss than did long rest periods at warm  $T_{As}$ . Covered and uncovered egg temperature drops differed similarly. Temperatures of covered eggs dropped  $4.1^\circ\text{C}$  ( $SD = 2.1$ ,  $N = 37$ ) while temperature of uncovered eggs dropped  $7.1^\circ\text{C}$  ( $SD = 3.7$ ,  $N = 30$ ). The correlations of covered and uncovered egg temperature drop per minute with  $T_A$  were significant ( $t = 4.875$ ,  $P < 0.001$ ;  $t = 2.499$ ,  $P < 0.025$ ) (Fig. 13). The importance of nest insulation and down is obvious.

#### THERMOREGULATION AND THE COST OF INCUBATION

Ducks remain on the nest during ambient temperature extremes. No female was ever seen off the nest when ambient temperatures exceeded  $32^\circ\text{C}$ . Generally ambient temperature was falling when ducks left the nest at temperatures between  $27^\circ\text{C}$  and  $32^\circ\text{C}$ . These periods also cor-

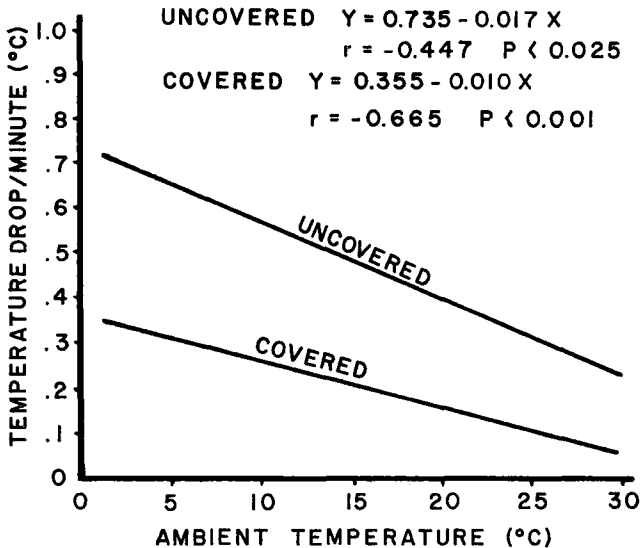


Fig. 13. Regression of egg temperature drop per minute on ambient temperature for eggs left covered with nest material by the female and left uncovered.

respond with periods of long shadow formation (late afternoon). Thus usually no direct solar radiation that could cause lethal increases in egg temperature reached the eggs (Snart 1970). After extended periods of extreme heat, the female may leave the nest for up to 102 min during late afternoon, presumably to meet her greater maintenance demands. Egg temperature during these periods generally did not drop significantly because of high ambient temperatures.

The nesting duck's behavior in high ambient temperatures probably reflects her need to maintain thermal homeostasis as well as maintain optimum egg temperature. She remains on the nest and shades the eggs, preventing overheating and embryonic mortality. When ambient temperatures rose above 27°C with slight or no wind, females were observed panting, but increasing wind speed had a cooling effect, decreasing panting at any given ambient temperature (Fig. 14). Wind was found to be a significant factor in reducing the occurrence of panting ( $\chi^2 = 13.607$ ). A  $2 \times 2$  contingency table, arbitrarily dividing wind speed (0–25 mph) and  $T_A$  (27–38°C) range into half was used. Female posture changed and ambient temperature increased; birds became more alert and sat higher in the nest exposing more body surface to cooling.

Egg wetting has been reported in several species of aquatic birds, but we saw it only once in this study. Its function is subject to considerable disagreement. Kossack (1950) and Crossley (1964) believe the bird is

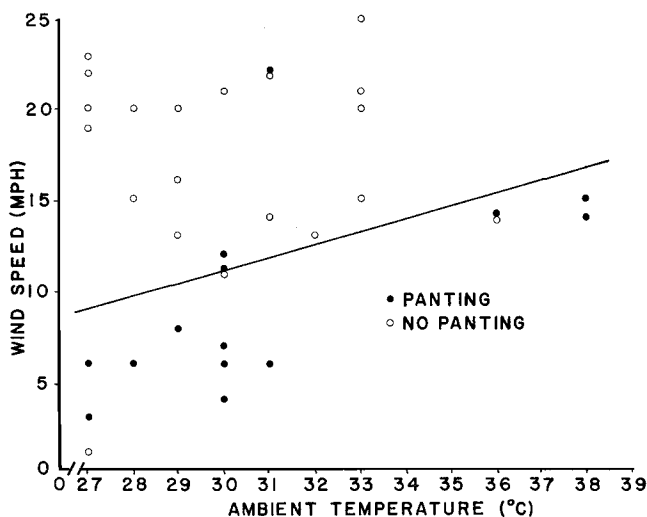


Fig. 14. The relationship between wind speed and temperature and its effect upon the occurrence of panting. The line represents the expected division between occurrences of panting and nonpanting.

attempting to cool the eggs or raise the humidity within the nest. Others believe the primary purpose of wetting is simply to help the female to thermoregulate, and egg moistening and cooling are secondary benefits (Tomkins 1942, Drent 1970). We believe the latter explanation more probable. Unpublished research conducted by Caldwell showed that Mallards have the ability to control heat loss through the feet under varying ambient temperatures. This also has been shown in other birds (Kahl 1963, Steen and Steen 1965). By leaving the nest and seeking cool water, a bird may dissipate excessive body heat more rapidly through the feet. After leaving and returning to the nest, evaporative cooling may continue to help lower the body temperature.

The cost of incubation to the female is great, especially when reneating is required. Kendeigh (1963) developed the following formula to calculate the heat needed to incubate House Wren (*Troglodytes aedon*) eggs:

$$\text{Kcal} = \frac{n \cdot w \cdot h \cdot b \cdot (t_e - t_{na}) \cdot i \cdot (l - c \cdot a)}{1000}$$

We used the following data in this formula:

- n = clutch size, 9.1 (N = 10) (Table 1).
- w = fresh egg weight, 50.6 g (SD = 3.81, N = 211) (Batt pers. comm.).
- h = specific heat of an egg, 0.80 g-cal (Kashkin 1961).
- b = egg cooling rate in nest, 0.64 °C/°C/h (text).

- te = average egg temperature (day 1-24), 36.3°C (text).  
tna = average nest air temperature 31.2°C (text).  
i = interval in hours, 24.  
c = percent of egg surface covered by female, 18% (Drent 1970).  
a = percent attentiveness per 24 h, 94.6% (text).

During normal incubation we estimate the duck expended 23.9 kcal during a 24-h period. This figure is similar to that obtained by Drent (1970) with Herring Gull and Cooper (1976) with Canada Goose. During a 24-day incubation period a female would expend 574.1 kcal if she bore the entire expense. As Drent points out, embryo thermogenesis contributes a considerable amount of heat towards the end of incubation. Using Cooper's (1976) figure, calculated from Drent (1970) (79% of the heat needed for incubation provided by the female) we estimate 453.6 kcal expended by the female; the embryo contributing 120.6 kcal. The duck during incubation probably takes in less food (energy) than is required for maintaining normal body functions and constant weight while providing an adequate environment for egg development. The resulting hen weight loss has been suggested by Folk et al. (1966) to be due to the rigors of nesting. Our estimate of the cost of incubation support the concept that the hen operates under a deficit energy budget. Such deficits may be important factors when considering renesting and desertion rates between years (cool weather requires more energy) and habitats (food quality and quantity).

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#### SUMMARY

The incubation period consists of two parts: time spent incubating (94.6%) and time spent on maintenance of body functions (5.4%). Two terms were used to describe the time spent on the nest: the bout (the time between rest periods) and the sitting spell (time between changes of position on the nest). The average bout lasted 356 min. Bout length seemed to increase with cold but did not with advancing incubation.

Sitting spell length averaged less than 1 h and was affected by weather. High temperatures tended to shorten it while rain and cold tended to lengthen it. Resettling occurred at the beginning of each new sitting spell on an average of 1.8 times per hour. Rest periods were more frequent and longer during warm weather. No rest period occurred during extreme ambient temperatures above 32°C and only rarely during rain. Ambient temperature was the most important factor affecting incubation behavior and rhythm. The eggs shift position relative to one another at least 1.2 times every hour, as a result of billing after resettling. The egg surface facing up during incubation was found nonrandom as was egg position within the nest. During incubation the average arc through which an egg turned was 122.4°.

The temperature of the embryo is probably even more constant than the data indicate. Embryo temperature varies in early incubation with egg position in the nest. Toward the end of incubation, embryo temperature becomes more constant from embryo heat production, size, and developing circulation. Egg temperatures during attentive periods were not affected by weather, but were affected during inattentive periods by cold ambient temperatures, with covered and uncovered eggs showing differences in heat loss.

Duck thermoregulation during incubation took precedence over attentiveness to the nest, which decreased as ambient temperature increased. The energetic cost of incubation was calculated to be approximately 23.9 kcal/day.

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