

- GÜTTINGER, H. R. 1974. Gesang des Grünlings (*Chloris chloris*). Lokale Unterscheide und Entwicklung bei Schallisolation. *J. Ornithol.* 115:321–337.
- KNECHT, A., AND U. SCHEER. 1968. Lautäusserung und Verhalten des Azoren Buchfinken (*Fringilla coelebs moreletti* Pucheran). *Z. Tierpsychol.* 25:115–169.
- KONISHI, M. 1985. Bird song: from behavior to neuron. *Annu. Rev. Neurosci.* 8:125–170.
- MARLER, P. 1970. A comparative approach to vocal learning: song development in White-crowned Sparrow. *J. Comp. Physiol. Psychol.* 71:1–25.
- MARLER, P., AND S. PETERS. 1977. Selective vocal learning in a sparrow. *Science* 198:519–521.
- MARLER, P., AND S. PETERS. 1987. A sensitive period for song acquisition in the Song Sparrow, *Melospiza melodia*: a case of age-limited learning. *Ethology* 76:89–100.
- MARSHALL, J. T., JR. 1948. Ecologic races of Song Sparrows in the San Francisco Bay Region Part I. Habitat and abundance. *Condor* 50:193–215.
- MULLIGAN, J. A. 1966. Singing behavior and its development in the Song Sparrow *Melospiza melodia*. *Univ. Calif. Publ. Zool.* 81:1–76.
- NICE, M. M. 1943. Studies in the life history of the Song Sparrow II. The behavior of the Song Sparrow and other passerines. *Trans. Linn. Soc. N.Y.* 6:1–238.
- NOTTEBOHM, F. 1969. The song of the Chingolo, *Zonotrichia capensis*, in Argentina: description and evaluation of a system of dialects. *Condor* 71:299–315.
- REED, T. M. 1982. Interspecific territoriality in the Chaffinch and Great Tit on islands and the mainland of Scotland: playback and removal experiments. *Anim. Behav.* 30:171–181.
- REMSEN, J. V. JR., K. GARRETT, AND R. A. ERICKSON. 1982. Vocal copying in Lawrence's and Lesser goldfinches. *West. Birds* 13:29–33.
- SORJONEN, J. 1986. Mixed singing and interspecific territoriality—consequences of secondary contact of two ecologically and morphologically similar nightingale species in Europe. *Ornis Scand.* 17:53–67.

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NEST COOLING AND RECESS LENGTH OF INCUBATING SPRUCE GROUSE¹

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Key words: *Spruce Grouse; Dendragapus canadensis; incubation; recess length; nest cooling.*

In birds with biparental care, foraging requirements of incubating parents can be met while maintaining relatively continuous coverage of the eggs if parents share incubation duties (e.g., gulls, kingfishers, pigeons, and woodpeckers; Skutch 1976), or if the foraging parent feeds the incubating parent (e.g., owls, parrots, some jays; Skutch 1976). However, in birds with uniparental care, the attendant parent may expose the eggs to cooling while absent from the nest on foraging recesses (e.g., pheasants, quails, and grouse; Skutch 1976). Such incubators may modify their attentiveness in response to conditions affecting the cooling of exposed eggs. Cartar and Montgomerie (1985) suggested that small-bodied incubators have a low fasting endurance and modify attentiveness by adjusting the frequency of recesses, while large-bodied incubators adjust the length of recesses.

Grouse are relatively large-bodied single-sex incubators that spend approximately 5% of each 24-hr period away from the nest foraging (e.g., Lennerstedt 1966; Pulliainen 1971, 1978; McCourt et al. 1973; Maxson

1977; Giesen and Braun 1979). We monitored the incubation rhythm of female Spruce Grouse (*Dendragapus canadensis*) in the wild to document the relationship between recess length and the cooling of exposed eggs (as measured by changes in nest-bottom temperature).

METHODS

The study was conducted during May and June in 1983 and 1984 near Gogama (47°30'N, 81°40'W), in north-eastern Ontario, Canada. The study area was a 20-year-old jack pine (*Pinus banksiana*) plantation with an understory of low woody shrubs including blueberry (*Vaccinium angustifolium*), sheep laurel (*Kalmia angustifolia*), and sweet-fern (*Comptonia peregrina*).

Nest bottom temperature was monitored in seven nests throughout incubation for a total of 2,760 hr with strip chart-thermister event recorders (Rustrak model 288). Thermisters were placed under the eggs on the surface of the needle litter comprising the floor of the nest bowl, and were anchored with 4-cm pins to avoid displacement. To ensure that they did not become buried in the needle litter, we checked the thermisters occasionally after hens departed for recesses. We present results for the period of continuous incubation (begins with clutch completion) because hens spent only short periods of time on nests during laying (Mccourt et al. 1973; Naylor et al., unpubl.).

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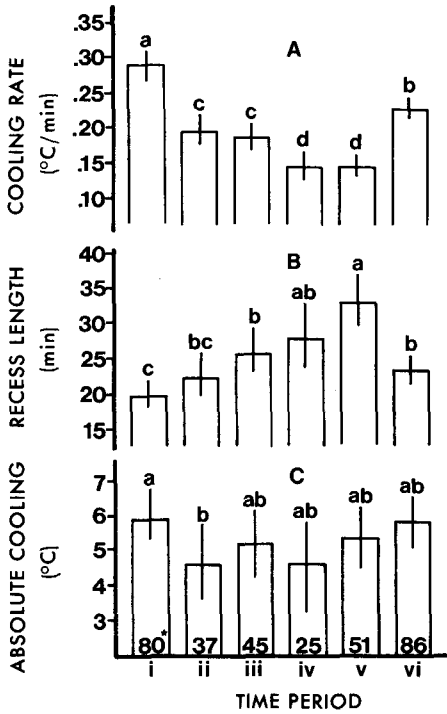


FIGURE 1. Mean cooling rate and absolute cooling of Spruce Grouse nests, and mean recess length of hens in six consecutive 3-hr time periods of the day (i = 04:00 to 07:00 to vi = 19:00 to 22:00). Sample size is denoted by *. Means sharing common letters are not significantly different ($P > 0.05$). Vertical bars represent 95% confidence intervals.

The timing and duration of inattentive periods (recesses) were interpreted from changes in nest temperature associated with the departure and return of hens as shown on the strip charts. To test the accuracy of our estimates of recess length, we compared values interpreted from the charts to those obtained when hidden observers recorded the actual time of departure and return of hens ($n = 30$). Estimates of recess length read from the charts did not differ significantly from that observed (mean deviation = 0.43 min, SE = 0.38 min; paired t -test, $t = 1.132$, $df = 29$, $P = > 0.20$). A linear regression equation predicting observed from estimated recess length ($r^2 = 0.917$) had a slope not significantly different from 1 ($t = -1.371$, $P > 0.10$) and an intercept not significantly different from 0 ($t = 1.675$, $P > 0.10$). Thus, we believe that our estimates of recess length provide an accurate indication of attentiveness.

Absolute cooling refers to the decline in nest temperature during a recess. Since the decline in nest temperature was approximately linear, cooling rate was calculated by dividing absolute cooling by recess length. We assume that changes in nest temperature were correlated with changes in the temperature of the eggs (see Barrett 1980).

TABLE 1. Correlations between recess length and cooling rate within six 3-hr time periods of the day (all hens pooled).

Time period	r	n recesses	P
04:00 to 07:00	-0.222	80	$P < 0.05$
07:00 to 10:00	-0.456	37	$P < 0.01$
10:00 to 13:00	-0.493	45	$P < 0.001$
13:00 to 16:00	-0.055	25	$P > 0.50$
16:00 to 19:00	-0.392	51	$P < 0.01$
19:00 to 22:00	-0.429	86	$P < 0.001$

Recess length, cooling rate, and absolute cooling were compared among six 3-hr time periods during the day and among the seven females using two-way analysis of variance (program BMDP2V; Dixon 1981:359-387). Since the interaction terms were not significant ($P_s > 0.10$), raw means were used throughout. Recess length and cooling rate were log-transformed to produce homoscedasticity and normality. Duncan's multiple range test was used for multiple comparisons. Statistical significance was accepted at the 5% level.

RESULTS AND DISCUSSION

Hens took two to four recesses per day, with three being most common (66% of 90 complete days monitored). When all hens were pooled, mean nest temperature at the onset of recesses was 28.6°C (SE = 0.3°C, $n = 324$) and nest temperature declined an average of 5.5°C (SE = 0.2°C) during recesses. Recess length averaged 26.4 min (SE = 0.8 min) and was inversely correlated with cooling rate ($r = -0.394$, $df = 322$, $P < 0.001$). Below we examine how this relationship varied within and among hens.

When variation among hens was controlled (two-way ANOVA), the cooling rate of nests showed significant diel variation ($F = 31.200$, $df = 5, 282$, $P < 0.001$). The lowest cooling rate occurred between 13:00 and 19:00 and the highest between 04:00 and 07:00 (Fig. 1A). Mean recess length also exhibited significant diel variation ($F = 7.581$, $df = 5, 282$, $P < 0.001$), with the longest recesses between 16:00 and 19:00 and the shortest between 04:00 and 07:00 (Fig. 1B). Thus, the diel pattern of recess length was opposite that of cooling rate ($r = -0.819$, $df = 4$, $P < 0.05$). Since hens took shorter recesses when cooling rate was high, the absolute cooling of nests was similar throughout the day. Although absolute cooling differed between the first and second time periods (Fig. 1C: $F = 2.270$, $df = 5, 282$, $P < 0.05$), cooling in these periods was not significantly different from that observed during the rest of the day.

Recess length was also inversely related to cooling rate within each time period except 13:00 to 16:00 (Table 1). Thus, recess length appeared to be associated with the cooling rate of nests both within and among time periods of the day. Diel variation in cooling rate likely reflects diel variation in ambient air temperature. Air temperature and recess length were positively correlated in Mallards, *Anas platyrhynchos* (Caldwell and Cornwell 1975), Black Ducks, *Anas rubripes* (Ringleman et al. 1982), Northern Shovelers, *Anas clypeata*

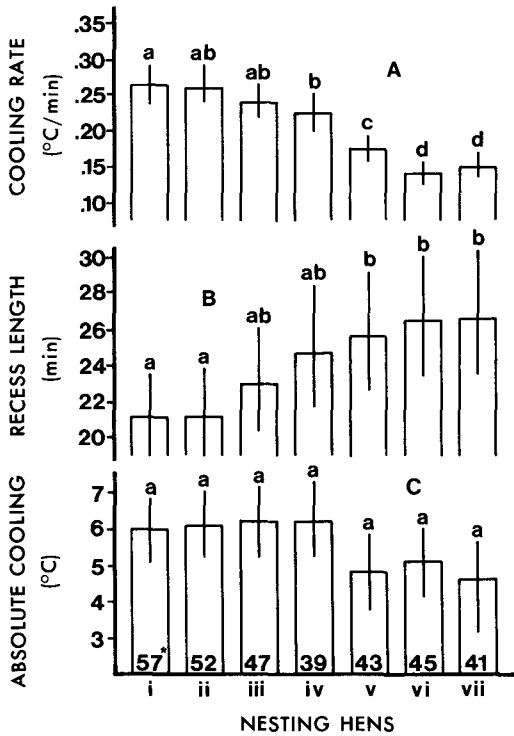


FIGURE 2. Mean cooling rate and absolute cooling of seven Spruce Grouse nests, and mean recess length of the corresponding hens. Sample size is denoted by *. Means sharing common letters are not significantly different ($P > 0.05$). Vertical bars represent 95% confidence intervals.

(Afton 1980), Goldcrests, *Regulus regulus* (Haftorn 1978), Willow Tits, *Parus montanus* (Haftorn 1979), and Great Tits, *Parus major* (Kluijver 1950).

When variation among time periods was controlled (two-way ANOVA), Spruce Grouse hens differed significantly in the mean cooling rate of their nests (Fig. 2A; $F = 22.583$, $df = 6, 282$, $P < 0.001$), and also in mean recess length (Fig. 2B; $F = 3.349$, $df = 6, 282$, $P < 0.005$). Since hens with nests that cooled rapidly took short recesses ($r = -0.947$, $df = 5$, $P < 0.01$), mean absolute cooling of nests was similar (Fig. 2C; $F = 1.742$, $df = 6, 282$, $P > 0.10$).

White and Kinney (1974) observed a similar relationship between attentiveness and variation in the cooling rate of nests of Village Weavers (*Ploceus cucullatus*). They speculated that differences in the cooling rate of eggs reflected variation in nest insulation. Spruce Grouse nest on the ground at the base of trees. Variation in cooling rate among nests could reflect differences in microclimate associated with characteristics of the nest site (e.g., Zerba and Morton 1983), or differences in weather related to year of nesting or date of nest initiation (e.g., Afton 1979). Cooling rate could also be affected by the mass of eggs in the nest (e.g., Frost and Siegfried 1977). However, there was no clear

relationship between clutch size and cooling rate as the hens in Figure 2 had clutches of 6, 6, 5, 7, 6, 7, and 5 eggs respectively.

Numerous studies suggest that incubating birds may respond to changes in egg temperature by modifying their behavior (Baerends 1959, Franks 1967, Baerends et al. 1970, Drent et al. 1970, Shallenberger et al. 1974) and by adjusting attentiveness (White and Kinney 1974, Zerba and Morton 1983, Davis et al. 1984, Drent et al. 1985, Morton and Pereyra 1985). The cooling rate of Spruce Grouse nests varied among time periods and among nests, but absolute cooling was approximately constant. Thus, assuming that nest bottom temperature parallels egg temperature (see Barrett 1980), hens may adjust the length of recesses in relation to cooling rate to regulate the absolute cooling of eggs. However, cooling rate explained only 15.5% of the variance in recess length ($r = -0.394$), and other factors may interact to influence attentiveness. For example, incubation behavior may be affected by food availability (e.g., Afton 1980, Drent et al. 1985) or the risk of predation (e.g., Thompson and Raveling 1987).

If recess length is at least partly related to cooling rate, an interesting question arises. How can incubating birds measure the cooling rate of eggs to permit them to make decisions concerning recess length? Drent (1972) suggested that birds might assess the cooling rate of eggs upon return to the nest following a recess. This might permit birds to adjust subsequent recesses and might even explain differences in mean recess length among hens. However, adjustments in recess length during the day in response to changes in air temperature would appear to require knowledge of the cooling rate before a hen returns to her nest. When away from the nest, a hen might monitor heat loss from the brood patch as an index to actual egg cooling (cf. White and Kinney 1974).

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LITERATURE CITED

- AFTON, A. D. 1979. Incubation temperatures of the Northern Shoveler. *Can. J. Zool.* 57:1052-1056.
- AFTON, A. D. 1980. Factors affecting incubation rhythms of Northern Shovelers. *Condor* 82:132-137.
- BAERENDS, G. P. 1959. The ethological analysis of incubation behaviour. *Ibis* 101:357-368.
- BAERENDS, G. P., R. H. DRENT, P. GLAS, AND H. GROENWOLD. 1970. An ethological analysis of incubation behaviour in the Herring Gull. *Behav. Suppl.* 17:135-235.
- BARRETT, R. T. 1980. Temperature of Kittiwake *Rissa tridactyla* eggs and nests during incubation. *Ornis Scand.* 11:50-59.
- CALDWELL, P. J., AND G. W. CORNWELL. 1975. Incubation behavior and temperatures of the Mallard Duck. *Auk* 92:706-731.

- CARTAR, R. V., AND R. D. MONTGOMERIE. 1985. The influence of weather on incubation scheduling of the White-rumped Sandpiper (*Calidris fuscicollis*): a uniparental incubator in a cold environment. *Behaviour* 95:261-289.
- DAVIS, S. D., J. B. WILLIAMS, W. J. ADAMS, AND S. L. BROWN. 1984. The effect of egg temperature on attentiveness in the Belding's Savannah Sparrow. *Auk* 101:556-566.
- DIXON, W. J. [ED.]. 1981. BMDP statistical software. Univ. of California Press, Berkeley.
- DRENT, R. H. 1972. Adaptive aspects of the physiology of incubation. *Proc. XV Int. Ornithol. Congr.* (1970):255-280.
- DRENT, R. H., K. POSTUMA, AND T. JOUSTRA. 1970. The effect of egg temperature on incubation behaviour in the Herring Gull. *Behav. Suppl.* 17: 237-261.
- DRENT, R. H., J. M. TINBERGEN, AND H. BIEBACH. 1985. Incubation in the Starling, *Sturnus vulgaris*: resolution of the conflict between egg care and foraging. *Neth. J. Zool.* 35:103-123.
- FRANKS, E. C. 1967. The responses of incubating Ringed Turtle Doves (*Streptopelia risoria*) to manipulated egg temperature. *Condor* 69:268-278.
- FROST, P.G.H., AND W. R. SIEGFRIED. 1977. The cooling rate of eggs of Moorhen *Gallinula chloropus* in single and multi-egg clutches. *Ibis* 119: 77-80.
- GIESEN, K. M., AND C. E. BRAUN. 1979. Nesting behavior of female White-tailed Ptarmigan. *Condor* 81:215-217.
- HAFTORN, S. 1978. Egg-laying and regulation of egg temperature during incubation in the Goldcrest, *Regulus regulus*. *Ornis Scand.* 9:2-21.
- HAFTORN, S. 1979. Incubation and regulation of egg temperature in the Willow Tit, *Parus montanus*. *Ornis Scand.* 10:221-234.
- KLUJVER, H. N. 1950. Daily routine of the Great Tit, *Parus major*. *Ardea* 38:99-135.
- LENNERSTEDT, I. 1966. Egg temperature and incubation rhythm of the Capercaillie (*Tetrao urogallus* L.) in Swedish Lapland. *Oikos* 17:169-174.
- MAXSON, S. J. 1977. Activity patterns of female Ruffed Grouse during the breeding season. *Wilson Bull.* 89:439-455.
- MCCOURT, K. H., D. A. BOAG, AND D. M. KEPPIE. 1973. Female Spruce Grouse activities during laying and incubation. *Auk* 90:619-623.
- MORTON, M. L., AND M. E. PEREYRA. 1985. The regulation of egg temperatures and attentiveness patterns in the Dusky Flycatcher (*Empidonax oberholseri*). *Auk* 102:25-37.
- PULLIAINEN, E. 1971. Behaviour of a nesting Capercaillie (*Tetrao urogallus*) in northeastern Lapland. *Ann. Zool. Fennica* 8:456-462.
- PULLIAINEN, E. 1978. Behaviour of a Willow Grouse, *Lagopus l. lagopus*, at the nest. *Ornis Fenn.* 55: 141-148.
- RINGLEMAN, J. K., J. R. LONGCORE, AND R. B. OWEN, JR. 1982. Nest and brood attentiveness in female Black Ducks. *Condor* 84:110-116.
- SHALLENBERGER, R. J., G. C. WHITTOW, AND R. M. SMITH. 1974. Body temperature of the nesting Red-footed Booby (*Sula sula*). *Condor* 76:476-478.
- SKUTCH, A. F. 1976. Parent birds and their young. Univ. Texas Press, Austin.
- THOMPSON, S. C., AND D. G. RAVELING. 1987. Incubation behavior of Emperor Geese compared with other geese: interactions of predation, body size, and energetics. *Auk* 104:707-716.
- WHITE, F. N., AND J. L. KINNEY. 1974. Avian incubation. *Science* 189:107-115.
- ZERBA, E., AND M. L. MORTON. 1983. Dynamics of incubation in Mountain White-crowned Sparrows. *Condor* 85:1-11.

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NONTERRITORIAL MALES IN POPULATIONS OF SPRUCE GROUSE¹

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Key words: Spruce Grouse; *Dendragapus canadensis*; nonterritorial; males; removal experiment.

Nonterritorial males have been observed in populations of several species of grouse (e.g., Herzog and Boag

1978, Zwickel 1980, Gullion 1981, Watson 1985, Dunn and Braun 1986). In addition, removal experiments have revealed a large number of males capable of breeding that replaced territorial birds when they were shot (e.g., Watson and Jenkins 1968, Lewis and Zwickel 1980, Hannon 1983). These studies suggest that many birds may be prevented from establishing territories, and thus that territorial behavior may limit the number of breeding males.

Nonterritorial yearling males were found in popu-

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