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# NEST ATTENTIVENESS AND EGG TEMPERATURE IN THE YELLOW-EYED JUNCO[1]

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*Abstract.* Egg temperatures ($T_{egg}$) and nest attentiveness were measured in *Junco phaeonotus* breeding at high altitude (2,560 m) in the Chiricahua Mountains of Arizona. Mean $T_{egg}$ for six nests was significantly higher at night than during the day (35.8°C vs. 34.9°C). Attentiveness averaged 76.9% during the 13.90-hr active day. Females left the nest (off bout) an average of 0.97 times per hour. Off-bout frequency was highest early in the day, declining from 1.5 bouts/hr at dawn to about 0.7 bouts/hr at midday. Off-bout duration averaged 13.7 ± 0.37 min (range = 3–44 min, $n$ = 158), and tended to be longest during midday. $T_{egg}$ fell to an average of 29.1 ± 2.1°C (range = 17.6–36.0°C) during off bouts. The minimum $T_{egg}$ during off bouts increased with embryo age. The junco's nest attentiveness pattern appears to be a compromise between two conflicting selection pressures—nest predation and egg cooling.

*Key words: Incubation; parental behavior; Passeriformes;* Junco phaeonotus.

## INTRODUCTION

Although egg temperature ($T_{egg}$) has been determined in over 36 passerine species (for reviews, see Webb 1987, Haftorn 1988), we still lack a full understanding of songbird incubation and nest attentiveness. Critical gaps in our knowledge include the range of temperatures experienced by eggs and how $T_{egg}$ and parental attentiveness vary with embryo age, weather, nest site, and egg size (Webb 1987). Such data are required for a complete recognition of how attentiveness patterns serve to resolve the conflicting selective pressures posed by the incubating parent's need to leave the nest and feed vs. its need to remain on the eggs to insure proper development.

To date, most studies of passerine incubation have involved species that nest in cavities or build cup nests situated above ground. Comprehensive data are unavailable for ground-nesting species, which generally face high rates of nest predation and thus may have different attentiveness requirements than cavity- or tree-nesting species. Accordingly, we determined $T_{egg}$ and nest attentiveness in the Yellow-eyed Junco (*Junco phaeonotus*), a small (19.5-g), ground-nesting passerine.

Yellow-eyed Juncos reside in montane habitats from southern Arizona and southwestern New Mexico south to Guatemala (AOU 1983). They are monogamous, maintain all-purpose breeding territories, and have biparental care of the young (Moore 1972). In Arizona's Chiricahua Mountains, they begin nesting in late April and continue until late August, with pairs producing up to three successful clutches in a single season (for details, see Sullivan 1988). Continuous incubation begins with the penultimate egg and lasts 13 days. Females carry out all of the nest-building, incubation, and brooding activities. Most nests (87%; Sullivan 1989) contain three or four eggs, and fresh eggs weigh an average of 2.43 ± 0.21 g ($n$ = 18; K-Tron model DS-10 electronic balance accurate to 0.05 g).

## METHODS

The study site (Rustler Park, Cochise County, Arizona: elevation = 2,560 m, 31°55′N, 109°17′W) consists of coniferous forest with little understory, short-grass meadows, and areas of bracken fern (*Pteridium* sp.). The predominant tree species are *Pinus ponderosa, P. strobiformis,* and *Pseudotsuga menziesii* (see Balda 1967 for detailed site description).

We studied six nests; three between 15 and 27 May 1986 and three between 25 May and 10 June 1988. Clutches ranged from 2 to 13 days in age, determined by checking nests daily during the egg-laying or incubation stage. Five of the

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nests contained four eggs, one held three eggs. Five nests were situated on the ground, one was located 2 m above ground in a building raingutter. The ground nests were concealed within clumps of dried bracken ferns or beneath fallen logs, and thus were shaded. The raingutter nest was partially exposed. Except for averaging fewer off bouts/hr (0.71 vs. 1.18) and exhibiting higher attentiveness (84.3% vs. 74.1%), the raingutter nest resembled the five ground nests. Even in these two respects, the raingutter nest data nearly overlapped that of the ground nests and thus they were included in all analyses.

$T_{egg}$ was measured using a 40-gauge Cu-Cn thermocouple that was inserted into the center of an infertile egg, spot-glued to the shell, threaded through the bottom of the nest, and connected to a Campbell Scientific CR21X micrologger. The original clutch size was maintained by replacing one of the nest's eggs with the thermocouple egg. Air temperature ($T_a$) was measured with a shaded 40-gauge thermocouple placed 0.1 m above nest level and within 0.5 m of the nest. The data logger measured the temperatures every 1 or 6 sec and averaged temperatures at 60-sec intervals. Because we assessed $T_{egg}$ 10–60 times per minute, we were able to determine to within 1 min when females left or returned to the nest. Temperatures were accurate to within 0.3°C (Campbell Scientific 1984).

Attentiveness was determined from the $T_{egg}$ record, with sudden temperature changes signaling the female's arrival or departure. $T_{egg}$ was monitored continuously at each nest for between 22.1 to 117.9 hr. At two nests, we continued to measure $T_{egg}$ after the clutch hatched. Usually females do not remove eggs which fail to hatch from the nest. They did, however, remove our thermocouple eggs within a day or two after the other eggs hatched, indicating that they somehow identified eggs with thermocouples as abnormal. Once ejected from a nest, thermocouple eggs could only be successfully returned after they were painted black. Such painted eggs were in intimate contact with the nestlings and, as they were usually shielded from the sun, provided an approximation of nestling temperature. Except as otherwise noted, values are presented as the mean ± one standard deviation.

## RESULTS AND DISCUSSION

We obtained 9,250 daytime and 6,665 nighttime measurements (1-min averages) of $T_{egg}$ in nests

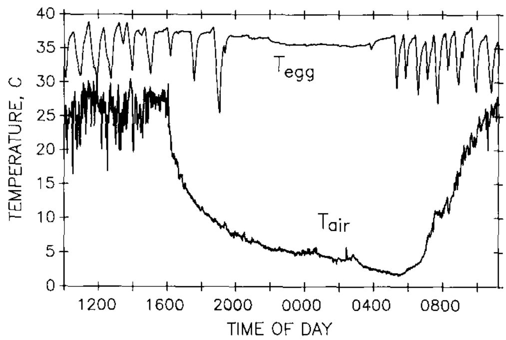


FIGURE 1. Egg ($T_{egg}$) and air ($T_{air}$) temperature with time of day in *Junco phaeonotus.* Data are for nest no. 2 (16–17 May 1986), day 10 of incubation.

containing eggs and 1,547 daytime and 1,340 nighttime $T_{egg}$ measurements in nests containing chicks. During these combined measurements the weather was mild with no rain. Mean daytime $T_a$ was similar during each of the 15 measurement days, ranging from 17.9 to 21.6°C ($\bar{x} = 19.5 \pm 5.4$°C). Mean nighttime $T_a$ was more variable, ranging from 4.9 to 14.1°C ($\bar{x} = 6.7 \pm 1.2$°C). Daytime $T_a$ measured at nest level showed larger variations over short time periods than typically seen when $T_a$ is measured 1–2 m above ground (Fig. 1, unpubl. data). These $T_a$ fluctuations probably resulted from the wind blowing boluses of sun-warmed, ground-level air past the nest. Such temperature fluctuations may make it difficult for female juncos to judge the rate of egg cooling when they are off the nest, and species which place their nests above ground in typical cup nests may have a more stable thermal environment upon which to base their behavioral decisions.

Mean daytime $T_{egg}$ varied among the six nests, ranging from 33.5 to 36.7°C. Similarly, mean nighttime $T_{egg}$ ranged from 33.3 to 36.8°C. For all measurements combined, $T_{egg}$ averaged 34.9 ± 3.2°C during the day and 35.8 ± 1.3°C at night (Table 1). Statistically, the difference between daytime $T_{egg}$ and nighttime $T_{egg}$ is highly significant ($t = 36.0$, $P < 0.001$). The mean $T_{egg}$ of the juncos we measured in this study is within the 34–36.5°C range reported for other passerines (Drent 1975, Haftorn 1988). There was no significant correlation between mean $T_{egg}$ and mean $T_a$ for either daytime or nighttime measurements. Nor was there a correlation between mean $T_{egg}$ and embryo age. As in other passerines (Haftorn 1983, Morton and Pereyra 1985), mean $T_{egg}$

TABLE 1. Incubation data for *Junco phaeonotus*.

| Parameter | $\bar{x} \pm$ SD ($n$) |
|---|---|
| Egg temperature, °C | |
| Daytime | 34.9 ± 3.2 (9,250) |
| Nighttime | 35.8 ± 1.3 (6,665) |
| Constancy of incubation, % | 76.9 ± 5.11 (6) |
| No. off bouts/hr | 0.97 ± 0.34 (154) |
| $T_{egg}$ at end of off bout, °C | 29.1 ± 2.1 (158) |
| Off-bout duration, min | 13.7 ± 0.37 (158) |
| On-bout duration, min | 49.8 ± 39.8 (138) |

of juncos does not appear to vary after the clutch is completed.

Like most single-sex intermittent incubators, *Junco phaeonotus* must periodically leave the nest to forage, preen, and defend the nest and territory (Fig. 1). In our study, females left the nest an average of 0.97 times/hr. Off bouts (time away from the nest) averaged 13.7 ± 0.37 min in duration (range = 3–44 min), with the frequency distribution of off bouts being skewed towards those of less than 14 min duration (Table 1, Fig. 2). Off-bout duration among Yellow-eyed Juncos was considerably longer than for two other montane passerines, the White-crowned Sparrow, *Zonotrichia leucophrys oriantha* (Zerba and Morton 1983b), and the Dusky Flycatcher, *Empidonax oberholseri* (Morton and Pereyra 1985), in which off bouts averaged 7.8 and 6.8 min, respectively. Furthermore, the number of off bouts/hr in Dusky Flycatchers and White-crowned Sparrows averaged 2.2/hr, more than twice that of Yellow-eyed Juncos. Consequently, on-bout duration in juncos, which averaged about 50 min (Table 1), was considerably longer than in Dusky Flycatchers (19 min, Morton and Pereyra 1985) or the White-crowned Sparrows (20 min, Zerba and Morton 1983b).

Off-bout duration varied with time of day, tending to be shorter both early and late in the day—times when $T_a$ was lowest (Fig. 3). Although females made more trips off the nest early in the day, when $T_a$ was lowest, these early trips were of relatively short duration. Towards midday, females made fewer but longer trips from the nest (Fig. 3). This pattern of absences from the nest with time of day would serve to reduce egg cooling, given the typical circadian rhythm in $T_a$. Although our sample sizes were small, Figure 3 resembles the pattern exhibited by the Dusky Flycatcher (Morton and Pereyra 1985). From this we infer that attentiveness is positively related to $T_a$, as has been shown for both the Dusky Flycatcher (Morton and Pereyra 1985) and the White-crowned Sparrow (Zerba and Morton 1983b). In those species, females increased their attentiveness during midday in order to protect their eggs from sunlight. Junco nests are typically concealed beneath logs or in dried vegetation and thus are shaded from direct sunlight. Hence increased female attentiveness at midday either reflects reduced hunger, a consequence of the female's efficient foraging and abundant food supply (Weathers and Sullivan, in press), or represents an adaptive response serving to reduce nest predation.

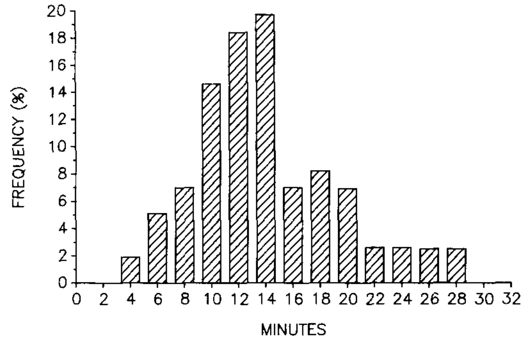


FIGURE 2. Frequency (%) of off-bout durations in incubating *Junco phaeonotus*. Bout classes encompassing fewer than 1% of cases are not shown.

During off bouts, $T_{egg}$ fell to an average of 29.1 ± 2.1°C (range = 17.6–36.0°C, Fig. 4), which is not significantly different from the average of 30.4°C found for six species of passerines in which $T_{egg}$ was measured at 1-min intervals (Haftorn 1988). Thus like other passerines, juncos time their return to the nest such that $T_{egg}$ usually remains above the presumed threshold (25 to 27°C) for embryonic development (see Webb 1987, Haftorn 1988).

For the six nests that we studied, mean minimum $T_{egg}$ during off bouts ($T_{min}$) correlated significantly with embryo age, ($T_{min}$ = 26.2 + 0.29 [days age]; $s_{yx}$ = 0.976, $s_b$ = 0.105, $r^2$ = 0.482, $P$ < 0.05), but not with $T_a$ ($r^2$ = 0.030), indicating that $T_{min}$ was actively regulated. Juncos appear unusual in this respect as Haftorn (1988) found no correlation between $T_{min}$ during off bouts and embryo age in 12 passerine species.

The increase in $T_{min}$ with embryo age results in part from females making more, but shorter, trips off the nest as incubation progresses. Observations at two nests in which $T_{egg}$ was mea-

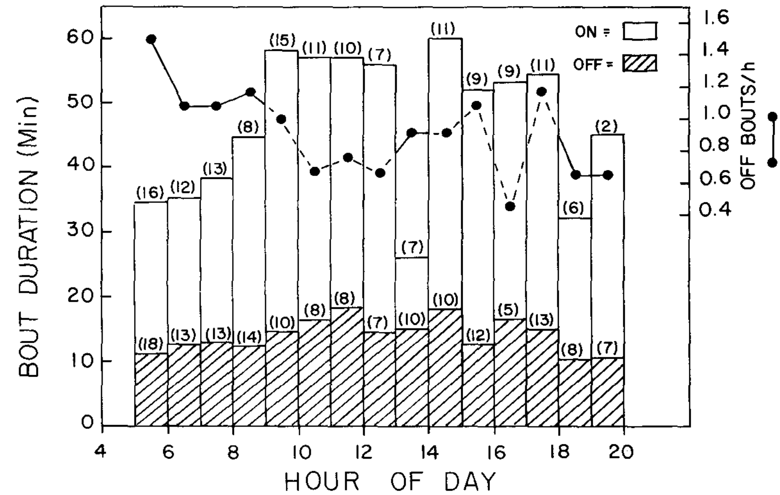


FIGURE 3. Mean duration of on and off bouts (histograms, left ordinate) and mean frequency of off bouts (dots, right ordinate) with time of day in *Junco phaeonotus*. Sample sizes in parentheses.

sured through late incubation and early brooding revealed a further increase in $T_{min}$ after the eggs hatched (Fig. 5). A number of factors may be involved in the observed increase in off-bout frequency and $T_{min}$ during the transition from incubation to brooding in Yellow-eyed Juncos. These include: decreased embryo tolerance to cold, female restlessness during pipping and hatching, and the feeding requirements of newly hatched nestlings. Clearly, additional studies are needed to resolve this issue. The number of off bouts/hour declined dramatically the second day after hatching, presumably as the male began to feed the young and thereby reduced the requirement for feeding by the female.

The active day is the period between the female's first departure from the nest in the morning and her last return to the nest in the evening. For juncos, the active day averaged 13 hr 54 min ($n$ = 12). Females first left the nest 38 ± 15.9 min (range = 19–59 min, $n$ = 12) after sunrise and last returned to the nest 34 ± 13.0 min (range = 11–50 min, $n$ = 12) after sunset. The duration of civil twilight was approximately 27 min. Thus females delayed their evening return to the nest until most other birds had ceased their activity. This may serve to reduce nest predation by Steller's Jays (*Cyanocitta stelleri*).

The constancy of incubation (total time on the nest during the active day) averaged 76.9%, which

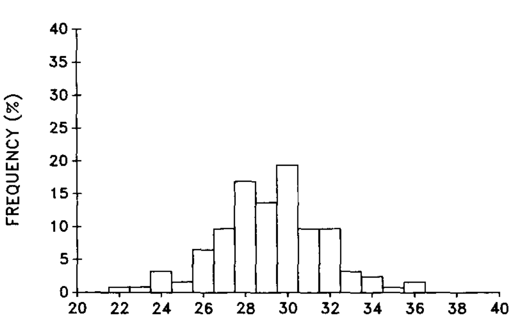


FIGURE 4. Frequency (%) of minimum $T_{egg}$ at end of off bouts ($n$ = 126) in incubating *Junco phaeonotus*.

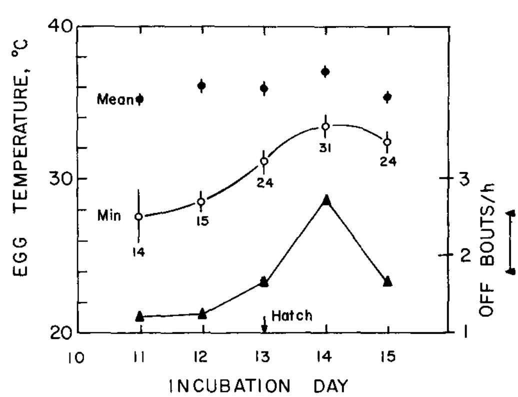


FIGURE 5. Egg temperature (left ordinate) and off-bout frequency (lower right ordinate) in *Junco phaeonotus* as functions of incubation day for nest no. 4. The dots denote mean $T_{egg}$ (±99% confidence interval). Circles denote mean minimum $T_{egg}$ at the end of off bouts (±95% confidence interval; sample size given). Triangles denote mean number of off bouts per hour. Lines were fitted to the data by eye.

is near the high end of the 60–80% range reported for numerous species by Skutch (1976). Males of many passerine species feed their mates at the nest and this may contribute to the relatively high constancy of incubation (about 75%) exhibited by species such as the Great Tit, *Parus major* (Haftorn 1981), Dusky Flycatcher (Morton and Pereyra 1985), or White-crowned Sparrow (Zerba and Morton 1983a). In contrast with these species, male *J. phaeonotus* rarely feed their mates on the nest (unpubl. data). High nest attentiveness in juncos may partly reflect the high food abundance at Rustler Park. Incubating females have little difficulty in obtaining sufficient prey (Weathers and Sullivan, in press). Indeed, unlike some species, both sexes of *J. phaeonotus* maintain their body mass throughout the breeding season (Sullivan 1989; unpubl. data).

## CONSTRAINTS ON ATTENTIVENESS PATTERN

Compared with other small passerines, juncos exhibit a fairly high level of attentiveness, make relatively few trips from the nest per day, and manifest an increase in $T_{min}$ throughout incubation. This nest-attentiveness pattern may represent a compromise between two conflicting selective pressures—predation and egg cooling. The success of a junco nest depends in large part on remaining concealed from predators. Juncos typically nest on the ground and experience a high nest-predation rate (all of the eggs or nestlings disappeared from 25.6% [76/296 nests] of the monitored nests over a 5-year period). Twin-spotted rattlesnakes (*Crotalus pricei*), striped skunks (*Mephitis mephitis*), coati (*Nasua nasua*), and Steller's Jays all prey on the eggs and nestlings of Yellow-eyed Juncos (Sullivan 1988). Stellar's Jays are diurnal and locate nests by following parent juncos (pers. observ.). To reduce jay predation, incubating females should engage in a few, relatively long, foraging bouts each day. However, long bouts off the nest result in eggs cooling to near $T_a$, which in the juncos' habitat is often well below the presumed temperature threshold for embryonic development (25–27°C). Although eggs survive exposure to low $T_a$, development is retarded and the length of time that the eggs are vulnerable to predation by snakes and nocturnal predators would be extended.

The daily attentiveness pattern depends upon several factors: (1) the hunger level and energy requirements of the female—which affects the total time the female needs to spend off the nest, (2) the availability of food—which also influences total time off the nest, (3) possible diurnal variation in predation pressure, and (4) ambient temperature—which determines how fast the eggs cool and hence limits off-bout duration. After fasting overnight, females have a high hunger level and need to spend relatively large amounts of time off the nest foraging. At the same time, the eggs cool rapidly because ambient temperature is low at dawn. Thus, females should make many short trips early in the day. At midday when hunger levels are lower, females are able to spend less time foraging. Furthermore, because ambient temperature is higher at midday and eggs cool less rapidly, females should not only spend less time foraging, but also forage in longer bouts at midday than at dawn. Both expectations are realized for Yellow-eyed Juncos, Dusky Flycatchers, and White-crowned Sparrows, which reflect the fact that nest-attentiveness patterns in these species evolved primarily to maintain egg temperature within the range required for embryonic development. Compared with Dusky Flycatchers and White-crowned Sparrows, however, juncos make relatively few trips from the nest/hour. This could reflect either greater food availability in the junco's habitat or higher levels of predation by diurnal predators such as Steller's Jays. Although we are unable to distinguish between these possibilities, it seems likely that the Yellow-eyed Juncos' nest-attentiveness pattern represents a compromise between conflicting selective pressures of nest predation vs. egg cooling.

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## LITERATURE CITED

AMERICAN ORNITHOLOGISTS' UNION. 1983. Check-list of North American birds. 6th ed. American Ornithologists' Union, Washington, DC.

BALDA, R. P. 1967. Ecological relationships of the breeding birds of the Chiricahua Mountains, Arizona. Ph.D.diss. Univ. of Illinois, Urbana.

CAMPBELL SCIENTIFIC. 1984. CR21X Micrologger Operator's Manual. Campbell Scientific, Logan, UT.

DRENT, R. 1975. Incubation, p. 333–420. *In* D. S Farner and J. R. King [eds.], Avian biology. Vol. 5. Academic Press, New York.

HAFTORN, S. 1981. Incubation rhythm in the Great Tit *Parus major*. Fauna Norv. Ser. C., Cinclus 4: 9–26.

HAFTORN, S. 1983. Egg temperature during incubation in the Great Tit *Parus major,* in relation to ambient temperature, time of day, and other factors. Fauna Norv. Ser. C., Cinclus 6:22–38.

HAFTORN, S. 1988. Incubating female passerines do not let the egg temperature fall below the 'physiological zero temperature' during their absences from the nest. Ornis Scand. 19:97–110.

MOORE, N. J. 1972. Ethology of the Mexican Junco (*Junco phaeonotus palliatus*). Ph.D.diss. Univ. of Arizona, Tucson.

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.

SKUTCH, A. F. 1976. Parent birds and their young. Univ. Texas Press, Austin.

SULLIVAN, K. A. 1988. Ontogeny of time-budgets in yellow-eyed juncos: adaptation to ecological constraints. Ecology 69:118–124.

SULLIVAN, K. A. 1989. Predation and starvation: age-specific mortality in juvenile juncos. J. Anim. Ecol. 58:275–286.

WEATHERS, W. W., AND K. A. SULLIVAN. In press. Juvenile foraging proficiency, parental effort, and avian reproductive success. Ecol. Monogr.

WEBB, D. R. 1987. Thermal tolerance of avian embryos: a review. Condor 89:874–898.

ZERBA, E., AND M. L. MORTON. 1983a. Dynamics of incubation in Mountain White-crowned Sparrows. Condor 85:1–11.

ZERBA, E., AND M. L. MORTON. 1983b. The rhythm of incubation from egg laying to hatching in Mountain White-crowned Sparrows. Ornis Scand. 14: 188–197.