

## INCUBATION PATTERNS IN HARRIS' SPARROWS AND WHITE-CROWNED SPARROWS IN THE NORTHWEST TERRITORIES, CANADA

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**Abstract.**—Nest attendance patterns during incubation were compared in sympatric populations of Harris' Sparrows (*Zonotrichia querula*) and Gambel's White-crowned Sparrows (*Z. leucophrys gambelii*) in the Northwest Territories, Canada. In both species, only females incubated. Females of both species spent similar proportions of their active day incubating, but duration of bouts on and off nests were significantly longer for Harris' Sparrows. Duration of bouts on nests decreased with increasing ambient temperature ( $T_a$ ) in White-crowned Sparrows. In Harris' Sparrows, duration of bouts on nests decreased with increasing  $T_a$  up to 20 C, but increased in length at higher  $T_a$ s. Interspecific differences in incubation patterns may have resulted from the greater risk of egg hyperthermia in Harris' than White-crowned Sparrow nests, because the former are placed in more open locations and exposed to increased solar radiation. In both species, duration of bouts off nests increased with  $T_a$ . Increased length of bouts away from nests in Harris' Sparrows may have resulted in part from reduced cooling rates of their eggs, as influenced by the species' nest microclimate and greater egg mass. Susceptibility to predation may also have affected incubation behavior. As Harris' Sparrow nests are subject to greater risk of predation than White-crowned Sparrow nests, female Harris' Sparrows could reduce risks to themselves and protect their nests more effectively by taking fewer, lengthier trips to and from the nest and remaining on their eggs for longer periods.

### **PATRÓN DE INCUBACIÓN DE *ZONOTRICHIA QUERULA* Y *Z. LEUCOPHRYS GAMBELII* EN LOS TERRITORIOS DEL NOROESTE DE CANADA**

**Síopsis.**—Los patrones de atención al nido fueron comparados en poblaciones simpátricas del gorrión de Harris (*Zonotrichia querula*) y el gorrión de corona blanca (*Z. leucophrys gambelii*) en los territorios del noroeste de Canadá. En ambas especies las hembras son las que incuban e invierten proporciones similares del día incubando. Sin embargo los episodios o períodos de incubación (entrando y saliendo del nido) fueron significativamente más largos en el gorrión de Harris. En el gorrión de corona blanca los períodos dentro del nido disminuyeron con aumentos en la temperatura ambiental. Por su parte, en el gorrión de Harris la duración de períodos dentro del nido disminuyeron según aumento la temperatura hasta llegar a los 20 C, pero incrementaron a temperaturas más altas. Las diferentes interespecíficas en los patrones de incubación entre ambas especies muy bien pudieran ser el resultado de un mayor riesgo de hipertermia en los huevos en el gorrión de Harris, ya que éste coloca sus nidos en lugares más abiertos y más expuestos a la radiación solar. En ambas especies la duración de los episodios de incubación se incrementaron con las temperaturas. Los períodos más largos fuera del nido por parte del gorrión de Harris muy bien podría ser el resultado de una menor tasa de enfriamiento de los huevos de éstos como consecuencia de su mayor masa y las condiciones microclimáticas del nido. La susceptibilidad a depredación muy bien pudiera también influir en la conducta de incubación. Dado el caso de que los nidos de gorriónes de Harris están sujetos a mayor riesgo de depredación que los nidos del gorrión de corona blanca, las hembras de Harris muy bien pudieran reducir el riesgo a

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éstas y a sus nidos dando menos viajes pero tomando períodos de incubación más prolongados.

Incubation is an important component of reproduction in passerine birds, but it presents the attending parent(s) with conflicting needs to maintain thermal conditions necessary for embryo development, while at the same time obtaining sufficient energy for metabolic requirements (Carey 1980, Drent 1973, Vleck 1981, Williams 1987). In some species, restrictions on time available for foraging may negatively affect reproductive output (Walsberg 1983), while incubating birds also may neglect their eggs in order to forage and "defend" their body temperature (Morton and Pereyra 1985). The incubation process often is strongly influenced by environmental conditions, especially air temperature ( $T_a$ ) (Drent 1975), and places a selective pressure on behavioral traits (Zerba and Morton 1983a).

In 1989–1991, I studied patterns of nest attendance during incubation in sympatric populations of Harris' Sparrows (*Zonotrichia querula*) and Gambel's White-crowned Sparrows (*Z. leucophrys gambelii*) breeding in the low Arctic of the Northwest Territories (NWT), Canada. Here I compare duration of bouts on and off nests during incubation, and effects of environmental conditions, especially air temperature, on incubation behavior in Harris' Sparrows and White-crowned Sparrows. As egg mass is smaller in White-crowned Sparrows than in Harris' Sparrows (Norment 1992a), and smaller eggs cool at a faster rate (Kendeigh et al. 1977), I also test the prediction that the durations of foraging trips away from nests should be shorter for incubating White-crowned Sparrows than for incubating Harris' Sparrows. Finally, I describe general activity patterns of females of the two species during the incubation period in a low Arctic environment where mid-summer cycles of daylight and darkness are not clear-cut.

Nest attendance by White-crowned Sparrows has been studied previously; incubation is by the female only, but both sexes feed young (DeWolfe 1968; Hubbard 1978; King 1986; Morton et al. 1972; Zerba and Morton 1983a, 1983b). Incubation in Harris' Sparrows is also by the female only (Norment and Shackleton 1993), although incubation behavior in the species has not been investigated in detail prior to this study. I chose a comparative approach because there are relatively few comparative studies of incubation behavior in closely related, sympatric species. Such an approach involving species with very similar breeding biologies (Norment 1992a) may be useful in examining the adaptive basis of differences in incubation behavior and the effects of body size and nesting ecology on these behaviors.

#### STUDY AREA AND METHODS

I conducted the study at Warden's Grove (WG), Thelon Game Sanctuary, NWT, Canada (63°41'N, 104°26'W) during the summers of 1989–1991. Daylight (civil daylength plus civil twilight) is continuous from late May to mid-July at this latitude. The study area lies near the southern

TABLE 1. June weather data recorded at Warden's Grove, 1989–1991.

	Temperature (C)			Mean wind speed (km/h)	Precipitation (mm)
	Maximum	Minimum	Mean		
1989	29.1	-3.2	9.7	6.5	4.6
1990	23.0	-3.4	7.5	12.3	42.1
1991	25.8	1.0	7.5	12.6	36.4

limit of the low arctic (Bliss 1981), and contains a mosaic of isolated spruce (*Picea* spp.) stands and extensive tundra vegetation. Tree "islands" from <0.01 to 12.3 ha typically are surrounded by shrubby dwarf birch (*Betula glandulosa*), willow (*Salix* spp.), and green alder (*Alnus crispa*) 0.3–1.5 m tall, which provide the primary nesting habitat for Harris' Sparrows and White-crowned Sparrows. Detailed descriptions of the study area are in Norment (1992a).

The study area is situated near the border between the arctic and boreal climatic regions (Hare and Thomas 1974). The climate is characterized by long, cold winters and short, generally cool summers. Weather conditions during June, when most female *Zonotrichia* at WG incubate eggs (Norment 1992a), were warmer and drier in 1989 than in either 1990 or 1991 (Table 1).

Nest attendance patterns during incubation were quantified by observing nests with 8× binoculars or a 25× spotting scope from concealed locations or distances >25 m, so as not to disturb the behavior of attending birds. Nests of banded birds of known sex were observed for ca. 1-h periods distributed throughout the daily activity periods. Incubating Harris' Sparrows were observed for 50 1-h periods ( $n = 9$  nests; clutch size: six nests with four eggs, three nests with five eggs) and incubating White-crowned Sparrows for 24 1-h periods ( $n = 4$  nests; clutch size: two nests with four eggs, two nests with five eggs); observations were distributed throughout the incubation periods of both species. Sample size for White-crowned Sparrows was limited in part by its lower breeding density, which was about 33% that of Harris' Sparrows (Norment 1992a). During incubation, sex of the attendant bird(s) and length of bouts on and off nests were recorded. Bouts on the nest were defined as the periods when the female was incubating the eggs; these began when the female settled on the nest and ended when she left. Bouts off the nest began when the female stopped incubating and left the nest; they ended when the female resumed incubation.  $T_a$  was measured at the beginning, midpoint, and end of each observation period with a Bailey thermometer (Bat-12 microprobe) and a thermocouple placed in the shade beneath a shrub with characteristics approximating those of the nest site. Measurements were averaged to obtain a mean  $T_a$  for each observation period.

In 1989 I also conducted one 24-h watch of a Harris' Sparrow nest during incubation. Personnel limitations made repeating the procedure for additional Harris' Sparrow and White-crowned Sparrow nests imprac-

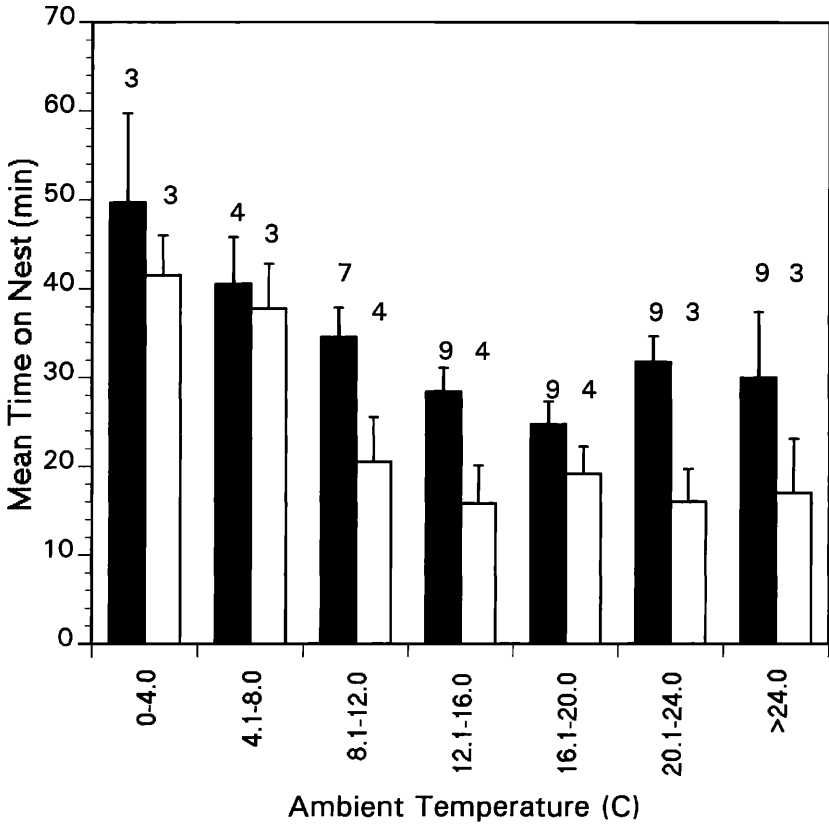


FIGURE 1. Average duration of incubation bouts for Harris' Sparrows (filled bars) and White-crowned Sparrows (open bars) at Warden's Grove, 1989-1991. Error bars indicate  $\pm 1$  SE. Numbers above bars refer to number of females observed within each  $T_a$  interval.

tical. Instead, I obtained additional data on daily activity periods of Harris' Sparrows and White-crowned Sparrows during incubation by extended observations of nests during periods spanning cessation of activity in the evening and resumption of activity in the early morning.

Average length for bouts on and off the nests were calculated for each female during each approx. 60-min observation period. I used Spearman's rank correlation (Sokal and Rohlf 1981) to examine the relationship between  $T_a$  and length of time on and off nests during incubation. To avoid violating assumptions of independence among samples, I divided the range of  $T_a$ s observed during the study into seven 4 C intervals, and averaged mean times on and off for each female within each temperature interval. Hence, each 4 C interval contained only one data point for each female. Although I attempted to observe each female at  $T_a$ s within each 4 C interval, fewer Harris' Sparrows were observed at  $T_a$ s <

TABLE 2. Length of bouts on and off the nest ( $\bar{x} \pm SD$  min) for Harris' Sparrows ( $n = 9$  females) and White-crowned Sparrows ( $n = 4$  females), 1989–1991. Means are based on average values of bouts on and off nest for each female.

Bout	Harris' Sparrow	White-crowned Sparrow	<i>t</i>	<i>P</i>
On nest	32.3 $\pm$ 7.3	21.3 $\pm$ 3.9	2.645	<0.05
Off nest	12.7 $\pm$ 3.2	8.7 $\pm$ 2.2	2.253	<0.05

8 C (Fig. 1). The Wilcoxon matched-pairs signed-ranks test was used for interspecific comparisons of time on and off the nests within the 4 C intervals. Percentages were arcsin transformed prior to statistical analysis. Significance level for all analyses was 0.05;  $\bar{x} \pm SD$  are given throughout, unless otherwise indicated.

#### RESULTS

During >98 h of nest observations, only female *Zonotrichia* incubated eggs. Average percentage of time spent incubating by Harris' Sparrows (70.4  $\pm$  7.2%,  $n = 9$  nests) and White-crowned Sparrows (71.7  $\pm$  2.8%,  $n = 4$  nests) did not differ significantly ( $t = 0.344$ ,  $df = 11$ ,  $P > 0.05$ ). During a 24-h nest watch in 1989, a female Harris' Sparrow spent 80.1% of the entire 24-h period, and 67.4% of her active period, on the nest. Although female Harris' Sparrows and White-crowned Sparrows spent approximately equal proportions of their active days incubating eggs, lengths of bouts on and off nests were significantly longer for Harris' Sparrows (Table 2). Lengths of bouts on (31.6  $\pm$  10.5 min,  $n = 19$ ) and off (14.0  $\pm$  5.4 min,  $n = 30$ ) the nest for an incubating female Harris' Sparrow during the 24-h nest watch were similar to those for the shorter observation periods. In both species, females foraged most of the time when away from nests (pers. obs.).

Mean length of continuous incubation during the arctic night was about 1 h longer for White-crowned Sparrows (8.86  $\pm$  0.20 h,  $n = 3$  females) than for Harris' Sparrows (7.95  $\pm$  0.80 h,  $n = 3$  females), although the means did not differ significantly (Mann-Whitney  $U = 8$ ,  $P = 0.10$ ). Length of the active day for incubating females thus was about 16 h for Harris' Sparrows and 15 h for White-crowned Sparrows. Observed bouts of continuous incubation tended to begin and end earlier for Harris' Sparrows (initiation: 1817–1938 hours MST; end: 0315–0429 hours MST) than for White-crowned Sparrows (initiation: 1930–2002 hours MST; end: 0322–0500 hours MST).

In both species, length of incubation bouts tended to be greatest at lower  $T_a$  (Fig. 1); the relationship was significant for White-crowned Sparrows ( $r_s = -0.821$ ,  $P < 0.05$ ) but not for Harris' Sparrows ( $r_s = -0.714$ ,  $P = 0.10$ ). Mean length of incubation bouts was shortest within the 12.1–16.0 C interval for White-crowned Sparrows, and within the 16.1–20.0 C interval for Harris' Sparrows (Fig. 1). White-crowned Sparrow incubation

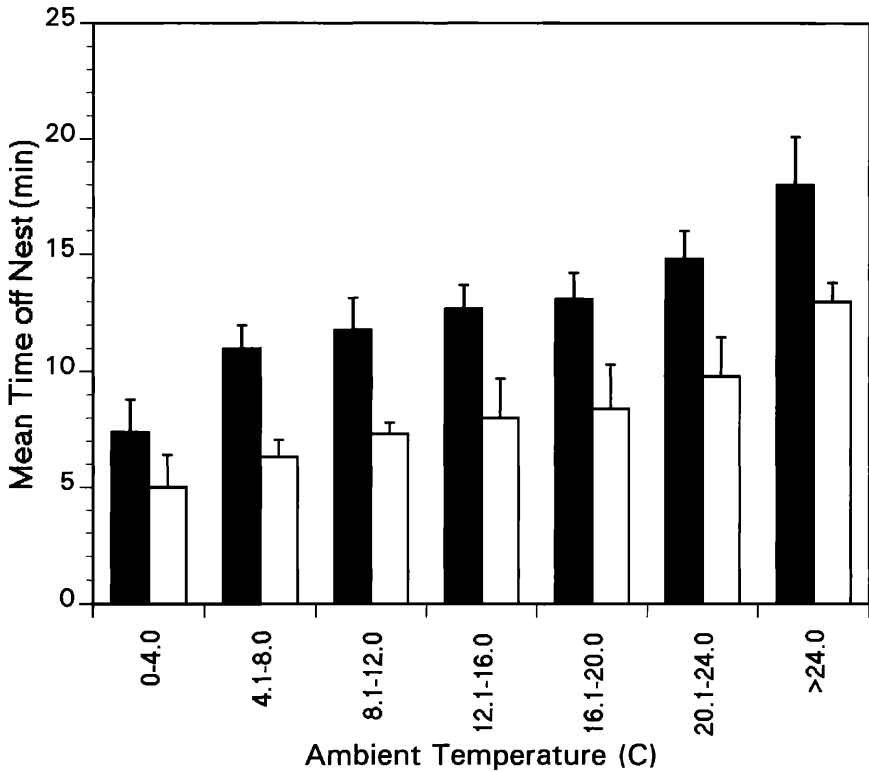


FIGURE 2. Average duration of bouts away from the nest for incubating Harris' Sparrows (filled bars) and White-crowned Sparrows (open bars) at Warden's Grove, 1989-1991. Error bars indicate  $\pm 1$  SE. Sample sizes given in Figure 1.

bouts were significantly shorter than Harris' Sparrow incubation bouts across the range of  $T_a$ s observed at WG (Wilcoxon signed ranks test,  $P < 0.01$ ).

Bouts off the nest increased in length with increasing  $T_a$  (Fig. 2); the relationship was significant for both White-crowned Sparrows ( $r_s = 1.0$ ,  $P < 0.001$ ) and Harris' Sparrows ( $r_s = 1.0$ ,  $P < 0.001$ ). White-crowned Sparrow bouts off the nest were significantly shorter than Harris' Sparrow bouts off the nest across the range of  $T_a$ s observed at WG (Fig. 2; Wilcoxon signed-ranks test,  $P < 0.01$ ).

#### DISCUSSION

General patterns of incubation in Harris' Sparrows and White-crowned Sparrows at WG were similar to those observed elsewhere in *Zonotrichia*. Incubation in White-crowned Sparrows, White-throated Sparrows (*Z. albicollis*), and Golden-crowned Sparrows (*Z. atricapilla*) is by females only (DeWolfe 1968, Hendricks 1987, Hubbard 1978, Lewis 1975, Lowther and

Falls 1968, Zerba and Morton 1983a), which spend about 70% of their active day on the nest (Hendricks 1987, Hubbard 1978, Zerba and Morton 1983a). Length of bouts on ( $\bar{x} = 19.6$  min) and off ( $\bar{x} = 7.8$  min) the nest for incubating female *Z. l. oriantha* in the Sierra Nevada of California was remarkably similar to that for White-crowned Sparrows at WG, as was length of continuous incubation ( $\bar{x} = 9.0$  h) (Zerba and Morton 1983a).

Both species spent similar proportions of their active days incubating, but duration of bouts on and off the nest were shorter in White-crowned Sparrows. Duration of bouts on the nest also correlated more strongly with  $T_a$  in White-crowned Sparrows than in Harris' Sparrows. As incubation behavior is influenced by a large number of factors, including  $T_a$  and other climatic variables (Cartar and Montgomerie 1985, Drent 1973), photoperiod (Zerba and Morton 1983a), food availability (Haftorn 1978a, Weeden 1966), and effects of hunger and predation on the incubating female (Webb and King 1983), I cannot evaluate all possible reasons for differences in the incubation behavior of Harris' Sparrows and White-crowned Sparrows. It seems, however, that  $T_a$ , with its differential effects on eggs of different mass, along with differences in the nesting ecologies of the two species, is at least partially responsible for patterns observed in this study.

In many passerines there is an inverse relationship between  $T_a$  and nest attentiveness during incubation (Drent 1973, 1975; Haftorn 1978b; Morton and Pereyra 1985; White and Kinney 1974; Williams 1993; Yom-Tov et al. 1978), although female incubation behavior should be correlated most strongly with equilibrium egg temperature ( $T_{eq}$ ), the equilibrium temperature that would occur in an egg if the female were off the nest (Webb and King 1983). Departure of females from the nest, and thus incubation time, appears to be controlled by warming of the eggs to a "set point" (White and Kinney 1974, Zerba and Morton 1983b). Duration of incubation bouts should be inversely related to  $T_a$ , at least at lower temperatures, because a greater transfer of heat is required for a longer period of time at low  $T_a$  (Zerba and Morton 1983a). Duration of incubation bouts at WG was inversely correlated with  $T_a$  in White-crowned Sparrows; a similar, but non-significant, relationship ( $P = 0.1$ ) existed for Harris' Sparrows, although duration of bouts on the nest increased above 20 C. Increased incubation times at high temperatures may be a response to potentially harmful effects of egg hyperthermia (Drent 1975) in an environment where ground temperatures above 30 C occur (Norment, unpub. data). White-crowned Sparrows may not have increased attentiveness at high  $T_a$ s because vegetation within 0.5 m of their nests was about 70% more dense than was vegetation near Harris' Sparrow nests (Norment 1993). Increased vegetation could have reduced insolation, and prevented egg temperatures from increasing to near lethal levels. Incubation patterns in *Z. l. oriantha* and *Empidonax oberholseri* nesting in high subalpine habitat in California are also affected by potential exposure of eggs to intense solar radiation, and subsequent heating to lethal temperatures (Morton and Pereyra 1985, Zerba and Morton 1983a). In *Z. l. oriantha*,

duration of incubation bouts decreased as  $T_a$  increased, up to about 12 C; above this temperature, duration of bouts on the nest increased (Zerba and Morton 1983a).

Duration of bouts off the nest increases with  $T_a$  in many incubating birds (Drent 1973), including *Z. l. oriantha* (Zerba and Morton 1983a). In another study of *Z. leucophrys*, shorter trips away from the nest were taken at all ranges of  $T_{eq1}$  (which increases with  $T_a$ ), while longer trips occurred only at moderate temperatures (Webb and King 1983). Length of foraging trips is limited by the need to maintain thermal conditions necessary for embryo development (Webb and King 1983, Zerba and Morton 1983b). Thus, increased duration of foraging trips at higher  $T_a$  for both Harris' Sparrows and White-crowned Sparrows at WG is to be expected.

Interspecific differences in lengths of bouts on and off the nest at WG are surprising. These differences may be explained partially by differences in body mass between the species. Female Harris' Sparrows weigh more than female White-crowned Sparrows at WG (HS:  $33.7 \pm 2.2$  g; WCS:  $26.6 \pm 1.7$  g), and they lay heavier eggs (HS:  $3.09 \pm 0.26$  g; WCS:  $2.48 \pm 0.13$  g; Norment 1992a). Cooling rate of an avian egg is inversely related to its mass (Kendeigh et al. 1977). Using the formula in Kendeigh et al. (1977), White-crowned Sparrow eggs should cool about 9% more quickly than Harris' Sparrow eggs. White-crowned Sparrow eggs may also cool more quickly than Harris' Sparrow eggs because of differences in nest placement. Thicker vegetation at White-crowned Sparrow nests could have reduced insolation and maintenance of stable egg temperatures; for example, increased cooling rate in Snow Bunting (*Plectrophenax nivalis*) eggs relative to Lapland Longspur (*Calcarius lapponicus*) eggs is due to decreased insolation at bunting nests (Lyon and Montgomerie 1987). Thus female White-crowned Sparrows, with smaller eggs and less insolation at their nests, should take shorter foraging trips than female Harris' Sparrows. Increased cooling rates of eggs might also explain the longer periods of continuous incubation and tendency to end these periods later in the morning in White-crowned Sparrows.

Thermal considerations, however, probably explain only part of the variation in incubation behavior; other factors, including susceptibility to predation, also may influence incubation behavior (Webb and King 1983). At WG, predation on nests during the incubation and nestling periods of the nesting cycle was much higher for Harris' Sparrows (34.4% of all known nests) than for White-crowned Sparrows (0% of all known nests) (Norment 1993). Female Harris' Sparrows also seem particularly vulnerable to predators during nesting because they forage in more open habitats than White-crowned Sparrows (Norment 1992b). Northern Shrikes (*Lanius excubitor*) were seen chasing foraging female Harris' Sparrows (but never White-crowned Sparrows), and three breeding Harris' Sparrow females, but no White-crowned Sparrows, were known to have been killed by shrikes in 1991. Females of the two species spent equal proportions of their active day incubating, and had to satisfy their energy



requirements in approximately the same proportion of their active days. Given this restriction, female Harris' Sparrows could reduce risk to themselves and their nests by taking fewer, lengthier trips to and from the nest. Length of bouts on and off nests observed in this study indicate that female Harris' Sparrows should average only 24 trips to/from their nests in a 16-h period, versus 32 for female White-crowned Sparrows. Longer attentive bouts also could maximize the parent's abilities to protect eggs (Drent 1973, 1975; Morton and Pereyra 1985) and nestlings (Breitwisch 1989, Finch 1984; see also Biedenweg 1983, Mugaas and King 1981) from predators.

As I did not control for clutch size, observed differences in incubation behavior between the species could have been affected by the higher proportion of five-egg clutches in the White-crowned Sparrow sample. Generally, incubation time and/or proportion of the day spent incubating increases with clutch size in passerines (Baltz and Thompson 1988, Moreno and Carlson 1989, Smith 1989). As mean clutch size in observed Harris' Sparrow nests ( $\bar{x} = 4.33$ ) was only slightly less than in observed White-crowned Sparrow nests ( $\bar{x} = 4.50$ ), however, I conclude that clutch-size effects were minimal in this study.

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