

Patterns of Nestling Feeding in Harris's Sparrows, *Zonotrichia querula* and White-crowned Sparrows, *Z. leucophrys*, in the Northwest Territories, Canada

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Patterns of nestling feeding by males and females were compared in sympatric populations of Harris's Sparrows (*Zonotrichia querula*) and Gambel's White-crowned Sparrows (*Z. leucophrys gambelii*) in the Northwest Territories, Canada. In both species, only the female brooded young. Total feeding rate (both parents), and male and female feeding rates, increased with nestling age in both species; total feeding rates did not differ significantly between species. Nestlings of both species were fed most frequently by females during the early part of the nestling period (day 0–5), and feeding rates did not approach parity until nestlings were 6–8 d old. Patterns of nestling feeding, including initially low male provisioning, in Harris's Sparrows and White-crowned Sparrows at my low arctic study site were similar to those in other populations of *Zonotrichia*. Low levels of male nestling care, relative to females, appears to be relatively uncommon among socially monogamous passerines. Reduced male care may be adaptive in temperate environments, as it would allow males to pursue other mating opportunities. However, reasons for persistence of the trait in the low arctic, where breeding is highly synchronous, remain unclear.

Key Words: Harris's Sparrow, *Zonotrichia querula*, White-crowned Sparrow, *Zonotrichia leucophrys*, breeding biology, nestling care, Northwest Territories.

Nestling care is an important component of reproduction in passerine birds and requires high parental investment (PI) (Ricklefs 1974; Walsberg 1983). Unequal male versus female PI during the nestling phase of the breeding cycle occurs in many passerines (e.g., Hegner and Wingfield 1987; Yasukawa et al. 1990; Haggerty 1992). These asymmetries may arise from conflict between the sexes (Gowaty 1996a, b) and may be linked to the evolution of avian mating systems (Emlen and Oring 1977). Because of the assumed "cost of reproduction," high levels of PI may reduce adult survival probabilities, and select for reduced clutch size (Williams 1966).

In 1989–1991, I studied nestling care in sympatric Harris's Sparrows (*Zonotrichia querula*) and Gambel's White-crowned Sparrows (*Zonotrichia leucophrys gambelii*) in the Northwest Territories (NWT), Canada. Here I compare effects of nestling age on parental feeding rates and the relative contribution of males and females to nestling feeding in these species. Nestling care has been studied previously in White-crowned Sparrows; both sexes feed the young, but only females brood nestlings (Chilton et al. 1995). The same pattern occurs in Harris's Sparrows (Norment and Shackelton 1993), although nestling care in the species had not been investigated in detail prior to this study. I used a comparative approach to investigate *Zonotrichia* nestling care because there are relatively few such studies in sympatric passerine populations.

Study Area and Methods

I conducted the study at Warden's Grove (WG), Thelon Wildlife Sanctuary, Northwest Territories (63° 41'N, 104°26'W), during the summers of 1989–1991. The low arctic study area contains a mosaic of isolated spruce (*Picea* spp.) stands and extensive tundra vegetation.

Tree "islands" are surrounded by shrubby Dwarf Birch (*Betula glandulosa*), willow (*Salix* spp.), and Green Alder (*Alnus crispa*) 0.3–1.5 m tall, which provide nesting habitat for *Zonotrichia*. The study area lies near the border between the arctic and boreal climatic regions (Hare and Thomas 1974), with cold winters and short, cool summers. In 1989–1991, mean ambient temperatures at WG ranged between 7.5 and 9.7°C in June and 12.5 and 16°C in July. Although the summers of 1989–1991 were relatively mild, violent storms may occur after breeding *Zonotrichia* arrive at WG (Norment 1985, 1992).

Nestling care was quantified by observing nests with 8× binoculars or 25× spotting scope from concealed locations or distances > 25 m, so as not to disturb attending birds. Nests of color-banded parents of known sex were observed for 1-h periods distributed throughout daily activity periods. Nests with young *Zonotrichia* were observed from day 0 to day 9 of nestling development, close to the average age of fledging for these species at WG (Norment 1992). Only nests observed on > 5 d, with nestlings of known

age with both parents present, and with broods in which nestling number remained constant, were used in analyses. Observation time was 78 h for Harris's Sparrow broods ($n = 9$ different broods; 3 broods with 3 nestlings, 4 broods with 4 nestlings, and 2 broods with 5 nestlings), and 36 h for White-crowned Sparrow broods ($n = 4$ different broods: 2 broods with 4 nestlings and 2 broods with 5 nestlings). White-crowned Sparrow sample size was limited by its breeding density, which was 33% that of Harris's Sparrows (Norment 1992). Number of broods observed for each species was almost constant across years (Harris's Sparrow: 3 broods in each year; White-crowned Sparrow: 1 brood each in 1989 and 1991, 2 broods in 1990). During the study, sex of the attendant bird(s) and their activities (feeding young or brooding) were recorded. Because adult *Zonotrichia* feeding nestlings usually perch in conspicuous locations before visiting the nest (personal observation), sex of attendant banded birds could be determined.

Male, female, and combined parental feeding rates were calculated for each nest during each 1-h observation period. I used linear regression to examine nestling age effects on nestling feeding rates using mean values for each age (0-9 d), based on all nests observed. I examined interspecific differences in nestling feeding rates by using the general linear model to do a two-factor ANOVA with feeding rate as the response variable, and nestling age (days 0-9) and species as factors. I also used the general linear model for an intersex comparison of Harris's Sparrow nestling feeding rates, with nestling age (days 0-9) and sex as factors. In these analyses, cells contained number of feedings/h for individual nests ($n = 9$ nests). I also used the general linear model to test for an interaction effect between Harris's Sparrow brood size and sex, based upon mean feeding rates for each nest. When sample sizes varied across days or species, I used the square-root transformation to reduce inequality among variances (Zar 1999). If a significant interaction term was present for any two-factor ANOVA, then a single-factor ANOVA was used to compare means of a factor separately at each level of the second factor (Underwood 1997). Finally, I used the Wilcoxon signed-ranks test (Sokal and Rohlf 1981) for an intersex comparison of Harris's Sparrow nestling feeding rates across the range of nestling ages; for this I compared

mean values for each member of each pair for early (day 0-2), middle (day 3-5) and late (day 6-8) stages of nestling care. Significance level for all analyses was 0.05; $\bar{x} \pm SD$ are given throughout, unless otherwise indicated.

Results

During > 114 h of nest observations, only female Harris's Sparrows and White-crowned Sparrows brooded nestlings. Males of both species fed nestlings, but attendant males never stayed > 2 min at a nest. Combined feeding rate (both parents) increased with nestling age in Harris's Sparrows ($r = 0.954$, $P < 0.001$) and White-crowned Sparrows ($r = 0.926$, $P = 0.006$) (Figure 1). Harris's Sparrows tended to feed day 0 and day 3 nestlings more frequently than did White-crowned Sparrows, but feeding rates for Harris's Sparrows were lower than for White-crowned Sparrows for day 5-9 nestlings (Figure 1). Across the range of nestling ages, there was no significant difference between species in combined feeding rates (Two-factor ANOVA; $df = 1$, $F = 0.54$, $P = 0.465$).

Harris's Sparrow and White-crowned Sparrow nestlings were fed most often by females during early stages of the nestling period; percentage of male feeding trips attained maximum values of ca. 47% of total feedings when nestlings were between day 6 and 9 (Figure 1). Male White-crowned Sparrows generally fed nestlings on day 0, whereas all banded male Harris's Sparrows known to be > 1 yr began feeding nestlings by day 1. However, a few Harris's Sparrow males appeared reluctant to feed nestlings < 3 d. At several nests, females returning from foraging trips perched within several m of the nest and gave a long series of "chink" calls. These were repeated until the male fed the young, at which time the female ceased calling and visited the nest. This behavior was not seen in White-crowned Sparrows and ceased after males began regular feedings.

Total feedings were higher for female than for male Harris's Sparrows (62.5%, $n = 748$) and White-crowned Sparrows (60.2%, $n = 304$). Male feeding rates increased with nestling age for Harris's Sparrows ($r = 0.965$, $P < 0.001$) and White-crowned Sparrows ($r = 0.951$, $P < 0.001$) (Figure 1). Female feeding rates also increased with nestling age for Harris's Sparrows ($r = 0.780$, $P = 0.005$) and White-crowned Sparrows ($r = 0.878$, $P < 0.001$) (Figure 1). Because there was a significant interaction term between sex and age (Two-factor ANOVA; Table 1), I used single-factor ANOVAs to compare male and female feeding rates at each nestling age (see Methods). Average feeding rates for Harris's Sparrow broods were significantly greater for females than for males from day 0 through day 4, but not for day 5 through day 9 (Figure 1). The Wilcoxon signed-ranks test also indicated that female Harris's Sparrows fed nestlings significantly more often than males through

TABLE 1. Two-factor ANOVA for effects of sex and nestling age on male and female feeding rates for Harris's Sparrows.

Source	df	SS	MS	F	P
Sex	1	12.7965	11.57774	57.97	0.000
Nestling age	9	20.0790	2.2310	11.17	0.000
Sex* nestling age	9	7.3311	0.8146	4.08	0.000
Error	134	26.7621	0.1997		
Total	153	66.9688			

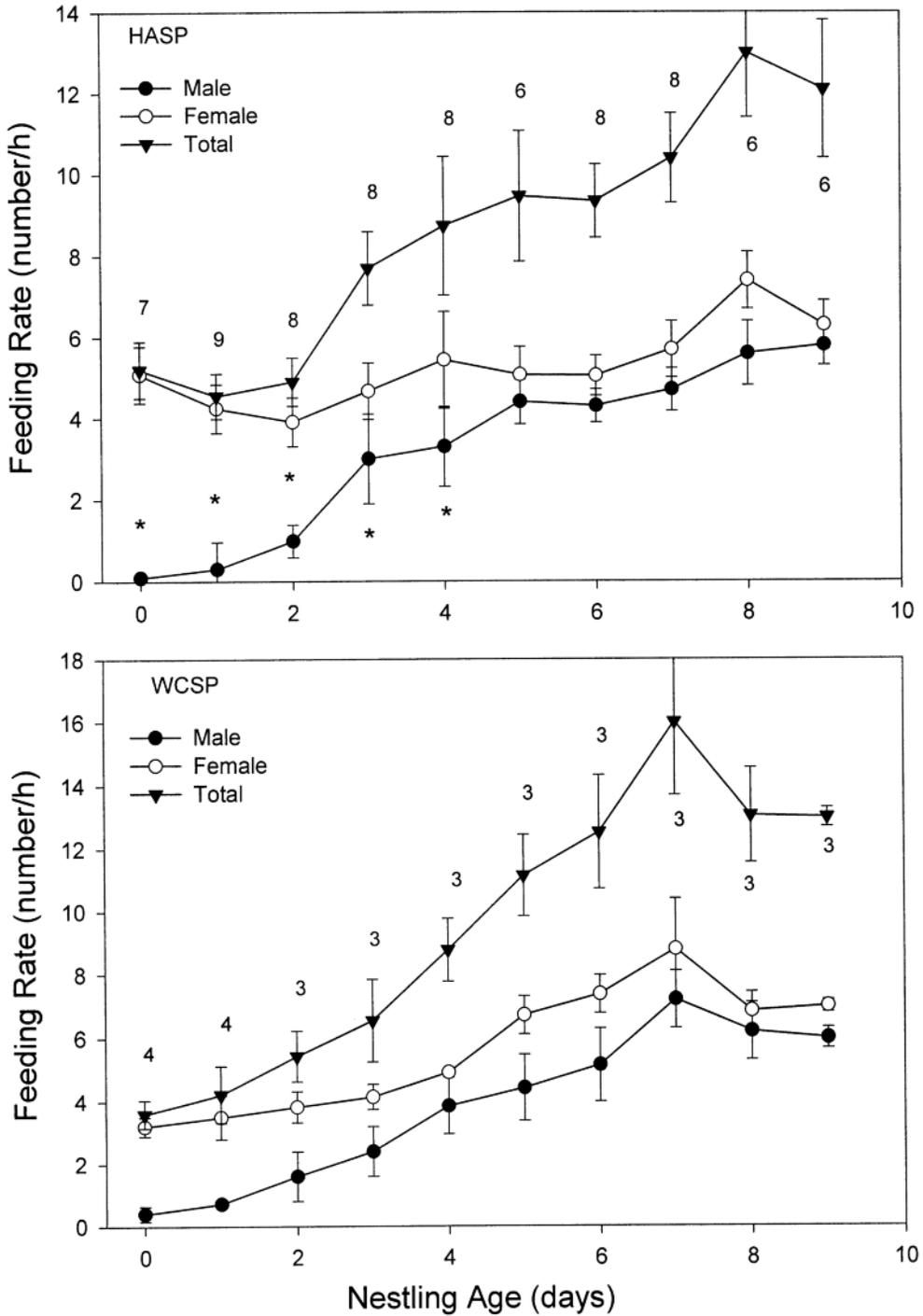


FIGURE 1. Mean feedings/h for both parents (Total), males, and females plotted against nestling age for Harris's Sparrows (HASp, top) and White-crowned Sparrows (WCSP, bottom) at Warden's Grove, 1989-1991. Error bars indicate ± 1 SE. Sample sizes (observation periods) given for each nestling age; * on the HASp graph indicate significant differences ($P < 0.05$) for single-factor ANOVAs comparing male and female feeding rates for broods of a single age (see Methods).

the early and middle stages of nestling care, but not during the late stage (Table 2, $P < 0.05$). Patterns were similar in White-crowned Sparrows, but sample sizes were too small for the Wilcoxon test (Table 2). Brood size significantly affected Harris's Sparrow feeding rates, with lower rates in smaller broods ($P = 0.003$), although male feeding rates were smaller than female feeding rates for all brood sizes ($P < 0.001$) and there was no significant interaction between sex and brood size (Two-factor ANOVA; Table 3).

Discussion

Patterns of nestling care in Harris's Sparrows and White-crowned Sparrows at WG were similar to those observed elsewhere in *Zonotrichia*. Both sexes feed nestlings, but only the female broods young, in White-crowned Sparrows (Chilton et al. 1995), Rufous-collared Sparrows (*Z. capensis*; Miller and Miller 1968) and Golden-crowned Sparrows (*Z. atricapilla*; Norment et al. 1998). In White-throated Sparrows (*Z. albicollis*) brooding is primarily by females, although males occasionally brood (Falls and Kopachena 1994). Male *Zonotrichia* usually feed nestlings less than females, with the proportion of male feedings remaining low during the first few days after nestlings hatch (DeWolfe 1968; Hendricks 1987a; Knapton and Falls 1983; Morton 2002).

Feeding nestlings, particularly as they approach fledging, is energetically expensive for arctic passerines (Custer et al. 1986). In Harris's Sparrows and White-crowned Sparrows, combined parental feeding rates and male feeding rates increased with nestling age; female feeding rates also increased, but less steeply than male rates. Both the relative contribution of males to feeding nestlings < 3d, and their overall feeding rates, were lower than for females of both species. These differences probably were not due to brood size effects. Brood size affects patterns of male and female parental investment in some socially monogamous passerines (Johnson and Best 1982; Hegner and Wingfield 1987; Westneat 1988; Carey 1990). However, I had equal numbers of White-crowned Sparrow broods of 4 and 5, and almost equal numbers of Harris's Sparrow broods of 3, 4 and 5, and the lack of an interaction effect between sex and brood size in the two-factor ANOVA (Table 3) suggests that brood size did not affect observed differences in male and female feeding rates in my study.

In four of the five *Zonotrichia* species, nestling feeding develops more slowly in males than in females, and males feed nestlings less frequently than females (Miller and Miller 1968; Hubbard 1978; King 1986; Hendricks 1987a; Morton 2002; this study). The only exception is the White-throated Sparrow. Males of the "white-striped" morph feed nestlings less than females, but "tan-striped" males feed nestlings at about the same rate as do females (Kopachena and Falls 1993). Thus, the general pattern in *Zonotrichia* differs from that of most socially monogamous passerines, in which males

TABLE 2. Mean parental feeding rates (number/h) for Harris's Sparrows and White-crowned Sparrows according to sex and nestling age. Means based on averages for each brood within 3-d stages of the nestling period. Levels of significance (between sexes): * = $P < 0.05$; ** = $P < 0.01$ (Wilcoxon signed-ranks test).

Stage	Harris's Sparrow		<i>P</i>	White-crowned Sparrow ^a	
	Male	Female		Male	Female
Early (0-2 d)	0.48	4.33	**	0.75	3.44
Middle (3-5 d)	3.12	4.67	*	3.62	5.22
Late (6-8 d)	4.84	5.77	NS	6.17	7.64

^a Sample sizes (see Figure 1) were too small for Wilcoxon signed-ranks test.

TABLE 3. Number of feedings/h/nest ($\bar{x} \pm$ SD) for male and female Harris's Sparrows according to brood size (all nestling ages pooled). Sample sizes (number of pairs) given in parentheses¹.

Sex	Brood size		
	3 (3)	4 (4)	5 (2)
Male	1.9 \pm 0.4	3.0 \pm 0.3	3.4 \pm 0.1
Female	4.0 \pm 0.3	4.8 \pm 0.8	6.0 \pm 0.4

¹ Two-factor ANOVA: Brood size: $df = 2$, $F = 9.86$, $P = 0.003$; sex: $df = 1$, $F = 30.96$, $P = 0.000$; interaction between sex and brood size: $df = 2$, $F = 0.18$, $P = 0.838$.

feed nestlings as often as, or more frequently than, females (Johnson and Best 1982; Grundel 1987; Hegner and Wingfield 1987; Hendricks 1987b; Buitron 1988; Haggerty 1992), and nestling age has little effect on male feeding rates (Biermann and Sealy 1982; Breitwisch et al. 1986; Leffelaar and Robertson 1986; Moreno 1987). In relatively few monogamous passerines do males increase feeding rate with nestling age (Westneat 1988; Carey 1990).

In this study, male parental care varied among nests, especially those with nestlings < 3d. This variation could be due to age-related effects, with younger males provisioning young less frequently than older birds, although this effect has not been found in Yellow Warblers (*Dendroica petechia*) or American Redstarts (*Setophaga ruticilla*) (Studd and Robertson 1989; Omland and Sherry 1994). Alternatively, differences in male provisioning could be due either to genetic effects (Freeman-Gallant 1999) or to environmental factors such as weather (Rosa and Murphy 1994).

Because I did not study load size, which may be greater in male passerines (Moreno 1987), and because feeding nestlings is only one aspect of male PI during the nestling period (Breitwisch 1989; Carey 1990), I cannot conclude that total PI by male *Zonotrichia* during the nestling period is less than for females. However, it is likely that reduced male care occurs

during the early part of the nestling period because males made fewer visits to the nest during the early part of the nestling period and did not brood nestlings. Males might benefit from such a strategy because they could allocate more time and energy to extra-pair copulations or territory defense (Westneat 1988). Male *Zonotrichia* in some populations may engage in extra-pair copulations at relatively high rates (Sherman and Morton 1988; Tuttle 1993). However, opportunity for extra-pair copulations may be reduced for *Zonotrichia* at WG because breeding is highly synchronized and few females lay eggs when other pairs are feeding nestlings (Norment 1992). Thus reasons for reduced male attention to *Zonotrichia* nestlings at WG remain unclear. Possibly this behavioral pattern may have adaptive significance in more temperate habitats, and has persisted in an arctic environment because it is a conserved trait within the genus. Alternatively, the pattern may not be maladaptive in the ecological context existing at WG, or if it is maladaptive, recent development of the forest-tundra transition in northern Canada (Nichols 1976) means the trait has not had sufficient time to allow for modification through habitat-mediated selection.

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