

GENDER DIFFERENCES IN PARENTAL FEEDING EFFORT OF CERULEAN WARBLERS AT BIG OAKS NATIONAL WILDLIFE REFUGE, INDIANA

Joseph Allen¹ and Kamal Islam: Department of Biology, Ball State University,
Muncie, Indiana 47306-0440 USA

ABSTRACT. As part of a broad study on Cerulean Warbler (*Dendroica cerulea*) breeding biology in southern Indiana, we examined parental feeding bouts. We hypothesized that females would feed nestlings more often than males, based on documented behavior of several closely related *Dendroica* warblers. Cerulean Warbler nests were observed for one hour every other day from hatching to fledging. Differences in frequency of feeding trips between males and females were recorded. Our hypothesis was supported; females were significantly more likely than males to feed nestlings at four nests.

Keywords: Cerulean Warbler, *Dendroica cerulea*, feeding bouts, parental investment, Indiana

The Cerulean Warbler (*Dendroica cerulea*) is a Neotropical migrant that has experienced overall steady population decline, as much as 3.4% per year, between 1966 and 1996 (Hamel 2000; Robbins et al. 1992). It winters in the Andes of northern South America but returns to breeding areas in North America in early May (Hamel 2000). The breeding range extends throughout the northeastern and midwestern regions of the United States and as far north as Ontario and Quebec in Canada (American Ornithologists' Union 1998; Hamel 2000). Cerulean Warbler populations have been decreasing for decades, with most of the dramatic losses having occurred during the last 30 years (Jones et al. 2001; Hamel 2000; Robbins et al. 1992).

Cerulean Warbler habitat has declined in the midwestern United States in recent years. Possible factors in the decline include loss of deciduous forest overall, habitat fragmentation, loss of key tree species, and a changing forest management regime (Hamel 2000). One consequence of habitat decline (due to increased urban sprawl) is a reduction of large tracts of mature hardwood forests, specifically in the midwestern United States (Indiana north to Quebec) (Jones et al. 2001). Urbanization, leading to increased habitat fragmentation, has left Cerulean Warblers more con-

centrated in the few remaining larger tracts of mature forests.

As part of an ongoing long-term study on the breeding biology of Cerulean Warblers, we investigated the role of parental investment as it relates to differences between sexes in frequency of feeding trips. Hamel (2000) stated that both sexes are present during nestling rearing. Initially, the male provides greater feeding effort with the female's proportion of the workload increasing later as she shifts from brooding to feeding. Currently only one study (in southeastern Ontario, Canada) has examined parental feeding bouts in Cerulean Warblers (Oliarnyk & Robertson 1996).

STUDY AREA

Big Oaks National Wildlife Refuge (NWR) is located in Jefferson, Jennings, and Ripley counties in southern Indiana (Fig. 1). This refuge contains over 20,000 ha of various habitats, including mature mixed hardwood forest. This type of habitat is critical to breeding Cerulean Warblers, which have been shown to occur there since 1990 (Bruner 1998).

METHODS

Nests were located beginning in early May 2003, and nest searching concluded in early July when no additional active nests were located. Cerulean Warbler females have characteristic nest-leaving behavior described by some as "bungee jumping," or deep dives when leaving the nest (Jones & Robertson

¹Current address: Department of Biology, North Dakota State University, Fargo, North Dakota 58105 USA.



Figure 1.—Location of Big Oaks National Wildlife Refuge in Jefferson, Jennings, and Ripley counties in southern Indiana.

2001). Other behaviors (nest construction, males delivering food to incubating females, females moving to and from nest during incubation, and the calls of nestlings) were also used to find nests. Similar methods are described in Jones & Robertson (2001) and Oliarnyk & Robertson (1996). Observations were recorded every second day from the time nests were located until young fledged or nests failed. Every nest was observed from the ground with a spotting scope for 1 h in the morning at variable times after sunrise (0600–0900 h).

Parental feeding bouts and the amount of time females spent brooding were recorded during each observation period. Each trip by a parent successfully delivering food to nestlings was equal to one feeding bout regardless of duration. Nestling age was determined in one of two ways. At nests located prior to hatching, observations were made of the incubating female until she and/or the male started bringing food to nestlings. If the nest was located after hatching, observations were made until fledging or nest failure and then age of the nestlings was calculated. If the age of nestlings was unknown, it was possible to calculate back from the time the nest was

found to fledging of the young (Oliarnyk & Robertson 1996). Young typically fledge 10–11 days after hatching (Hamel 2000).

The weather was unseasonably cool for several weeks after nesting had begun and likely chilled eggs. This factor, combined with predation, resulted in only 7 of 26 clutches actually hatching and providing data on parental feeding (Roth 2004). Our best comparison of parental feeding bouts was of four nests with data collected on the sixth day after hatching. These four nests were compared using paired *t*-tests (LeBlanc 2004). Analyses was conducted using SPSS for Windows (V11.0.1, 2001) at $\alpha = 0.10$.

RESULTS

Females were found to brood for an average of 37.3 mins per h ($n = 3$; Table 1). In some instances, males were seen feeding the female on the nest while the female was brooding. Sometimes both sexes fed young simultaneously while, at other times, a female would move to the edge of the nest while a male fed the young. Generally, both parents did not feed nestlings at the same time. Females fed nestlings more often than males (mean feedings/h \pm SE; males = 1.5 ± 0.75 , females = 4.0 ± 2.0 , $n = 4$, *t*-value = 2.89, *P* value = 0.063; Table 1).

Parents were seen either feeding nestlings separately or males feeding females with the female delivering food to nestlings. In some situations, females perched on the side of the nest while the male fed nestlings. These observations of adults feeding nestlings are similar to those observed for Prairie Warbler (*Dendroica discolor*) (Nolan 1978).

DISCUSSION

There was a significant difference between female and male feeding rates (*P* value = 0.063; Table 1). Females were still spending a great amount of time brooding (37.3 minutes/hour) on the sixth day after hatching.

Lovette & Bermingham (1999) conducted molecular analyses of *Dendroica* warblers. Based on their results of the phylogenetic relationships, Cerulean Warblers are alone in one clade; thus, we have chosen to make comparisons with the clade most closely related to the Cerulean Warbler.

In Black-throated Blue Warblers (*Dendroica caerulescens*), females fed nestlings more

Table 1.—Comparison of gender differences in feeding bouts of Cerulean Warblers (*Dendroica cerulea*) between southeastern Ontario, Canada in 1996 (Oliarnyk & Robertson 1996) and Big Oaks National Wildlife Refuge, Indiana in 2003.

	Southeastern Ontario, Canada (1996)	Big Oaks NWR, Indiana (2003)
Age of nestlings for data being reported	Averaged for entire brooding period	Day 6 post-hatching
Nest sample size	8	4
Male feeding bout (mean feedings/h \pm SE)	3.5 \pm 1.81	1.5 \pm 0.75
Female feeding bout (mean feedings/h \pm SE)	3.5 \pm 3.7	4.0 \pm 2.0
Average female brooding time (min/h)	49.2 ($n = 5$)	37.3 ($n = 3$)
Paired t -Test	Not used	t -value = 2.89 P value = 0.063

often than males (Chuang-Dobbs et al. 2001), although Holmes (1994) reported no differences in number of feeding bouts between the sexes. In Prairie Warblers (Nolan 1978), females also fed nestlings more often than males. In contrast, Hunt & Eliason (1999) reported no difference between feeding bouts of males and females in Blackpoll Warblers (*Dendroica striata*).

In their study of Yellow Warblers (*Dendroica petechia*) Yezerinac et al. (1996) reported that males fed nestlings more often than females. This same pattern was reported in Chestnut-sided Warblers (*Dendroica pensylvanica*) (Richardson & Brauning 1995) and Magnolia Warblers (*Dendroica magnolia*) (Hall 1994).

Oliarnyk and Robertson (1996) reported no difference in number of feeding trips by male and female in Cerulean Warblers for eight nests; however, they produced no day-specific analysis on feeding bouts. While our field methods were similar to theirs, we did find a significant difference for four nests on the sixth day post-hatching. Because both studies used very similar methods, questions arise as to the source of the difference in results (Table 1).

We considered two explanations for the difference between the results of this study and that of Oliarnyk & Robertson (1996). There may be a temporal (time of day) difference between frequency of feeding trips of males and females. But neither study investigated evening feeding bouts; therefore, this explanation is not valid. Many species increase feeding effort as the nestling period progresses. During this increase, the female most like-

ly changes her workload from brooding to an increasing number of feeding bouts while, at the same time, the male decreases his feeding bout rate. One difficulty in making this comparison is that the majority of published studies only report overall feeding bout rates while disregarding day-to-day comparisons (e.g., Oliarnyk & Robertson 1996). Only additional research which examines and reports day-to-day differences over the brooding period will answer this question.

Many avian studies examine feeding bouts but present only an average feeding frequency for the entire nestling period. These analyses are incomplete. Perhaps many species have been reported as having no difference between feeding frequency for males and females when, in fact, there may be a temporal difference. Feeding bout research needs to address this problem by making more complete analyses and reporting day-to-day comparisons. In order to tease apart individual roles of each parent, daily differences must be investigated and reported to allow for the best possible conclusions. This would allow a more complete understanding of the behaviors of breeding biology and how they change over time.

ACKNOWLEDGMENTS

The Indiana Academy of Science and the United States Fish and Wildlife Service funded this research. We thank Joe Robb, Refuge Manager of Big Oaks National Wildlife Refuge for providing logistical support, as well as guidance, in the field. Thanks to David LeBlanc for supervision of statistical analyses. Kirk Roth and Jason Jones provided guidance, support, and encouragement. Kelly Jones and

the rest of the field assistants helped immensely with data collection. This manuscript has benefited from the comments and suggestions of J. Dan Webster, Jim Berry, and an anonymous reviewer.

LITERATURE CITED

- American Ornithologists' Union. 1998. Check-list of North American Birds. 7th ed. American Ornithologists' Union, Washington, D.C.
- Bruner, A.W. 1998. Cerulean Warbler. Pp. 260–261, *In* Atlas of Breeding Birds of Indiana (Castro, J.S., E.M. Hopkins & C.E. Keller, eds.). Indianapolis: Nongame and Endangered Wildlife Program, Indiana Department of Natural Resources.
- Chuang-Dobbs, H.C., M.S. Webster & R.T. Holmes. 2001. Paternity and parental care in the Black-throated Blue Warbler, *Dendroica caerulescens*. *Animal Behaviour* 62:83–92.
- Hall, G. 1994. Magnolia Warbler (*Dendroica magnolia*). *In* The Birds of North America, no. 136. The Birds of North America, Inc., Philadelphia.
- Hamel, P.B. 2000. Cerulean Warbler (*Dendroica cerulea*). *In* The Birds of North America, no. 511 (A. Poole & F. Gill, eds.). The Birds of North America, Inc., Philadelphia.
- Holmes, R. 1994. Black-throated Blue Warbler (*Dendroica caerulescens*). *In* The Birds of North America, no. 87. The Birds of North America, Inc. Philadelphia.
- Hunt, D. & B. Eliason. 1999. Blackpoll Warbler (*Dendroica striata*). *In* The Birds of North America, no. 431. The Birds of North America, Inc. Philadelphia.
- Jones, J. & R.J. Robertson. 2001. Territory and nest-site selection of Cerulean Warblers in eastern Ontario. *Auk* 118:727–735.
- Jones, J., R. Debyrn, J. Barg & R. Robertson. 2001. Assessing the effects of natural disturbance on a Neotropical migrant songbird. *Ecology* 82:2628–2635.
- LeBlanc, D. 2004. *Statistics: Concepts and Applications for Science*. Jones and Bartlett Publishers, Massachusetts.
- Lovette, I.J. & E. Bermingham. 1999. Explosive speciation in New World *Dendroica* warblers. *Proceedings of the Royal Society of London: Biological Sciences* 266:1629–1636.
- Nolan, V. 1978. The ecology and behavior of the Prairie Warbler (*Dendroica discolor*). *Ornithological Monograph* no. 26. The American Ornithologists' Union.
- Oliarnyk, C. & R. Robertson. 1996. Breeding behavior and reproductive success of Cerulean Warblers in southeastern Ontario. *Wilson Bulletin* 108:673–684.
- Richardson, M. & D. Brauning. 1995. Chestnut-sided Warbler (*Dendroica pensylvanica*). *In* The Birds of North America, no. 190. The Birds of North America, Inc. Philadelphia.
- Robbins, C., J. Fitzpatrick & P. Hamel. 1992. A warbler in trouble: *Dendroica cerulea*. *In* Ecology and Conservation of Neotropical migrant landbirds. Smithsonian Institution Press, Washington, D.C.
- Roth, K.L. 2004. Cerulean Warbler breeding biology. M.S. thesis, Ball State University, Muncie, Indiana. 46 pages.
- Yezerinac, S.M., P.J. Weatherhead & P.T. Boag. 1996. Cuckoldry and lack of parentage-dependent paternal care in Yellow Warblers: A cost-benefit approach. *Animal Behaviour* 52:821–832.

Manuscript received 8 May 2004, revised 1 September 2004.