



Fledgling Adoption in Hooded Warblers (*Wilsonia citrina*): Does Extrapair Paternity Play a Role?

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Adoption is a widespread phenomenon in birds and generally occurs at a low frequency within a species (reviewed in Rohwer 1986, Meek and Robertson 1991). Adoption of fledglings is common in seabirds due to the mobility of chicks soon after hatch (e.g. Hébert 1988, Morris et al. 1991, Pierotti 1991, Brown et al. 1995). In songbirds, studies of adoption have focussed on the behavior of replacement males during the nestling stage (Meek and Robertson 1991). Little is known about fledgling adoption in songbirds because the fledgling period is poorly described for many species (Smith 1978, Moreno 1984). We report two cases of fledgling adoption in the Hooded Warbler (*Wilsonia citrina*) observed in the course of an intensive study of fledgling care (Evans Ogden 1994).

In passerines, the main hypotheses for the adaptive significance of adoption by males are: (1) increased opportunities for fathering offspring with the offspring's mother in the future (Power 1975, Rohwer 1986); and, (2) as a result of extrapair matings, the adopting bird may be the genetic parent of the young it adopts (Meek and Robertson 1991). The first hypothesis is supported by comparative evidence that adoption tends to occur in species where females are likely to reneest with the adoptive male (Rohwer 1986). Recent reports that extrapair fertilizations occur at high frequency in many Temperate Zone passerines (e.g. Westneat 1987, 1993, Morton et al. 1990, Stutchbury et al. 1994) indicate that the extrapair-paternity hypothesis for adoption may be more important than previously recognized. We used DNA fingerprinting of Hooded Warblers to examine whether extrapair paternity played a role in adoption.

Our study was conducted from May through August 1991-1993 in Crawford Co., Pennsylvania (41°N, 79°W). The study site is a 150-ha continuous hardwood forest that supported about 40 breeding pairs of Hooded Warblers each year. Adults were captured with mist nets, banded with U.S. Fish and Wildlife aluminum bands, and individually color banded. Each brood member that fledged also was banded with an aluminum band, and all nestlings within a brood were given color-band combinations different from those of other broods. For most adults and nestlings, we collected 30 to 100 μ L of blood for use in parentage analysis. Multilocus DNA fingerprinting (with Jef-

frey's probe 33.16) was used to determine actual paternity of the adopted fledgling (for detailed methods, see Stutchbury et al. 1994). Unrelated adults had a band-sharing coefficient of 0.301 ± 0.017 ($n = 22$), so young were considered unrelated to their social father if they had a band-sharing coefficient of less than 0.42 and had more than two novel bands when compared with their social parents.

Territories of color-banded males were mapped by following singing individuals and noting border disputes. The social father was the male that defended the territory at the time of egg laying and fed the young at nests on the territory. The social mother was the female that incubated the eggs and fed the young.

Each year, we systematically attempted to locate family groups after fledging to determine the period of fledgling care and food-delivery rates to fledglings. In Hooded Warblers we rarely saw both parents feeding a given fledgling. Instead, the brood was usually divided and each parent assumed full care of one or two fledglings (Evans Ogden 1994). When the social mother attempted a second brood, the male assumed full care of all fledglings from the first brood. In the forested habitat, it was difficult to see young fledglings and determine color-band combinations to confirm the nest from which they fledged. To identify whether or not a parent had adopted fledglings, we used only those cases where adults were seen feeding color-banded fledglings on more than two occasions.

Using these criteria, we observed fledgling care by 17 parents from 13 different families. Two of these 17 parents (12%) were observed to adopt young (i.e. they fed young on their own territory that had fledged from a neighbor's nest). Below we describe the two case histories in detail. The cases were similar in that the social father of the fledglings was no longer present on his territory at the time of adoption, and the social mother had reneested to attempt a second brood. The second case was perhaps unnatural, because the social father died accidentally during handling early in the nestling stage.

In the first case, a fledgling was fed by a neighboring male on the adjacent territory, beginning when the fledgling was 28 days old postfledging. At this time, the adoptive male was also feeding two of his own young (nine days postfledging) on his territory.

The adoptive male was seen repeatedly feeding the adopted fledgling (and his own young) on two occasions, 28 July and 5 August 1991. The adopted fledgling was seen with this same family group on two more occasions during the subsequent week (9 and 11 August). The adopted fledgling's social mother was incubating her second brood at the time of the adoption. The adopted fledgling's social father had assumed full care of the first brood, but we could no longer find this male or his other young after early July. DNA fingerprinting revealed that the adoptive male was not the genetic father of the fledgling he adopted. The adopted fledgling's social father had a high band-sharing coefficient (0.48–0.59) with all the fledglings from his first brood, and these fledglings had no novel bands when compared with their social parents (Stutchbury et al. 1994). We do not know if the adoptive male fathered young in the social mother's second brood, because the nest was preyed upon at the egg stage.

In the second case of adoption, two fledglings (16 days postfledging) were fed repeatedly by a male on the neighboring territory. The feeding rate to these fledglings was high. On 30 June 1992 one adopted fledgling was fed 10 times in 11 min and, in a subsequent observation, the other was fed 7 times in 13 min. The young from the adoptive male's own nest were only two days postfledging. The adopted fledglings were seen again with the neighbor male on 3 and 6 July. This male was seen feeding only the adopted fledglings; his mate was feeding their three fledglings in nearby thickets. The social father of the adopted young had accidentally died during handling when his first brood had just hatched. Their social mother fed the nestlings alone, and began laying a second clutch at about the same time that her fledglings were adopted by the neighboring male. DNA fingerprinting revealed that the genetic father of both adopted fledglings was their social father (band-sharing coefficient 0.46–0.55, no novel bands), not the adoptive male (band-sharing coefficient <0.21). The adoptive male was not seen near her second nest and did not feed the nestlings when they hatched. However, the adoptive male appeared to be the genetic father (band-sharing coefficient 0.42–0.56) of two of three nestlings from the social mother's second brood.

Although adoption of fledglings in passerines has not received attention in the literature (Rohwer 1986, Meek and Robertson 1991), we documented adoption by 2 of the 17 parents (12%) that were systematically observed. It is difficult to compare this rate of fledgling adoption with the rate of nestling adoption in other songbirds. Reports of nestling adoption usually involve replacement males (Meek and Robertson 1991) and, under natural conditions, males rarely disappear from their breeding territories. Even when breeding males are experimentally removed at the nestling stage, the adoption rate by replacing males (10–30%;

Meek and Robertson 1991) is comparable to the frequency of fledgling adoption in this study. The natural rate of fledgling adoption may be higher than that for nestling adoption because the mobility of fledglings creates frequent opportunities for fledglings to seek parental care from neighboring adults, as occurs in seabirds (e.g. Pierotti 1991, Brown et al. 1995).

Fledgling adoption does not necessarily benefit the adoptive parent and could simply represent a case of misdirected parental care (Rohwer 1986) or an intergenerational conflict won by the adopted fledgling (Pierotti 1991, Brown et al. 1995). Adoptive males likely could identify the adopted young as foreign, because the fledglings were much older than their own young. One banded fledgling was seen aggressively giving begging calls while pursuing a female that was not its social mother, and this female simply evaded the fledgling. It is possible that the fledglings sought adoption due to reduced parental care from their social parents. In both cases the social father was absent and the social mother was attempting a second brood. Assuming that fledglings seek adoption to gain additional parental care (Pierotti 1991), we expect that fledgling adoption in songbirds should be more common in double-brooded species because parents are more likely to reduce parental care to first brood fledglings.

There appeared to be little cost of adoption to adult males, since there was no partial brood reduction after adoption. Both adoptive males had mates who were feeding some or all of the young from their own nest, which may have mitigated the costs of adoption. We do not have sufficient data on fledgling feeding rates to compare adoptive with nonadoptive families. We expect that the costs of adoption would be much higher for males who are caring for their brood without the help of their mate (e.g. when their mate attempts a second brood).

Adoption could be beneficial to adult males in two ways: increasing the probability of acquiring a social mate in the future (Rohwer 1986); and increasing direct fitness by providing care to young fathered via extrapair fertilizations (Meek and Robertson 1991). In our study, adoptive males did not form a social pair-bond with the social mother of the adopted young either in the same year, or in the next breeding season. However, in the second case the adoptive male apparently did obtain fertilizations with the social mother when she began a second brood. In Hooded Warblers, about 40% of females produce young that are the result of extrapair fertilizations with neighboring males (Stutchbury et al. 1994). Thus, future "mate acquisition" (Rohwer 1986) may take the form of extrapair fertilizations rather than social pair bonds. By adopting fledglings, males may increase the availability of fertile females on neighboring territories by increasing the likelihood that females will renest.

Meek and Robertson (1991) suggested that males

may adopt young if they obtained extrapair matings with that female earlier in the breeding season. The adoptive males in our study were not the genetic fathers of the fledglings they adopted. However, high rates of extrapair fertilizations (36% of nestlings) in the population (Stutchbury et al. 1994) may increase the average degree of relatedness between a male and fledglings on a neighboring territory. Females also could potentially benefit in a similar way from adoption, but intraspecific brood parasitism is rare in Hooded Warblers (Stutchbury et al. 1994), so females are usually unrelated to neighboring young.

In summary, we suggest that fledgling adoption may be widespread in songbirds. Fledglings likely benefit from adoption by receiving higher levels of parental care than they would on their own territory, but it is not known whether there is a net benefit to adoptive males. Extrapair fertilizations could increase the benefits of adoption to males in two ways: (1) acquisition of genetic mates by facilitating the re-nesting of neighboring females; and (2) increasing the average degree of genetic relatedness between males and neighboring offspring.

Acknowledgments.—We thank Rob Fleischer, Judy Rhymer, Garth Fuller, and Walter Piper for their collaboration in DNA fingerprinting at the Molecular Genetics Laboratory, National Zoological Park, Smithsonian Institution, Washington, D.C. Joan Howlett, David Mark, Mark DeBoer, Abby Neufeld, and Diane Neudorf assisted with fieldwork. We especially thank the Willis family and other landowners on Brown Hill for allowing us to conduct fieldwork on their property. E. S. Morton and S. Rohwer provided helpful comments on the manuscript. This research was supported by a Smithsonian Post-doctoral Fellowship and a Natural Sciences and Engineering Research Council of Canada Research Grant to B.J.S., as well as a Smithsonian Migratory Bird Center internship, Frank M. Chapman Research Grant, and Sigma Xi Grant-in-Aid of Research to L.J.E.O.

LITERATURE CITED

- BROWN, K. M., M. WOUFFE, AND R. D. MORRIS. 1995. Patterns of adoption in Ring-billed Gulls: Who is really winning the intergenerational conflict? *Anim. Behav.* 49:321–331.
- EVANS OGDEN, L. J. 1994. Cross-seasonal effects on the breeding strategy of the Hooded Warbler (*Wilsonia citrina*). M.Sc. thesis, York Univ., North York, Ontario.
- HÉBERT, P. N. 1988. Adoption behaviour by gulls: A new hypothesis. *Ibis* 130:216–220.
- MEEK, S. B., AND R. J. ROBERTSON. 1991. Adoption of young by replacement male birds: An experimental study of Eastern Bluebirds and a review. *Anim. Behav.* 42:813–820.
- MORENO, J. 1984. Parental care of fledged young, division of labor, and the development of foraging techniques in the Northern Wheatear (*Oenanthe oenanthe*). *Auk* 101:741–752.
- MORRIS, R. D., M. WOUFFE, AND G. D. WICHERT. 1991. Hatching synchrony, chick care and adoption in the Common Tern: Can disadvantaged chicks win? *Can. J. Zool.* 69:661–668.
- MORTON, E. S., L. FORMAN, AND M. BRAUN. 1990. Extrapair fertilizations and the evolution of colonial breeding in Purple Martins. *Auk* 107:275–283.
- PIEROTTI, R. 1991. Infanticide versus adoption: An intergenerational conflict. *Am. Nat.* 138:1140–1158.
- POWER, H. W. 1975. Mountain Bluebirds: Experimental evidence against altruism. *Science* 189:142–143.
- ROHWER, S. 1986. Selection for adoption versus infanticide by replacement “mates” in birds. *Curr. Ornithol.* 3:353–395.
- SMITH, J. N. M. 1978. Division of labour by Song Sparrows feeding fledged young. *Can. J. Zool.* 56:187–191.
- STUTCHBURY, B. J., J. M. RHYMER, AND E. S. MORTON. 1994. Extra-pair paternity in Hooded Warblers. *Behav. Ecol.* 5:384–392.
- WESTNEAT, D. F. 1987. Extra-pair fertilizations in a predominantly monogamous bird: Genetic evidence. *Anim. Behav.* 35:877–886.
- WESTNEAT, D. F. 1993. Polygyny and extrapair fertilizations in eastern Red-winged Blackbirds (*Agelaius phoeniceus*). *Behav. Ecol.* 4:49–60.

Received 11 October 1994, accepted 25 April 1995.