SHORT COMMUNICATIONS

Evidence of Reproductive Error in Adoption of Nestling Eastern Bluebirds (*Sialia sialis*)

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Adoption can be defined as parental care of presumed nonlinear offspring (PNLO) by an individual replacing an original caregiver—usually a biological parent—of those offspring. Published reports of avian adoptions often are limited to anecdotal notes (see Skutch 1961; see Rohwer 1986 for a comprehensive review of this literature). Some authors have suggested explanations for such apparently maladaptive behavior, and others have devised experimental removals and specific observational studies to explore the evolutionary significance of such behavior (Power 1975, Pierotti 1980, Rutberg and Rohwer 1980, Crook and Shields 1985, Rohwer 1986).

Adoption, indifference, or infanticide are three potential reactions of replacement individuals toward PNLO (Rohwer 1986). On the assumptions that adopters and adoptees are unrelated and that the behavior of replacement individuals is determined by a strategy of maximizing the probability of future reproductive success through acquisition of mates, nest sites, breeding status, or all of these, Rohwer (1986) offered predictions of ecological factors favoring adoption or infanticide by replacement mates. The first assumption eliminates a hypothesis of adoption as a kin-selection strategy, in which replacement individuals may care for nestlings with a high probability of genetic similarity by aiding or replacing siblings or other kin (Eshel and Cohen 1976). The second assumption is acceptance of an individual-selection hypothesis for adoption by replacement individuals. The hypothesis predicts that adoption will evolve because survival of the offspring and a demonstrated ability to care for dependent young increases reproductive potential through acquisition of breeding territory or mates directly (Eshel and Cohen 1976, Allan 1979, Rutberg and Rohwer 1980). In suggesting an adaptive value for the occurrence of adoption by replacement individuals, Rohwer (1986) forcefully argued against the potentially significant role of reproductive error in stimulating parental care of PNLO. Despite these arguments, the potential for nonadaptive adoptive behavior under infrequently encountered circumstances may be associated directly with intense selection for normal parental care and present the selective dilemma of a behavioral response to equivalent or near-equivalent stimuli that is highly favorable in one context and unfavorable in another (Williams 1966).

An important question is, What causes replacement? This is different from the question of what causes replacement of PNLO. The significance of the cause of replacement is apparent in considering that kin selection alone cannot determine the evolution of adoption, for an individual would presumably defer care of related nonlinear offspring in favor of presumed linear offspring when such an option is presented. Therefore, the reproductive condition of a replacement individual, reflected by its recent history, is valuable in determining both the potential for adoption to occur and the applicability of hypotheses for its occurrence. We report here the circumstances of replacement and adoption that include detailed knowledge of the prior reproductive history of the adopting individuals.

Eastern Bluebirds (*Sialia sialis*) are secondary cavity nesters. Their populations are nest-site limited, with implication of a nonbreeding "floater" population of sexually mature birds that are potential replacement individuals. The breeding habits of bluebirds have been reported extensively (Hamilton 1943, Krieg 1971, Pinkowski 1977, Gowaty 1981). Replacements have been observed in cases of both natural disappearance of males and females (Hamilton 1943, Pinkowski 1978, Gowaty 1983b) and male removal experiments (Gowaty 1983a). The response of replacement individuals to eggs and nestlings apparently varies widely and includes indifference, adoption, and probably infanticide (Rohwer 1986).

In 1985 we uniquely marked breeding Eastern Bluebirds in three noncontiguous areas near Clemson, South Carolina, and observed breeding at nest boxes in each area. We were able to ascertain the breeding associations of many individuals throughout the breeding season. In the populations we observed, opportunity for replacement at active nests was apparently rare, and adoptive behavior was observed at only one nest. Of more than 220 nesting attempts, disappearance of individual caregivers of nestlings was known to have occurred at only 2 nests. In one case the resident male remained alone on the territory and unsuccessfully attempted to rear 5 nestlings after the disappearance of the caregiving female; at a second box an unbanded male quickly replaced the deceased resident male, exhibited no parental behavior toward the nestlings, but was probably the same male that successfully bred with the female at the same box after the young fledged. In three cases females alone disappeared from nests during incubation. The remaining males subsequently attracted new mates, but abandoned eggs were uncared for by either the original males or replacement females.

During the first week of June 1985, color-banded females F223 and F262, along with unbanded males, initiated second nesting attempts at two nest boxes (B109 and B108, respectively) from which each had successfully fledged their first broods of the season. The boxes were located along a fencerow bordering experimental orchards, with B108 located 175 m east of B109. No interactions were observed between the two pairs while the nests were simultaneously active, and no intrasexual aggression such as that reported by Gowaty (1981) and Gowaty and Wagner (1987) were observed in the area. On 24 June, 2 of 4 eggs incubated by F223 in B109 hatched, 4 days before the complete hatching of 5 eggs incubated by F262 in B108. On 28 June, when nestlings were 4 days old, we color-banded a male (M631) that entered B109 as he delivered food to the nestlings within. (We routinely attempt to catch male caregivers early in the nestling stage when caregiving males are highly motivated to go all the way into boxes when they deliver food to relatively small nestlings.) Three days later we discovered the disappearance of the 2 nestlings and unhatched eggs from B109; the nest cup was undisturbed, a condition we associate with predation by snakes, and no evidence of eggshells or chicks was found near the nest, conditions we associate with predation by other birds and some mammals. Thus, we believe the chicks' disappearance was due to predation by a rat snake (*Elaphe obsoleta*) observed within 5 m of the box earlier that week. The adult birds, which had frequently swooped at us as we approached the active nest, were absent and we observed no further activity at B109 for the duration of the breeding season.

On 1 July at B108 we recaptured F262 but failed to observe a male bluebird. Ten minutes after we released the female, F262 reappeared at the box accompanied by M631. Both birds perched on the box front and "peered in" through the entrance hole, though neither brought food to the box or entered the box completely. At the same time, we observed a banded female on a telephone wire 50 m south-southeast of the box, and we heard contact calls from a fourth bird hidden in trees 75 m north of the box.

On 4 July a banded female and M631 were observed at B108. Neither carried food, although all 5 4-day-old nestlings were extremely active, indicating abnormal hunger. On 8 July M631 and F223 swooped toward us as we approached the box. F262 was never observed subsequently. Note that the replacement of the original nest caregivers did not occur simultaneously: M631 and F262 appeared at the box together without evidence of aggression before F262's replacement by F223. On 8 July we banded and weighed each of the 10-day-old nestlings and extracted less than 0.1 ml of blood from each for electrophoretic analysis. The nestlings ($n = 5$, $\bar{x} = 21.9 \pm 1.78$ g [SD]) were significantly lighter than the 10-day-old nestlings in the population ($n = 334$, $\bar{x} = 25.9 \pm 2.37$ g [SD], $t = 3.7680$, df = 334, $P = 0.0002$).

Observations at B108 continued until the nestlings fledged on 18 July. We conducted 40-min behavioral samples on 6 days between 9 July and 15 July, during which the male was observed carrying food to the box on 22 occasions and the female on 8. The male was identified as M631, but the female was identified only as a banded individual. A female identified as F223 was observed at the box during regular box checks on 14, 15, and 16 July, strongly suggesting we observed the same bird during the behavioral samples. We did not observe aggressive interactions between any birds and cannot discriminate among the possibilities of desertion, death, or displacement of both original caregivers that coincided with the availability of M631 and F223 as replacement individuals. Disappearance of adults from boxes with nestlings was exceedingly rare in the study populations and was not correlated with capture or banding.

Knowledge of the recent breeding history of the adopting individuals represents significant information that often has been absent from other anecdotal reports. Because M631 and F223 had lost their nestlings immediately before adopting the brood in B109, we believe reproductive error was an important contributing factor in this adoption. Hormonal variation mediating reproductive behavior is likely to be associated with reproductive error (Emlen 1976). Given the degree of nest-cycle synchrony between these two nests, it is obvious that the adopting individuals were in hormonal states appropriate to caregiving. Other explanations for this adoption include the possibility that male 631 consorted polygynously with females at both B108 and B109; we doubt this possibility because we simultaneously observed two different males at these nests earlier. Kin selection may have played a role in the adoption, a possibility we cannot comment on because we have no evidence bearing on the relatedness of the adult birds. Final possibilities include that M631 fathered some or all of the chicks at B108 through extrapair copulation with F262 or conspecific egg dumping by F223 (Gowaty 1985). Electrophoretic data (Gowaty and Karlin 1984) on kinship indicate that M109 was not likely to be the genetic father of the nestlings in B108 (Table 1). Based on her behavior, we assume that F262, the original female caregiver, was the genetic mother of the nestlings in B108. Consistency of her electrophoretic phenotype with that of the nestlings weakly corroborates our assumption of maternity. If M631 or F223 were the genetic parent(s), we would have expected to observe one or more nestling genotypes at the Est2 locus equal to "12." The electrophoretic data do not prove nongenetic parentage of M631 or F223, but suggest that M631 and F223 adopted nestlings not directly descendant from themselves.

TABLE 1. Electrophoretic phenotypes of caregiving adults and nestlings seen at box 108. (B. May, Cornell Laboratory of Ecological and Evolutionary Genetics, performed the electrophoresis.)

		Electrophoretic locus[b]					
Box[a]	Name	Est2	Est1	MPI	GR	GPI	IDH
109	M631	12	11	11	11	11	11
109	F223	12	11	11	11	11	11
108	F262	11	11	11	11	11	11
108	N691	11	11	11	11	11	11
108	N692	11	11	11	11	11	11
108	N693	11	11	11	11	11	11
108	N694	11	11	11	11	11	11
108	N695	11	11	11	11	11	11

[a] Box at which bird was banded.

[b] Es2 = esterase-2 (E.C. 3.1.1.1), Est 1 = esterase-1 (3.1.1.1), MPI = mannosephosphate isomerase (5.3.1.8), GR = glutathione reductase (1.6.4.2), GPI = glucosephosphate isomerase (5.3.1.9), IDH = isocitrate dehydrogenase (1.1.1.42) (Nomenclature Committee Int. Union Biochem. 1984).

The events observed at boxes 108 and 109 fit temporal and behavioral patterns suggestive of misdirected parental care, i.e. reproductive error. The elapsed time between loss of nestlings at B109 and attendance at B108 may have been less than 2 h and, for M631, a maximum of 3 days. The discrepancy in the timing of replacement by the male and female may be accounted for by delayed stimulation of adoptive behavior by F223, or greater intensity of nest-defense behavior by F262 than by the unbanded male seen with her. The possible displacement of the adopted nestlings' original caregivers indicates a strong motivational state as predicted for birds redirecting parental behavior following brood loss. The low masses of the nestlings suggest that the adoptive caregivers discriminated between care of adoptees and care of nestlings at the box originally attended, a disparity unlikely to be associated with reproductive error alone. While the masses may have resulted from reduced feeding rates during periods of increased nest attentiveness and defense, the few feeding trips recorded for the replacement female during behavior samples instead suggest decreased motivation at the onset of adoption, possible conflicts of stimuli, or an inability to adapt to feeding 5 nestlings rather than 2.

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A 3:1 Ratio of Mandible Crossing Direction in White-winged Crossbills

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There are few examples of polymorphisms occurring in simple Mendelian ratios in wild populations of birds (Cooke and Cooch 1968, Smith 1987). Most studies of morphological variation in bird species show continuous variation (e.g. Grant 1986). The direction the lower mandible curves in crossbills (*Loxia*) is an example of a discrete dimorphism. The lower mandible in Red Crossbills (*L. curvirostra*) crosses in equal frequency to the right and to the left (e.g. Ticehurst 1910, Knox 1983, James et al. 1987). In White-winged Crossbills (*L. leucoptera*) the mandibles do not cross in equal frequencies to the left and right (Ticehurst 1910, James et al. 1987). I found that the ratio of mandible crossings in White-winged Crossbills differed from 1:1, however, and that the lower mandible crosses to the right approximately 3 times more often than to the left.

A 3:1 ratio in the frequency of the lower mandible crossings was found in wild-caught White-winged Crossbills (*L. l. leucoptera*) in 1987 in northern Ontario (43 of 145 birds, 29.7%) and in Riding Mountain National Park, Manitoba (11 of 49 birds, 22.4%). Similar frequencies occurred in the collections of White-winged Crossbills accumulated since the late 1800's in the National Museum of Canada (88 of 309 birds, 28.5%), American Museum of Natural History (39 of 141 birds, 27.7%), and Museum of Vertebrate Zoology (37 of 140 birds, 26.4%). None of these alone or in sum (218 of 784 birds, 27.8%) differs from that expected if the ratio of lower mandible crossings of right to left occurs in a 3:1 ratio (Chi-square tests, $P > 0.10$). The frequency of females with lower mandibles crossing to the left (0.312, 90 of 288 females) was significantly greater than expected if the ratio is 3:1 ($\chi^2 = 4.50$, df = 1, $P < 0.05$), but not for males (0.243, 100 of 411 males). The biological significance of this difference for females is not known; it may be a statistical artifact because there is nearly a 50% chance that 1 in 8 comparisons would be significant at the 0.05 level. James et al. (1987) also examined White-winged Crossbill specimens from the National Museum of Canada and from three other Canadian museums and found similar ratios overall and between sexes.

These data support the hypothesis that the direction of crossing is determined by a single autosomal diallelic locus, with lower mandible crossing to the right dominant over crossing to the left. The frequencies of the two alleles equal 0.5. This interpretation is consistent with observations of two families of White-winged Crossbills I observed in 1987 where all 4 adults and 7 offspring had lower mandibles that crossed to the right. Convincing support for this hypothesis, or any other genetic hypothesis, requires breeding experiments.

A nongenetic hypothesis for different ratios of mandible crossings has been suggested (James et al. 1987). James et al. (1987) pointed out that the cone scales spiral in two directions about the axis of the cone and that there are two types of cones. They argued that the direction the lower mandible crosses may be influenced by the structure of the cones on which juvenile crossbills forage before their mandibles cross and that the differences in the ratios of bill crossings are related to variation in the spiraling of scales on the cones (phyllotaxy). Whether the different cone types influence foraging behavior and feeding rates is unknown, although such an effect is central to their argument.

Several comments about their hypothesis are in order. First, crossbills foraging on closed cones begin at the base of the cone and progress toward the tip, sequentially prying apart the scales. Consequently, the scale they next separate is usually free of most of the scales that overlap it from below. If this is true, it is difficult to see how such slight differences in cone scale spirals (see James et al. 1987: fig. 1) could influence foraging efficiency. Second, juvenile crossbills forage infrequently and awkwardly before the mandibles begin crossing (pers. obs.). Furthermore, juvenile crossbills often do not orient in the "proper" direction to the cone (see below), and before the mandibles cross juveniles cannot separate closed cone scales (Benkman 1988). Thus, whether slight differences in scale spiraling cause consistent differences in mandible crossing ratios is doubtful. Third, while watching captive crossbills of both species foraging for more