

The Wilson Journal of Ornithology 121(4):830–834, 2009

Adoption by a Territorial Passerine

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ABSTRACT.—We observed and video-taped actively nesting adult Eastern Bluebirds (*Sialia sialis*) repeatedly feeding abandoned conspecific juveniles in a nearby nest. We used molecular techniques to confirm these nestlings were unrelated to the adults that fed them. The most likely explanation for the observed behavior is that it was a mistake resulting from parental response to the begging vocalizations in the nearby nest. Received 24 November 2008. Accepted 1 May 2009.

Adoption is the phenomenon wherein individuals provide sole parental care to foreign young (Riedman 1982). This seemingly maladaptive behavior has been documented in a wide range of animals including fish (McKaye and McKaye 1977), mammals (Bridges 1990), and birds (Pierotti 1988). There are two main pathways in birds to alloparental care and adoption. First, mobile young may abandon their original nest and seek additional care from unrelated adults (Pierotti and Murphy 1987, Redondo et al. 1995, Roulin 1999, Bize et al. 2002). Nestlings of colonial species (e.g., Ring-billed Gulls [*Larus delawarensis*], Brown et al. 1995) have more opportunities to receive care from foster parents, and adoption is especially common when adults are unable to discriminate between related and unrelated young (Graves and Whiten 1980, Pierotti 1988, Morris et al. 1991, Brown et al. 1995, Jouventin et al. 1995). Second, adults may adopt unrelated young following territorial takeover events (Rowher 1986). Individuals in these instances may increase the likelihood of main-

taining newly formed pair bonds and territorial control by providing care to unrelated young (Rowher 1986). Our objectives are to: (1) report adoption of Eastern Bluebird (*Sialia sialis*) nestlings by a pair of concurrently nesting, unrelated adults from a neighboring territory; and (2) present a third pathway to alloparental care. We confirmed field observations with evidence from videotaped parental behaviors and molecular genotyping.

METHODS

Study Species.—Eastern Bluebirds are socially monogamous, territorial, obligate cavity-nesting passerines that frequently breed in artificial nest boxes (Gowaty and Plissner 1998). Eastern Bluebirds, like some other socially monogamous passerines (e.g., Great Tits [*Parus major*] and Eurasian Blue Tits [*Cyanistes caeruleus*] (Gullberg et al. 1992), experience high levels of extra-pair paternity in some populations (Gowaty and Plissner 1998). Male and female bluebirds defend all-purpose territories around their nest boxes during the breeding season, and breeding pairs are aggressive to other bluebirds. Male bluebirds intensively guard their partners during the egg-laying period of the nesting cycle, and females aggressively defend their nests from other females to reduce conspecific brood parasitism (Gowaty and Plissner 1998).

Field Procedures.—We conducted this study on a banded population of Eastern Bluebirds in Lee County, Alabama, USA (32° 35' N, 82° 28' W). We collected feathers and blood samples from adults by trapping males and females at their nest boxes when nestlings were 2 days of age.

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We placed one video camera at each of two adjacent nest boxes (Box # 28 and Box # 29) when nestlings in both boxes were 5 days of age (18 Jul 2008) to record the feeding behavior of any adults that visited these nest boxes. This allowed us to identify adults visiting each box and the rate at which these visits occurred. We videotaped Box # 29 for 195 min beginning at 0610 hrs CST and Box # 28 for 189 min beginning at 0613 hrs.

We collected blood from the nestlings at Box # 29 on day 8. Two nestlings from Box # 28 had disappeared by nestling day 6 and we decided to collect blood from the remaining two nestlings at that time. We also collected blood from both adults upon capture at Box # 29. No other adults were observed in the immediate vicinity of Box # 28 or # 29.

Laboratory Procedures.—We extracted genomic DNA from blood using proteinase K digestions and phenol-chloroform-isoamyl extraction. Samples were washed in ethanol following extraction, dried in a vacuum centrifuge, and DNA samples were resuspended and stored in TE buffer (Sambrook and Russell 2001). We used three dinucleotide microsatellite loci (EABL129, MOBL49, MOBL 87; primers reported in Balenger et al. 2009) for microsatellite genotyping of bluebirds. Each 10 μ L polymerase chain reaction (PCR) contained \approx 250 ng of genomic DNA, 5 μ L of Fidelity TaqTM PCR Master Mix (USB Corporation, Santa Clara, CA, USA), 0.25 μ M of forward primer, 0.25 μ M of WellRED (Beckman Coulter, Fullerton, CA, USA) fluorescent-labeled M13 primer (Sigma-Proligo, St. Louis, MO, USA), and 0.5 μ M of reverse primer (Invitrogen Life Technologies, Carlsbad, CA, USA). The forward primer was an M13 tailed primer (Balenger et al. 2009). A PTC-100 thermocycler (MJ Research, Waltham, MA, USA) was used to amplify the microsatellite loci using 94° C for 4 min, 30 cycles of 1 min at 94° C, 1 min at 50° C, 2 min at 72° C, and final elongation at 72° C for 10 min. PCR products were separated and sized on a CEQTM 8000 Genetic Analysis System Version 10 (Beckman Coulter Inc., Fullerton, CA, USA). Alleles were visually scored on rounding fragment size calls to the nearest base.

OBSERVATIONS

We set traps on 15 July 2008 in two adjacent nest boxes (Boxes # 28 and # 29) \sim 100 m apart.

Both boxes contained active nests, each with four, 2-day old chicks. An unbanded female was captured at Box # 29 at \sim 0900 hrs CST and banded with one numbered metal band and three color bands. An unbanded male was captured at Box # 29 at \sim 0930 hrs and similarly banded. No adult was captured at Box # 28 during this time. We left the trap in Box # 28 until 1030 hrs when we returned to the box to find the freshly banded female previously captured in Box # 29. The following morning we again placed a trap in Box # 28, but failed to capture any adult over the course of 2 hrs.

Neither of the nestlings in Box # 28 was related to the adults captured and banded at Box # 29 based on microsatellite data. These adults were the genetic parents of the nestlings in Box # 29, although one extra-pair young was sired by another male. The extra-pair nestling was not related to either nestling in Box # 28.

Both parents from Box #29 visited the unrelated nestlings in Box # 28 in addition to feeding their own young. The adults visited their own nest a combined 27 times during 195 min of recorded behavior for Box # 29. The parents from Box # 29 visited a total of 5 times during 189 min recorded for Box # 28. However, the male and female allocated their visits between the two boxes differently. The female fed her own nestlings only six times during this period while feeding and brooding the nestlings in Box # 28 four times during the same period. The male, however, visited Box # 28 only once, but fed his own (and one extra-pair) young 21 times between 0610 and 0925 hrs (Table 1).

Nestlings from Box # 28 began to disappear on 18 July. Only three nestlings remained in the nest on this date and the following day only two nestlings remained. The nestlings were then 6 days of age, but were developmentally equivalent to normal 2-day old nestlings (Fig. 1). The infrequent feedings by the adults from Box # 29 appeared to provide inadequate nutrition to maintain normal growth of the adopted nestlings. On nestling day 8 we found one of the two remaining nestlings on the ground, just outside of the nest box. This individual was still alive, and we returned it to the nest box. However, within 2 days this individual and its nestmate had disappeared.

DISCUSSION

Adoption is a rare behavior across all vertebrates, but observations of alloparental care by

TABLE 1. Visits during ~3 hrs by a nesting pair of Eastern Bluebirds to their own and a nearby nest box containing unrelated nestlings. Visits were recorded simultaneously when nestlings in both boxes were 5 days of age.

	Own nest ^a	Unrelated nest ^b
Male		
Visits	21	1
Feeding rate ^c	1.62	0.11
Female		
Visits	6	4
Feeding rate	0.46	0.42
Total		
Visits	27	5
Feeding rate	2.08	0.53

^a Four chicks.

^b Three chicks.

^c Visits/chick/hr.

adult Eastern Bluebirds are not uncommon (e.g., Pinkowski 1978, Gowaty 1983, Plissner and Gowaty 1988, Wetzel and Chandler 2008). The apparent frequency of this behavior and documentation in bluebirds is likely a result of intensive monitoring efforts in the eastern United States combined with increased density of bluebird nests in artificial boxes (Gowaty and Plissner 1998). Higher densities of breeding bluebirds increase the likelihood of contact between breeding birds and actively begging, unrelated young. This is the first account of alloparental care

directed to nestlings <7 days of age despite a number of reports detailing adoptive behavior in Eastern Bluebirds. Abandoned bluebird nestlings younger than 7 days are typically ignored or killed by replacement females (Gowaty and Plissner 1998).

Individual bluebirds may occasionally benefit by caring for unrelated young (e.g., Gowaty 1983, Wetzel and Chandler 2008), but it seems unlikely there is an unrecognized advantage for the adoption we observed. The bluebirds in our study were probably stimulated to provision young by simple, proximate cues. These stimulus-response systems lead to adaptive responses in most circumstances, but occasionally cause responses that are maladaptive (misallocation of resources, Riedman 1982). Rearing the occasional unrelated young may carry a fitness cost but, because the opportunities for such mistakes are scarce and costs of ignoring begging young are usually high (Knudsen and Evans 1986, Hebert 1988), bluebirds remain vulnerable to feeding unrelated young.

Only an unusual set of circumstances—orphaned chicks of the same age as those of a neighboring pair, and neighboring adults passing sufficiently close to hear begging—created the opportunity for a pair of bluebirds to feed young outside their own nest. There is no opportunity for bluebird parents to be stimulated to feed nestlings outside their own nest in a typical breeding situation because adults aggressively exclude both male and female intruders from the area around

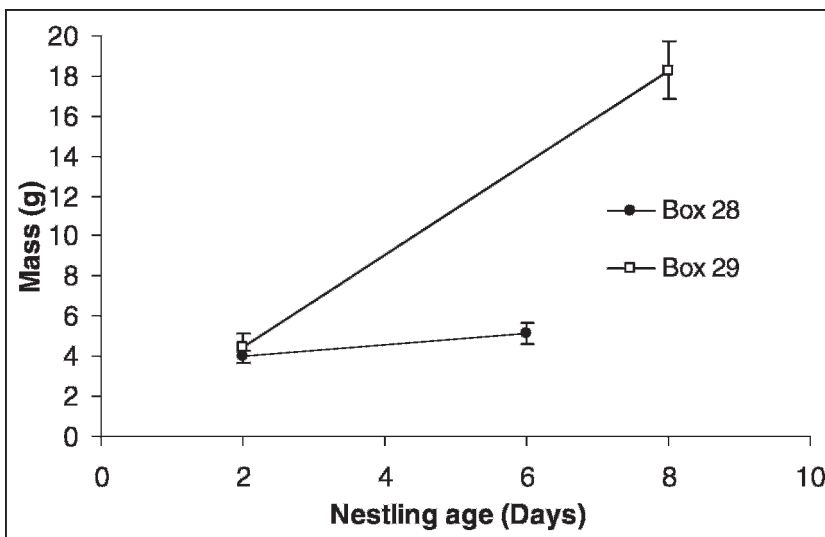


FIG. 1. Average (\pm SE) nestling mass in Box # 28, abandoned by true parents, and Box # 29, fed by true parents.

their nests. Box # 28 in our study had no adults associated with it (a pair of Cooper's Hawks [*Accipiter cooperii*] was observed multiple times near this box and we suspect both parents of the nestlings in Box # 28 were killed by these raptors) which allowed the adoptive parents to frequently move past the unattended nest to forage. The small number of total visits by the foster parents to the adopted nest (Table 1), coupled with the low growth rate of the adopted nestlings (Fig. 1), suggest the parents from Box # 29 were stimulated to feed their adopted young less than their own, likely because they only occasionally moved sufficiently close to the secondary nest to hear begging of these nestlings. The alloparental behavior we report was likely a hard-wired response of hormonally-primed breeding adults to begging of the abandoned chicks (Emlen 1976).

The male and female in this study provided different levels of care to the adopted nestlings in Box # 28. Divergence in foraging behavior or location may have contributed to these differences. The increased alloparental care exhibited by the female could have arisen if she foraged more frequently near Box # 28 and was more frequently exposed to the begging vocalizations of the unrelated nestlings. Only the female was observed to brood nestlings during our study in accordance with the species account of Gowaty and Plissner (1998). The increased investment by the female with respect to brooding behavior may have contributed to her generally lower feeding rate, as well as her more equitable distribution of visits to each nest box. Consistently lower body temperatures of the nestlings in Box # 28 might have caused the female to invest more time brooding these young (70 min) than her own young (38 min), decreasing the total amount of time spent foraging and feeding nestlings.

Many alloparental behaviors are simply the result of misdirected parental care on a proximate level (Riedman 1982). Alloparental behavior will persist in territorial species, like Eastern Bluebirds, where the frequency or costs of adoption are relatively low as long as the behavioral patterns of individuals are adaptive in the majority of cases, and there is no simple and better alternative behavioral pattern.

ACKNOWLEDGMENTS

We thank J. M. Hill and M. A. Buschow for dedicated assistance in the field. We also thank C. E. Braun, B. C. Faircloth, J. D. Lang, J. D. Ligon, H. L. Mays Jr., and

members of the Hill laboratory for helpful comments on this manuscript. This research was supported by a grant from the National Institute of Allergy and Infectious Diseases, Project # R01AI049724 to GEH and by grants from the Birmingham Audubon Society, Sigma Xi, and the American Ornithologists' Union to RAL.

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