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DO RED-WINGED BLACKBIRD PARENTS AND THEIR NESTLINGS RECOGNIZE EACH OTHER?

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Abstract.—To examine whether parent-nestling recognition occurs in Red-winged Blackbirds (*Agelaius phoeniceus*) we exchanged 11 pairs of nestlings matched for sex, mass, and age (6–9 d old) between pairs of experimental nests. To control for possible effects of nestling removal and handling, we also removed and then returned one nestling from each of nine control nests. Data on nestling feeding and fecal sac removal by care-givers, and on begging behavior of nestlings, were gathered by videotaping for 2 h at each focal nest. We found no significant differences in parental care or nestling responses between resident and exchanged nestlings in experimental nests, and no significant differences between manipulated and unmanipulated nestlings in control nests. Our findings are consistent with the hypothesis that parent-nestling recognition does not occur in this species.

¿SE RECONOCEN CENTRE SÍ LOS PADRES Y CRÍAS DE *AGELAIUS PHOENICEUS*?

Sinopsis.—Intercambiamos once pares de crías pareadas para sexo, masa y edad (6 a 9 días de edad) entre pares de nidos experimentales para examinar si ocurre el reconocimiento parental-filial en *Agelaius phoeniceus.* También removimos y devolvimos una de las crías de cada uno de los nidos de control para controlar los efectos posibles de la remoción y manipulación de pichones. Se obtuvo información mediante videocintas de dos horas de duración en cada nido focal sobre alimentación de pichones y sobre la remoción de sacos fecales por los atendientes del nido, y sobre la conducta de peticionar de las crías. No hallamos diferencias significativas en el cuidado parental o en las respuestas de las crías entre los pichones residentes y los intercambiados en los nidos experimentales, y tampoco entre los pichones manipulados y no-manipulados en nidos de control. Nuestros hallazgos son consistentes con la hipótesis de que el reconocimiento parental-filial no ocurre en esta especie.

Parent-offspring recognition has been defined by Medvin and Beecher (1986) as the differential treatment of offspring by parents, or vice versa based on certain characteristics such as odor or calls. Whether or not parent-offspring recognition occurs in different species of birds has been addressed in many studies (e.g., Beer 1970, 1979; Beecher 1982; Medvin and Beecher 1986; Burke et al. 1989; Lifjeld et al. 1992; Buitron and

Nuechterlein 1993; Frumkin 1994; Leonard et al. 1995; Westneat et al. 1995). In general, parent-offspring recognition is expected in species or ecological circumstances, such as in colonial species where young are free to intermingle, in which the probability and cost of misdirecting care are high (Beer 1970; Colgan 1983; Medvin and Beecher 1986; Medvin et al. 1992a,b).

Determining whether parent-offspring recognition occurs is difficult, however (Beer 1970, Beecher 1991). If an individual reacts specifically against an alien, or is able to locate displaced parents or young, it seems clear that recognition of some sort has taken place. Lack of discrimination, however, may or may not indicate lack of recognition. For example, a care-giving adult might recognize that a nestling is not its offspring, but continue to care for it anyway because the cost of "misdirected" care, or the benefit of discriminatory behavior, is minimal. It also may be advantageous for an alien nestling to accept care even if it were to recognize that the care-giver is not a parent. Alternatively, failure to discriminate could be due to an inability to perform a more optimal action such as ejecting a foreign nestling from a nest.

The Red-winged Blackbird (*Agelaius phoeniceus*) is a species in which parents continue to feed their fledglings for several weeks after nest-leaving (Yasukawa and Searcy 1995). We would expect redwing parents and their fledglings to recognize one another (Peek et al. 1972, Leonard et al. 1995) as a result of the redwing's high nesting density, the potentially large number of simultaneously active sets of fledglings, and the continued feeding of fledglings even after they have dispersed beyond the boundaries of their own territories (Yasukawa and Searcy 1995). Parent-fledgling recognition may develop towards the end of the nestling period in Red-winged Blackbirds. Peek et al. (1972) replaced or exchanged entire broods of redwing nestlings and showed that once the young are 10–11 d old (i.e., approaching nest-leaving age) the female was able to find them at a different nest 6–9 m away on the same territory. Peek et al. (1972) suggested that females used calls to identify their young because after first hovering over their own nests for a short time, they flew directly to the nests containing their young even though these nests could not be seen from their own nest sites.

Brood manipulation experiments also provide evidence that female Red-winged Blackbirds learn to recognize their young late in the nestling period. Both Peek et al. (1972) and Yasukawa et al. (1993) found that female redwings would readily accept replacement nestlings younger than 7 d old. When Peek et al. (1972) exchanged pairs of nestling younger than 5 d old, then re-exchanged them at 10–11 d old, however, females continued to care for their foster nestlings, which were no longer in the females' own nests, even though their original nestlings were back in their own nests just prior to nest leaving. Apparently these females had learned to recognize the foreign nestlings in the intervening 7–8 d.

Perhaps because Peek et al. (1972) presented evidence that offspring recognition by female Red-winged Blackbirds does not occur until late in the nestling period, many experimental studies of parental behavior in this species have assumed that no parent-nestling recognition occurs. For example, nestlings have been added to Red-winged Blackbird broods to study the evolution of clutch size (Cronmiller and Thompson 1980) and parental investment strategies (Whittingham 1989, Teather 1992), and brood exchanges have also been used to study parental investment (Yasukawa et al. 1993). Clearly, however, if parents discriminate against foreign nestlings, or if the behavior of alien nestlings differs from that of residents, then the results of such brood manipulations will be difficult to interpret.

There is some evidence for recognition between parents and younger nestlings in Red-winged Blackbirds, however. Peek et al. (1972) performed one brood replacement involving nestlings 7 d (removed brood) and 6 d (replacement brood) old. They reported that although the female did accept the replacement nestlings, she showed signs of "distress." Teather (1992) used transfers of redwing nestlings 6 d old to produce experimental broods of two males and two females, and reported some evidence of discrimination. Foreign male, but not female, nestlings begged less and were fed less than were same-sex residents. Perhaps most importantly, recent videotaping at nests into which foreign conspecific nestlings were placed has shown what appears to be discriminatory behavior by adult female Red-winged Blackbirds (A. B. Clark, pers. comm.). In some cases, adult females appeared to persecute foreign nestlings, and some females were even recorded ejecting 4–5 d old aliens from their nests. Although the persecution was dramatic, the potential advantages of early recognition are unclear. Nestling Red-winged Blackbirds do not ordinarily find themselves in "foreign" nests. Intraspecific brood parasitism does not seem to occur in this species (Yasukawa and Searcy 1995), and nestlings are unable to move among nests. Even though is it unclear to us why discrimination should occur in parents and young nestlings, Clark's observations prompted us to re-investigate whether adult Red-winged Blackbirds discriminate between their own 6–9 d old nestlings and those of other conspecifics.

To test the hypothesis that Red-winged Blackbirds recognize their nestlings and/or their parents, we conducted nestling exchanges and temporary removals. For the purpose of our study, we tested the prediction that male and female Red-winged Blackbirds would discriminate against foreign nestlings, and that foreign nestlings would discriminate against nonparental care-givers.

METHODS

Study population.—Our study population of Red-winged Blackbirds was located on Diehls Prairie, a privately owned, 12-ha grass and sedge meadow in south-central Rock County, Wisconsin, USA (42°32′N, 89°08′W; see Clotfelter 1997). This habitat supported approximately 30 territorial males and nearly 100 nests. We performed manipulations during June and July 1996 as nests were available.

General field methods.—In early June, we performed and videotaped two pilot manipulations on separate nests to determine the feasibility of the current study. We then designed a protocol for all subsequent experimental and control manipulations.

We videotaped both control and experimental nests to examine parental and nestling behavior with respect to recognition. Only nests that contained two or more nestlings 6–9 d old and that were unparasitized by Brown-headed Cowbirds (*Molothrus ater*), were considered for the study. All manipulations were performed between 0530 and 1030 h. Using two-way radios, we coordinated all actions performed at pairs of experimental nests.

Nestling exchange methods.—We performed experimental manipulations when two nests contained nestlings of similar age (±1 d). Using nestlings 6–9 d old allowed time for recognition to be established while minimizing the risk of premature fledging as a result of our manipulations. The bills of all but one nestling were distinctively marked with a nontoxic, black permanent marker (e.g., in a brood of four, one was marked at the tip of the bill, another was marked with a ring around the bill, one was marked on the flanges, and one was unmarked) to facilitate identification of individuals when viewing the taped sessions at a later date. We marked both nestlings that were to be exchanged (hereafter, "foreign nestlings") with the same arbitrarily chosen identification mark (tip, ring or flanges). Exchanged nestlings were of the same sex, as determined by size (mass and tarsus length), and were otherwise chosen randomly.

We weighed each foreign nestling using a 50-g Pesola balance and a small sock to hold the nestling securely during weighing and transporting. Fecal sac expulsion was induced prior to each weighing. After weighing, we simultaneously transported the two foreign nestlings to the opposite nests and started both video cameras. After 2 h, both foreign nestlings were re-weighed and transported back to their original nests.

Control manipulation methods.—All manipulations were duplicated for the control nests, except for the exchange. A nest was videotaped as a control when no brood of similar age was available to make an exchange. One nestling was arbitrarily chosen as the manipulated nestling and was weighed. We then took this nestling away from the nest for approximately 2 min to simulate an exchange. The manipulated nestling was then placed back into the nest and the camera was started. After 2 h we re-weighed the manipulated nestling.

Videotaping methods.—To habituate our subjects to the video camera, we placed a tripod supporting a black wooden box, which resembled a video camera, approximately 1 m from the nest 24 h before videotaping was to occur. On the day taping occurred we replaced the boxes with video cameras. In the case of inclement weather, a plastic bag was tied securely around the camera to protect it.

Videotape scoring methods.—We employed an independent viewer to minimize bias when gathering data from our videotapes. Each tape was viewed by the independent viewer and one of the authors (SE or EM).

Each time an adult visited the nest we recorded the type of feed (whole feeds, shared feeds, insertions, and partial feeds; see below), the time a nestling kept its mouth open to receive food (gape time) for that visit, whether a nestling responded to a feeding visit by a care-giving adult, the number of times the adult elicited begging, and fecal sac removals. Whole feeds were recorded when one nestling received all food brought to the nest by the care-giver. Shared feeds were recorded when more than one food article was brought to the nest and distributed to more than one nestling. Insertions were recorded when a food article was inserted into the mouth of a nestling and was then completely removed by the adult. A partial feed was recorded when the adult inserted an article of food as if to perform a whole feed, only to remove some of the food seconds later to give to another nestling. In all cases the identities of the nestling or nestlings involved were recorded.

When results for a 2-h recording session differed between observers by more than three units (e.g., the number of whole feeds or insertions), the videotape was simultaneously reviewed by all three observers and a consensus was reached. In cases of differences less than three, the results were averaged.

Statistical methods.—All statistical tests comparing foreign experimental with resident experimental nestlings and manipulated control with unmanipulated control nestlings were performed with a one-way ANOVA using JMP version 3.0.2. Statistical significance was accepted at the 0.05 level. When differences were not statistically significant, we performed power analyses in JMP to determine the sample size necessary to produce significance ($\alpha = 0.05$) for the observed group means.

RESULTS

We obtained recordings from 11 pairs of experimental nests and from 9 control nests. Feeding by females was recorded at all 31 nests. Male feeding was recorded at six experimental and three control nests (males were not observed to feed nestlings in the remaining nests). In general, we found no evidence for nestling discrimination by parents or for parent discrimination by nestlings.

Mean total gaping time per 2-h observation (experimental, $F_{1,42} = 0.023$; $P = 0.88$; control, $F_{1,16} = 0.0008$, $P = 0.98$) and the mean gape time per feeding (experimental, $F_{1,42} = 0.10$, $P = 0.75$; control, $F_{1,16} = 0.0083$, $P = 0.93$) did not differ significantly between foreign and resident nestlings of the experimental nests and between manipulated and unmanipulated nestlings of the control nests (Fig. 1). Nonresponses to begging elicited by the female (Fig. 2) also did not differ significantly between the two classes of nestlings in both types of manipulations (experimental, $F_{1,42} = 0.044$, $P = 0.84$; control, $F_{1,16} = 0.13$, $P = 0.73$). Fecal sac removal (Fig. 2) also did not differ significantly between resident and foreign nestlings of experimental nests ($F_{1,42} = 2.10$, $P = 0.15$) or manipulated and unmanipulated nestlings of control nests ($F_{1,16} = 0.74$, $P = 0.40$).

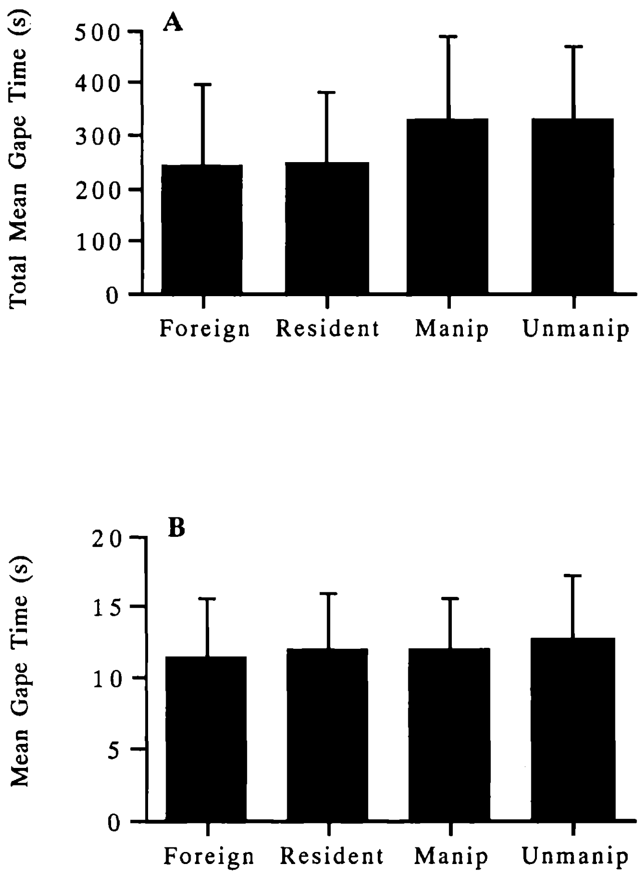

FIGURE 1. Mean (±SD) total gape time per 2-h observation and mean (±SD) gape time per nestling (in seconds) for Foreign and Resident Red-winged Blackbird nestlings in experimental nests, and for Manipulated and Unmanipulated Red-winged Blackbird nestlings in control nests.

There were no significant differences in the four types of feeds: whole feeds (experimental, $F_{1,58} = 0.29$, $P = 0.45$; control, $F_{1,16} = 0.055$, $P = 0.82$); shared feeds (experimental, $F_{1,42} = 0.38$, $P = 0.54$; control, $F_{1,16} = 0.010$, $P = 0.92$); insertions (experimental, $F_{1,42} = 1.63$, $P = 0.21$; control, $F_{1,16} = 1.57$, $P = 0.23$); and partial feeds (experimental, $F_{1,42} = 1.51$, $P = 0.23$; control, $F_{1,16} = 0.0$, $P = 1.0$) (Fig. 3).

The only data we were able to obtain from males was for whole feeds and shared feeds (Fig. 4); there were no significant differences in these two types of feeds: whole feeds (experimental, $F_{1,10} = 0.077$, $P = 0.79$; control, $F_{1,6} = 0.070$, $P = 0.80$), shared feeds (experimental, $F_{1,10} = 0.0$, $P = 1.00$; control, $F_{1,6} = 0.0$, $P = 1.00$).

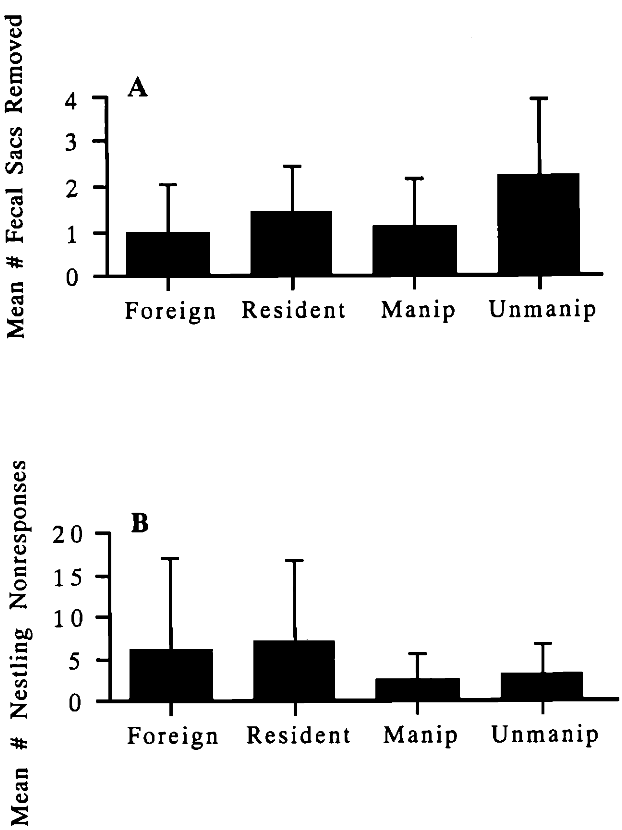

FIGURE 2. Mean (±SD) number of fecal sacs removed by the female and the mean number of nonresponses by the nestlings for Foreign and Resident Red-winged Blackbird nestlings in experimental nests, and for Manipulated and Unmanipulated Red-winged Blackbird nestlings in control nests.

DISCUSSION

Studies of parent-offspring recognition in birds have long employed the technique of moving nestlings from one nest to another (Lashley 1915, Tinbergen 1953, Davies and Carrick 1962). The existence of discrimination by parents or young following such a manipulation is usually taken as evidence for recognition in these studies (Beecher 1991). Our results show no evidence of parent-nestling discrimination in Red-winged Blackbirds, however. There were no significant differences in comparisons of foreign and resident nestlings. In addition, lack of a significant effect of nestling manipulation in control nests gives us some confidence that our manipulations of the broods did not affect the results of our experiment. We suspect that lack of discrimination in this case is evidence for

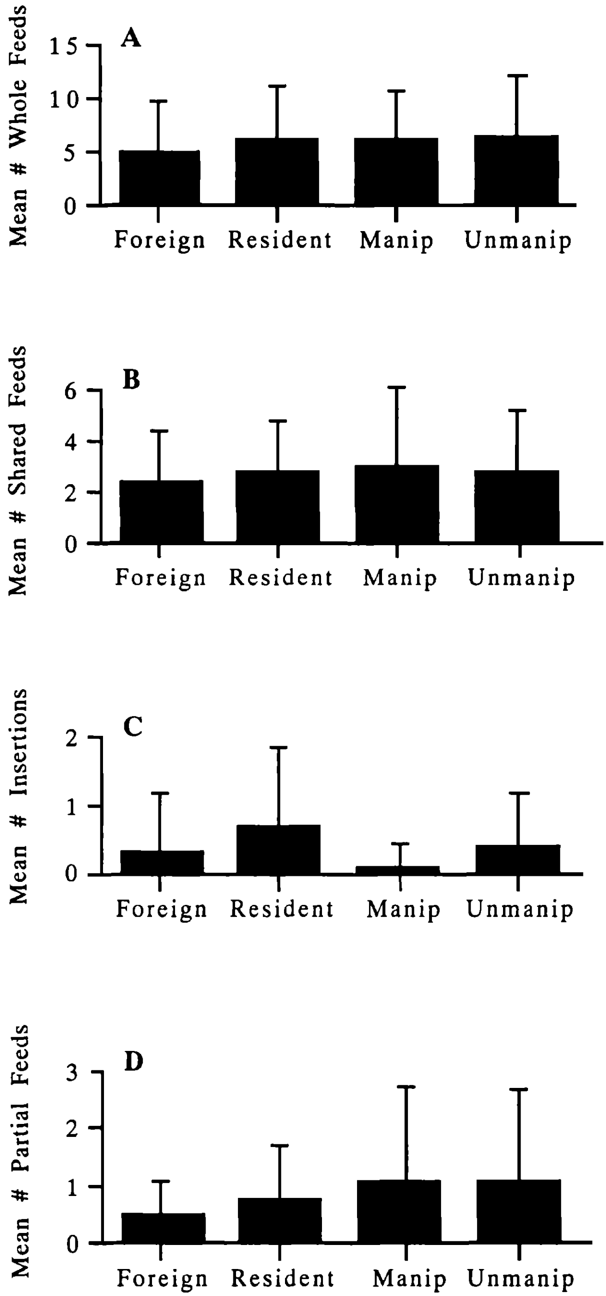

FIGURE 3. Mean (±SD) number of whole, partial and shared feeds, and insertions by the female for Foreign and Resident Red-winged Blackbird nestlings in experimental nests, and for Manipulated and Unmanipulated Red-winged Blackbird nestlings in control nests.

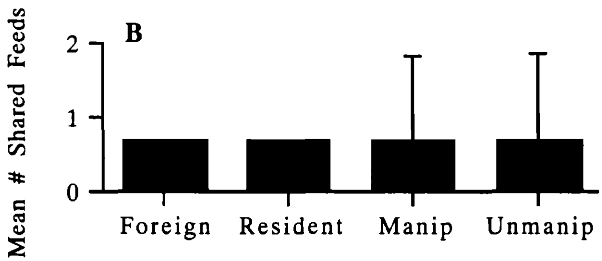

FIGURE 4. Mean (±SD) number of whole and shared feeds by the male for Foreign and Resident Red-winged Blackbird nestlings in experimental nests, and for Manipulated and Unmanipulated Red-winged Blackbird nestlings in control nests.

lack of recognition, although as we discuss below, our evidence is far from conclusive.

Limitations of the study.—The obvious limitation to our study was the sample size of 22 experimental nests. Power analysis indicated that we would have needed sample sizes in excess of 100 nests to achieve statistical significance at the 0.05 level for many of the differences (effect sizes) we observed. This analysis also showed, however, that the sample size we attained was sufficient to detect effect sizes of 25–50% at the 0.05 level. Our sample should therefore be able to detect large differences of the sorts reported by Peek et al. (1972) and Anne B. Clark (pers. comm.).

Feeding behavior of the adults.—We examined feeding behavior to determine whether adult Red-winged Blackbirds discriminate between their offspring and foreign nestlings. If discrimination were occurring, we would expect the foreign nestling to receive fewer feeding attempts, or more insertions (food item inserted then completely removed), or more partial and shared feeds. We found no significant difference between the foreign nestling and the resident nestlings in any feed type, however. Furthermore we saw no evidence of persecution of the foreign nestlings, as A. B. Clark (pers. comm.) observed. These results would indicate that the adult Red-winged Blackbirds in our study did not discriminate against foreign nestlings.

Fecal sac removal.—Although we examined fecal sac removal in this study, we did not expect to observe discrimination by adults. By not removing the fecal sacs of the foreign nestling, care-givers might endanger the survival of their own nestlings by increasing the risk of predation or the abundance of parasites and pathogens in the nest.

Gape time and nestling nonresponses.—Total gaping time, mean gape time, and nestling nonresponses to the adult's presence were analyzed to determine whether recognition of the adults by the nestlings took place. We found no significant difference in any of these variables between foreign and resident nestlings, demonstrating that resident and foreign nestlings did not differ in their responses to care-givers.

Comparison with previous studies.—Our failure to document parent-offspring recognition in Red-winged Blackbirds supports assumptions of several brood-manipulation studies of this species (Cronmiller and Thompson 1980, Whittingham 1989, Yasukawa et al. 1993), but is in contrast to results of Peek et al. (1972) and A. B. Clark (pers. comm.). Peek et al.'s (1972) brood exchanges and Anne Clark's remarkable videotape footage of persecution and ejection of foreign nestlings by female Red-winged Blackbirds seem to provide clear evidence for offspring discrimination by females in this species. Peek et al. (1972) exchanged pairs of similar-aged broods between nests 3–6 m apart on the same territory. Females readily accepted substitute nestlings younger than 7 d old, but followed their own 10–11-d-old nestlings to new nest sites even though their original nests contained (foreign) nestlings. The one female whose 7-d old nestlings were exchanged with a 6-d old brood showed some distress before accepting the substitute nestlings. Peek et al. (1972) therefore demonstrated that nestling recognition develops in female Red-winged Blackbirds just before the young depart the nest.

As suggested by Beer (1970), nestling-exchange experiments do not necessarily provide evidence that parents recognize their own young. Apparent discrimination by a parent might occur because the young discriminate among adults or because the exchanged young react to their foreign surroundings. Perhaps the females in Anne Clark's study were responding to abnormal behavior by the foreign nestlings (we attempted to account for this possibility with our control manipulations). Two other potentially important differences between Clark's study and ours are that Clark exchanged nestlings 4–5 d old whereas our nestlings were 6–9 d old, and Clark's exchanges were of opposite sex, whereas we attempted to exchange same-sex nestlings. It may be more difficult for females to remove older than younger nestlings, and exchanges of opposite sex may be more easily identified because male and female nestlings are dimorphic in size (Holcomb and Twiest 1970, Fiala 1981) and perhaps in begging behavior (Teather 1992). Alternatively, perhaps there are geographic differences in recognition ability. In any case, the issue of parent-offspring recognition in Red-winged Blackbirds is far from settled. Parents and offspring may still be able to perceive individual variation in signature calls or other cues, and parents or offspring might still discriminate in other situations such as among fledglings.

Conclusions.—It is possible that true nestling recognition is not generally advantageous for female Red-winged Blackbirds. There is no evidence of intraspecific brood parasitism in this species (Gibbs et al. 1990, Westneat 1993, Weatherhead and Boag 1995, Gray 1996) or in our population (Yasukawa, unpubl. data), so the female does not risk this form of misdirected nestling care. In addition, female Red-winged Blackbirds readily care for Brown-headed Cowbird nestlings even though such care is clearly misdirected and the nestlings of these two species are distinguishable to a human observer. Adult Red-winged Blackbirds are able to eject nestlings from their nests, so perhaps errors in such discrimination are too costly and therefore make nestling discrimination disadvantageous (Rothstein 1975, Røskaft et al. 1990).

Although nestling discrimination would seem to be advantageous to male Red-winged Blackbirds (Whittingham et al. 1992, Westneat and Sherman 1993), there is no evidence for its existence in this species. Extra-pair fertilizations account for a substantial proportion of young in this species (Gibbs et al. 1990, Westneat 1993, Weatherhead and Boag 1995, Gray 1996) and in our population (Yasukawa, unpubl. data). Despite the potential for misdirected paternal care, Westneat et al. (1995) showed that male Red-winged Blackbirds do not discriminate between their own and extra-pair nestlings. Our very limited data are consistent with this result.

Even if an extra-pair nestling were able to recognize that a care-giving male was not its father, it would be in its best interests to mask any potential signature cues to ensure care from that male (Beecher 1991). Likewise it would be to the female's advantage for any potential signature cues to be masked to ensure help from the territorial male in caring for extra-pair young. Alternatively, selection for a male's ability to discriminate between his own and extra-pair young may not have had time to produce an evolutionary response. Another possibility is that mistakes in correctly identifying young may be costly enough to oppose selection for this ability (Westneat et al. 1995).

Even if recognition were occurring, however, it would be advantageous for a foreign nestling to accept any care provided regardless of the identity of the care-giver. Whether or not the nestling is capable of signaling its relationship in the nest is unclear. Medvin et al. (1992a), found that there was strong sib-sib call similarity in the colonial Cliff Swallow (*Hirundo pyrrhonota*), but not in the noncolonial Barn Swallow (*Hirundo rustica*). We suspect that the Red-winged Blackbird does not have strong sib-sib call similarity among nestlings because it is a species in which nestlings do not normally intermingle, and because playback of foreign begging calls increased feeding rates of care-givers (Burford et al. 1998). If strong sib-sib similarity in calls existed, however, recognition of the difference between calls of resident and foreign nestlings could be relatively easy. Nestling call behavior may be an interesting area for further study in Red-winged Blackbirds. In addition, because fledglings from several broods can occupy a single territory, and because care-giving Red-winged Blackbirds must locate fledglings beyond their territorial boundaries, fledgling call behavior is also of interest.

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