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## An Experimental Test of Offspring Recognition in Western Bluebirds

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Recognition of offspring by parents should occur when the risk of provisioning unrelated young is high. Offspring recognition has been demonstrated mainly for colonial species in which large numbers of young intermingle after fledging and parents need to recognize their own offspring for feeding (e.g. Bank Swallows, *Riparia riparia* [Beecher et al. 1981]; Cliff Swallows, *Hirundo pyrrhonota* [Stoddard and Beecher 1983]). However, offspring recognition might also be favored during the nestling stage if intraspecific brood parasitism and/or extrapair matings are frequent (Beecher 1991). DNA fingerprinting suggests that both are common features of many bird populations (Birkhead and Møller 1992).

In general, parent birds will feed foreign young that are experimentally placed in the nest (Beecher 1991), but only one study has directly examined offspring recognition in a species in which broods are known to have mixed paternity. In Dunnocks (*Prunella modularis*), pairs of males sharing one nest appear not to recognize their own offspring, but rather feed all nestlings at a rate based on their mating access to the female (Davies et al. 1992). The situation for the polyandrous Dunnock, however, may not apply to socially monogamous species with high levels of brood parasitism or extrapair fertilizations. Offspring recognition in species of this type has received little attention and "it would be rash to conclude that it cannot occur" (Beecher 1991).

The purpose of our study was to determine whether male and/or female Western Bluebirds (*Sialia mexicana*) discriminate between their own offspring and unrelated nestlings. In our population, 34.5% of nests (16.5% of offspring) contain at least one nestling unrelated to the resident male ( $n = 29$  nests, brood size  $\bar{x} = 4.40 \pm \text{SE of } 1.07$ ; Dickinson in prep.), so there may be selection on males to recognize their own young. Egg dumping by conspecifics occurs infrequently (less than 1% of nests; Dickinson in prep.), so females are expected to show less discrimination. We tested for discrimination by presenting parents with broods containing both their own nestlings and nestlings transferred from other broods. We assumed that, if Western Bluebirds do not recognize this extreme difference in relatedness, they are unlikely to recognize subtler differences due to extrapair paternity.

Western Bluebirds are ideal for such a study for at least two reasons. First, these bluebirds are solitary nesters and even after fledging broods remain on the territory until they are independent, making extra-

pair fertilization a more likely explanation of recognition than interbrood mixing. Second, at 15 to 19 days of age, both broods and individuals can be identified by the structure of their begging calls (Monk and Koenig in prep.), providing at least one cue by which parents potentially could discriminate between their "own" and "unrelated" nestlings.

*Methods.*—This study was conducted at Hastings Natural History Reservation, central coastal California (36°23'N 121°33'W) between 1 May and 14 June 1990. As part of another study examining sex-biased provisioning in Western Bluebirds (Leonard et al. 1994), we experimentally altered the sex ratio of 10 broods by moving male and female nestlings between nests. This manipulation also allowed us to compare feeding rates by parents to their own versus unrelated young. We videotaped inside nests to identify which nestlings were fed and by which parent. We removed the nest box, with the nest and nestlings, 24 h before videotaping. We replaced the original box with a nest box with one plexiglass side and then returned the nest and nestlings. All nestlings were marked on the head with an individually distinctive pattern of white paint before being placed in a new box. The patterns applied to own and unrelated nestlings were randomized. A tripod covered with a plastic bag was attached to the box around the plexiglass plate. This bag protected the camera and kept the nest box near natural light levels, which were still high because of light entering the nest hole. Parents resumed feeding within 5 min of our departure from the box (for more details on methodology, see Leonard et al. 1994). We videotaped each nest for 4 h, between 0400 and 0900 PST, using a video camera mounted on the tripod. Each 2-h tape was changed midway through the 4-h period. We calculated feeding rates separately for each tape and then averaged them, so feeding rates are given as feeds per 2 h.

To determine whether parents distinguish between their own and unrelated nestlings, we exchanged nestlings (when 14 days old), while controlling for brood size, in broods matched for age (fledging occurs between 18 and 22 days). On day 15 we videotaped at these nests and then returned nestlings to their original nests and performed a reciprocal exchange. For example, in the first switch male young from nest A were exchanged for females from nest B and, in the reciprocal switch, females from nest A were exchanged with males from nest B. Nestlings were returned to their home nests after taping on day 16. Both switches were conducted 24 h before taping to

allow parents and nestlings time to adjust to the manipulation. Both own and unrelated nestlings were handled in the same manner. In 3 of the 10 nests, nestlings were only exchanged once because nestlings fledged before the second switch ( $n = 1$ ) or nests were only of one sex ( $n = 2$ ). The order of switches for each trial and the nestlings used were chosen at random. These manipulations resulted in a mean proportion of  $0.45 \pm 0.06$  (range 0.20–1.00) unrelated nestlings/nest, assuming that the original nestlings were the offspring of the resident male and female. We used the mean values from each nest to avoid pseudoreplication. The overall feeding rates to nests biased toward male or female offspring did not differ significantly for either parent (Leonard et al. 1994).

**Results.**—Both male and female Western Bluebirds fed unrelated nestlings at the same rate as their own offspring (Table 1). In general, females tended to feed at higher rates than males, although these differences were not significant based on a paired *t*-test (own nestlings,  $t = 2.16$ ,  $df = 8$ ,  $P = 0.06$ ; unrelated,  $t = 2.03$ ,  $df = 9$ ,  $P = 0.07$ ; Table 1). The proportion of unrelated nestlings in a nest may affect the ability of parents to discriminate between their own and unrelated nestlings. However, there was no correlation between the proportion of unrelated nestlings and the difference in feeding rate between their own and unrelated young by male ( $r_s = 0.18$ ,  $n = 9$ ,  $P = 0.60$ ) or female ( $r_s = -0.52$ ,  $n = 9$ ,  $P = 0.37$ ) parents.

**Discussion.**—Neither male nor female Western Bluebirds preferentially fed related nestlings, suggesting that they may not recognize their own young. The failure of Western Bluebirds to identify their offspring should not be a result of the timing of the experiment. Our study was conducted a few days before fledging, when vocal differences among broods and individuals are present in this species (Monk and Koenig in prep.) and when parents, in species with recognition, begin to discriminate (e.g. Medvin and Beecher 1986; Lessells et al. 1991).

We do not know the exact relationship of the nestlings in each nest to the attending adults, so some of the nestlings that we classified as "own" may have been extrapair nestlings. However, the analyses are based on the mean feeding rates to own versus unrelated nestlings rather than to individuals, so any effect of misclassified nestlings should be reduced. Also, our sample size was small, but a power test (Taylor 1990) showed we had a 90% chance of detecting a difference of 2.3 feeds·nestling<sup>-1</sup>·(2 h)<sup>-1</sup>, and we did detect overall sex differences in provisioning rates, which were less than 1.3 feeds·nestling<sup>-1</sup>·(2 h)<sup>-1</sup>.

Several factors might select against discrimination. Discrimination may increase the chance of starving one's own young and, even if this chance is small, discrimination will be selected against. This argument applies to cases in which parents that mistakenly feed foreign young do so at the exclusion of

TABLE 1. Mean ( $\pm$ SE) feeds·nestling<sup>-1</sup>·(2 h)<sup>-1</sup> by male and female Western Bluebirds to their own and unrelated nestlings. Feeding rates were compared using a paired *t*-test with 8 df (both tests  $P > 0.05$ ).

Sex	Own	Unrelated	<i>t</i>
Male	4.03 $\pm$ 0.94	3.74 $\pm$ 0.57	0.76
Female	5.33 $\pm$ 0.70	5.00 $\pm$ 0.75	1.31

their own young. This may happen if foreign chicks monopolize feedings, as in parasitism by Common Cuckoos (*Cuculus canorus*; Beecher 1991), but probably does not apply to Western Bluebirds, in which own and unrelated young are similar in size and age.

Nestlings may be selected to suppress cues for recognition (Davies et al. 1992). For instance, in Dunnocks the female and young may benefit from the inability of males to recognize their own offspring because nestlings are potentially fed by two males rather than by one (Davies et al. 1992). Western Bluebirds are monogamous, so this added benefit would not apply, but unrelated nestlings might still benefit by suppressing paternity cues. Nonetheless, it is unclear how these benefits would balance against the benefits of own nestlings to advertise their relatedness and of fathers to discriminate subtle differences in cues.

In Western Bluebirds, males might reduce the cost of feeding unrelated nestlings by reducing their overall feeding rate when the likelihood of extrapair paternity is high (as in Dunnocks), rather than by discriminating among young within the nest. Indeed, this partly may explain why males tended to have lower feeding rates than females. Nonetheless, more tests for offspring recognition in species with high extrapair paternity are needed before it is assumed that offspring recognition is restricted only to species in which young mix outside the nest.

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## Accelerational Implications of Hummingbird Display Dives

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Gravitationally induced forces and hydrostatic pressures in blood columns are well known to impose hypertension in various animals (e.g. giraffes [*Giraffa camelopardalis*], Hargens 1987; climbing snakes, Lillywhite 1987). Less well studied is transient imposition of high forces and dynamic induction of physiological pressures above resting values. In birds, rapid turns, sudden decelerations, and high-speed appendicular motions can impose substantial external and internal forces (e.g. Larimer and Dudley 1994) and, concomitantly, elevated internal pressures. Hummingbirds are particularly known for engaging in rapid display behaviors, which can be used in courtship toward a potential mate or in intra- and interspecific aggression. Such displays often incorporate a species-specific diving component at variable speeds and curvature radii at the bottom of the dive (Bent 1940, Wagner 1946, Johnsgard 1983, Miller and Inouye 1983, Stokes and Stokes 1989, Tamm et al. 1989, Scott 1993). Common Nighthawks (*Chordeiles minor*) also have high-speed display dives with low-frequency acoustic components (Miller 1925, Bent 1940, Breland 1972).

The display behaviors of Allen's Hummingbirds (*Selasphorus sasin*; Pearson 1960) and Anna's Hummingbirds (*Calypte anna*; Stiles 1982) are particularly spectacular and are among the best described of avian display dives. In both species, the display usually begins with a long steep dive initiated 20 to 35 m above a conspecific bird. When the diving bird is about 1 m of the display target and moving probably at maximal velocity, an abrupt pullout ensues during which radial accelerations must be substantial. Seg-

ments of the display are accompanied by species-specific vocalizations.

Because of the high velocities associated with hummingbird displays, it is of interest to calculate centrifugal forces and the corresponding accelerations associated with the pullout phase of the dives. Although dive trajectories have not been described quantitatively, the pullout consists of motion along an approximately circular arc leading into the ascent portion of the display (Stiles 1982). Thus, one can estimate radial forces and accelerations assuming circular motion. For this case, centrifugal force is given by  $mv^2/r$ , where  $m$  is the object mass,  $v$  is the velocity, and  $r$  is the local radius of curvature. Centripetal acceleration is correspondingly given by  $v^2/r$ . In circular motion, the centrifugal force is directed outwards and is orthogonal to the local tangent, whereas body orientations during diving are likely to be parallel to the flight trajectory (e.g. see Stiles 1982).

Available information on display dive velocities and geometry in *S. sasin* and *C. anna* is summarized in Table 1. Radii of curvature for dives of *C. anna* were approximated from graphic representations (see Stiles 1982); dive velocities reported by Stiles (1982) include a mean and maximum values. For *S. sasin*, the reported mean velocity at the bottom of the dive was used in acceleration and force calculations; although dive geometry was not specified in the original paper, a possible range of values for the radius of curvature can be estimated from description of the dive in relation to local landmarks (see Pearson 1960).

Calculated centripetal accelerations at the bottom of hummingbird display dives equal 70 to 100 m/s<sup>2</sup>