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## Specialized Extrapair Mating Display in Western Bluebirds

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Western Bluebirds (*Sialia mexicana*) are socially monogamous, maintain long-term pair bonds, and share equally in biparental care (Dickinson et al. 1996). Females often have extrapair young in their nests even though males exhibit kin-based winter sociality and sometimes help at the nests of relatives

(Dickinson and Akre 1998). DNA fingerprinting has revealed that more than 45% of females have at least one offspring sired by a male outside the family group and that 19% of offspring are sired by extrapair males (Dickinson and Akre 1998). Paired males follow their mates closely during the receptive period, a behavior that dramatically reduces the frequency of extrapair copulation (EPC) attempts (Dickinson and Leonard 1996, Dickinson 1997). As a con-

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TABLE 1. Comparison of female receptivity and male display frequency during extrapair and within-pair copulation attempts by Western Bluebirds.

Period	Copulations <sup>a</sup>	No. of males displaying	No. of males mewing	No. of dyads
<b>Extrapair interactions</b>				
During laying	0.28 ± 0.06	19	9	50
<b>Within-pair interactions</b>				
More than 10 days before laying	0.23 ± 0.16	0	0	7
During laying	0.89 ± 0.05 <sup>b</sup>	0	0	24

<sup>a</sup> Proportion of copulations accepted by female ( $\bar{x} \pm SE$ ).

<sup>b</sup> Mean proportion of copulations accepted by female was greater for within-pair interactions during laying than for within-pair interaction more than 10 days before laying or for extrapair interactions (Mann-Whitney *U*-tests,  $z > 3.4$ ,  $P < 0.001$  for both comparisons).

sequence, EPCs are only rarely observed under natural circumstances, indicating that they are typically covert. Here, we report on a specialized display that extrapair males perform during copulatory interactions with females.

**Methods.**—We have followed 36 to 130 Western Bluebird pairs per year since 1985, monitoring 360 artificial nest boxes on a 7-km<sup>2</sup> study area in Carmel Valley, California. Nestlings and adults are banded for individual recognition. We monitored copulatory behavior of unmanipulated pairs of Western Bluebirds from 1990 to 1998 (see Dickinson and Leonard 1996).

Females are highly receptive to their mates from about 10 days before laying through the last day of laying. We conducted observations both before and after the onset of peak female receptivity. Observations before the onset of peak receptivity were conducted 10 to 60 days before laying, and those after the onset of peak receptivity were conducted the day after the first egg was laid. We also created opportunities for EPCs by detaining resident males for 1 to 1.5 h the day after the first egg was laid, when we could be certain that females were highly receptive (Dickinson and Leonard 1996). Males were detained on 34 territories. Detained males were placed within 3 m of the nest where they were visible in open cages ( $n = 19$ ) or visually occluded behind a cloth bag ( $n = 15$ ). One observer monitored the female continuously while one to three observers recorded the identities and behaviors of extrapair males that interacted with the female. During detention, we were able to keep the extrapair male in view continuously and determine whether he displayed for 50 different extrapair male-female dyads.

Females do not usually solicit copulations by obvious tail raising or crouching, so copulations were scored as refused or accepted (Dickinson 1997). Refusal behaviors included leaving the perch, which often results in the male chasing the female in a looping flight through the air, frontal attack on the male by the female, and more rarely, the female flattening her body against a branch. Behaviors were described

on tape and transcribed the same day. They were then compiled by cross-checking times to create a single sequential record.

**Results.**—Males attempting copulations during extrapair visits to a female's territory exhibited a distinctive display that we have never observed during pair interactions. The display was only given during copulatory interactions when the male was within 1 m of the female. During the display, males typically shivered or flipped their wings rapidly while tilting forward to position their body axis parallel to the substrate. In 47% of cases (9 of 19) where males gave the visual display, they also gaped and gave a high-pitched "mew" call that resembled a kitten's mewing (Table 1). This call is distinct from the quiet "tch-tch" call sometimes given by males sneaking onto the territories of other pairs (Dickinson 1997). The extrapair mating display is similar in form to begging by adult female Western Bluebirds, but it differs in that begging females sit upright and give a high "chittering" vocalization. Both the posture of the male and the vocalization were distinctly different from those of begging females and fledglings.

The extrapair mating display occurred during 38% of the 50 extrapair encounters we observed (Table 1), and in 89% of cases it involved wing-shivering rather than rapid wing-flipping. We never observed a paired male give the display to his own mate (Fisher exact tests for comparisons with extrapair interactions;  $P = 0.048$  vs. within-pair interactions more than 10 days before laying;  $P = 0.001$  vs. within-pair interactions during laying; Table 1). Laying females were less receptive to extrapair than to within-pair copulation attempts; however, it is unlikely that the display was simply a response to mate refusal because males did not give the display to their own mates more than 10 days in advance of laying when females were similarly nonreceptive (Table 1).

The display was not associated with pair formation, because 89% of 19 identifiable displaying males were neighboring breeders that returned to their mates after the extrapair visit. In 12 cases (63%) where the extrapair male displayed, the female's mate was

visually present on the territory. Furthermore, we have never seen extrapair males give the display during pair formation in winter groups or in spring. The display did not appear to function as a signal to the resident breeder male, because the extrapair male displayed as frequently when the female's mate was in full view (41% of 29 dyads) as when he was visually occluded (33% of 21 dyads; Fisher exact test,  $P = 0.39$ , power = 0.63).

The display was not associated with female acceptance of EPCs. Males displayed in 42% (8 of 19) of EPC bouts resulting in at least one successful EPC compared with 35% (11 of 31) of bouts where the female was completely nonreceptive (Fisher exact test,  $P = 0.78$ , power = 0.97). Displaying males were just as likely to obtain a successful EPC before they displayed (6 of 18) as after they displayed (2 of 9), suggesting that the display does not function to increase copulatory success (Fisher exact test,  $P = 0.45$ , power = 0.68).

Females behaved aggressively toward males in 15 (30%) of the 50 extrapair encounters. Aggressive behaviors included pecking the male, bill snapping, reverse mounting, and frontal attack, which resulted in aerial grappling. Extrapair males displayed more often when females behaved aggressively (67% of 15 interactions) than when females did not show any of these aggressive behaviors (26% of 35 interactions; Fisher exact test,  $P = 0.008$ ).

*Discussion.*—Because the male display is performed by extrapair males that have mates of their own and does not occur during within-pair interactions, we conclude that the display is specific to extrapair interactions and is not involved in pair formation. The display occurred more frequently during extrapair interactions where the female behaved aggressively toward the male. This association suggests that the display is a submissive signal to the female that functions to reduce female aggression. An experimental test using a mechanical or robotic model of a male could be used to test this hypothesis. The extrapair display did not appear to be associated with the visual presence of the resident male, suggesting that it does not function as a signal to the resident male.

In Western Bluebirds, the display was associated with EPC attempts, but not with EPC success, suggesting that it does not have a courtship function. EPCs are rarely observed, particularly in passerines, so it is not clear how common specialized extrapair mating displays are in birds. In the Superb Fairy-Wren (*Malurus cyaneus*), a cooperative breeder with exceptionally high levels of extrapair paternity, males not only display and vocalize during extrapair encounters, they present females with flower petals (Mulder 1997). However, these displays are never fol-

lowed directly by EPCs and therefore are viewed as self-advertisement behaviors rather than as direct solicitations (Mulder 1997).

We were able to observe extrapair interactions in Western Bluebirds only by detaining resident males, both to increase the frequency of occurrence of EPC attempts and to reduce the chaos that ensues when the female's mate is free to interfere. In the absence of such manipulations, we might not have detected the display, and we certainly would not have sufficient data to determine whether the display is specific to extrapair interactions. Although this is the first description of an extrapair display in a bird with moderate levels of extrapair paternity, specialized EPC displays may be more common than current evidence indicates (Birkhead and Møller 1992).

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