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REGIONWIDE POLYGyny IN WILLOW FLYCATCHERS¹

JAMES A. SEDGWICK AND FRITZ L. KNOPF

U.S. Fish and Wildlife Service, National Ecology Research Center, 1300 Blue Spruce Drive, Fort Collins, CO 80524-2098

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Most species of North American flycatchers (Tyrannidae) are believed to be normally monogamous (Skutch 1960, Verner and Willson 1969). Some instances of bigamy are known for the Eastern Phoebe (*Sayornis phoebe*; Sherman 1952), Eastern Wood-Pewee (*Contopus virens*; W. J. Smith, cited in Eckhardt 1976), Western Wood-Pewee (*C. sordidulus*; Eckhardt 1976), and Acadian Flycatcher (*Empidonax virens*; Mumford 1964). Recently, local incidences of polygyny have also been reported for the Least (*E. minimus*; Briskie and Sealy 1987) and Willow (*E. traillii*; Prescott 1986) flycatchers. Here, we present details on two additional instances of polygyny in Willow Flycatchers in different regions of North America, including information on the behavior and nesting ecology of polygynous trios.

We observed instances of polygyny in Willow Flycatchers in 1987 incidental to other studies on two national wildlife refuges in the western United States: Arapaho National Wildlife Refuge (ANWR) in north-central Colorado, and Malheur National Wildlife Refuge (MNWR) in southeastern Oregon. ANWR is located in a high-elevation (2,500 m), intermountain glacial basin. Willow Flycatchers in this area occur along the floodplain of the Illinois River, wherever there are extensive stands of shrub willows (*Salix* spp.). The shrub willow community at ANWR is dominated by four species of willows—*S. geyeriana*, *S. monticola*, *S. caudata*, and *S. planifolia* (Cannon and Knopf 1984). MNWR is located at the northern edge of the Great Basin province (elevation = 1,280 m). Flycatchers at MNWR occur along the Blitzen River, also in stands of shrub willows. *Salix exigua* and *S. lutea* dominate the willow community at MNWR.

We observed apparent polygyny at MNWR on 11 June. At that time most flycatchers were paired and in the early stages of nest construction. Birds presumed to be females were actively carrying nesting material, and birds presumed to be males were alternately accompanying females to and from nests and singing at

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high rates from elevated perches. Along one stretch of the Blitzen River, we observed four singing males, but located five nests under construction. Three males were associating with only one female each, whereas one male was clearly consorting with two different females. The nests of these two females were 75 m apart along the stream and the primary song perch of the male was approximately midway between the two nests. From a vantage point on the opposite side of the river (ca. 15 m from the male's primary song perch and ca. 40 m from each nest), we were able to observe both females and the male simultaneously. The male often left his song perch and alternately pursued the two females to sites where they were gathering nesting material. This was accompanied on the male's part by *fitz-bews* and *churrs* (after Stein 1963). The most common vocalizations of females were alarm notes (*pits* or *whits*), and less frequently, slow *churr* calls, *creets*, and from one of the females, a few soft *fitz-bews* from low perch sites near the nest (cf. Seutin 1987). When either female returned to her nest, the male gave either *churr* calls from his song perch or he flew to the nest bush and gave these calls. During a 4-hr observation period, this male divided his time about equally between the two females. The two females never interacted with one another during this period; however, the male did have a few territorial encounters with another male involving chases near apparent territorial boundaries.

Our studies at ANWR occurred from 18 June to 6 August 1987. Willow Flycatchers were paired and in the nest construction phase on 18 June. We found two flycatcher nests in close proximity (35 m) on 25 June and within the territory of a single, singing male. Both nests were at approximately the same phenological stage: nest HQ-1 contained three flycatcher eggs and one Brown-headed Cowbird (*Molothrus ater*) egg (cf. Sedgwick and Knopf 1988), and nest HQ-2 contained two flycatcher eggs. Neither female had begun incubating. Nest HQ-1 was depredated between 26 and 28 June, and a completed re-nest (HQ-1a) was found 65 m from HQ-2 on 2 July. Sometime before 7 July, nest HQ-1a had also been destroyed. We observed the female building a third and final nest (HQ-1b) on 8 July only 21 m from the HQ-2 nest. Egg laying began on 9 July and a clutch of two eggs was laid in this nest.

We observed the male and two female flycatchers intermittently during incubation. The only obvious evidence of polygyny during this time—other than both nests being clearly within the male's territorial boundaries—was that the male occasionally accompanied the females when they left their respective nests to forage. Vocalizations associated with these episodes were *pits* and occasional *weeeos* and *zweeoos* by the females (after Stein 1963) and *fitz-bews* by the male. Rattle calls, heretofore undescribed (Sedgwick and Knopf, unpubl. data), and which we interpret as *wheak-dee-dee*, were frequently given by the male when he approached a female, either at or off of the nest.

Because the two nests were not both visible at the same time from a single vantage point, and because none of the flycatchers had any obvious distinguishing markings, we mist-netted and color-banded the three adults on 16 July. Nest HQ-2 had three, 1-week-old chicks on 16 July and nest HQ-1b had two eggs. Both the male and the HQ-2 female were observed feeding

young at nest HQ-2 on 17, 23, and 24 July. The female made most of the feeding trips (80.8%; $n = 78$; 5.5 hr observation on days 7, 13, and 14 of the nestling period), and devoted most of her time to feeding nestlings. When not feeding nestlings at HQ-2, the male spent his time foraging, advertising, and in maintenance activities, often <20 m from the HQ-1b nest; he occasionally accompanied the HQ-1b female when she was foraging. By 30 July, the young at nest HQ-2 had fledged, and on 30 and 31 July both the male and HQ-2 female were observed feeding fledglings.

Hatching at nest HQ-1b occurred between 24 and 26 July. By 6 August, the male and HQ-1b female were sharing feeding of the nestlings at this nest. As was the case for nest HQ-2, the female made most of the feeding trips (84.6%; $n = 39$; 4 hr observation on day 12 of the nestling period). The fledglings from nest HQ-2 were still within the male's territory on 6 August and were still being fed by the HQ-2 female; the fledglings were also doing some flycatching on their own. Male parental duties were apparently limited to the HQ-1b nest as we did not observe any feedings of the HQ-2 fledglings by the male on 6 August (315 min observation).

We can suggest at least four factors that may promote polygyny in Willow Flycatchers: a shortage of males in combination with female site fidelity, female-female tolerance, nonmandatory biparental care, and a habitat with productivity concentrated into a narrow, vertical belt. Whereas an unbalanced sex ratio (i.e., a shortage of males) is no longer generally believed to have an overriding influence on a species' mating system (Verner and Willson 1966), a local shortage of males in combination with female site fidelity may have resulted in incidental polygyny. Both male and female Willow Flycatchers display strong site fidelity (Walkinshaw 1966) and, in fact, one of the two females of the polygynous trio at ANWR in 1987 returned to the same territory in 1988 (Sedgwick and Knopf, unpubl. data). Site fidelity is especially strong in individuals that were successful the previous year (Greenwood and Harvey 1982, Gavin and Bollinger 1988) which suggests the following possible scenario. One of the females, after having bred successfully in 1986, returned to her territory in 1987 but failed to find her mate from the previous year. She may have then chosen to stay with the site because of her past success, and mated polygynously.

Female-female aggression was rare at ANWR; we observed only two instances of aggression between the females, in spite of the proximity of their nests (21 m). Similarly, there were no interactions between females at MNWR (4 hr of observation). If aggression is rare between female Willow Flycatchers, then polygyny may be promoted because competition for essential resources (e.g., food, nest sites, and/or male attention) is weak (Nolan 1978). The frequency of intrasexual aggression we observed, however, is in contrast to that reported by Prescott (1986) who observed "numerous" aggressive encounters between females. Furthermore, it should be noted that although our observations coincided with two periods of high female activity (nest building and feeding nestlings), they did not coincide with the early settling period when aggressive encounters may have been at their peak. Finally, recent evi-

dence that female aggression in Red-winged Blackbirds (*Agelaius phoeniceus*) does not limit settling patterns or densities (Searcy 1988) (suggesting that female aggression may not be a factor in the promotion of polygyny) may make the question of how aggressive female Willow Flycatchers are or are not, moot.

Biparental care of nestlings in Willow Flycatchers may not be mandatory. The male made only 17.9% ($n = 117$) of all feedings at both nests at ANWR; all three young successfully fledged from nest HQ-2, and both nestlings also fledged at HQ-1b in spite of a low male feeding rate. Similarly, Holcomb (1972) reported that females did most of the feeding of Willow Flycatcher nestlings in Nebraska, and Ettinger and King (1980) reported male visits to the nest being about 0.75 times as frequent as those of the female in Washington. Thus, biparental care in the Willow Flycatcher may not be essential to reproductive success, especially in the case of small brood sizes ($n = 3$ and $n = 2$ at ANWR). Low demands for male feeding of the young may reduce the advantage of monogamy and promote polygyny (Oring 1982).

Finally, Willow Flycatcher habitats at both MNWR and ANWR are savannah-like, shrub-willow associations along rivers. These habitats are vertically narrow and characteristic of those of most North American polygynous species (Verner and Willson 1966). Such habitats are highly productive and typically have abundant food supplies compared to more strictly terrestrial habitats (Orians 1980). In addition, the potential for differences in food supplies between territories is presumably enhanced in such habitats (Verner and Willson 1966). Such differences in food abundance raise the "polygyny threshold," thus tending to make polygyny adaptive (Verner and Willson 1966).

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