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BREEDING ECOLOGY OF THE GRAY FLYCATCHER IN PINYON–JUNIPER WOODLANDS IN NEW MEXICO

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ABSTRACT: We studied the breeding ecology of the Gray Flycatcher as part of a long-term study of bird communities of pinyon–juniper in northeastern New Mexico, 1992–2002. All years combined, we located and monitored 37 nests and measured vegetation and habitat characteristics at most nests. Clutch-initiation dates ranged from 12 May through 14 July with a peak from late May to early June. Mean clutch size was 3.65 eggs but was significantly lower in later nests than in early nests. Mayfield nest success was 31% with most (93%) unsuccessful nests failing because of predation. Only one nest (3%) was parasitized by a cowbird. Nest height averaged 2.32 m with most nests placed close to or against the main trunk within the middle portion of a tree. Positioning the nest close to the trunk increases nest concealment and may represent a strategy to avoid predation. Gray Flycatchers nested primarily in pinyon pines (*Pinus edulis*; 62% of nests) and junipers (*Juniperus* spp.; 35%). On average, the flycatchers built nests in areas with taller and denser canopies, steeper slopes, and higher densities of trees, especially junipers.

The Gray Flycatcher (*Empidonax wrightii*) is a small (~12.5 g) migratory songbird that breeds through much of the interior western United States and winters primarily in Mexico (Sterling 1999). It nests in a wide variety of arid habitats ranging from taller sagebrush (*Artemisia* spp.) shrublands to open pinyon pine (*Pinus edulis*)–juniper (*Juniperus* spp.) woodlands to mature ponderosa pine (*Pinus ponderosa*) forests (Sterling 1999). Its population density varies substantially by habitat and location but tends to be greatest in shrubland habitats, particularly on the Columbia Plateau, and lower in woodland or forested habitats (Sterling 1999). Unlike many other migratory songbirds, the Gray Flycatcher does not appear to be suffering declines in

abundance but rather is increasing over much of its range (Peterjohn et al. 1995) and expanding its distribution (Sterling 1999).

Despite the Gray Flycatcher's abundance and broad distribution, surprisingly little is known about many aspects of its natural history. For example, although a few published studies have described the species' nesting behavior and nest sites (Russell and Woodbury 1941, Johnson 1963, Yaich and Larrison 1973), most have been based on observations of only one or a few nests. In addition, there have been no detailed studies of the reproductive success of any Gray Flycatcher population (Sterling 1999). We studied the breeding ecology of Gray Flycatchers nesting within pinyon–juniper woodlands in northeastern New Mexico. The objective of this paper is to describe the nesting success, causes of nest failure, nest sites, and nesting habitat of this population.

METHODS

Study Site

Our study took place in Colfax County, northeastern New Mexico, along the eastern edge of the foothills of the Sangre de Cristo Mountains at the western edge of the Great Plains. It was part of a long-term research program studying the behavior of the Brown-headed Cowbird (*Molothrus ater*) and its effects on hosts nesting in pinyon–juniper woodlands. During these studies, we established 14 study plots of 35 ha each within pinyon–juniper woodlands distributed among four adjacent properties, and we studied the breeding-bird communities on a subset of plots each year from 1992 to 2002 (NRA Whittington Center, 4 plots, 1992–2000; V-7 Ranch, 4 plots, 1992–1997; CS Ranch, 2 plots, 2001; Vermejo Park Ranch, 4 plots, 2001–2002). All properties are largely undeveloped, but two were grazed seasonally by cattle (V-7 Ranch, CS Ranch), one was grazed by American bison (*Bison bison*; Vermejo Park Ranch), and one was ungrazed by domestic livestock or bison (NRA Whittington Center); see Goguen and Mathews (1998) and Goguen et al. (2005) for detailed descriptions of these sites.

Although distributed among four properties, all study plots were located within 50 km of each other and were similar in habitat structure and topography. In our study region, pinyon–juniper habitat occupies a narrow elevational zone (~1990–2130 m) between shortgrass prairie and mixed-conifer forests of ponderosa pine and Douglas fir (*Pseudotsuga menziesii*). All plots were covered by an open woodland dominated by pinyon, with one-seed juniper (*Juniperus monosperma*) scattered throughout. The shrub layer consisted primarily of oaks (*Quercus* spp.), alder-leaf mountain mahogany (*Cercocarpus montanus*), and skunkbrush sumac (*Rhus aromatica*). The herbaceous layer was generally sparse.

Over 40 bird species breed in the pinyon–juniper woodlands of this region (Goguen and Mathews 1998). Among the most common breeding species are the Spotted Towhee (*Pipilo maculatus*), Chipping Sparrow (*Spizella passerina*), Bushtit (*Psaltriparus minimus*), Blue-gray Gnatcatcher (*Polioptila caerulea*), Western Wood-Pewee (*Contopus sordidulus*), and Western Scrub-Jay (*Aphelocoma californica*). The Brown-headed Cowbird is also

common and parasitizes several species heavily (Goguen and Mathews 1998). The Gray Flycatcher is a regular breeder at low densities (typically <2 pairs/35 ha plot).

Nesting Success

We located and monitored Gray Flycatcher nests on a subset of study plots from May through July each year while searching broadly for nests of any cowbird hosts. We located nests by observing adults' behavior and revisited nests every 2 or 3 days to monitor the nests' fate and contents. For all nests, we estimated the date of clutch initiation from direct observation or by back-calculation from hatching or fledging dates. To calculate average clutch size, we used only nests that were checked during the incubation stage to ensure that clutches were complete. To estimate the parasitism rate, we used only nests that survived through the egg-laying stage to ensure that each nest was available to be parasitized for at least the entire egg-laying period.

We calculated nesting success by the Mayfield method (Mayfield 1961, 1975). We considered a nest successful if it fledged at least one young flycatcher. We considered a nest to have failed because of cowbird parasitism if it was abandoned within three days of the appearance of a cowbird egg. In calculations, we used published estimates of the Gray Flycatcher's incubation (14 days) and nestling periods (16 days; Sterling 1999), as these agreed with our observations. Because clutch size varied from nest to nest, we used the mean clutch size observed in our study to estimate the average length of the egg-laying period (period between the laying of the first and last egg).

Nest Site and Habitat Characteristics

After nests were no longer active, we measured habitat characteristics at most nests by a protocol modified from James and Shugart (1970). At each nest, we used a measuring tape or clinometer to measure nest height, height and diameter at breast height (dbh) of the nest tree, distance of the nest from the main tree trunk, and distance of the nest from the outer foliage edge. We used a compass to determine the orientation of the nest relative to the trunk. We measured canopy cover with a spherical densiometer by averaging four measurements taken 1 m from the nest in the four cardinal directions. We estimated the proportion of the nest concealed by foliage from 1 m above the nest and from 1 m in each of the four cardinal directions at the level of the nest. Within a subplot of radius 5 m (0.008 ha) centered on the nest, we counted shrubs and saplings (all woody plants <8 cm dbh), and we determined slope and the average height of the canopy. Within a subplot of radius 11.3 m (0.04 ha) centered on the nest, we counted trees (all woody plants >8 cm dbh), by species.

To evaluate whether nests were oriented nonrandomly, we assigned each nest to one of six sectors (60° each) according to its orientation and used a Pearson chi-squared test to evaluate whether the nests' distribution by sector differed from even.

To evaluate whether Gray Flycatchers were selecting specific microhabitats within pinyon–juniper woodlands, we compared characteristics of nest sites on the four study plots on the V-7 Ranch to similar measurements made

systematically within these four plots. We limited these comparisons to this single property because plot-level habitat measurements were available for only two properties (NRA Whittington Center and V-7 Ranch), and 23 of 24 flycatcher nests found on these two properties were on the V-7 Ranch. We quantified the habitat on each plot on the V-7 Ranch in 1992 in order to describe the pinyon–juniper woodland for a related study (see Goguen and Mathews 1998). Within a given plot, we sampled the habitat in a manner similar to that used at nest sites, centering on 12 bird-survey points arranged systematically within the plot in a 3 × 4 grid, with points separated by 200 m. We used ANOVA to compare the means of seven variables (slope; overstory canopy height; canopy cover; total number of shrubs and saplings per 0.008 ha; total number of pinyon, juniper, and all trees per 0.04 ha) at the flycatcher nest sites with those at the systematically located points representing potential flycatcher nesting habitat. Although plot-level habitat measurements were made during only one year (1992) whereas nest measurements were spread over six years (1992–1997), we believe that the habitat variables we were comparing were unlikely to change significantly over this relatively brief period in this arid habitat. Three systematically located points that were in prairie (no trees) did not represent potential Gray Flycatcher nesting habitat and were removed prior to analyses. Percent canopy cover was arcsine-square-root transformed prior to being tested to approximate normality (Sokal and Rohlf 1981). All analyses were carried out with SYSTAT, version 10 (Systat Software, Inc.).

RESULTS

Nesting Success

We located and monitored 37 nests over the 11 years of the study. The number of flycatcher nests located annually varied from 0 to 12, but in most years (9 of 11) we located between 1 and 6 nests. Although we tried to locate nests as early in the nesting cycle as possible, only 13 (35%) were found during the nest-building or egg-laying stages, whereas 10 (27%) and 14 (38%) were found during the incubation and nestling stages, respectively. Because so few nests were found each year we did not attempt to analyze data by year but instead combined nests from all years for analyses.

Clutch-initiation dates ranged from 12 May through 14 July with a peak in initiations from the last week of May to the first week of June (Figure 1). Although the birds were not banded, the proximity of some of the later nests to recently failed nests (<100 m) suggests they were replacement nests. We were unable to determine if any later attempts were second broods of previously successful pairs.

Mean clutch size was 3.65 eggs (n = 17; standard error 0.15). Four-egg clutches were most frequent (12 nests; 71%), but three-egg (4 nests, 24%) and two-egg (2 nests, 6%) clutches were also observed, particularly later in the season. Nests initiated in the first half of the breeding season (before June 9) averaged 3.9 eggs (n = 10), while later nests averaged 3.3 eggs (n = 7; Mann–Whitney U test: U = 52.00, P = 0.04).

Of 33 nests whose fates we confirmed, 19 (58%) were successful, 13

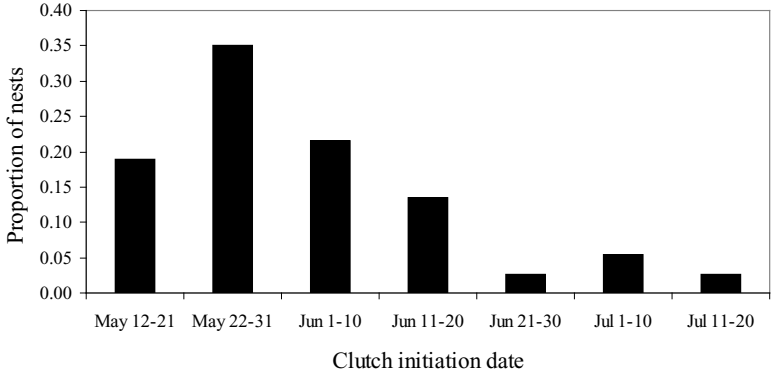

Figure 1. Seasonal distribution of clutch-initiation dates for Gray Flycatcher nests (n = 37) in pinyon–juniper woodland in northeastern New Mexico, 1992–2002.

(39%) failed because of predation, and 1 (3.0%) failed because of cowbird parasitism. Mayfield nest success (30.7%) was substantially lower than the observed proportion successful (57.6%) because of the large number of nests located during the incubation and nestling stages (Table 1).

On the basis of nests for which the number of fledglings was known, Gray Flycatchers fledged an average of 1.78 young per nesting attempt (n = 32 attempts) but an average of 3.17 young per attempt when only successful nests (n = 18) were considered. In the one parasitized nest a single cowbird egg was laid during the flycatcher's egg-laying period, and this nest was deserted within two days.

Nest Site and Habitat Characteristics

Gray Flycatchers nested primarily in pinyon (23 of 37 nests, 62%) but also used one-seed juniper (12 nests, 32%), Rocky Mountain juniper (*Juniperus*

Table 1 Nest Success Calculated by the Mayfield Method for Gray Flycatchers Nesting in Pinyon–Juniper Woodlands in Northeastern New Mexico, 1992–2002

Phase of nesting interval	Phase duration (days)	Exposure (days)	Nests failed (n)	Daily survival (mean, SE[a])	Phase survival (mean, SE)
Egg-laying	2.67[b]	21	1	0.952 (0.046)	0.878 (0.11)
Incubation	14.0	163	7	0.957 (0.016)	0.541 (0.13)
Nestling	16.0	223.5	6	0.973 (0.013)	0.647 (0.12)
Overall nest survival				0.307 (0.098)	

[a]SE, standard error.

[b]Duration of the egg-laying stage was calculated from the mean clutch size observed in this study (3.67) minus 1 day since the egg-laying stage consists of the interval from the laying of the first egg to the laying of the final egg in a clutch.

Table 2 Characteristics of Gray Flycatcher Nest Sites in Pinyon–Juniper Woodlands of Northeastern New Mexico, 1992–2002

Nest-site characteristic[a]	Mean (SE)	Minimum	Maximum	*n*
Nest height (m)	2.32 (0.18)	0.60	6.10	37
Nest-tree height (m)	5.58 (0.36)	2.70	13.50	36
Relative nest height	0.44 (0.026)	0.12	0.84	36
Nest-tree diameter[b] (cm)	18.9 (1.7)	6.5	48.0	34
Nest distance from trunk (cm)	28.6 (8.3)	0.0	175.0	35
Nest distance from tree's outer edge (cm)	75.1 (9.1)	0.0	200.0	28
Relative distance from trunk	0.17 (0.04)	0.0	0.78	34
Concealment from 1 m above (%)	63.3 (5.68)	0.0	100.0	27
Concealment from sides (%)	64.9 (4.48)	11.3	91.3	26
Nest-patch characteristic				
Slope (degrees)	16.1 (1.2)	5.0	32.0	34
Canopy height (m)	6.3 (0.3)	3.5	13.0	34
Canopy cover (%)	69.4 (3.76)	36.7	95.8	24
Shrubs/0.008 ha (*n*)	51.3 (12.4)	1	367	34
Trees/0.04 ha (*n*)	24.4 (2.0)	6	70	34
Pinyons/0.04 ha (*n*)	18.7 (1.8)	3	57	34
Junipers/0.04 ha (*n*)	5.5 (0.8)	0	14	34
Ponderosa pines/0.04 ha (*n*)	0.2 (0.2)	0	534	

[a]See Methods for a more complete description.

[b]At breast height (dbh).

scoparum; 1 nest), and ponderosa pine (1 nest). In all cases, nests were placed in live trees. In general, flycatcher nests were compact, well-hidden, and placed close to or against the main trunk within the middle portion of the tree (results summarized in Table 2). Nest height averaged 2.32 m with the majority of nests (76%) located between 2 and 4 m in height. Nest heights were distributed approximately normally in relation to the height of the nest tree, with most nests (61%) located between 40 and 60% of the height of the nest tree. Nest placement within the foliage, however, was highly skewed towards the trunk; 60% of nests were built against the main trunk. Nest orientation relative to the trunk was non-random (χ^2 =11.55, 5 df, P = 0.04); 24 of 33 nests (74%) were oriented to either the north or east (between 316° and 135°).

Within the pinyon–juniper woodland of the V-7 Ranch, Gray Flycatchers selected specific microhabitats. They built nests in areas with taller and denser canopies, steeper slopes, and higher densities of trees, particularly junipers, than at points located systematically (Table 3).

DISCUSSION

In northeastern New Mexico, Gray Flycatchers typically initiated their first nesting attempts in late May or early June, with some clutches initiated as early as mid-May. Although the earliest nests in our population include the earliest initiation dates observed in this species to date, the date of peak egg-

Table 3 Comparison of Habitat at Gray Flycatcher Nest Sites and at Points Located Systematically

Habitat variable	Nest sites[a] (mean, SE)	Systematic points[b] (mean, SE)	F[c]	*P*
Canopy height (m)	5.95 (0.26)	4.93 (0.33)	4.30	0.042
Slope (degrees)	17.28 (1.34)	11.84 (1.28)	7.11	0.010
Canopy cover (%)	68.82 (3.89)	39.60 (5.14)	14.30	<0.001
Shrubs/0.008 ha (n)	31.83 (6.98)	54.36 (8.30)	3.16	0.080
Pinyons/0.04 ha (n)	19.30 (2.55)	16.84 (1.45)	0.82	0.37
Junipers/0.04 ha (n)	5.83 (0.98)	1.68 (0.44)	19.93	<0.001
Total trees/0.04 ha (n)	25.13 (2.86)	18.53 (1.49)	5.13	0.027

[a]n = 23.

[b]n = 45. Points within four study plots of 35 ha each in pinyon–juniper woodland on the V7 Ranch, northeastern New Mexico, 1992–1997.

[c]Test statistic from ANOVA with 1, 66 degrees of freedom for all variables.

laying conforms closely with the timing of nesting at other locations throughout the range (Sterling 1999). For example, in Colorado Sedgwick (1998) reported that first broods hatched during mid-June, which would correspond to egg-laying in late May or early June. The Gray Flycatcher rears two broods in some locations (Russell and Woodbury 1941, Johnson 1963), and the length of the breeding season in our study region appears to allow time for pairs successful in their first nesting attempt to attempt a second brood. We were unable to confirm any instances of double-brooding, however, and the approximately unimodal distribution of clutch-initiation dates suggests that if double-brooding does occur, it is not particularly common.

Clutches consisted primarily of either three or four eggs, as reported previously (Sterling 1999). The ratio of three- to four-egg clutches, however, was not consistent through the season. Most early clutches contained four eggs, while many later nests contained three or, in one case, two eggs, resulting in a decline in the average clutch size across the season. This pattern has also been observed in other species of *Empidonax* such as the Dusky Flycatcher (*E. oberholseri*; Sedgwick 1993), Willow Flycatcher (*E. traillii*; McCabe 1991), and Acadian Flycatcher (*E. virescens*; Wilson and Cooper 1998), perhaps because the energetic demands of multiple nesting attempts or seasonal patterns of food availability constrain the females to lay fewer eggs.

The Mayfield success of Gray Flycatchers in our study area (30.7%) appears to be slightly low in comparison to other songbirds building open cup nests in trees (Martin 1992), although a larger sample of nests found early in the nesting cycle is probably needed for a more accurate assessment. Predation was the primary cause of nest failure for Gray Flycatchers, as it is for most species building open cup nests (Martin 1988). Thirteen of 14 nests that failed in this study failed because of predation. Although we did not identify the predators, the primary predators of tree-nesting songbirds in this habitat include the Western Scrub Jay, Steller's Jay (*Cyanocitta stelleri*),

Pinyon Jay (*Gymnorhinus cyanocephalus*), Rock Squirrel (*Spermophilus variegatus*), and Pinyon Mouse (*Peromyscus truei*). Although there are few records of cowbird parasitism of the Gray Flycatcher nests, Friedmann et al. (1977) reported the flycatcher to be moderately parasitized (25%) in Oregon. At our site, cowbirds are abundant and parasitize several species heavily, for example, >50% of nests of the Blue-gray Gnatcatcher, Plumbeous Vireo (*Vireo plumbeus*), and Western Tanager (*Piranga ludoviciana*) (Goguen and Mathews 1998, Goguen et al. 2005), but the Gray Flycatcher appears to be an unimportant host.

Gray Flycatchers tended to place their nests in the middle portion of a tree, both vertically and horizontally. The average nest height we observed (2.3 m) is comparable to that reported from pinyon–juniper woodlands in Arizona (0.6–3.4 m; T. Corman in Sterling 1999) and Jeffrey pine (*Pinus jeffreyi*) forest in California (2.7 m; Johnson 1963) but is substantially lower than that reported from a ponderosa pine forest in California (5.4 m; L. George in Sterling 1999). Gray Flycatchers appear to favor placing nests in the inner portion of a tree near the trunk regardless of habitat type: flycatcher nests were placed at the base of a branch against the trunk in 59.5% of nests in a Jeffrey pine forest (Johnson 1963) and in 64.7% of nests in a ponderosa pine forest (L. George in Sterling 1999), proportions similar to that observed in our study (60%). Positioning the nest close to the stem may increase nest concealment and act as a predator-defense strategy.

As >90% of trees in our study area are pinyons (Goguen and Mathews 1998), it is unsurprising that we found Gray Flycatchers nesting primarily (62% of nests) in pinyons,. Nevertheless, Gray Flycatchers apparently prefer juniper trees: given the dominance of pinyon, flycatchers nested more frequently in junipers (35% of nests) than expected, and they favored habitats with a higher density of junipers (Table 3). Although further study is needed, juniper may be favored because its foliage structure provides high-quality nesting or foraging sites. Strips of juniper bark also appear to be a favored component in the outer structure of Gray Flycatcher nests (Russell and Woodbury 1941).

In addition to a preference for juniper, Gray Flycatcher nests in our study were associated with taller trees, denser overstory cover, steeper slopes, and higher tree densities. The association of flycatchers with these features probably results from the flycatchers' preference for mature pinyon–juniper woodland (Pavlacky and Anderson 2001) and the effect of elevation on that woodland's structure in our region. Pinyon–juniper habitat in our study area tends to be shorter and more open (i.e., lower tree density) at lower elevations at or near the edge of the prairie than at higher elevations away from the edge. Flycatchers were generally not found in these flatter, open habitats but instead favored the denser, taller woodlands on steeper slopes at higher elevations. Given that the Gray Flycatcher is a pinyon–juniper specialist in a large part of its range (Balda and Masters 1980), additional research examining the breeding ecology of this species in pinyon–juniper woodlands would be beneficial. Particularly beneficial would be studies that can also address the effects of land uses that promote early successional stages, such as timber or firewood harvesting and clearing or chaining for livestock grazing.

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Gray Flycatcher

Sketch by George C. West