suggest differential digestion between adults and young.

We do not know the reason for these differences between adults and young. They may be related to higher feeding rates for nestlings, a wider selection of prey by adult birds that are attempting to meet the demands of hungry nestlings, or a broader availability of different prey during the nesting period. Since both total prey numbers and number of prey taxa were higher in nestlings than adults, the higher prey diversity may simply be an artifact of higher prey numbers. Our analysis did not allow us to examine this possibility. Some food items were found only in samples from young birds (termites, lepidopterans, isopods, and plant matter). This could reflect differential food selection for the young or could be a sampling artifact (except for termites, total numbers for these items were 15 or less).

Males and females

There was not a significant overall difference in diet between males and females. However, our samples sizes were small, resulting in relatively low power to detect differences. Individual comparisons by prey taxon showed a significant difference between the sexes in the relative contribution of flies (higher in males). There are potential behavioral reasons for differences in diet between males and females during the nesting season (e.g., foraging in proximity to the nest vs. farther away, or differences in roles between the sexes in feeding the young); this comparison warrants further examination in future studies.

COMPARISONS WITH OTHER PUBLISHED STUDIES

Other studies (Beal 1912, Bent 1942, McCabe 1991) have all reported bugs, various hymenopterans, and flies as prominent food items of Willow Flycatchers (these reports are based on data from Willow Flycatchers in various parts of their North American range, but not the Southwest). Species of flies (Diptera) made up a consistently high portion of the diet at the Kern River and in other areas. The Kern River samples had higher numbers of some taxa, notably beetles and spiders, than reported in previous works. The spiders (and probably some of the beetles and homopterans) are of interest because many of them are presumably taken by gleaning. Large numbers of termites (Isoptera) were found in samples from the Kern River, but were not reported for samples from other areas across the Willow Flycatcher's range (Beal 1912, McCabe 1991).

On the other hand, the observed diet at the Kern River included quite low numbers of flying Hymenoptera (bees and wasps) compared to reports from elsewhere in the flycatcher's range. This paucity of Hymenoptera in the diet may be due to the relative scarcity of flowering shrubs at the Kern River site. Willows at the Kern River site flower by early May, so insects attracted to flowering willows are not represented in our samples. Malaise trap samples for flying insects at the Kern River site support this idea, being heavily dominated by flies, with few Hymenoptera (M. Whitfield, unpubl. data). The Kern River diet samples also contained relatively few Lepidoptera larvae (caterpillars), which make up a moderate proportion of the diet in other studies.

MANAGEMENT IMPLICATIONS AND RESEARCH NEEDS

Southwestern Willow Flycatchers take a wide range of invertebrate prey, including flying, and ground- and vegetation-dwelling species. This diverse prey base, in conjunction with the variety of foraging techniques used by the birds (and suggested by the food data), indicates significant flexibility in the diet. Such flexibility and range in the diet should be advantageous in the face of variable conditions (e.g., from site to site, or year to year).

The dual issues of exposure to chemical toxins and effects of adjacent land use are important to Southwestern Willow Flycatcher conservation efforts. Of 209 breeding sites known in the year 2000, at least 37 (18%) were associated with runoff and other water inputs (e.g., irrigation canals, sewage treatment outflows) from agricultural and urban sources (Table 6 in U.S. Fish and Wildlife Service 2001). Chemical toxins are one possible explanation for deformities observed in Southwestern Willow Flycatchers (Sogge and Paxton 2000; cf. Mora et al. *this volume*), and exposure to pesticides and other harmful chemicals is particularly a threat at sites surrounded by intensive agriculture and along lowland riparian sites downstream from pollution sources. The wide variety of invertebrate prey taken by Willow Flycatchers provides many potential avenues for accumulating environmental toxins. The prey base includes species of terrestrial and aquatic origins, so harmful chemicals may be accumulated from either of these sources. Because flycatchers feed on many strong-flying prey species (such as bees, wasps, flies, and dragonflies), toxins could be introduced into the diet even from sources relatively distant from breeding sites. In light of this, additional research is needed on the level of harmful compounds present in the food base, and potential impacts to Southwestern Willow Flycatchers (Stoleson et al. 2000a, Mora et al. *this volume*).

Willow Flycatcher prey base may be strongly influenced by habitats and land uses adjacent to riparian breeding sites. Adjacent invertebrate-rich habitats such as mesquite or wetlands may provide good source areas for strong-flying "tourist" species that can travel to the flycatcher's breeding patch. Adjacent areas with intensive agriculture likely provide fewer (or at least different) prey taxa, especially if the area is treated with pesticides to control insects. On the other hand, some agricultural activities or crops may attract pollinators and other potential prey taxa. Finally, conversion of surrounding habitats to urban use is likely to dramatically alter the local distribution and abundance of the flycatcher's invertebrate prey, especially where insect control measures are aggressively pursued.

This study documents the diet composition and diversity only at the Kern River, a native-dominated riparian site. It is unknown whether the same patterns hold true at flycatcher breeding sites dominated by non-native saltcedar (*Tamarix ramosissima*). This is an important consideration in that almost half of all known Southwestern Willow Flycatchers territories are in sites dominated by saltcedar or by mixtures of native vegetation and saltcedar (Sogge et al. *this volume*). Although Tracy and DeLoach (1999) suggest that saltcedar habitats do not support an adequate prey base for nesting flycatchers, the relative quality of saltcedar habitats is not clearly known (Stoleson et al. 2000a). Specific data on flycatcher diet composition in saltcedar habitats are needed to help address these questions.

ACKNOWLEDGMENTS

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THE STATUS OF THE WILLOW AND PACIFIC-SLOPE FLYCATCHERS IN NORTHWESTERN CALIFORNIA AND SOUTHERN OREGON

C. JOHN RALPH AND KIMBERLY HOLLINGER

Abstract. The Willow (*Empidonax traillii*) and Pacific-slope (*E. difficilis*) flycatchers are generally similar in their morphology and foraging, but differ in their habitat and population dynamics. Through a concentration of constant-effort mist-netting stations, we documented the movements and composition of populations over a relatively large geographical province of southern Oregon and northern California. Although the Pacific-slope Flycatcher is far more common as a breeding species in much of the province, it becomes much less common than the Willow Flycatcher during migration. After breeding, the Willow Flycatcher has a previously undocumented major influx of birds into the province from breeding sites to the north, including both young and adults. By contrast, the Pacific-slope Flycatcher appears to migrate differentially, with adults moving south before the young.

Key Words: California, demography, *Empidonax traillii, Empidonax difficilis*, Klamath Province, migration, mist-nets, Oregon, Pacific-slope Flycatcher, Siskiyou Province, Willow Flycatcher.

As a group, the *Empidonax* flycatchers of the Americas have always challenged ornithologists. With many sibling or superspecies that differ only slightly on the basis of morphology, identification is sometimes difficult, even in breeding individuals with species-specific songs. In the post-breeding season, identification becomes even more difficult as they fall silent and become another small, greenish bird among the foliage. Careful examination of birds captured at constant-effort mist-netting stations can give us new insight into the life history attributes during all seasons, especially outside of the breeding season.

Our objectives were to document, for the Willow Flycatcher (*Empidonax traillii*) and Pacific-slope Flycatcher (*E. difficilis*), the timing and magnitude of their use of various regions and the implications to land management. Little is known about dynamics of population and age structure at any time of the year for either species, and especially in the post-breeding and migration seasons when much of the selection takes place. The few previous studies during these seasons have been at a single station or in a small, restricted area (Ralph 1968, Otahal 1998, Yong and Finch 1997). Our data are based upon captures of birds in mist nets at stations in what we term the Klamath Physiographic Province of Oregon and California: a complex of the Siskiyou and Klamath mountains, drained by many rivers including the Rogue, Klamath, Trinity, northern Sacramento, and Eel (Fig. 1).

THE WILLOW FLYCATCHER

Gaining knowledge of the distribution and status of the Willow Flycatcher has been challenging to ornithologists, due in large part to the difficulty in separating forms of the genus. As Pyle (1997) pointed out, the majority of individuals of the Willow Flycatcher are not distinguishable from the very closely related Alder Flycatcher (*E. alnorum*). Based upon the geographic breeding ranges of the two flycatchers (AOU 1998), in our area we assume that all birds we captured are *E. traillii.*

In much of its range the Willow Flycatcher is rather habitat specific, occurring in "moist, brush thickets, open second growth, and riparian woodland" (AOU 1998). In Oregon it can be one of the most abundant birds in young, regenerating clear cut forests (Altman et al. *this volume*), in addition to the more typical riparian habitats. In California it was previously common in certain riparian woodlands (Grinnell and Miller 1944). However, it has been essentially extirpated from the Central Valley and remains in only a few sites along the western side of the Sierras and in the extreme northern part of the state. In 1990 all of the subspecies were listed by the state of California as endangered.

In the mountains of the Klamath Province, the Willow Flycatcher breeds very rarely in the upper Klamath River Valley (Harris 1996), and more commonly north and east of Mount Shasta, into the Upper Klamath Basin. Although known to occur as a migrant from its more northern breeding areas, its abundance was largely unknown in much of these mountains. Because of the paucity of breeding birds, forest and range management plans in the Province have not taken the species into account, except in the very few areas where an occasional bird has been recorded singing.

THE PACIFIC-SLOPE FLYCATCHER

The former "Western" Flycatcher (*E. difficilis*) has been split into two morphologically very

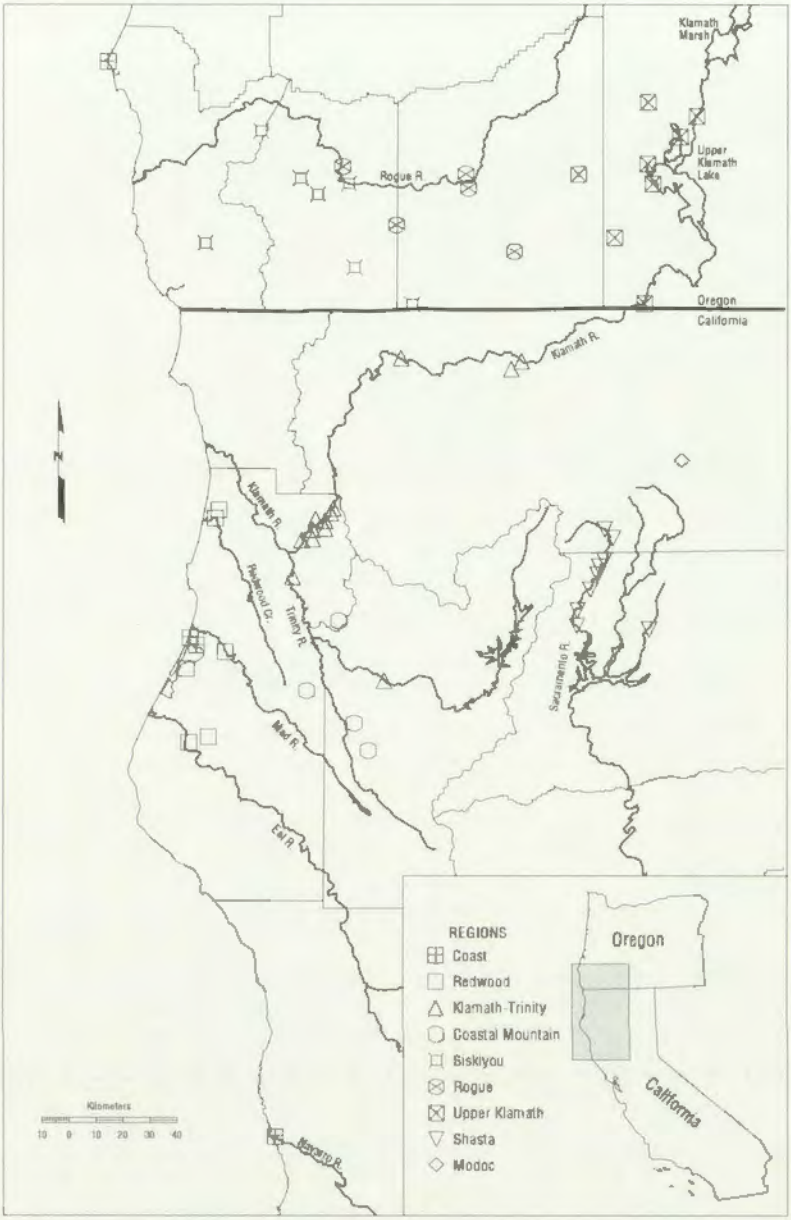

FIGURE 1. Study area with regions, mist-netting stations, and major rivers.

similar species (Johnson 1994, AOU 1998): (1) the Pacific-slope Flycatcher (which retained the former specific name), found in the Pacific coastal coniferous forests; and (2) the Cordilleran Flycatcher (*E. occidentalis*), which occurs in more inland coniferous habitats in the western mountains of North America. Johnson and Marten (1988) found the two taxa to be sympatric without interbreeding in north-central California, on the margin of our study area in Siskiyou County. Unfortunately, only about 60% of individuals can be identified as either Pacific-slope or Cordilleran Flycatcher even in the hand (Pyle 1997), making species separation imprecise. Although our easternmost stations are near or in the suggested range of the Cordilleran Flycatcher, we assume that the vast majority of birds breeding and moving through our study area can be safely referred to as the Pacific-slope form. We also assume that the migratory route of the

Cordilleran Flycatcher lies largely to the east of our stations, as that is the direct route to its wintering grounds. Additionally, we have noted no birds with the song type of the Cordilleran Flycatcher during our extensive censuses in the area.

The Pacific-slope Flycatcher is more of a habitat generalist than the Willow Flycatcher, inhabiting both deciduous and coniferous forests throughout its range (Bent 1942, Thomas 1979). In addition, it occupies many seral stages, from shrub-seedling to old-growth (Meslow and Wight 1975).

Most arrive in our study area by mid-April (Sakai 1987), and nesting is well underway by mid-May. Sakai (1987) found that peak incubation is during June, and fledging is from mid-July to the first week of August. The birds leave their territories beginning about the third week of July, peaking about the first of August, with the last departing in mid-August. Post-breeding up-slope movements have been suggested by Ziener et al. (1990) in California, and down-slope by Swarth (1904) in Arizona.

METHODS

For all analyses except recapture rate, we used only the first capture of an individual in each year. This results in an assay of new birds moving into the area around a capture station.

CONSTANT-EFFORT MIST-NETTING

These data were derived from birds captured in arrays of 12-m mist nets at 54 stations (Fig. 1), each operated from 1 to 18 years. Methods followed the protocol outlined in Ralph et al. (1993). Nets were operated during the breeding season from the beginning of May through the end of August, and on into the fall at many stations (Appendix). For analyses, we used 10-day periods, with the first period beginning 1 May and ending on 10 May (Table 1). We had a total of 2306 station ten-day periods (Appendix), all years and stations combined.

Each station consisted of 10 to 14 12-m long nets, opened within 15 min of dawn and closed after 5–6 hrs. Each station operated on a separate and regular schedule (every 1–10 days) during a season, with the same number of nets, in permanent net lanes, and for the same number of hours, weather permitting. For analyses, we grouped nearby stations with similar physiographic features into Regions (Fig. 1).

AGEING AND SEXING

Each captured bird was aged as young (hatched that year) or adult based on plumage or skull (Pyle 1997). Birds were considered males if they showed any sign of a cloacal protuberance. We have observed that these two species have relatively small protuberances as compared to other taxa, such as thrushes and sparrows, which may result in an underestimate of males. Females develop well-defined brood patches and are easily sexed by this trait that develops usually by June, indicating that incubation is underway. Birds maintain cloacal protuberances and brood patches for a period after the cessation of active breeding.

TABLE 1. DATES OF 10-DAY PERIODS USED FOR ANALYSES

Period	"Month"	Dates
1	May	1–10 May
2	May	11–20 May
3	May	21–30 May
4	June	31 May–9 June
5	June	10–19 June
6	June	20–29 June
7	July	30 June–9 July
8	July	10–19 July
9	July	20–29 July
10	August	30 July–8 August
11	August	9–18 August
12	August	19–28 August
14	September	29 August–7 September
15	September	8–17 September
16	September	18–27 September
17	October	28 September–7 October
18	October	8–27 October

Notes: The "month" indicates the notation used in Figures 2 and 6 for convenience of viewing. Note that the last period is longer, and includes all late migrants.

AGE RATIO

We used the average proportion young in each Region as the age ratio metric. It was calculated separately for each station, for each year, and for each season the station was operated. Specifically, we divided the capture rate of young by the total capture rate of both adults and young for that season and year at the station. We averaged these proportions for all station-seasons in a Region, and tested the significance of differences between age ratios by a Duncan's Multiple Range test from the General Linear Models Procedure of SAS (1996). Age ratio is a unique metric that provides an estimate of the location of the route of the migrants, as hypothesized in Ralph (1981). An even age ratio (approximately 50% young) indicates the center of a species' migration route, while a high proportion of young suggests the edge of the route.

CAPTURE RATE AS AN INDEX OF ABUNDANCE

The capture rate per 10-day period at each station is our basic index of abundance. We calculated it by summing all the captures of a species at a station in a 10-day period and dividing by the number of net-hrs (one 12-m net operated for one hr is a net-hr), multiplied by 1000, giving the number of birds per 1000 net-hrs at the single station. This index is widely employed at single stations such as bird observatories, and has been expanded into multiple stations in various studies such as Ralph (1981), the Constant Efforts Sites Scheme of the British Trust for Ornithology (e.g., Baillie and Holden 1988, Peach et al. 1991), and the Monitoring Avian Productivity and Survivorship (MAPS) program (DeSante 1992).

For both abundance and age ratio, the Regional averages of these station-season data were used in various comparisons. We considered this to be a relatively conservative approach, as we treated all the captures of a species in a season at a station as an independent datum.

SEASONS

For our seasonal analyses, we defined two seasons—breeding and the fall migration. The breeding season was centered on the two periods with the peak of abundance of birds in breeding condition. This resulted in the breeding season being the eight 10-day periods from 1 May to 19 July. The migration season was the seven 10-day periods centered on the peak of fall migration, which for both species was the 10-day period of 19–28 August; therefore, the migration season included the periods from 20 July to 27 September. With this convention, a small number of birds were captured after the main migration season and were included in the last migration period.

By contrast, for purposes of discussion (especially in Figures 2 and 3), we characterize birds as undergoing spring migration, breeding, post-breeding, or fall migration. These refer to the state of each individual bird, rather than the date of capture, and separate birds in breeding condition from others that were not. This was important because during spring, some individuals can be migrating north through an area while others there are breeding.

RESULTS

The two species differ markedly in several aspects of their biology. We present the Pacific-slope Flycatcher first, as it provides a basis of comparison for the more variable Willow Flycatcher. Both species have substantial breeding populations to the north of the study area.

PACIFIC-SLOPE FLYCATCHER

Timing of events

Overall, this species breeds fairly commonly in most of the study area, is more abundant towards the coast, and the adults migrate south before the young (Fig. 2). The young appear to have two autumnal pulses of movement into the province, the post-breeding and then the fall migration.

We found substantial numbers of adult birds in non-breeding condition, and presumably spring migrants, moving through in May (Fig. 2). We captured breeding birds (those with a cloacal protuberance or brood patch) from late May through the end of June, when the first young appeared. In July and early August, we noted an increase in new adults (still in breeding condition) in most regions; this pulse of post-breeding adults was especially marked in the Klamath-Trinity, Redwood, and Coast regions. Adults then rapidly departed on their fall migration, leaving all regions by late August, with only a few captured in the Coast Region in very early September.

By July, young birds began to make up the majority of new captures. This post-breeding influx of young continued into early August in most areas, at times overshadowing the numbers in other seasons. In many regions the fall migration of young was signaled by an increase of captures in late August and September. In the inland and higher elevations of the Upper Klamath Region, the fall movements were largely concluded by mid-August. In the Coast, Redwood, and Siskiyou Regions, this influx of young was a separate pulse. In others, it apparently overlapped with the earlier post-breeding movements of adults and young.

Comparison of abundance between regions

In the breeding season (until 19 July), both adults and young were most commonly captured towards the coast, with higher capture rates at the Coast and Redwood Regions for adults (6 to 14 birds per 1000 net-hrs, respectively; Table 2). The highest abundance of young was at the Redwood and the nearby Coastal Mountain Regions (about 3 birds per 1000 net-hrs).

During the fall migration (after 19 July), relative abundance can give an indication of the route taken. Overall, adults were captured much less often than young (Table 3) and showed little propensity for any particular region. Young birds were abundant in all regions from the Coast to the inland river valleys (4 to 7 per 1000 net-hrs), and became less common far inland.

Determination of routes through age ratio

We found little difference among Regions in the percent young captured during the migration season (Table 4), except at the three stations at Shasta, which had only 33% young. The great majority of birds in all regions were young, suggesting a broad front of migration throughout most of the Province.

WILLOW FLYCATCHER

Timing of events

The pattern of Willow Flycatcher captures (Fig. 3) differed markedly from that of the Pacific-slope Flycatcher, notably in the relative paucity of breeding populations, the greater post-breeding abundance in the inland regions, the synchronous migration of adults and young, and the prolonged passage in the fall.

We captured adults that were not in breeding condition moving through in late May and early June. These adults were in moderate numbers in most inland regions, in general avoiding the Coast and Redwood Regions. From late May through June, small to moderate numbers of birds in breeding condition were captured in the

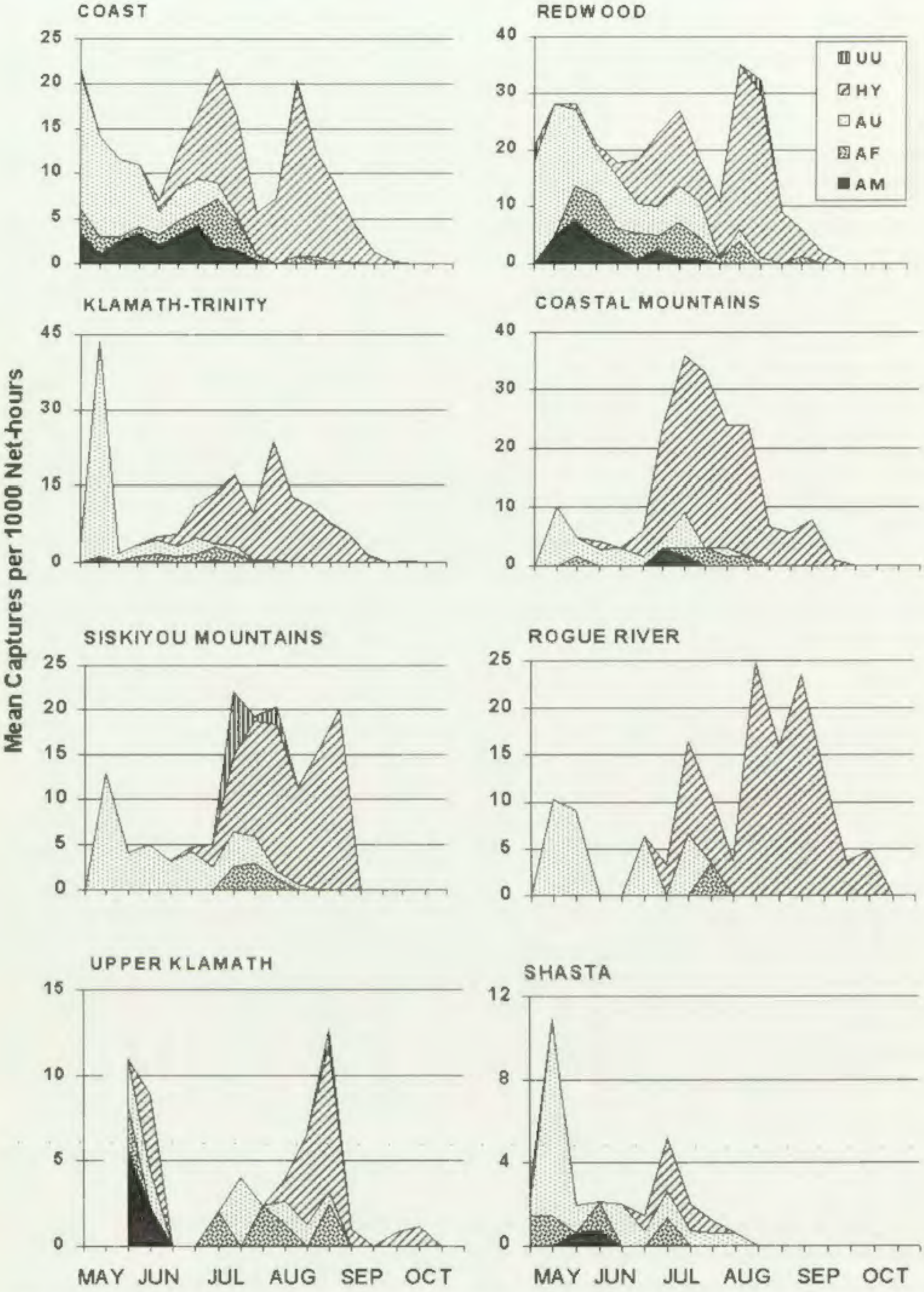

FIGURE 2. Average capture rate of adult, young, male, and female Pacific-slope Flycatchers per 1000 net-hours at stations in various regions of northern California and southern Oregon from May through October. Each station-season contributed a datum to the mean of a region. Age and sex classes are: UU = Unknown age and sex; HY = Hatching year, less than one year old; AU = Adult, unknown sex; AF = Adult female; and AM = Adult male. The "month" is as shown in Table 2.

TABLE 2. BREEDING SEASON AVERAGE CAPTURE RATES (NUMBER PER 1000 NET-HOURS) OF ADULT AND YOUNG PACIFIC-SLOPE FLYCATCHERS WITH EACH STATION-SEASON CONTRIBUTING A DATUM TO THE MEAN OF A REGION

	Young				Adult			
Region	Capture rate	SD	N	Duncan grouping[a]	Capture rate	SD	N	Duncan grouping[a]
Coast	1.8	1.6	19	A B C	5.7	2.0	19	A B
Redwood	3.3	1.8	19	A	14.3	1.3	19	A
Klamath-Trinity	1.4	1.8	51	A B C	2.4	2.3	51	B C
Coastal Mountains	2.8	2.3	13	A B	2.7	1.8	13	B C
Siskiyou	0.6	1.3	40	C D	2.4	2.1	40	B C
Rogue	0.9	1.6	6	B C D	1.0	2.5	6	C D
Upper Klamath	0.2	0.9	9	C D	1.0	2.1	9	C D
Shasta	0.3	0.8	32	C D	1.1	1.8	32	C D
Modoc	0.0	0.0	4	D	0.0	0.0	4	D

[a] Regions not significantly different from others have the same letter.

farther inland and more northerly Klamath-Trinity, Rogue, Shasta, and Upper Klamath Basin Regions; elsewhere, few breeding birds were captured. During July, Willow Flycatchers were captured only in the Upper Klamath Basin Region, where they likely breed in small numbers. No post-breeding influx was noticeable in any other Region, in contrast to the Pacific-slope Flycatcher in which many adults still in breeding condition were moving through. In all regions except the Upper Klamath, a distinct and prolonged fall migration of Willow Flycatchers was evident. Beginning in mid-August and on into September, we captured large numbers of mostly young birds, far more than in other seasons. Capture rate was remarkably high in the Rogue, Klamath-Trinity, and Coastal Mountain Regions, with moderate numbers in all other regions except the Coast and Redwood, where the Willow Flycatcher was scarce. In contrast to the Pacific-slope Flycatcher, moderate numbers of Willow Flycatcher adults were still present through the migration at most regions.

The fall migration of Willow Flycatchers peaked in early September in the northern regions. Surprisingly, at the Farallon Islands (Point Reyes Bird Observatory, unpubl. data), some 500 km to the south and some 30 km offshore, the peak of fall migration was somewhat earlier, during August (Fig. 4). This indicates that their presence in the riparian habitats of most of our Regions was generally later than on this offshore island, though the movement of young through the Upper Klamath Region was similar in timing to the Farallones.

Comparison of abundance between regions

Although few Willow Flycatchers bred in the Province, adults were significantly more abundant (based on average capture rate) during the breeding season only in the Rogue and Klamath-Trinity Regions (Table 5). In the fall migration, moderate numbers of adults were captured in some inland regions (i.e., the Shasta and Rogue Regions at 1.8 birds per 1000 net-hrs) as compared to the other inland and coastal regions (from 0 to 0.5 per 1000 net-hrs).

When the young Willow Flycatchers appeared

TABLE 3. FALL MIGRATION SEASON AVERAGE CAPTURE RATES (NUMBER PER 1000 NET-HOURS) OF ADULT AND YOUNG PACIFIC-SLOPE FLYCATCHERS WITH EACH STATION-SEASON CONTRIBUTING A DATUM TO THE MEAN OF A REGION

	Young				Adult			
Region	Capture rate	SD	N	Duncan grouping[a]	Capture rate	SD	N	Duncan grouping[a]
Coast	4.0	1.2	27	A B	0.3	0.4	27	B
Redwood	6.6	1.3	19	A	1.5	1.3	19	A
Klamath-Trinity	6.5	1.7	50	A	0.3	0.7	50	B
Coastal Mountains	7.0	0.8	13	A	0.5	0.8	13	A B
Siskiyou	5.7	3.7	38	A	0.7	1.9	38	A B
Rogue	5.4	1.9	7	A	0.2	0.8	7	B
Upper Klamath	1.5	1.4	13	B C	0.7	1.2	13	A B
Shasta	0.1	0.4	31	D	0.1	0.7	31	B
Modoc	0.5	1.2	4	C D	0.0	0.0	4	B

[a] Regions not significantly different from others have the same letter.

TABLE 4. FALL MIGRATION PERCENT YOUNG OF PACIFIC-SLOPE FLYCATCHERS AND WILLOW FLYCATCHERS WITH EACH STATION-SEASON CONTRIBUTING TO THE MEAN OF A REGION

	Pacific-slope Flycatcher				Willow Flycatcher			
Region	Percent hatch year	SD	N	Duncan grouping[a]	Percent hatch year	SD	N	Duncan grouping[a]
Coast	91.4	10.2	24	A B	94.9	10.2	17	A
Redwood	76.6	23.8	18	A B	100.0	—	1	A
Klamath-Trinity	95.1	11.1	44	A B	96.8	8.2	47	A
Rogue	91.7	20.4	6	A B	87.9	17.8	7	A B
Coastal Mountains	87.8	16.2	13	A B	99.3	2.3	10	A
Siskiyou	88.2	24.6	27	A B	80.2	32.6	12	A B
Upper Klamath	67.9	40.5	10	B	68.4	35.4	8	B
Shasta	33.3	57.7	3	C	29.3	31.2	12	C
Modoc	100.0	—	1	A	0.0	—	0	

[a] Regions not significantly different from others have the same letter.

after the breeding season, they were much more common overall than Pacific-slope Flycatchers (cf. Table 3). Abundance of young also differed markedly between regions (Table 6); they were significantly more common in the river valleys of the Rogue and the Klamath-Trinity regions, reaching high levels of 20–23 birds per 1000 net-hrs. In comparison, moderate numbers (1.0 to 3.6 per 1000 net hrs) were captured in most other regions, both inland and coastal. This pattern of abundance indicates the young migrate in the inland river valleys.

Determination of routes through percent young

While almost no young Willow Flycatchers were captured during the breeding season (before 19 July), almost all captured after that were young. In the fall, only the Shasta and Upper Klamath Regions had a significantly lower proportion young than the other regions, all of which had >80% young (Table 4). If higher proportions of adults occur in the center of the migration route, these age ratios indicate a more inland route than do the capture rates, with the main route generally to the east of the Province.

RECAPTURE RATE

The recapture rate is a measure of the site persistence within a season (Table 7). Combining all regions, the Willow Flycatcher was recaptured much less often than the Pacific-slope Flycatcher, indicating that the Willow Flycatcher was more mobile in the study areas, with few birds apparently remaining for more than a day at a station. The return rate of birds captured in previous years (a measure of site fidelity between years) was 3.8% for the Pacific-slope Flycatchers during the breeding season; no Willow Flycatchers were recaptured (during breeding or migration periods), suggesting a largely transient population.

DISCUSSION

SCALE OF STUDY AND INDEPENDENCE OF DATA

Utility of combining stations

Our study combined data from many stations, because individual stations can have differing abundances and age ratios due to habitat and locality differences. However, an inspection of the data found no evidence that timing of age or sex classes capture rate peaks differed between stations within a region (C. J. Ralph, unpubl. data). Differences in habitat were related to abundance, but when three or more stations were combined in a Region, any such biases were minimal. In combining stations it is important that each station contributing to a regional mean was operated consistently through the season in question, on a constant-effort schedule (whether daily or weekly); the stations included in this study met this criterion.

Independence of data

The basic datum of our study was the abundance or age ratio at each station, in a unit of time (either a season or a 10-day period) and in a year. This station-season-year datum was not strictly independent. For instance, a station run multiple years contributes more data to a Regional mean than a station with only one year's data. At a given station, each year's datum would be expected to have a strong relationship with the datum from another year. In practice, we have found that the between-year differences were as marked as the between-station differences (C. J. Ralph, unpubl. data), and for purposes of this paper we considered them independent. Further, mist netting data may experience less site bias than some other methods, as a station will likely capture birds from over a large area, especially during the migration sea-

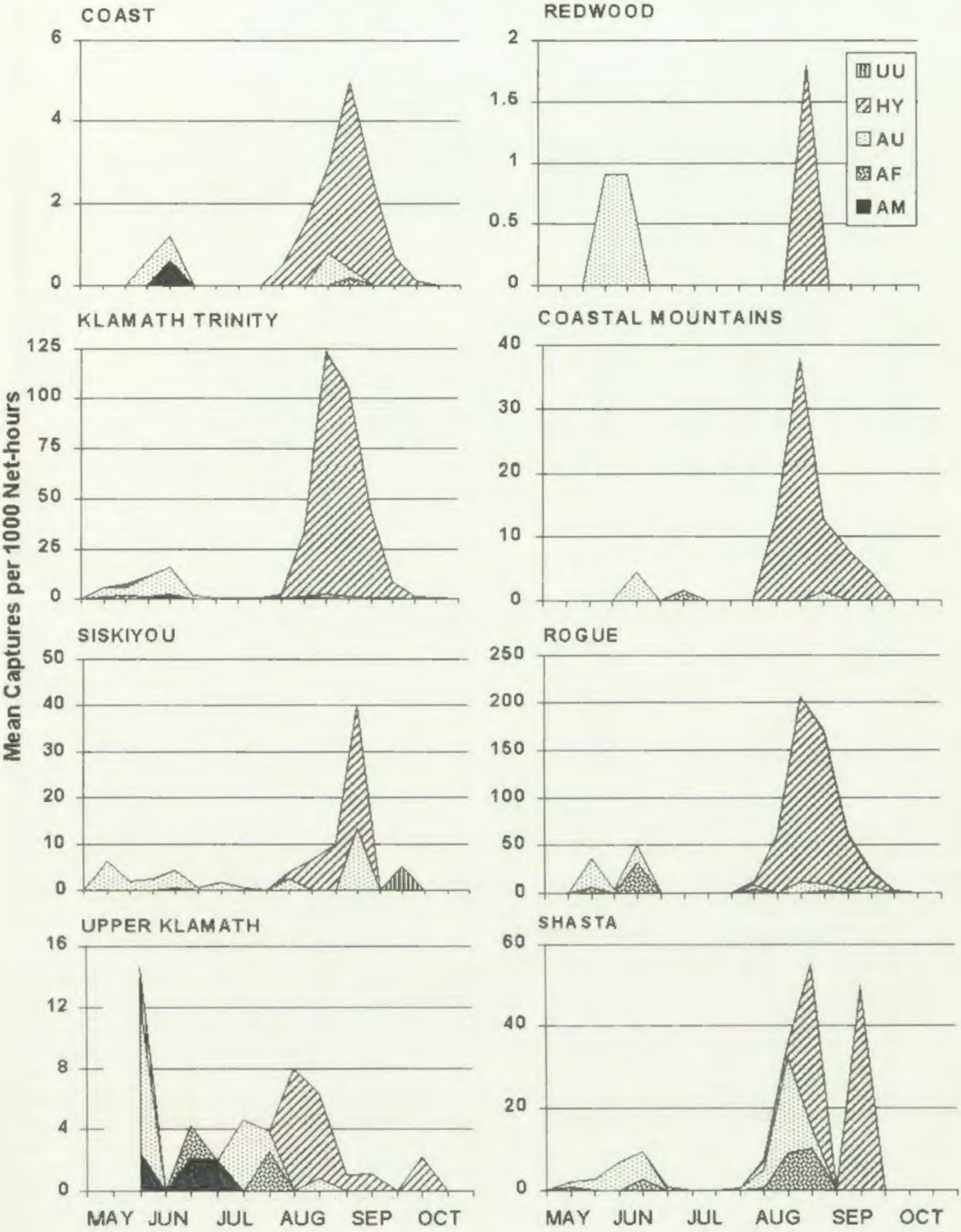

FIGURE 3. Average capture rate of adult, young, male, and female Willow Flycatchers per 1000 net-hours at stations in various regions of northern California and southern Oregon from May through October. Age and sex classes are: UU = Unknown age and sex; HY = Hatching year, less than one year old; AU = Adult, unknown sex; AF = Adult female; and AM = Adult male. The "month" is as shown in Table 2.

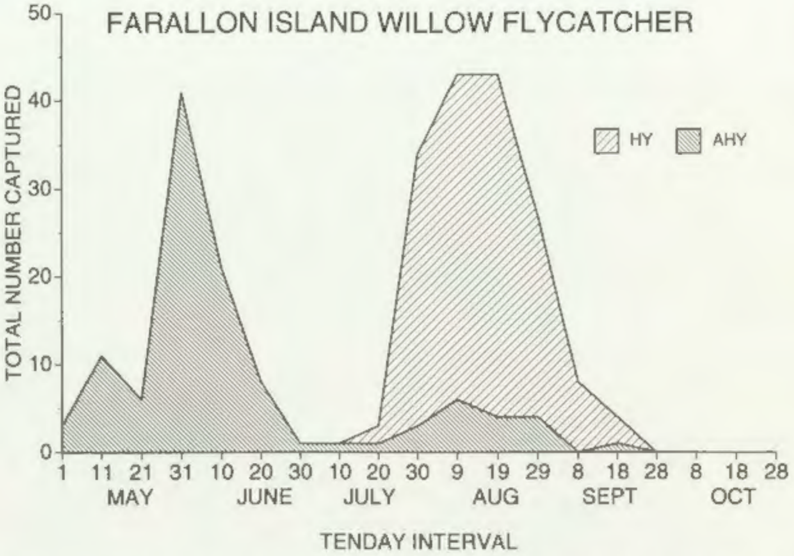

FIGURE 4. Total number of Willow Flycatchers caught on the Farallon Islands, 30 km west of San Francisco, California, by 10-day intervals. Each date is the beginning of a 10-day interval. Capture effort was constant throughout year.

son, when birds are moving in from their more northerly breeding areas.

Importance of mist-netting data

Mist netting is the preferred method of determining the local abundance of these birds, especially in the non-breeding season. In our study areas, censuses alone would not have provided the insight into the two species' abundances and migration. Most censuses are done during the breeding season, as this has been felt to be the time of critical habitat relationships. The breeding season is also the time when *Empidonax* can be identified by song, the most reliable field characteristic. However, the use of only one method in one season would not have identified the complexity of the species' differences nor the importance of the inland river valleys to the Willow Flycatcher. Although it is one of the most common birds netted in our region in the fall, the Willow Flycatcher has almost never been detected on censuses in the region, even by expert censusers (C. J. Ralph, unpubl. data). Additionally, the metrics of age composition cannot be gathered in any other fashion.

TABLE 5. BREEDING SEASON AVERAGE CAPTURES RATES (NUMBER PER 1000 NET-HOURS) OF ADULT (NO YOUNG WERE CAPTURED) WILLOW FLYCATCHERS WITH EACH STATION-SEASON IN A YEAR CONTRIBUTING A DATUM TO THE MEAN OF A REGION

	Adult			
Region	Capture rate	SD	N	Duncan grouping[a]
Coast	0.1	1.6	19	A B C
Redwood	0.1	0.4	19	C
Klamath-Trinity	2.5	2.2	51	A B
Coastal Mountains	0.4	1.0	13	C
Siskiyou	1.3	1.9	40	B C
Rogue	4.6	3.9	6	A
Upper Klamath	1.1	2.1	9	B C
Shasta	1.0	1.7	32	B C
Modoc	0.0	0.0	4	C

[a] Regions not significantly different from others have the same letter.

BREEDING SEASON ABUNDANCE

We have shown that the Pacific-slope Flycatcher is relatively common towards the coast. As Johnson (1980) noted, the Pacific-slope Flycatcher becomes much less common away from the coast, towards and into the suggested range of the very closely-related Cordilleran Flycatcher. Breeding Willow Flycatchers were, by contrast, most common in the far inland areas. They do breed in the far inland Upper Klamath Basin, the only region where adults in breeding condition were captured during the July post-breeding period, and censuses in the area had modest numbers of singing birds (C. J. Ralph, unpubl. data).

SPRING MIGRATION

The two species migrated on quite different schedules. Pacific-slope Flycatchers migrate early (late March into April), as noted by Garrett

TABLE 6. Fall Migration Season Average Captures Rates (Number per 1000 Net-Hours) of Young and Adult Willow Flycatchers with Each Station-Season in a Year Contributing a Datum to the Mean of a Region

	Young				Adult			
Region	Capture rate	SD	N	Duncan grouping[a]	Capture rate	SD	N	Duncan grouping[a]
Coast	1.0	1.0	27	B C	0.1	0.4	27	B
Redwood	0.1	0.3	19	C	0.0	0.0	19	B
Klamath-Trinity	20.5	2.2	50	A	0.4	0.8	50	B
Coastal Mountains	3.6	2.1	13	B	0.0	0.3	13	B
Siskiyou	1.3	3.0	38	B C	0.3	1.1	38	B
Rogue	22.6	1.1	7	A	1.8	1.4	7	A
Upper Klamath	1.0	1.0	13	B C	0.5	0.9	13	A B
Shasta	0.8	1.8	31	C	1.8	3.6	31	A
Modoc	0.0	0.0	4	C	0.0	0.0	4	B

[a] Regions not significantly different from others have the same letter.

and Dunn (1981), Davis et al. (1963), and Ralph (1968). Most have passed through or established in breeding areas in the region by mid-May and June, when most Willow Flycatchers move through. The highest spring capture rates for the Pacific-slope Flycatchers were in the Rogue, Siskiyou, and Coastal Mountain regions, where virtually no breeding birds were captured. This could indicate that the area functions largely for movements of birds to breeding areas to the north.

Post-breeding/Fall Migration

The contrast between the two species is marked in the post-breeding period. In July and early August, we found a pulse of post-breeding adult Pacific-slope Flycatchers, as had been documented by Ralph (1968). After this influx, the adults apparently rapidly left the area. The early departure of adult Pacific-slope Flycatchers is contrary to the assertion of Ralph (1968), based on a single station in coastal central California, where he assumed that adults moved on inland routes, but at the same time, as young. Our present results agree with Johnson (1973), who hypothesized that a preponderance of young in southern California and Arizona was in part due to the faster speed and earlier departure of the adults. Johnson (1973) also demonstrated that adult Pacific-slope Flycatchers are already on the wintering grounds in Mexico by early August, long before the first juveniles. The adult Willow Flycatchers, although being relatively scarce in our study areas, appeared to migrate later and at about the same time as the young. Similarly, Yong and Finch (1997) found adults with only a slight tendency to migrate earlier than young along the Rio Grande in New Mexico.

TABLE 7. The Number and Percent of First Captures and Recaptures in a Year, and The Number Returned in Subsequent Years by Species and Season

	Breeding		Migration	
	N	Percent	N	Percent
Pacific-slope Flycatcher				
First capture	752		853	
Recapture	78	9.0	38	4.2
Return	33	3.8	7	0.8
Total	863		898	
Willow Flycatcher				
First capture	220		1270	
Recapture	0	0.0	23	1.8
Return	0	0.0	0	0.0
Total	220		1293	

The adults and young of most species of landbirds appear to move southward together (Ralph 1981), including western populations of the Willow Flycatcher (from our data) and the Hammond's Flycatcher (*E. hammondii*; Johnson 1970). However, this is not the case for all populations of *Empidonax* flycatchers. Adults migrate earlier than young in the Pacific-slope Flycatcher (in our western regions), and in all four taxa of eastern *Empidonax* in Ontario (Hussell 1991b), including Least Flycatchers (*E. minimus*), Yellow-bellied Flycatchers (*E. flaviventris*), Alder Flycatchers, and (in contrast to our results) the Willow Flycatcher.

Routes Based on Age Ratios and Abundances

The route of migrants can be inferred by two metrics in this study, their relative abundance and age ratios. As hypothesized in Ralph (1981), a high proportion of young could indicate the edge of the route, as misoriented young would be more common away from the center of a route.

Based on abundance, the route of the young Pacific-slope Flycatchers was throughout the study area, especially from the Coast inland to the Klamath-Trinity and Coastal Mountain regions. Since the adults had departed earlier and apparently rapidly, they provided no information on routes from age ratios.

Inferred from abundance, the fall migration route of young and adult Willow Flycatchers is likely through the inland river valleys and to the east, with the age classes together. However, based on age ratios, the main route would appear to be to the east of the study area, as the age ratios were most even in the Upper Klamath Region, and heavily skewed towards young in the inland river valleys and farther west. The great abundance of young in the inland valleys might suggest a difference in route, with the young preferring those valleys, while the adults migrated to the east. However, in the areas with large numbers of adults, we also found large numbers of young, largely precluding a difference in routes of the age classes. Perhaps habitat segregation may occur with adults preferring upland areas.

In both species, the proportion of young in migration was much larger than can be explained by normal reproduction. The preponderance of young, certainly in the case of the Pacific-slope Flycatcher, is likely due to the young delaying migration, perhaps lingering longer as their relative inexperience required longer to provision for their migration south.

TIMING OF MIGRATION

Our fall peak migration of Willow Flycatcher was about August 19 to 28, approximately a week earlier than the midpoint noted in the San Francisco Bay Area (Otahal 1998), as would be expected. However, on the offshore Farallon Islands, at the same latitude as Otahal's study site, the peak of birds was much earlier (in early August), similar to the far inland and farther north Upper Klamath Region. The birds on the Farallones were young birds orienting over the ocean that were forced to fly long distances without stopping, and so arrived farther south and sooner on the inhospitable Farallones. By contrast, birds in the more salubrious inland riparian valleys could linger, building energy stores for their southward migration.

The data from recaptures are difficult to reconcile with this overstaying scenario, as the recapture rate was lower for the Willow Flycatcher than the Pacific-Slope Flycatcher. If Willow Flycatchers were lingering at a site, their recapture rate should be higher than for Pacific-slope Flycatchers, unless (1) both species linger similarly, or (2) Willow Flycatchers move slowly and continuously through the regions. It should be added that these data were not standardized for effort; rather, all captures were pooled because relatively few birds were recaptured, which may obscure patterns. Yong and Finch (1997) also documented little stopover of Willow Flycatchers, with only seven recaptures of 84 migrants, and all within one day of initial capture.

In the Pacific-slope Flycatcher, our peak of migration was late in August or early September. At a coastal site at Point Reyes Bird Observatory, Ralph (1968) found a peak in mid-September of young migrants, indicating a relatively slow transit period of the young.

IMPLICATIONS FOR MANAGEMENT

Young Willow Flycatchers appear to move into and possibly linger in our study area in large numbers during this previously undocumented pre-migration period. It is possible that the riparian systems, both at the lower elevation inland river valleys and the higher elevation meadows, become vital to the survival of the species. In the case of the Pacific-slope Flycatcher, we have also shown that while the adults appear to leave rapidly after breeding, the young also linger in the region prior to their fall migration to the tropics.

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APPENDIX. CONSTANT-EFFORT MIST-NET STATION LOCATIONS, OPERATOR ORGANIZATION, NUMBER OF YEARS SAMPLED, NUMBER OF TEN-DAY PERIODS, AND NUMBER OF CAPTURES OF EACH SPECIES BY REGION

				Number of Captures	
Region and location	Operator	Years sampled	Ten-day periods	Pacific-slope Flycatcher	Willow Flycatcher
Coast					
Cape Blanco, OR	Siskiyou NF (SNF)	1994–1997	26	1	34
Mad River Slough (HOME site), Arcata, CA	Humboldt Bay Bird Observatory	1982–1997	208	347	787
Mad River Slough (PARK site), Arcata, CA	Humboldt Bay Bird Observatory	1992–1997	97	100	155
Navarro River, Mendocino, CA	California State Parks, Mendocino	1997	17	15	20
	Total		348	463	996
Redwood					
Lostman Creek, Orick, CA	Redwood National Park	1993–1995	10	25	32
Mad River, Korbel, CA	Simpson Timber Company	1996–1997	19	24	39
Redwood Creek, Orick, CA	Redwood Sciences Laboratory (RSL)	1994–1997	34	102	73
Wright Refuge, Eureka, CA	Humboldt State University	1993–1997	65	89	0
Van Duzen River, CA	LBJ Enterprises (LBJ)	1997	9	5	9
Yager Creek, Carlotta, CA	Pacific Lumber Company, RSL, LBJ	1994–1997	58	45	64
	Total		194	290	217
Klamath-Trinity					
Seiad Valley, Klamath River, CA	Klamath NF (KNF)	1993–1997	87	148	99
Humbug Creek, Klamath River, CA	KNF	1994	11	0	11
West Humbug Creek, Klamath River, CA	KNF	1995	17	1	20
Whitmore Creek, Orleans, CA	RSL	1992	11	4	11
Ishi Pishi Road, Orleans, CA	RSL	1992–1997	54	32	59
Camp Creek, Orleans, CA	RSL	1992–1997	103	56	118
Red Cap Cr. 7.2 km SW Orleans, CA	RSL	1992–1996	82	40	97
Red Cap Cr. 7.6 km SW Orleans, CA	RSL	1992–1997	101	48	120
Red Cap Rd., 1.5 km SW Orleans, CA	RSL	1992–1997	97	103	118
Red Cap Rd., 2.2 km SW Orleans, CA	RSL	1992–1996	53	27	54
Weitchpec, CA	Six Rivers NF, RSL	1991	7	24	55
Aikens Creek, CA	RSL	1992	11	0	11
Trinity River, Big Bar, CA	Shasta-Trinity NF	1991–1997	87	26	148
	Total		721	509	921
Coastal Mountains					
Grove's Prairie, Denny, CA	RSL	1994–1997	52	33	79
Grouse Creek, Hyampom, CA	RSL	1994	10	4	0
Quail Meadows, Hayfork, CA	RSL	1994–1997	41	74	79
Indian Valley Creek, Hayfork, CA	RSL	1994–1997	41	33	78
	Total		144	144	236

APPENDIX. CONTINUED

				Number of Captures	
Region and location	Operator	Years sampled	Ten-day periods	Pacific-slope Flycatcher	Willow Flycatcher
Siskiyou					
Bear Creek Botanical Area, OR	SNF	1991–1997	57	26	63
Carberry Creek, OR	Rogue River NF (RRNF)	1993–1997	52	5	64
Clear Creek, OR	SNF	1985	6	1	8
Gray Back Creek, OR	SNF	1991–1997	39	25	11
Horse Creek Meadows, OR	SNF	1987–1997	104	97	107
Long Ridge, OR	SNF	1992–1997	40	13	60
White Horse Prairie, OR	SNF	1985	5	6	8
	Total		303	173	321
Rogue					
Applegate River, OR	RRNF	1997	19	5	21
Bear Creek, OR	RRNF	1997	8	0	11
Whetstone Savannah, OR	SNF	1997	15	2	15
Rogue River, Medford, OR	BLM, Medford District	1994–1996	31	41	58
	Total		73	48	105
Upper Klamath					
Williamson River, OR	RSL	1997	6	0	9
Wood River, Upper OR	RSL, BLM, Lakeview District (LVB)	1997	16	1	19
Seven Mile Creek, OR	RSL	1996–1997	25	2	30
Recreation Creek, OR	RSL	1996–1997	25	12	73
Odessa Creek, OR	RSL	1996–1997	25	3	31
Johnson Creek, OR	RSL, LVB	1997	16	2	19
Skeeter Swamp, OR	RRNF	1994–1997	33	19	41
Topsy, Klamath River Canyon, OR	RSL, LVB	1997	1	0	1
	Total		147	39	223
Shasta					
Mile 36, Sacto R.[a] Dunsmuir, CA	Point Reyes Bird Observatory (PRBO)	1993–1996	44	1	44
Prospect, Sacto R. Dunsmuir, CA	PRBO	1993–1996	44	0	44
Soda Creek, Sacto R. Dunsmuir, CA	PRBO	1993–1996	44	10	46
Castella, Sacto R. Dunsmuir, CA	PRBO	1993, 1994, 1996	33	2	33
Conant, Sacto R. Dunsmuir, CA	PRBO	1993, 1994, 1996	40	3	45
Sims Creek, Sacto R. Dunsmuir, CA	PRBO	1993–1996	50	6	54
Pollard Flat, Sacto R. Dunsmuir, CA	PRBO	1993, 1994, 1996	25	1	25

APPENDIX. CONTINUED

Region and location	Operator	Years sampled	Ten-day periods	Number of Captures	
				Pacific-slope Flycatcher	Willow Flycatcher
Dog Creek, Sacto R. Dunsmuir, CA	PRBO	1993, 1994, 1996	32	1	33
Madrone Campground, Squaw Creek, CA	PRBO	1993–1996	42	21	44
	Total		354	45	368
Modoc					
Antelope Creek, Tennant, CA	KNF, RSL	1994–1997	22	2	49

Notes: Abbreviations are: BLM = Bureau of Land Management, NF = National Forest, CA = California, OR = Oregon.

[a] Sacto R. = Sacramento River.

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EFFECTS OF MONOGAMY AND POLYGYNY ON REPRODUCTIVE SUCCESS IN SOUTHWESTERN WILLOW FLYCATCHERS (*EMPIDONAX TRAILLII EXTIMUS*) IN ARIZONA

REBECCA F. DAVIDSON AND LINDA J. ALLISON

Abstract. We analyzed the reproductive consequences of a mixed mating strategy for the endangered Southwestern Willow Flycatcher (*Empidonax traillii extimus*) in central Arizona. We monitored 286 birds in 1998 and 1999; 243 active nests (including renests) were located. Of these, 124 (51%) were built by polygynously paired females. In 1998, 52% of all monitored females and 29% of monitored males were mated polygynously. In 1999, 59% of monitored females and 37% of monitored males were mated polygynously. Because sources of variability in reproductive success can be crucial in understanding the ability of endangered species to maintain stable or increasing populations, we examined whether mating status affected the probability of fledging one or more young or the number of young fledged. For females, none of our measures of reproductive success differed as a function of mating tactic; instead, female annual success showed significant between-year variability. The odds of a polygynous male fledging at least one young were 17.8 times greater than for monogamous males, and polygynous males fledged more young over the breeding season than did monogamous males. We interpret this difference as a simple function of the number of mates and/or nesting attempts, since average number of young per nest did not differ between monogamous and polygynous males. Mixed mating tactics also affect our ability to estimate population size of breeding adults. If polygyny occurs range wide, and at higher rates than previously suspected, simple use of male territorial song (assuming one female with every male) to estimate the number of birds at a site will underestimate population size.

Key Words: Empidonax traillii extimus; fledging success; mating systems; polygyny; reproduction; Southwestern Willow Flycatcher.

There is continuing development and elaboration of models to describe the evolution and maintenance of both monogamy and polygyny within single populations of birds (Verner and Willson 1966, Orians 1969, Emlen and Oring 1977, Searcy and Yasukawa 1989, Petit 1991, Soukup and Thompson 1997a, Johnson and Burley 1998). These models are built on the theory that mating systems are structured by male-male and female-female competition for resources and mates (Kempenaers 1995). The relative importance of intra-sexual competition depends on environmental features such as resource availability, quality, and distribution (Verner and Willson 1966), and on adult sex ratio (Smith et al. 1982). The mating system of a particular species is comprised of tactics that birds use under different situations (Johnson and Burley 1998). Here, we refer to polygynous and monogamous nesting as separate tactics.

Polygyny is generally assumed to be advantageous to males because polygynous males have the potential to produce more fledglings each breeding season (Wheelwright et al. 1992, Soukup and Thompson 1997b, Parish and Coulson 1998, Lubjuhn et al. 2000) and more recruits to future breeding populations (Carey and Nolan 1975, Soukup and Thompson 1997b). However, fitness consequences or trade-offs for females can be more difficult to assess (Smith et al. 1982, Bart and Tornes 1989, Petit 1991, Wheelwright et al. 1992, Bensch 1996, Soukup and Thompson 1997a). Females may pair with an already mated male if male parental care contributes relatively little toward fledging success (Bart and Tornes 1989, Webster 1991, Parish and Coulson 1998), if territories of polygynous males contain higher quality habitat (Verner and Willson 1966, Orians 1969), if females are unable to discern pair status (Searcy and Yasukawa 1989), and/or if the genetic quality of the male is greater than that of unpaired males (Verner and Willson 1966, Soukup and Thompson 1997b, Slagsvold and Drevon 1999).

The Willow Flycatcher (*Empidonax traillii*) is considered a typically monogamous species (Sedgwick 2000), although polygyny has been reported in Canada (Prescott 1986), north-central Colorado and southeastern Oregon (Sedgwick and Knopf 1989, Sedgwick 2000), southern California (Whitfield et al. 1998), and on the lower Colorado River in Arizona and California (McKernan and Braden 2001). Within these populations, polygyny rates have been documented as high as 15% in Oregon, 50% in southern California (Sedgwick 2000), and 10% on the lower Colorado River (McKernan and Braden 2001).

To describe breeding status and reproductive consequences for monogamous and polygynous Southwestern Willow Flycatchers (*E. t. extimus*) in central Arizona, we compared their fledging

TABLE 1. Annual Mating Tactic Information for Southwestern Willow Flycatchers in Central Arizona

	1998			1999		
	San Pedro	Roosevelt	Combined	San Pedro	Roosevelt	Combined
Females						
Total	35	31	66	52	43	95
Monogamous	13 (37%)	19 (61%)	32 (48%)	15 (29%)	24 (56%)	43 (41%)
Polygynous	22 (63%)	12 (39%)	34 (52%)	37 (71%)	19 (44%)	56 (59%)
Males						
Total	26	28	54	35	34	69
Monogamous	13 (50%)	19 (68%)	32 (59%)	15 (43%)	23 (68%)	38 (55%)
Polygynous	10 (38%)	6 (21%)	16 (30%)	17 (48%)	9 (26%)	26 (38%)
Unmated	3 (12%)	3 (11%)	6 (11%)	3 (9%)	2 (6%)	5 (7%)
Active nests produced						
Total	63	43	106	79	58	137
By monogamous females	28 (24%)	29 (67%)	57 (54%)	27 (33%)	35 (60%)	62 (47%)
By polygynous females	35 (76%)	14 (33%)	49 (46%)	52 (66%)	23 (40%)	75 (53%)
Fledglings produced						
Total	92	70	162	93	76	169
By monogamous females	38 (41%)	40 (53%)	78 (48%)	33 (35%)	46 (61%)	79 (47%)
By polygynous females	54 (59%)	30 (43%)	84 (52%)	60 (65%)	30 (39%)	90 (53%)

success (probability of fledging one or more young), and the number of fledglings per nest and per breeding season. We also examined whether these measures of reproductive success differed between two breeding areas during the two years of the study.

METHODS

Data were collected during the breeding seasons of 1998 and 1999 as part of ongoing studies conducted at Roosevelt Lake (at the Salt River and Tonto Creek inflows) and the San Pedro and Gila Rivers (near the town of Winkelman), two of the largest Southwestern Willow Flycatcher breeding areas in Arizona (Paradzick and Woodward *this volume*). Cowbird trapping has been conducted within our study sites since 1996, and brood parasitism was < 1% in 1998 and 1999 (Paradzick et al. 1999, 2000). Vegetation in the study areas was comprised of varying proportions of native and exotic flora including saltcedar (*Tamarix ramosissima*), Goodding willow (*Salix gooddingii*), Fremont cottonwood (*Populus fremontii*), seepwillow (*Baccharis salicifolia*), and mesquite (*Prosopis* spp.).

Territorial males arriving on the breeding grounds were first located in late-April to early-May. As females began arriving in early-May, we followed pairing activities closely and conducted nest searches from mid-May through August. We monitored nests every two to four days following Rourke et al. (1999) and a modification of Martin et al. (1997). All nests in which at least one egg was laid were considered active.

A nest was defined as successful when one of four conditions were met: (1) one or more young were visually confirmed fledging from the nest or were located near the nest; (2) color banded adult flycatchers were seen feeding fledglings; (3) parents behaved as if dependent young were nearby when the nest was empty; and (4) nestlings were observed in the nest within two

TABLE 2. Nest Success of Monogamous and Polygynous Southwestern Willow Flycatchers in Central Arizona, 1998–1999

	Total	Monogamous	Polygynous
Active nests monitored	243	119	124
Successful nests (fledged ≥1 young)	138 (57%)	66 (55%)	72 (58%)
Unsuccessful nests	105 (43%)	53 (45%)	52 (42%)
Females	161	71	90
Successful (fledged ≥1 young season)	118 (73%)	52 (73%)	66 (73%)
Proportion of nests successful	0.61 ± 0.4 SD	0.65 ± 0.4 SD	0.58 ± 0.4 SD
Males	112	70	42
Successful (fledged ≥1 young season)	91 (81%)	50 (71%)	41 (98%)
Proportion of nests successful	0.61 ± 0.4 SD	0.63 ± 0.4 SD	0.58 ± 0.3 SD

TABLE 3. ODDS RATIOS OF THE LOGISTIC REGRESSION MODEL DESCRIBING FACTORS ASSOCIATED WITH FLEDGING SUCCESS (THE PROBABILITY OF FLEDGING ONE OR MORE YOUNG PER SEASON) OF SOUTHWESTERN WILLOW FLYCATCHERS IN CENTRAL ARIZONA IN 1998 AND 1999

			Males			Females		
Factor	Baseline category (1)	Comparison category (2)	N (1)/(2)	Odds ratio for (2) vs. (1)	95% CI	N (1)/(2)	Odds ratio for (2) vs. (1)	95% CI
Mating tactic	Monogamy	Polygyny	70/42	17.8	2.2–141.7	71/90	1.1	0.5–2.3
Area	Winkelman	Roosevelt	55/57	0.4	0.1–1.1	87/74	1.1	0.5–2.3
Year	1998	1999	48/64	0.8	0.3–2.4	66/95	0.5	0.2–0.98

Notes: Analyses considered all nests for each male or female that successfully hatched young, including re-nests. Odds ratios describe the proportional change in the odds for every unit change in the variable, so odds of success for polygynous males were 17.8 times higher than for monogamous males. Odds of success for females in 1998 were two times (= 1/0.5) greater than in 1999. If the confidence interval for an odds ratio estimate includes 1, that variable is not associated with annual success ($\alpha = 0.05$).

days of the estimated fledge date. Nests not meeting these criteria, or from which eggs or nestlings were missing before hatch/fledgling dates, were considered unsuccessful. Similar criteria have been used in other studies (Conner et al. 1986, Patnode and White 1992, Martin et al. 1997, Drobney et al. 1998, Clotfelter and Yasukawa 1999). For each successful nest, we determined the number of young fledged.

Adult flycatchers were captured (per Sogge et al. 2001) and uniquely color banded by the U.S. Geological Survey. Throughout the breeding season, we confirmed the color band combination of each bird through multiple field observations by multiple observers, enabling us to describe pairing and breeding activities in each territory.

DESCRIBING MATING TACTICS

We defined monogamy as a mating tactic in which both male and female were mated to a single individual at any one time during the breeding season (Ford 1983, Møller 1986). Males were polygynous if more than one female nested simultaneously in the male's territory; females that mated with a polygynous male were also classified as polygynous. We identified each bird's mating tactic based on pair interactions, feeding behaviors, and nest placement within territories. Unbanded males and males with unconfirmed color bands were excluded from analyses along with their mates, because their mating tactic could not be determined. We were, however, able to determine mating tactic for many unbanded or unconfirmed females. Provided that their mates were banded, female mating tactic could be determined through observation of male interactions with females (or associated nests), and the combination of two or more nests found active concurrently within the same male's territory.

STATISTICAL ANALYSES

The large number of failed nests (usually late in the nesting cycle) resulted in a non-normal distribution for the number of fledged young per nest and adult. Therefore, in addition to calculating average productivity per nest and per breeding season for each sex and mating tactic, we proceeded through a series of hypothesis tests based on only successful nests to describe different components of productivity and their association with mating tactic. Activities of the same female or male in different years were treated as independent. All statistical tests were performed using SPSS for Windows (2000). ANOVA and logistic regression models were built starting with main effects and all possible interaction terms. Interaction terms with the largest non-significant ($\alpha = 0.05$) P-values were removed from the model sequentially; all main effects were retained in the iterative and final models. Each time, the model was rebuilt before evaluating statistical significance of the remaining interaction terms.

We used logistic regression to test whether nesting area (Roosevelt vs. Winkelman) or mating tactic was associated with fledging success (having at least one fledgling in a season), generating separate models for females and males, and including year as a blocking factor to account for between-year variability. Overall model fit was evaluated using the biserial correlation (Pearson's R; Pampel 2000) between observed and predicted success. We used the resulting odds ratios to estimate effect sizes on nesting success (Hosmer and Lemeshow 1989). We also calculated the proportion of nesting attempts that were successful, and used Fisher's Exact Test to examine whether the proportion of successful nests was independent of mating tactic.

To examine possible differences in the way mating tactic affects the ability of adults to maximize young fledged from otherwise intact nests (e.g., through parental care), we included only successful nests in our hypothesis test of factors related to number of young fledged per nest. We applied Fisher's Exact Test to the contingency table of number of young fledged by each adult using the two mating tactics over all nesting attempts in the breeding season. In the case of a significant hypothesis test, we interpreted the standardized residuals to describe how the distributions differed.

RESULTS

Seventy-five percent (286 of 380) of birds found within the nest monitoring sites in both 1998 and 1999 were included in these analyses based on color band identification and pairing confirmations. There were 112 mated, territorial, banded males (16 were monitored in both years); 80 of their 161 mates were banded (11 of which were monitored in both years). In both years, more than half of monitored females were mated with a polygynous male, and roughly one-third of males were polygynous (Table 1). Each year, some monitored males remained unpaired

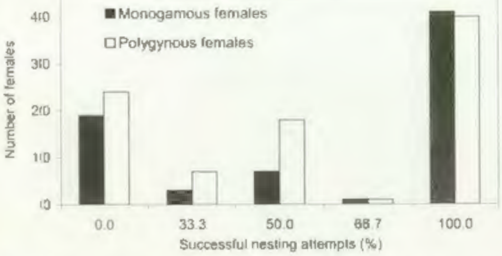

FIGURE 1. The number of monogamous and polygynous female Southwestern Willow Flycatchers experiencing different percentages of successful nesting attempts (i.e., nest fledged at least one young) in central Arizona, 1998–1999. Maximum number of nesting attempts = 3.

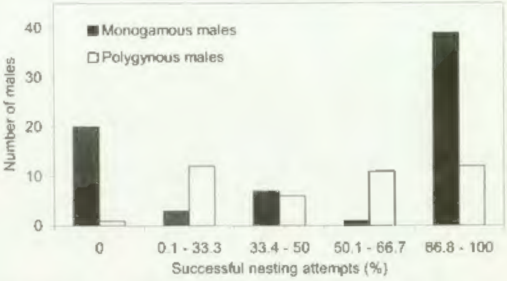

FIGURE 2. The number of monogamous and polygynous male Southwestern Willow Flycatchers experiencing different percentages of successful nesting attempts (i.e., nest fledged at least one young) in central Arizona, 1998–1999. Maximum number of nesting attempts = 7.

for the entire breeding season (Table 1). We located 243 active nests, of which 124 were built by polygynous females. At the San Pedro River, the majority of nests and fledglings were produced by polygynous females; at Roosevelt Lake, monogamous females built more of the nests and raised the majority of the fledglings (Table 1).

FLEDGING SUCCESS

Of the 243 active nests, 188 (77%) reached the nestling stage and 138 (57%) successfully fledged at least one bird. The majority of nests from both monogamous and polygynous matings were successful. Most (83 of 105) unsuccessful nests were attributed to predation.

Seventy-three percent of females fledged at least one young during the breeding season (Table 2). The logistic regression model did not indicate differences in fledging success between monogamous and polygynous females (χ^2 = 4.40, df = 3, P = 0.221; biserial correlation coefficient = 0.162; Table 3). Within each mating tactic, the proportion of successful nesting attempts did not differ by year or study area, so data were combined for testing differences by mating tactic. Monogamous females and polygynous females did not differ in expected nesting success (proportion of nesting attempts that were successful; Fisher's Exact Test, P = 0.266; Fig. 1; Table 2).

Eighty-one percent of males fledged at least one young during the breeding season (Table 2). The logistic regression model with main effects alone fit the data (χ^2 = 18.391, df = 3, P < 0.0005; biserial correlation coefficient = 0.371; Table 3) and no interaction effects were statistically significant. Polygynous males increased their odds of fledgling at least one young per season almost 18-fold over monogamous males (Table 3). Within each mating tactic, the proportion of successful nesting attempts did not differ by year or study area, so data were combined for testing differences by mating tactic. Despite the larger proportion of monogamous males that failed to fledge young, the proportion of successful nesting attempts was higher for monogamous than polygynous males (Fisher's Exact Test, P < 0.001; Table 2). Examination of standardized residuals indicated that polygynous males were much less likely to fail completely or to fledge young from all of their nests (Fig. 2).

PRODUCTIVITY

We confirmed the number of fledglings at 241 of the 243 monitored nests. Overall, 1.4 ± 0.09 SE (N = 241) young fledged per nest. Mating tactic was not significantly associated with per-nest productivity of successful females (Table 4), and successful monogamous and polygynous females had similar annual productivity (Table 5; Fig. 3). Productivity per nest was similar between monogamous and polygynous males. Although the pattern of differences depended on study year, annual productivity was consistently higher for polygynous males (Table 6). Among successful males, average number of fledglings at successful nests did not differ between mating tactics (Tables 4 and 6), but annual productivity was greater for polygynous males (Fisher's Exact Test, P <0.005 in 1998, P = 0.005 in 1999; Fig. 4).

DISCUSSION

The polygyny rates we documented were higher than reported for other Willow Flycatcher studies (Sedgwick 2000, McKernan and Braden 2001), but were comparable with those reported in southern California (Whitfield et al. 1998). Approximately half of our female population was associated with polygynous males each

TABLE 4. RESULTS OF ANOVA MODELS TESTING FOR DIFFERENCES IN AVERAGE NUMBER OF FLEDGLINGS PER SUCCESSFUL NEST FOR SOUTHWESTERN WILLOW FLYCATCHERS IN CENTRAL ARIZONA IN 1998 AND 1999

	Males				Females			
Source	df	Mean square	F	P	df	Mean square	F	P
Mating tactic	1	0.020	0.039	0.847	1	0.002	0.004	0.953
Area	1	<0.0005	0.001	0.976	1	0.018	0.030	0.862
Year	1	0.070	0.137	0.712	1	0.898	1.53	0.218
Error	86	0.511			112	0.586		

year; therefore, the notion that Willow Flycatchers are largely monogamous should be reconsidered and better quantified in future studies. We found the likelihood of a female fledging at least one young over the season was independent of whether her mate was monogamous or polygynous. Instead, fledging success varied significantly from year to year (P = 0.043; Table 3), apparently as a function of causes other than mating system (e.g., nest predation, habitat quality, weather).

Because neither mating tactic affected female fledging success or productivity over the breeding season, there may be no strong selection for females to pursue a particular strategy at our study sites. Rather, females can apparently choose to be more flexible in their mating tactic, perhaps due to an inability to predict a male's paternal care (Wheelwright et al. 1992) and/or a poor correlation between a male's mating tactic and his assistance at the nest (Ettinger and King 1980, Slagsvold and Drevon 1999, Sedgwick 2000). If male parental care is minimal, and level of care is unpredictable (Sedgwick 2000), then males that occupy territories with better habitat, food supply, and nest sites may be more likely to attract multiple mates (Verner and Willson 1966, Soukup and Thompson 1997b, Slagsvold and Drevon 1999). The presence of unpaired territorial males during both breeding seasons suggests that females may choose among males and/or their territories (Bensch and Hasselquist 1992).

We found that fledging success (the probability of fledging one or more young) for males was improved for the breeding season by mating with more than one female, which is consistent with other studies (Smith et al. 1982, Wheelright et al. 1992, Kempenaers 1995, Soukup and Thompson 1997b, Lubjuhn et al. 2000). Polygynous males also fledged more young over the entire breeding season than did monogamous males. The pattern of differences was not the same across study years, however. In 1998, some polygynous males fledged up to nine young, compared to only four for monogamous males. In 1999, the maximum that were fledged was similar for the two mating tactics, but more monogamous males failed to fledge any young. Thus, the productivity of monogamous males appears to be more uncertain than that of polygynous males, for which multiple-mating decreases the odds of complete reproductive failure. Monogamous males had slightly higher per-nest success. In other avian species, monogamous and polygynous male tactics can include a trade-off, whereby polygynous males reduce parental care to acquire extra mates, even if it results in lower survival of nestlings per nest (Webster 1991, Soukup and Thompson 1997b). Unfortunately, comparative data are lacking on parental care by monogamous and polygynous male Willow Flycatchers. Ultimately, true reproductive success of both polygynous and monogamous males could be affected by factors that were not part of our study, such as extra-pair copulations and rates of offspring survival to breeding age.

Through analyses of only successful nests, we sought to determine if mating tactic influenced per-nest and/or annual productivity in nests that were not lost to predation or other factors. Such differences in productivity could arise through

TABLE 5. PRODUCTIVITY (PER NEST AND ANNUAL) OF FEMALE SOUTHWESTERN WILLOW FLYCATCHERS IN CENTRAL ARIZONA, 1998–1999

	Productivity per nest						Annual productivity	
	All nests of all females			Successful nests of successful females			All females	
Tactic	$\bar{x}$	95% CI	N	$\bar{x}$	95% CI	N	$\bar{x}$	95% CI
Polygyny	1.5	1.2–1.7	90	2.5	2.3–2.7	66	2.2	1.8–2.5
Monogamy	1.6	1.3–1.9	71	2.5	2.3–2.7	52	2.1	1.7–2.5

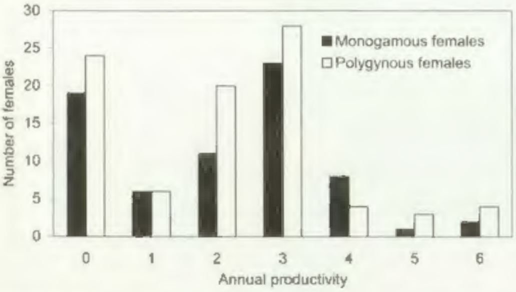

FIGURE 3. Annual productivity (total number of young fledged) for monogamous and polygynous female Southwestern Willow Flycatcher in central Arizona, 1998–1999.

differences in how monogamous and polygynous parents provide nestling care and/or protect against partial clutch losses (such as cowbird parasitism). However, neither male or female mating tactic significantly affected the number of fledglings per successful nest. Examining all nests (successful and unsuccessful), we also found that mating tactic did not influence the likelihood of a female failing to fledge young. Taken together, the lack of mating tactics effects suggest that male flycatchers may not play a major role in hatching or fledging of young. The same may not be true in other populations, especially where cowbird parasitism is more common and male nest defense therefore more important in deterring parasitism.

We found that the San Pedro River had higher rates of polygyny than Roosevelt Lake, and a sex ratio more strongly biased towards females. A more strongly biased sex ratio (Smith et al. 1982), as well as the distribution and quality of resources (Verner and Willson 1966, Emlen and Oring 1977), could influence an individual's mating tactic and therefore explain the differences in rates of polygyny between our study areas.

MANAGEMENT IMPLICATIONS

We do not know whether the high polygyny rates within our study areas are typical for the southwestern subspecies, or if they represent an adaptive strategy for members of a population

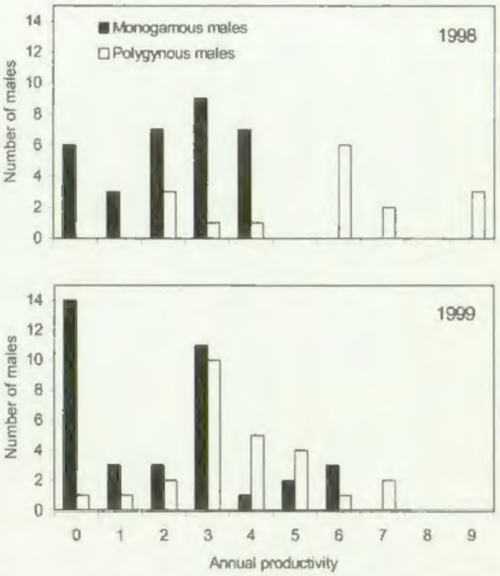

FIGURE 4. Annual productivity (total number of young fledged) for monogamous and polygynous male Southwestern Willow Flycatcher in central Arizona, 1998 and 1999.

in decline (Kunin and Gaston 1993). Polygyny may be advantageous for declining populations because within small populations of passerines, strictly monogamous species are more likely to suffer extirpation (Legendre et al. 1999). However, polygyny also results in lower effective population sizes (Nunney 1993), which may place endangered species in further genetic jeopardy. Small populations are also more likely to experienced unbalanced sex ratios, which could force some females to become polygynous despite any negative reproductive costs.

Considering the rates of polygyny that we documented, efforts to estimate the number of breeding flycatchers may be confounded by polygynous breeding and by fluctuating rates of polygyny from year to year. At our study sites, for example, surveyors assuming that each singing male represented only a breeding pair would have substantially underestimated the number of birds present. Underestimates would have been

TABLE 6. PRODUCTIVITY (PER NEST AND ANNUAL) OF MALE SOUTHWESTERN WILLOW FLYCATCHERS IN CENTRAL ARIZONA, 1998–1999

	Productivity per nest						Annual productivity					
	All males			Successful nests only			All males in 1998			All males in 1999		
Tactic	$\bar{X}$	95% CI	N	$\bar{X}$	95% CI	N	$\bar{X}$	95% CI	N	$\bar{X}$	95% CI	N
Polygyny	1.5	1.3–1.8	42	2.5	2.3–2.7	41	5.6	4.3–6.9	16	3.7	3.0–4.3	26
Monogamy	1.6	1.3–1.9	70	2.5	2.2–2.7	49	2.2	1.7–2.8	32	2.0	1.3–2.7	38

more extreme at San Pedro (21% in 1998; 24% in 1999) than at Roosevelt (11% in 1998, 15% in 1999). Such site-specific differences in estimate errors are troubling, and demonstrate that estimates of the total number of flycatchers should not be based on singing males alone; accurate estimates require information on the number of nesting females as well. Between-site differences in levels of polygyny could exacerbate difficulties in comparing flycatcher counts among sites, if those counts are based only on singing males.

It is possible that longer-term studies may reveal more subtle effects of mating tactic on reproductive success of Southwestern Willow Flycatchers. As recovery efforts for this flycatcher continue, a better understanding of mating tactics and associated ramifications could prove important when evaluating the stability of populations into the future.

ACKNOWLEDGMENTS

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SINGING BEHAVIOR OF SOUTHWESTERN WILLOW FLYCATCHERS IN ARIZONA

HELEN K. YARD AND BRYAN T. BROWN

Abstract. We studied the singing behavior of a small population of Southwestern Willow Flycatchers (*Empidonax traillii extimus*) along the Verde River in central Arizona from May–August, 1996–1998. Our objectives were to document patterns of daily and seasonal song rates and to evaluate sex differences. Most *fitz-bew* songs were given from perches, as only 2% of male songs and 7% of female songs were given in flight. Males were never detected singing from or within 2 m of nests, but females occasionally sang from or near nests. Rates of male *fitz-bew* song appeared greatest during courtship/nest-building; female song rates appeared greatest during incubation. Rates of male *fitz-bew* song during morning and midday appeared similar, but both appeared greater than evening; female song rates also appeared to differ, with morning > midday > evening. Mean rates of *fitz-bew* song for all years, nesting phases, and times combined appeared similar between sexes. Females gave an adjusted 20% of all *fitz-bew* songs detected (four male songs for each female song). Male rates of *creet* song appeared greater during both courtship/nest-building and incubation than during both nestling and post-fledging phases, while female rates did not appear to differ by nesting phase. Male rates of *creet* song appeared greater in morning than evening, while female rates of *creet* song appeared greater during midday than evening. Determination of sex and estimation of population size based solely on singing behavior should be considered unreliable for this subspecies.

Key Words: Arizona; behavior; *Empidonax traillii extimus;* riparian; song; Southwestern Willow Flycatcher; Verde River; vocal behavior.

Passerine song functions to attract mates, establish and defend territories, maintain pair bonds, and initiate other breeding phenomena (Catchpole and Slater 1995, Kroodsma and Miller 1996). Song rates in particular can provide information on the status of the singer (Staicer 1989), the presence of potential predators (Preston et al. 1998), and nest-site quality (Hoi-Leitner et al. 1995). Quantitative evaluations of singing behavior and song rates can be useful in addressing management concerns about parameters such as the potential influence of human intrusion (Gutzwiller et al. 1994, 1997) and determining the relative accuracy of auditory survey protocols (McShea and Rappole 1997), yet this information does not exist for most bird species.

The advertising-song performance of the Willow Flycatcher (*Empidonax traillii*) consists of a variable sequence of three vocalizations: *fitz-bew*, a similar *fizz-bew*, and *creet* (Kroodsma 1984, Sedgwick 2000). Where singing behavior and sex have been correlated through observations of color-banded individuals, males produce most songs (Sedgwick 2000). Females have been reported to sing uncommonly (Seutin 1987) to regularly (Sogge 2000), but quantitative data on female song are lacking. The only evidence of daily or seasonal differences in song frequency is qualitative (e.g., McCabe 1991, Sedgwick 2000, Sogge 2000b).

We studied the singing behavior of a small population (≤20 individuals) of the endangered Southwestern Willow Flycatcher (*E. t. extimus*) to document this little-known aspect of its natural history. Our objectives were to describe some aspects of singing behavior, investigate patterns of daily and seasonal song rates, evaluate sex differences in singing behavior, and discuss the implications of these findings with respect to determining sex and estimating breeding population size during field surveys. More information on the singing behavior of Southwestern Willow Flycatchers would be of value because the current protocol for presence-absence surveys relies primarily on vocal detection techniques (Sogge et al. 1997a,b).

METHODS

Our study was conducted at Camp Verde, central Arizona, along the Verde River (elevation ca. 1070 m), a perennial stream in a broad floodplain. The river at our site exhibited several small braided channels, and discharge from an irrigation ditch periodically caused standing water to occur in low-lying areas. Beaver (*Castor canadensis*) activity resulted in occasional inundation of part of the site. Riparian vegetation was dominated by discrete patches of native gallery forest composed of Fremont cottonwood (*Populus fremontii*) and Goodding willow (*Salix gooddingii*) which formed a discontinuous canopy up to ca. 22 m in height. Dense stands of non-native saltcedar (*Tamarix ramosissima*) up to 8 m in height occurred both as understory associated with gallery forest and as discrete patches between stands of gallery forest. Other associated vegetation included *Baccharis* spp., boxelder (*Acer negundo*), netleaf hackberry (*Celtis reticulata*), and honey mesquite (*Prosopis glandulosa*). The site received regular, but apparently low, use by livestock, hikers, bird-

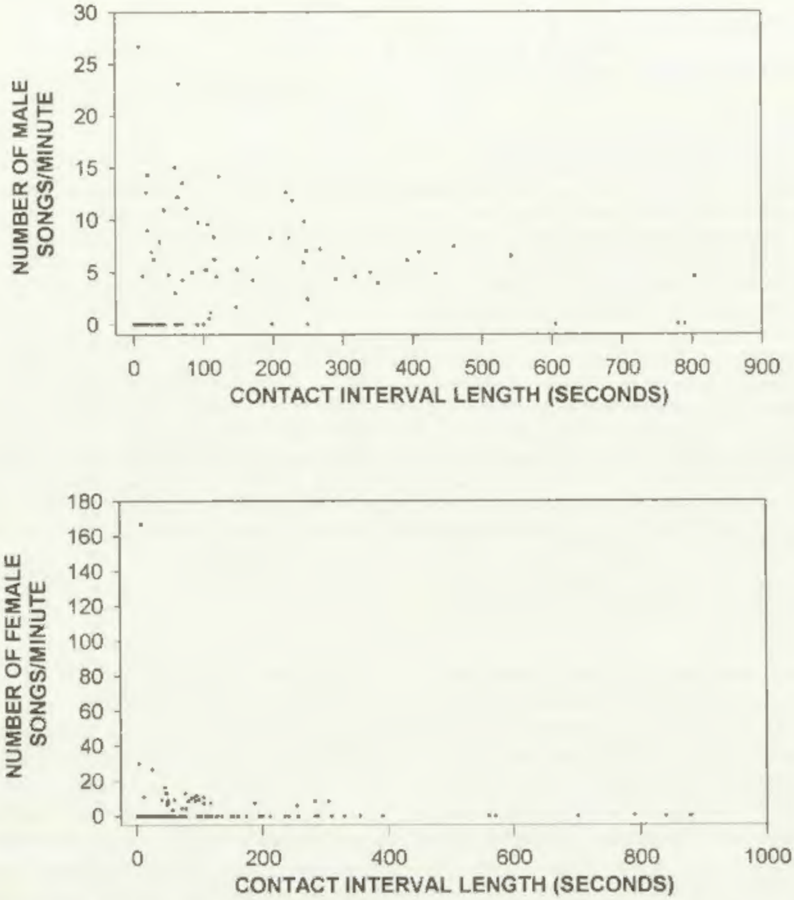

FIGURE 1. Number of songs/min by contact interval length, for male (top) and female (bottom) Southwestern Willow Flycatchers at Camp Verde, Arizona, May–August, 1996–1998.

watchers, fishermen, all-terrain-vehicle enthusiasts, and others.

The focal-animal continuous-observation technique (Bradley 1985) was used to sample singing behavior from mid-May through early August, 1996–1998. Vocalizations of flycatchers visible to observers were recorded during 15-min sample intervals (with few exceptions) occurring from 0500 to 2045 hrs (Mountain Standard Time), for up to four days/week. Contact intervals, in contrast, were those times during the sample interval when potentially singing flycatchers were actually in sight. Observers attempted to keep potentially singing flycatchers in sight throughout the sample interval; most observations were made from approximately 20–30 m.

We recorded the following variables for each song event: date and time, band color-combination, location (in nest, within 2 m of nest, or > 2 m from nest), position of individual (perched or in air/flight), and song type (*fitz-bew* or *creet*). Our "*fitz-bew*" song type included both *fitz-* and *fizz-bews,* which are difficult to differentiate in the field. Both are given at our study site, with *fitz-bews* given about twice as often as *fizz-bews* (Sedgwick 2000; J. Sedgwick, pers. comm.). We selected 2 m for our nest proximity threshold because preliminary observations suggested very little flycatcher activity not directly related to maintenance of the nest or eggs/young (i.e., foraging, perching, singing, vigilance) took place within this distance. We were simultaneously monitoring flycatcher nest and territory locations, nesting activity, population dynamics, and other behaviors, which were the source of our information on banded birds and nesting phase (H. Yard and B. Brown, unpubl. data). Sex was determined for individually color-banded birds by brood patch (females) and cloacal protuberance (males), and by a genetic technique (Busch et al. 2000). Unbanded birds, birds whose band color-combinations could not be accurately determined, and birds for which both the physical examination and genetic techniques failed to precisely identify sex were categorized as unknown sex.

Scatter plots of male and female *fitz-bew* songs/min by contact interval length were made to evaluate visibility bias (Fig. 1). We defined visibility bias as the brief observation of an individual (<5 sec) during which several songs were uttered in quick succession. Subsequent conversion to songs/min would produce

TABLE 1. SOUTHWESTERN WILLOW FLYCATCHER SONG TYPES BY SEX AND LOCATION FOR ALL COMBINATIONS OF NESTING PHASE AND TIME OF DAY, CAMP VERDE, ARIZONA, MAY–AUGUST, 1996–1998

	Number of male songs (452.2 contact min)				Number of female songs (920.2 contact min)				
Song type	Perched >2 m from nest	Perched on or <2 m from nest	In air	Total	Perched >2 m from nest	Perched on or <2 m from nest	In air	Total	Total
Fitz-bew	1,225	0	23	1,248	560	40	45	645	1,893
Creet	257	0	8	265	147	8	15	170	435
Total	1,482	0	31	1,513	707	48	60	815	2,328

inflated values for these observations, which were not produced during longer contact intervals. Visual inspection of outliers revealed no apparent bias in rates of male song and only one instance of female bias, which was eliminated from further analysis.

We compared song rates (i.e., frequencies) by nesting phase (courtship/nest-building, egg-laying/incubation, nestling, and post-fledging) and time of day (morning, 0500–0959 hrs; midday, 1000–1459 hrs; and evening, 1500–2045 hrs). Song rates were calculated by computing songs/min over all contact periods, not just those in which songs were observed. Statistical tests for differences between and within parameters have not been presented due to serious concerns regarding pseudoreplication. Most individuals were sampled multiple times within years, resulting in a lack of independence between observations. All years were combined for analysis to maximize sample sizes for comparison, which further compounded pseudoreplication because some individuals were present and sampled in >1 year. Therefore, different mean values between or within sampled variables have been described as "apparently different." Data summaries and song rates were calculated using SPSS software (Norusis 1993). Some sample sizes differed due to missing data.

RESULTS

Nineteen flycatchers were banded and their sex determined from 1996–1998; song data were gathered on 18 of these during 723 sample intervals for a mean of 40 intervals/individual (SD = 41, range = 1–141, median = 24). Three individuals were present and sampled in both 1996 and 1997, seven in 1997 and 1998, and one individual in all three years.

Most *fitz-bew* songs given by males and females were from perches. Of all male songs detected, 2% were given in flight; 7% of all female songs were given in flight (Table 1). Aerial song by males, females, or individuals of unknown sex occurred throughout the nesting season. No male *fitz-bew* songs and only 6% of female songs were given on or <2 m from nests (Table 1), so all following rates of male and female song were calculated for those given from perches >2 m from nests (males: N = 1225 songs, females: N = 560 songs).

Male and female *fitz-bew* songs were detected in 66% (N = 96) and 46% (N = 76), respectively, of total contact intervals of perched individuals >2 m from active nests for which nesting phase and time of day was known. Males and females uttered 1–20 songs during 41% and 37% of total contact intervals, respectively, and gave ≥21 songs during 25% and 9% of intervals, respectively. Most (71%) of the total (N = 66) female song bouts occurred earlier in the nesting season, during either May or June (Table 2).

Mean rates of male *fitz-bew* song appeared to differ between nesting phases, with the greatest difference in means between courtship/nest-building (Table 3) and nestling phases. Mean rates of female song also appeared to differ by nesting phase, with egg-laying/incubation and post-fledging both noticeably greater than courtship/nest-building or nestling phases (Table 3). Mean rates of male *fitz-bew* song by time of day appeared to differ between morning/midday and evening (Table 4). Mean female song rates also appeared different by time of day, with morning > midday > evening (Table 4).

TABLE 2. NUMBERS OF FEMALE SOUTHWESTERN WILLOW FLYCATCHER *FITZ-BEW* SONG BOUTS OBSERVED AT ALL LOCATIONS BY MONTH AND NESTING STAGE, CAMP VERDE, ARIZONA, MAY–AUGUST, 1996–1998

Nesting phase	May	June	July	August	Total
Courtship/nest-building	2	1	1	0	4
Egg-laying/incubation	0	25	4	1	30
Nestling	0	1	6	0	7
Post-fledging	0	0	5	0	5
Unknown	18	0	2	0	20
Total	20	27	18	1	66

TABLE 3. MEANS ($\bar{X}$), STANDARD DEVIATIONS (SD), AND SAMPLE SIZES (N = NUMBER OF CONTACT INTERVALS) FOR SOUTHWESTERN WILLOW FLYCATCHER *FITZ-BEW* SONGS/MIN BY SEX AND NESTING PHASE, CAMP VERDE, ARIZONA, MAY–AUGUST, 1996–1998

	Male songs/min				Female songs/min			
Nesting phase	N	$\bar{X}$	SD	Range	N	$\bar{X}$	SD	Range
Courtship/nest-building	29	5.2	6.3	0–27	5	0.1	0.2	0–0.5
Egg-laying/incubation	46	2.1	5.3	0–30	54	2.3	4.0	0–16
Nestling	18	0.1	0.2	0–1	79	0	0	0
Post-fledging	15	2.2	4.7	0–15	45	0.5	2.1	0–12
Total	108	2.6	5.3	0–30	183	0.8	2.6	0–16

Mean (± SD) *fitz-bew* song rates for males (2.9 ± 5.2; Table 4) and females (1.4 ± 4.0) appeared similar when perched individuals >2 m from nests were compared. However, males sang during a greater proportion of their contact intervals than females, and produced a greater overall number of songs than females despite their contact time of <50% that of females (Tables 1 and 4). Female contact time was 2.035 times more than male contact time when all locations, times of day, and nesting phases were combined (Table 1). To correct for discrepancies in contact time by sex, we multiplied the total number of male songs (N = 1248) by 2.035. This resulted in 645 female songs and an adjusted 2540 male songs, for a total of 3185 songs by individuals of known sex. Females gave an adjusted 20% of all *fitz-bew* songs detected, or, males gave an adjusted four songs for each female song.

Males gave the *creet* song 3.6 times more than females when the abundance of this call was corrected for overall contact minutes by sex (Table 1; songs >2 m from nest). Males were never observed giving this song from or near nests, but females occasionally gave it from nests (Table 1). Both sexes gave this song in flight on rare occasions (Table 1).

Male *creet* song was relatively common during courtship/nest-building and egg-laying/incubation but was not detected during nestling and post-fledging phases (Table 5). Female rates of *creet* song appeared highest during egg-laying/incubation (Table 5), a phase when the mean rate of female *creet* song appeared much higher than any male phase. Both male and female rates of *creet* song appeared to decrease with time of day (Table 6).

DISCUSSION

Sedgwick (2000) and Sogge (2000b) reported that Willow Flycatcher song (presumably by males) was most common shortly after arrival on the breeding grounds and early in the nesting cycle, declining with the season and particularly after pairing. Our findings are consistent with this general pattern for both *fitz-bew* and *creet* songs by males. An exception was the high rate of male *fitz-bew* song in the post-fledging phase, which, due to the prevalence of second clutches, was probably early in the following nesting cycle when male song would be expected to exhibit another peak.

Sedgwick (2000) and Sogge (2000) also reported that males sang throughout the day, but that the highest rates of song were in the early morning. In contrast, McCabe (1991) found that male song was not as consistent or vigorous in morning compared to late evening. Our findings were consistent with the former pattern, as the males at Camp Verde sang throughout the day, and mean song rates of both *fitz-bews* and *creets* were greater for males during morning. However, our need to combine data from all years and nesting phases for analysis may have masked subtle differences between phases that

TABLE 4. MEANS ($\bar{X}$), STANDARD DEVIATIONS (SD), AND SAMPLE SIZES (N = NUMBER OF CONTACT INTERVALS) FOR SOUTHWESTERN WILLOW FLYCATCHER *FITZ-BEW* SONGS/MIN BY SEX AND TIME OF DAY FOR ALL NESTING PHASES COMBINED, CAMP VERDE, ARIZONA, MAY–AUGUST, 1996–1998

	Male songs/min				Female songs/min			
Time of day	N	$\bar{X}$	SD	Range	N	$\bar{X}$	SD	Range
Morning (0500–0959 hrs)	88	3.1	5.3	0–30	83	3.0	5.7	0–30
Midday (1000–1459 hrs)	57	3.4	5.5	0–27	100	0.8	2.6	0–16
Evening (1500–2045 hrs)	18	0.8	1.9	0–6	48	0.0	0.0	0
Total	163	2.9	5.2	0–30	231	1.4	4.0	0–30

TABLE 5. Means ($\bar{X}$), Standard Deviations (sd), and range of Willow Flycatcher *Creet* Songs/Min (N = sample size of contact intervals) by Sex and Nesting Stage for all Times of Day, Camp Verde, Arizona, May–August, 1996–1998

	Male songs/min				Female songs/min			
Nesting phase	N	$\bar{X}$	SD	Range	N	$\bar{X}$	SD	Range
Courtship/nest-building	29	0.6	0.6	0–2	5	0	0	0
Egg-laying/incubation	46	0.5	1.2	0–6	55	2.8	16.1	0–120
Nestling	18	0	0	0	79	0.1	0.4	0–3
Post-fledging	15	0	0	0	46	0.1	0.4	0–2
Total	108	0.4	0.9	0–6	185	0.9	8.8	0–120

we were not able to evaluate. We observed male song in late evening but could not evaluate the evening song peak described by McCabe (1991). Flycatcher activity was reduced during evenings, making it much more difficult for us to locate individuals for observation of singing behavior.

Our study of a small population of flycatchers resulted in a high rate of pseudoreplication due to repeated samples of the same individuals. This lack of independence between most of our samples was a potential source of bias, as it is in all studies of endangered species or small populations (Mannan and Meslow 1984, Noon and Block 1990). The necessity of netting, color-banding, and then accurately determining sex of individuals to be sampled for singing behavior will limit sample sizes and hinder efforts to duplicate this study elsewhere. We recommend that future studies of Southwestern Willow Flycatcher singing behavior attempt to gather samples from many geographic areas in order to determine if the descriptive (i.e., not statistically confirmed) patterns we observed exist rangewide. Until this study can be duplicated elsewhere, our findings should be interpreted cautiously.

The finding that females sang commonly at rates similar to males was contrary to findings of other investigators. Females gave an adjusted 20% of all *fitz-bew* songs detected during our study, suggesting a probability of 0.2 that any song detected at random during presence-absence surveys (with or without a simultaneous visual contact) would be a female. Flycatcher plumage is sexually monomorphic and few reliable behavioral cues exist to differentiate sex. With an estimated probability of only 0.8 that a randomly-encountered, singing individual is a male, determining sex based on song alone should be considered unreliable.

Our examination of female song identified several issues which should be considered in similar future studies. First, the probability that a randomly-encountered singing individual is a female might be even greater than our data indicated. This is because while female contact intervals were three times more numerous than males', their contact minutes were only two times greater. Thus, female contact intervals were on average shorter than males', which could have led to bias against detection of female song. Second, we were unable to determine the extent to which potential pseudoreplication might have influenced our determination of female song rate (i.e., only a few females might sing frequently while most might rarely or never sing), and future studies should consider this issue. Finally, our study was not designed to determine the purpose and function of female song, and this topic awaits examination.

The implications of relatively high rates of female song in an endangered subspecies whose population size is estimated by auditory techniques are profound. Males and females regularly sang while in flight and we occasionally observed both members of a pair singing simultaneously, behaviors which could cause observers to conclude that more singing males were

TABLE 6. Means ($\bar{X}$), Standard Deviations (sd), and range of Willow Flycatcher *Creet* Songs/Min (N = sample size of contact intervals) by Sex and Time of Day for all Nesting Phases Combined, Camp Verde, Arizona, May–August, 1996–1998

	Male songs/min				Female songs/min			
Time of day	N	$\bar{X}$	SD	Range	N	$\bar{X}$	SD	Range
Morning (0500–0959 hrs)	88	1.2	3.1	0–23	85	2.2	13.1	0–120
Midday (1000–1459 hrs)	57	0.4	0.6	0–2	100	0.2	0.8	0–5
Evening (1500–1845 hrs)	18	0.3	0.6	0–2	48	0	0	0

present on more territories than were actually present at a site. Quick estimates of population size at breeding sites with ≥5 pairs may be particularly unreliable because of unavoidable simultaneous contacts with multiple singing birds. Intensive nest and population monitoring would produce more reliable estimates of population size, but such monitoring is expensive and time-consuming. Marshall (2000) pointed out that only 25 sites with ≥5 pairs exist rangewide out of a total of 109 Southwestern Willow Flycatcher breeding sites, but they support almost one-half of all known territories. Therefore, even a small element of unreliability could substantially influence rangewide estimates of population size that are employed to measure recovery.

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MANAGEMENT, CONSERVATION, AND RESEARCH NEEDS—INTRODUCTION

SUSAN J. SFERRA, MARK K. SOGGE, MARY J. WHITFIELD, AND BARBARA E. KUS

One of the primary goals of this volume is to provide information that will be useful in the management of Willow Flycatcher populations, especially the recovery of the federally endangered Southwestern subspecies *Empidonax traillii extimus*. Although the Southwestern Willow Flycatcher Recovery Plan (USFWS 2002) outlines a recovery strategy for *E. t. extimus*, the actual recovery of the Southwestern Willow Flycatcher is dependent on the actions of managers. These managers will need reliable and up-to-date information to achieve recovery goals. Three threats identified in the recovery plan are habitat loss and degradation, cowbird parasitism, and environmental contamination. This section brings together papers addressing each of these threats, as well as information relevant to research techniques used to study and monitor flycatchers.

HABITAT RESTORATION

A major part of the recovery plan addresses habitat restoration as a strategy to reverse widespread loss and degradation of riparian habitat. Compliance with the Endangered Species Act of 1973 has often provided the otherwise unavailable motivation and financial means to improve ecosystem function by protecting and restoring habitat. Conversely, in many cases, managers working to improve riparian ecosystems in the Southwest for reasons other than Endangered Species Act compliance, will also be improving flycatcher habitat.

Many past attempts at riparian habitat restoration have been costly and largely ineffective at creating suitable Willow Flycatcher habitat because they often lacked the natural processes needed to regenerate and maintain the habitat (Briggs 1996). Restoration methods and results need to be documented so that we may learn from successful and unsuccessful efforts.

Paul Boucher and colleagues provide an example of an approach that can benefit Southwestern Willow Flycatchers by creating breeding habitat in the process of achieving other goals. They describe how the Gila National Forest in southwestern New Mexico used a combination of managed and natural processes to stabilize banks and create riparian habitat. Retiring grazing, excavating the riverbank to the water table level, constructing a temporary berm, and planting native riparian tree cuttings set the stage for the naturally occurring flooding, sediment deposition, and revegetation that followed. Southwestern Willow Flycatchers colonized this site and a nearby site on private property managed in a similar way. The rapid colonization of these two restoration sites was due, in part, to their proximity to a large core population of flycatchers upstream in the Cliff-Gila Valley.

COWBIRD MANAGEMENT

Cowbirds were identified as a major threat to Southwestern Willow Flycatchers in the listing proposal (USFWS 1993), despite relatively little information on the actual ecological impacts that cowbirds have on local and regional flycatcher populations. The chapters in this section caution that managing cowbirds at a local scale may not result in increased flycatcher populations.

GRAZING MANAGEMENT

Some of the grazing management for the flycatcher has been based on assumptions about the relationship between cowbirds and livestock (Goguen and Mathews 1999, Robinson 1999). It is generally believed that livestock attracts cowbirds and that livestock removal will reduce cowbird density and, subsequently, the number of parasitized nests (Verner and Ritter 1983, Airola 1986, Young and Hutto 1999). Yet, there is much literature suggesting that local and landscape features such as habitat type, canopy cover, distance from edges, human development, agriculture, and host density also influence cowbird abundance and distribution (Chace and Cruz 1999, Donovan et al. 1997, Goguen and Mathews 1999, Robinson et al. 1995b, Rothstein 1994, Staab and Morrison 1999, Young and Hutto 1999). Throughout much of the western U.S. cowbirds are most abundant in riparian habitat, regardless of distance to foraging habitat (Robinson 1999). In landscapes where feeding areas are abundant and cowbirds saturate breeding habitat, parasitism may not decline with removal of livestock (Robinson 1999). Without multiscale and site-specific information on the relationship between cowbirds, landscape variables, and livestock, it is difficult to predict whether removing livestock alone will result in decreased cowbird densities.

Chapters by Juddson Sechrist and Darrell Ahlers, and Rinda Tisdale-Hein and Richard Knight reinforce this concern, and raise important questions that need to be considered regarding the effectiveness of cowbird control via cattle management. On the Rio Grande in New Mexico, they found no difference in daily distance traveled or density of cowbirds in habitat where cattle and anthropogenic activity were present vs. where cattle and anthropogenic activity were absent. Although they did not evaluate the direct impacts of grazing on habitat, they concluded that removing livestock may not benefit flycatchers if other local factors promote cowbird persistence. If adequate food is available within the commuting distance of cowbirds, then potential host densities likely determine local cowbird densities, regardless of cattle presence or absence. Thus, managers should carefully assess the relationship between cowbirds, livestock, and habitat across the landscape when considering management options. The approach used in these studies should be extended to a larger scale to determine whether riparian sites more distant from cattle support fewer cowbirds and lower parasitism rates.

COWBIRD TRAPPING

Cowbird trapping is popular as a local and short-term management tool, but with concerns about its effectiveness in increasing host populations (Hall and Rothstein 1999, Smith 1999) it is not applied as systematically in some areas as it was a few years ago. Several papers in the 1997 cowbird symposium held in California (Morrison et al. 1999b) cautioned against using cowbird trapping as a permanent fix for reversing declining songbird populations.

Stephen Rothstein and co-authors provide a comprehensive overview of this issue, and provide guidance as to considerations about, and methods for, cowbird management relative to the flycatcher. For example, although cowbird control may reduce parasitism rates and increase the reproductive output of Southwestern Willow Flycatchers, giving the appearance that it is an effective management tool, increasing reproductive output does not necessarily equate to stabilized or increased flycatcher populations. Also, endangered passerines that are impacted at the population level by parasitism are also impacted by reduction or degradation of habitat due to anthropogenic factors; if the habitat in these areas were restored, these endangered birds may be able to coexist with cowbirds. Therefore, cowbird management alone will not increase flycatcher populations limited by habitat. Rothstein et al. also recommend that the decision to trap cowbirds should be based on whether the population in question is significantly parasitized, as determined by baseline data collection; to date, this has seldom been the case.

INVESTIGATING ENVIRONMENTAL CONTAMINANTS

Many of the potential threats to flycatchers have been studied and are understood well enough to develop management recommendations (Green et al. 2003, USFWS 2002). However, little is known about the potential effects of environmental contamination resulting from agriculture, mining, industry, and urban activities. Even less is known about contaminant levels toxic to birds, especially passerines. Birds may accumulate contaminants from one or more sources over broad geographic areas, including migration routes, so isolating the source and determining the effects on flycatchers requires substantial sampling and analyses in both the breeding and wintering grounds.

One chapter in this volume begins to fill this data void. Deformities observed in Willow Flycatchers across the Southwest (Sogge and Paxton 2000) prompted Miguel Mora and colleagues to assess environmental contaminants in central Arizona. Testing for inorganic and organic contaminants in surrogate bird species and potential insect prey, they did not find contaminant levels high enough to be implicated in the deformities. Thus, the physical deformities observed in flycatchers at these central Arizona sites may be due to other factors, including exposure to other contaminants that were not measured. A related study similarly concluded that organochlorine compound concentrations in flycatcher nestlings and eggs, surrogate birds, and insect prey at sites in Arizona and California were below known thresholds for adverse effects on birds (King et al. 2002).

Although results from these studies regarding excessive contaminant levels did not directly link contaminants and flycatcher deformities, the potential for contaminant impacts on flycatchers remains high. Mora et al. in this volume, and in a report based on the following year's data (Mora 2002), found elevated levels of selenium and strontium. Similarly, King et al. (2002) found some contaminants (selenium and possibly boron) above typical background levels. More research should be conducted on (1) the rates of bioaccumulation and sensitivity of Willow Flycatchers, surrogate species, and eggs to these and other potential contaminants, and (2) contaminant levels in surrogate species at additional flycatcher breeding sites (within and between drainages) and wintering sites.

RESEARCH TECHNIQUES

This section concludes with three papers addressing research techniques and approaches for future research. One paper tests the survey protocol in an attempt to improve measures of flycatcher abundance, another improves research methodology for color-banding, and the last explores radiotelemetry to quantify habitat use and home range.

IMPROVING MEASURES OF FLYCATCHER ABUNDANCE

Tracking recovery progress will be achieved partly through monitoring Southwestern Willow Flycatcher distribution and abundance (USFWS 2002). Adequate survey coverage across the broad range of this species can be a challenge, given the limited funding, volume of habitat needed to be surveyed, and narrow time frame to conduct surveys. As pointed out in papers in Section 1, most survey data collected to date have limited usefulness in determining population trends because of inconsistent coverage and effort across years. The current flycatcher protocol (Sogge et al. 1997a, with USFWS 2000 supplement) provides a standardized survey methodology and is widely used; a similar protocol is recommended for Sierran populations (Bombay et al. 2000). However, these tape playback-based survey protocols have not been extensively field tested, especially for use by non-experts. Although the survey protocol was not designed to precisely determine flycatcher abundance at any given breeding site, it is often used this way, especially when time and financial resources are limited. Roland Shook and co-workers present information that will be useful in developing methods for measuring abundance. The field test they conducted reinforced that experienced surveyors familiar with all vocalizations are more likely to attain accurate counts than inexperienced surveyors. While this is an important first test of the methodology, additional and more extensive tests are needed to better determine the protocol's effectiveness of detecting populations of different sizes, in differing habitats, and during different parts of the breeding season.

In addition to response to tape-playback, other aspects of flycatcher behavior can affect survey results and population estimates. High polygyny rates, if undetected, can lead to underestimates of population size (Davidson and Allison *this volume*). Female song (Yard and Brown *this volume*) can result in overestimating local population size if surveyors make the common assumption that all singing birds are males. The presence of floaters (birds without territories) and unmated males may also affect population estimates. More data are also needed on how mating strategies and behavior can affect survey estimates, and how variable they are among populations.

IMPROVING RESEARCH METHODOLOGY

While research generates information critical to conducting and evaluating management and conservation actions, it can also generate improved techniques that minimize impacts to the study species. Therefore, it is important to track and evaluate the effects that research may have on the target species. William Haas and Lori Hargrove present information on how to maximize the safety of a widely-used technique that provides otherwise unavailable data on individual animals. They describe banding injuries similar to those noted by Sedgwick and Klus (1997) and other researchers (M. Sogge and M. Whitfield, unpubl. data), and recommend techniques that have been successful in reducing these impacts.

USING RADIOTELEMETRY TO DETERMINE HABITAT USE AND HOME RANGE

Papers in Sections 1 and 2 of this volume indicate the need for quantitative habitat characteristics, use, and selection studies at different scales. Where data have been collected, habitat characteristics have been measured within nest sites, territories, and habitat patches (U.S. Fish and Wildlife Service 2002). Although it is typically assumed that the area most important to a flycatcher is that in which it is most frequently observed, the geographic extent of area used cannot be known if the bird travels beyond the territory or patch. A flycatcher's home range can be greater than its defended territory, and can change throughout the breeding season. Unfortunately, it is very difficult to visually track flycatchers as they move through dense habitats or across large distances, so determination of home range and habitats used is problematic. Knowing how flycatchers use a local area can be important in predicting impacts of potential projects.

Eben Paxton and colleagues tested the feasibility of using radiotelemetry techniques for studies on Willow Flycatcher home range, habitat use, and local movement. This pilot study documented frequent use of adjacent non-riparian habitat and local exploration forays, suggesting that flycatchers may regularly use larger areas than their defended territories. Future radiotelemetry studies of Willow Flycatchers will help determine the relative importance of non-riparian habitat types at breeding sites, and how landscape composition influences flycatcher home range size and habitat use at different sites.

OTHER RESEARCH NEEDS

The research needs presented here were largely generated from the studies published in this volume. More detailed research needs and guidelines can be found in the Sedgwick (2000), the Southwestern Willow Flycatcher Recovery Plan (USFWS 2002), and the U.S. Forest Service conservation assessments for the Southwestern Willow Flycatcher (Finch and Stoleson 2000), and those in the Sierra Nevada (Green et al. 2003). These resources, and the many Willow Flycatcher studies published elsewhere, have already contributed greatly to improved management for this species. We hope the papers in this section provide additional guidance towards achieving recovery and conservation of Willow Flycatcher populations.

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RIPARIAN RESTORATION ON THE GILA RIVER, NEW MEXICO, CREATES BREEDING HABITAT FOR SOUTHWESTERN WILLOW FLYCATCHERS

Paul F. Boucher, Scott H. Stoleson, Roland S. Shook, Ralph D. Pope, and Jerry Monzingo

Abstract. In 1995, the Gila National Forest in southwestern New Mexico was faced with a legal obligation to reduce severe erosion of riverbanks in the Gila River Bird Area. A combination of managed and natural processes stabilized banks and created riparian habitat. Retiring grazing, excavating the riverbank to the water table level, constructing a temporary berm, and planting poles set the stage for the naturally occurring flooding, sediment deposition, and revegetation that followed. Southwestern Willow Flycatchers (*Empidonax traillii extimus*) colonized and bred for the first time in this restored habitat and nearby natural regeneration in 1997. A similar project undertaken upstream on private property on the U Bar Ranch was colonized in 1999. The rapid colonization of these two restoration sites was due, in part, to their proximity to a large core population of flycatchers upstream in the Cliff-Gila Valley. This project demonstrates that landowners can simultaneously stabilize banks, reduce erosion, and create or improve Willow Flycatcher habitat.

Key Words: bank stabilization, colonization, *Empidonax traillii extimus*, Gila River, revegetation, riparian restoration, Southwestern Willow Flycatcher.

The Southwestern Willow Flycatcher (*Empidonax traillii extimus*) is currently endangered, primarily because of the loss of its riparian habitat (U.S. Fish and Wildlife Service 1995). Throughout the American Southwest, riparian habitats have been degraded or destroyed through a variety of anthropogenic factors. Some estimates suggest that over 90% of the riparian areas in the region have been lost, altered, or degraded (Ohmart 1994). Factors impacting these areas include water management, urban and agricultural development, livestock grazing, channelization, and invasion of exotic woody vegetation (Knopf et al. 1988, Marshall and Stoleson 2000). Recovery of the Southwestern Willow Flycatcher will depend on increasing the quantity and condition of riparian habitat in the region through restoration, rehabilitation, and creation of riparian woodlands (Finch et al. 2000, U.S. Fish and Wildlife Service 2001).

Management for federally listed endangered species, such as the Southwestern Willow Flycatcher, may be viewed by federal or state land managers as conflicting with other goals. This perceived conflict might result from the fact that, within the Forest Service (and other agencies), wildlife and other issues are addressed by separate staffs with separate budgets and directives. However, we suggest that riparian restoration for Willow Flycatchers or other species of concern need not be viewed as an alternative to management for other goals. Rather, land managers may be able to address a variety of goals in a manner that creates or restores riparian habitat. The objectives of this paper are to describe a case study of riparian restoration using bank stabilization by revegetation as well as passive restoration, and to present mostly qualitative results including colonization and breeding by Southwestern Willow Flycatchers.

STUDY SITE

The Gila River Bird Area (GRBA), a part of the Gila National Forest, is located within the North Burro Mountains approximately 11 km west and downstream of the communities of Cliff and Gila, and approximately 91 km northwest from the town of Silver City, in southwestern New Mexico (32° 49′ N, 108° 36′ W). The GRBA comprises a broad (0.5–1.5 km wide) floodplain approximately 5 km long along the Gila River (Fig. 1).

The valley has been continuously grazed and intermittently farmed since it was first settled in the early 1880s. E. O. Wooton surveyed the area for possible inclusion in the Gila National Forest in 1902; he described bottomlands devoid of herbaceous ground cover. The degraded watersheds he reported likely resulted from the severe drought of the late 1800s and early 1900s combined with large numbers of domestic livestock (Wildeman and Brock 2000). In the 1940s and 1950s, another prolonged drought and increased stocking rates due to the war effort concentrated livestock use in river bottoms, thereby exacerbating their impact on the sparse riparian vegetation (F. McCauley, pers. comm.). Although active hay farming ceased in the GRBA in the 1960s, cattle still had yearlong access to the river corridor. Early photographs from the 1970s depict a lack of woody riparian vegetation resulting from uncontrolled grazing and phreato-

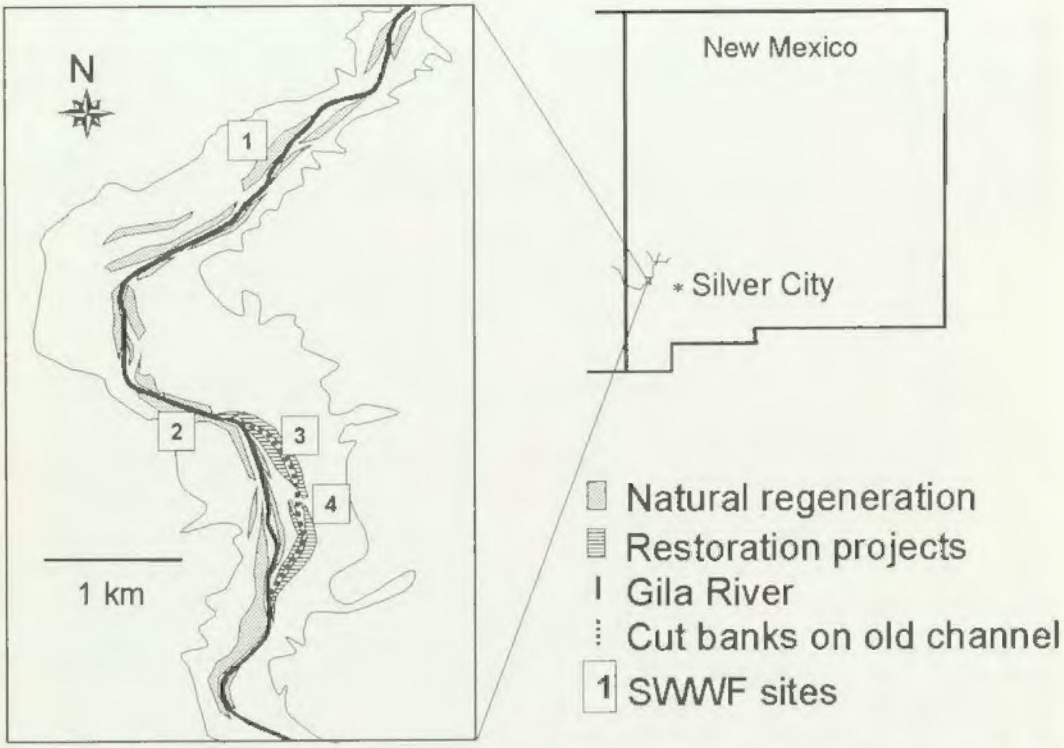

FIGURE 1. Gila River Bird Area, Gila National Forest, New Mexico, based on 1998 aerial photos and ground truthing, indicating floodplain area, restoration project, areas of natural regeneration, and Southwestern Willow Flycatcher (SWWF) breeding sites.

phyte control (the intentional removal of trees and shrubs in the belief that such actions helped to conserve water).

The Gila National Forest established the GRBA as a riparian emphasis area in 1972. Fencing to exclude livestock was completed in 1976, although it proved to be ineffective due to lack of permittee compliance. An off-highway vehicle closure was implemented in 1988. In addition to grazing impacts, the site was likely affected by the Gila National Forest's long and successful policy of fire suppression prior to 1989, which caused a reduction in nutrient-rich ash transferred to downstream riparian habitats by seasonal runoff (New Mexico Environment Department 1999). Without this influx of essential sediments, nutrient stores became depleted in riverine areas downstream (New Mexico Environment Department 1999). Regeneration of riparian plants was mostly limited to nursery bars along overflow channels (Brady et al. 1985), which were subject to grazing (P. Boucher, pers. obs.).

In 1989, the Upper Gila watershed experienced its first two large (>10,000 ha) wildfires in forty years. They produced abundant ash that was carried down the river corridor and deposited throughout the lower gradient sections of the Gila Valley. Areas with woody riparian vegetation trapped much of the nutrient-rich materials (P. Boucher, pers. obs.). After 1990, areas that were once open cobble flats began to collect new sediments during annual runoff events. Cottonwood (*Populus fremontii*), willows (*Salix* spp.), alder (*Alnus oblongifolia*) and sycamore (*Platanus wrightii*) began to grow in the new deposits. Additional large fires, both wild and managed, occurred between 1992 and 1994. With the aggradation of new sediments, the river channel began to constrict and deepen (P. Boucher, pers. obs.).

BANK EROSION

After farming in the GRBA ceased in the 1960s, no efforts were made to protect the alluvial fields or remove obstructions from the river. At the same time, a series of levees constructed from the 1940s into the 1960s on private land upstream constricted and channelized the river, promoting progressive downcutting (New Mexico Environment Department 1999). In the winter of 1992–1993, heavy precipitation

TABLE 1. GILA RIVER BIRD AREA, GILA NATIONAL FOREST, NEW MEXICO, RIPARIAN RESTORATION PROJECT EFFORT AND COSTS BY YEAR

Year	River length treated (m)	Earthwork (wks)	Cost ($)	Funding Source
1995	790	1.5	45,000	NFS[a] Soil Water Improvement grant
1996	1380	3.0	70,000	EPA[b] 319 funds
1999	100	1.0	18,000	NFS[a] Chief's Grant

[a] National Forest System appropriated funds.

[b] Environmental Protection Agency appropriated funds.

in the Mogollon Mountains resulted in severe high water events. One large flood lodged a large cottonwood snag in the river channel of the GRBA, which diverted water away from the existing channel directly into the farm fields. Phreatophyte control had left the riverbanks unprotected, so the energy deflected toward the banks caused large volumes of materials to be eroded away with each high water event (total $\approx 2.2 \times 10^6$ m^3). The New Mexico Environment Department's Surface Water Quality Bureau is responsible for water quality monitoring and enforcement of the Clean Water Act administered by the U.S. Environmental Protection Agency (1977 U.S.C. 33 §§1251–1387). In the early 1990s, the GRBA segment of the Gila River exceeded allowable levels of suspended sediments (mean daily load) and turbidity, and streambank destabilization was specifically cited as a probable cause (New Mexico Environment Department 1992, 1994). This put the Gila National Forest in a predicament; although the state cannot issue a citation to a federal agency, the U.S. Forest Service was in violation of the Clean Water Act and was obliged to comply. The Forest Service chose to avoid the conventional mechanical procedures used to stabilize banks (e.g., riprap, jetty jacks, revetment fences; see Patterson et al. 1984 for definitions) because of their negative impacts on riparian habitats, and instead opted for active restoration using native plants.

In 1992, Southwestern Willow Flycatchers were found on Gila National Forest land 24 km upstream of the GRBA, where the subsurface flow of water from an irrigation ditch created swampy wetlands (Monzingo 1994). This population is part of the very large breeding aggregation in the Cliff-Gila Valley (Maynard 1995, Marshall 2000), in which flycatchers inhabit multiple-storied stands of mixed broadleaf deciduous trees with a thick willow or boxelder (*Acer negundo*) understory in association with backwaters (Stoleson and Finch *this volume*). At the same time, on private land 22 km upstream of the GRBA, the U Bar Ranch in association with the Grant County Soil Commission and the Army Corps of Engineers had begun a project to stabilize approximately 950 m of eroding stream banks adjacent to private farmland. They used a system of excavation to the water table, grading eroding banks, constructing a berm, and pole planting of native trees along the abandoned river oxbow. This project was used as a model for the active restoration in the GRBA.

RESTORATION PROJECT GOALS

The Gila National Forest chose to achieve compliance with the CWA by using bank stabilization and riparian revegetation techniques that simultaneously created habitat like that occupied by flycatchers upstream. Active revegetation techniques were chosen for several reasons in addition to their environmental benefits. Compared to mechanical techniques, bank stabilization by revegetation is less expensive, more resilient, self-perpetuating, and often the most effective method for long-term stability (Kondolf and Curry 1984, Elmore and Beschta 1989, Brown and Decker 1999). Active revegetation of riparian zones can rapidly accelerate the natural recovery process, and is particularly useful where natural recovery fails due to extreme erosion or other factors (USDA 1998, Kauffman et al. 1997).

The main goals of the project were to (1) stabilize eroding banks in the GRBA to reduce the extreme levels of sedimentation and turbidity, and thereby bring the area into compliance with the Clean Water Act, and (2) supplement natural revegetation to create riparian habitat for the Southwestern Willow Flycatcher and other wildlife species.

PROJECT METHODS

The project was undertaken in three phases, beginning in 1995 (Table 1). First, the entire riparian corridor was retired from livestock grazing. This was accomplished in 1996 with the full cooperation and compliance of the current permittee, the U Bar Ranch. Second, heavy machinery was used to slope the vertical eroded banks, and to excavate the cobble bed to expose the water table. This work was conducted during the low-water periods of summer, thereby garnering the highest benefit for the newly created wetlands during periods of peak run-off. In New Mexico, to divert water for a wetland requires legal water rights, while to expose the existing water table for restoration requires none (Clark 1964). Third, poles and cuttings of native woody species were planted on both sides of the excavated channel. Species planted were Fremont cottonwood, Goodding (*Salix gooddingii*) and coyote willow (*Salix exigua*), Arizona sycamore, and Arizona alder. To maintain the genetic integrity of the riparian vegetation, all plantings used material originally from the Gila River valley (Montalvo et al. 1997). Poles were obtained from the Plant Materials Center, Las Lunas, NM, grown from parent material from Gila Valley. Cuttings were obtained on-site. In total, approximately 8000 cuttings (1–2 cm diam, 1 m length) and approximately 200 larger poles (5–10 cm diam) were planted on approximately 40 ha. In 2000, based on studies of habitat preferences of Willow Flycatchers in this area (Stoleson and Finch *this volume*), approximately 1700 sapling boxelders were planted within the recovering habitat patches. Exposed stream banks and weedy fields adjacent to the project were planted with a mix of native grass seed (*Bouteloua gracilis, Buchloe dactyloides, Elymus smithii*, and *Sporobolus cryptandrus* at approx. 15.6 kg/ha) to reduce erosion.

A temporary berm was constructed of excavated cobble and gravel on the river side of the new wetland to protect the newly planted vegetation from flooding until it could become established. We expected these coarse materials would be transported downstream gradually over time by the river's normal action, thereby avoiding the negative impacts of levees. Their gradual erosion and coarse nature precluded their becoming an additional non-point pollution source. The general project layout is indicated in Figure 1.

PROJECT ASSESSMENT

We conducted surveys for Southwestern Willow Flycatchers through the entire GRBA each year beginning in 1994 following standardized survey protocols (Tibbitts et al. 1994, Sogge et al. 1997a). This protocol utilizes tape playback of songs to elicit responses from flycatchers. In addition, the projects were included in a larger study of the GRBA avifauna using weekly or biweekly variable distance point counts (Bibby et al. 1992, Ralph et al. 1993) from 1997–2000. All point counts began within 15 min of sunrise, followed the same route, were traversed at a constant rate of 0.8 km/hr, and were conducted by the same observer. All birds detected were plotted on a field map noting number of individuals, species, and type of detection (visual, aural or both). We compared the average number of detections per count among years (1997–2000) for the ten most frequent bird species (Killdeer [*Charadrius vociferans*], Western Wood-Pewee [*Contopus sordidulus*], Black Phoebe [*Sayornis nigricans*], Brown-crested Flycatcher [*Myiarchus tyrannulus*], Lucy's Warbler [*Vermivora luciae*], Yellow Warbler [*Dendroica petechia*], Common Yellowthroat [*Geothlypis trichas*], Yellow-breasted Chat [*Icteria virens*], Red-winged Blackbird [*Agelaius phoeniceus*], and Bullock's Oriole [*Icterus galbula*]) using ANOVA. We predicted that we would find increases in those species dependent on early successional riparian habitats concomitant with the regeneration of that habitat.

No quantitative measures of vegetation growth and survival or stream morphology were taken due to financial constraints. These parameters were estimated from photographs taken annually at photo points.

RESULTS

VEGETATIVE AND GEOMORPHIC RESPONSES

The pole plantings of woody vegetation responded rapidly to the long growing season and abundant water available at the site. The first set of poles planted in 1995 had reached average heights in excess of 6 m by August of 2000 (Figs. 2 and 3). Survivorship of poles was >90%. The wetlands were colonized naturally by marsh vegetation including cattails (*Typha* spp.) and bulrush (*Scirpus* spp.) (Fig. 2, bottom). Abundant natural regeneration occurred both within and outside of the active restoration projects as well, such that it became difficult to differentiate between the poles and natural regrowth. Natural regeneration, predominantly willows and seepwillow (*Baccharis glutinosa*), brought the overall of density of woody plants up to 5 plants/square meter (Fig. 1). Concomitant with the regeneration of vegetation, the stream channel narrowed and deepened (P. Boucher, pers. obs.), while levels of turbidity and suspended sediments dropped to allowable levels (New Mexico Environment Department 2000).

WILLOW FLYCATCHERS IN THE GRBA

In 1996, the first Southwestern Willow Flycatcher was detected in the project area when a lone singing male appeared in mid-July (Cooper 1997). In 1997, the first breeding pairs were discovered: one pair in the 1995 project (site 3 in Fig. 1), and another three upstream in natural regeneration (site 1 in Fig. 1). Since then the number of flycatchers in the GRBA has fluctuated between 4 and 8 pairs (Table 2). The number of territories dropped in 2000 to 5, mirroring drops of similar proportions upstream on the U Bar Ranch and at the Kern River Preserve in California (S. Stoleson and D. Finch, unpubl. data; M. J. Whitfield, pers. comm.).

A total of 12 flycatcher nests have been monitored in the GRBA since 1998. Eight of these fledged one or more young. Although no cowbird trapping program has been implemented because of ongoing research, none of the 12 flycatcher nests monitored was parasitized by Brown-headed Cowbirds (*Molothrus ater*). In contrast, 12–22 km upstream in the Cliff-Gila Valley, nest success averaged 44% (N = 384 nests) and parasitism rates averaged 19% (N = 214 nests) from 1997 to 2000 (U.S. Forest Service, unpubl. data).

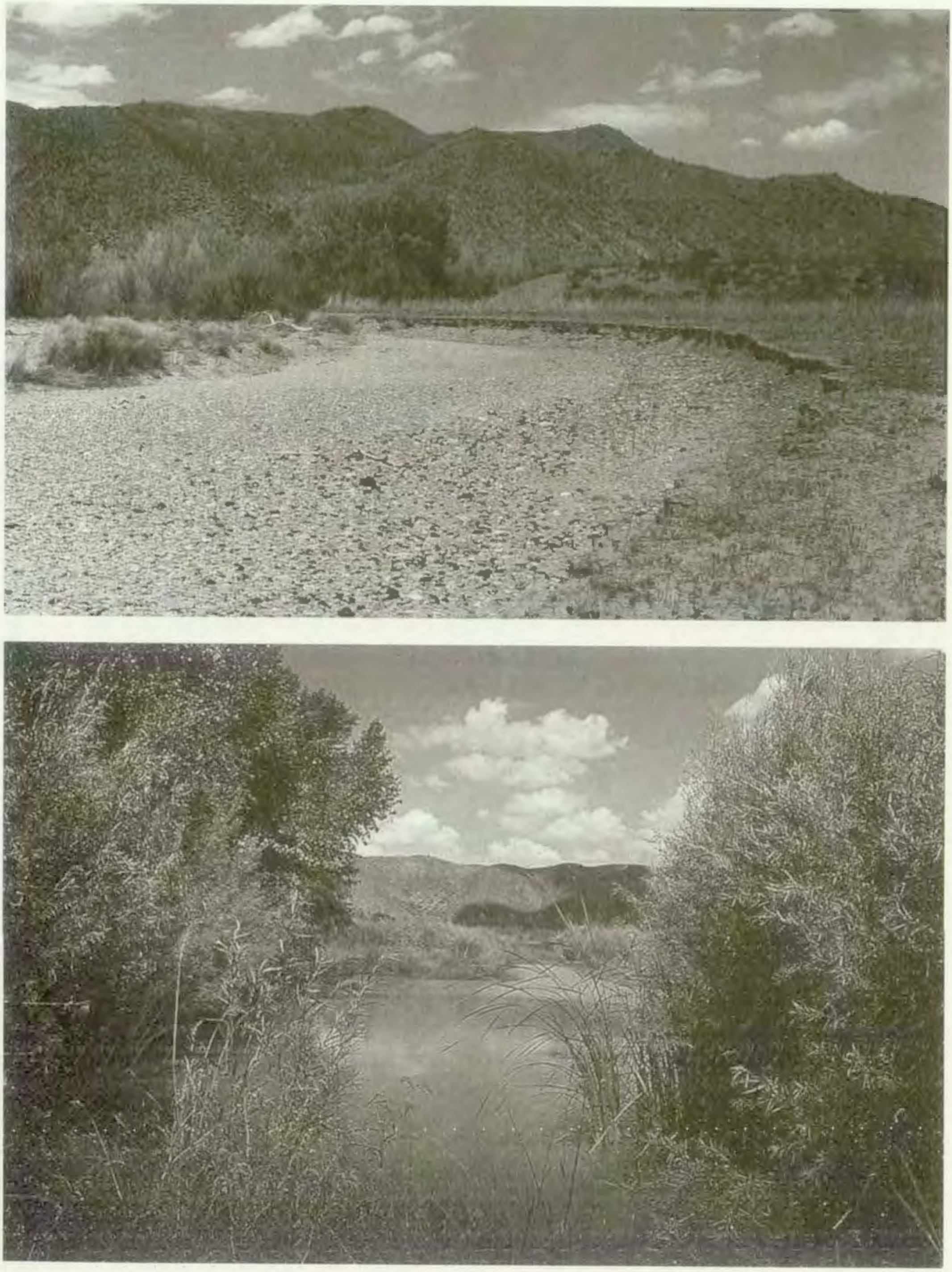

FIGURE 2. North half of the Gila River Bird Area project, Gila National Forest, New Mexico, looking west-northwest from SWWF site 3 in Figure 1: (top) in May of 1995 before restoration began, showing cut banks and paucity of riparian vegetation; and (bottom) approximately the same view in August of 1997 after two years of growth, showing wetland created by excavating to water table. Southwestern Willow Flycatchers nested in 1997 in tallest trees on right.

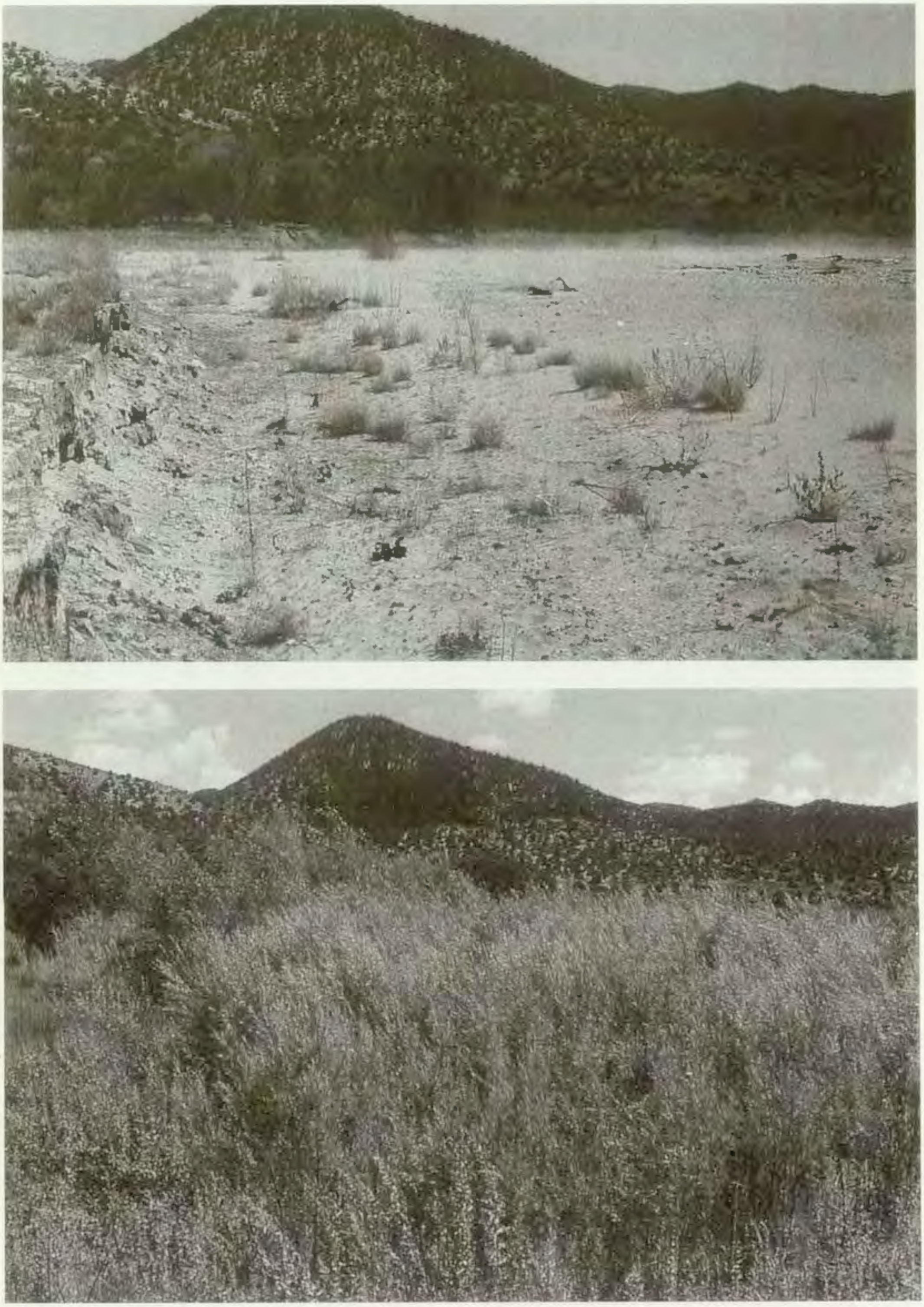

FIGURE 3. South half of the Gila River Bird Area project, Gila National Forest, New Mexico, looking south-southwest from SWWF site 4 in Figure 1: (top) in May of 1995, before restoration began, showing cut banks and paucity of riparian vegetation; and (bottom) same view in August of 1999 after three years of growth. In 1998, Southwestern Willow Flycatchers nested in tallest willows visible in middle left of picture.

TABLE 2. OBSERVED NUMBERS OF SOUTHWESTERN WILLOW FLYCATCHER TERRITORIES[a] IN THE GILA RIVER BIRD AREA, GILA NATIONAL FOREST, NEW MEXICO, 1994–2000

Site[b]	1994	1995	1996	1997	1998	1999	2000
1	0	0	0	2	3	5	3
2	0	0	0	1	2	3	0
3	0	0	0[c]	1	2	0	2
4	0	0	0	0	1	0	0
Total	0	0	0[c]	4	8	8	5

[a] Based on standard flycatcher survey protocols (Sogge et al. 1997).

[b] Sites refer to numbered areas in Fig. 1, and include areas of natural regeneration (1, 2) and two bank stabilization projects where pole plantings augmented natural regeneration (3, 4).

[c] A single singing male was detected in mid-July after all surveys were completed.

OTHER WILDLIFE

Benefits of the newly-created wetland were soon realized with the arrival of several species of waterfowl and shorebirds not regularly seen in this part of New Mexico because of the paucity of marsh habitats (Hubbard 1978). Point counts showed that Yellow-breasted Chats, an inhabitant of young thickets, increased significantly from 1997 to 2000 (ANOVA, $F_{3,69} = 4.38$, $P < 0.001$). In contrast, numbers of the cobble-inhabiting Killdeer peaked in 1998, probably in response to the scouring caused by the high flow event from Hurricane Linda, but then declined significantly as vegetation increased and the stream narrowed (ANOVA, $F_{3,61} = 5.18$, $P < 0.001$). Patterns of abundance for the other 8 species examined showed no clear trends (all ANOVA, $P > 0.32$).

Point counts revealed that a variety of neotropical migrant birds now used the project's riparian habitats for migration and breeding. These include several species that are state listed, considered sensitive by the Forest Service's Southwest Region, or high priority by Partners in Flight (New Mexico Dept. Game and Fish 1988, New Mexico Partners in Flight 2000), such as Common Black-Hawk (*Buteogallus anthracinus*), Sora (*Porzana carolina*), Yellow-billed Cuckoo (*Coccyzus americanus*), Bell's Vireo (*Vireo bellii*), Lucy's Warbler, Summer Tanager (*Piranga rubra*), and Hooded Oriole (*Icterus cucullatus*) (R. Shook, unpubl. data).

As the river has aggraded, a reduction in fine sediments on cobble and gravels in riffles created ideal habitat for the loach minnow (*Rhinichthys cobitis*), a fish species federally listed as threatened. Monitoring has indicated the presence of healthy numbers of both loach minnow and spike dace (*Meda fulgida*), another threatened fish (U.S. Forest Service, unpubl. data). No spike dace were found during similar monitoring in the mid-1980s (J. Rinne, pers. comm.), although the cause of this apparent increase is unclear. Extensive sampling in the GRBA has shown that the fish community, including these two listed species, now averages 99% native versus 1% nonnative (U.S. Forest Service, unpubl. data).

DISCUSSION

RIPARIAN RESTORATION

Wetland and riparian restoration projects nationwide have been subject to criticism for not fulfilling their ecological or conservation goals (Brown and Smith 1998, Malakoff 1998). Often, newly-restored vegetation does not last because the factors that caused the habitat degradation are not addressed by the restoration (Briggs et al. 1994). The restoration project described here successfully accomplished its main goals. Banks were stabilized, resulting in substantial reduction in erosion and a concomitant reduction in suspended sediments to levels in compliance with the Clean Water Act. The project also created over 40 ha of dense riparian habitat where there had been only cut banks and cobble. The rapid growth of the project's pole plantings and natural regeneration throughout the GRBA appeared to result at least in part from the retirement of grazing from the area. Both also likely benefited from extensive ash and sediment deposition. Pole-plantings exhibited high survival, probably because excavation to the water table ensured the poles were planted in saturated soils.

During project design, we had hoped for 5 yr of flood-free recovery to allow the developing vegetation to better withstand the effects of a high water event. However, in mid-September of 1997, a large tropical depression in the eastern Pacific, Hurricane Linda, deposited approximately 10 cm of rain in 48 hrs on the Mogollon Mountains upstream in the Gila drainage. Flow in the Gila increased from 1.5 m^3/sec (55 cfs) to over 538 m^3/sec (19,000 cfs) in little over 30 hrs, making it the third highest flow event ever recorded at the Gila gauging station 17 km upstream of the GRBA (USGS 2001). Although the project areas were completely inundated by this runoff event, the new vegetation suffered very little damage. In fact, large amounts (up to 58 cm) of new materials were deposited throughout the project and along the shoreline. The ability of the project to withstand such an extreme flood event so soon after its creation is strong evidence that this technique of riparian habitat construction can be an effective method of bank stabilization.

In 2000, the GRBA was included in an area designated as a Stream Corridor Restoration Demonstration Project by the Environmental

Protection Agency, one of only 10 such areas to receive this designation in the entire United States.

CREATION OF WILLOW FLYCATCHER HABITAT

Southwestern Willow Flycatchers rapidly colonized both the restoration project and natural regeneration within the GRBA. Similarly, the stabilization project undertaken upstream on the U Bar Ranch was first colonized in 1999 by two pairs of flycatchers. Although the sample size is small, the relatively high nest success (U.S. Fish and Wildlife Service 2001:15) suggests the GRBA may be quality habitat. Still, there appears to be much more habitat available for flycatchers in both the GRBA and U Bar projects than is currently occupied.

For both the GRBA and the U Bar projects, excluding livestock, excavating the banks to water table level, grading eroding banks, constructing berms, depositing sediment by floods, and planting poles helped stabilize banks and accelerate the revegetation process. The rapid colonization of these two restoration sites was likely due, in part, to their proximity to the large core population of flycatchers upstream in the Cliff-Gila Valley. Similarly, occupation of restored riparian habitat by Least Bell's Vireos (*Vireo bellii pusillus*) in southern California was more likely when adjacent to occupied mature habitat (Kus 1998). Although recovery of the species will depend on broad-scale riparian restoration across its range, we concur with the Willow Flycatcher Recovery Plan (U.S. Fish and Wildlife Service 2001:112) that developing new habitat near extant populations should be a high recovery priority as this strategy will increase the likelihood of colonization of those habitats.

BENEFITS TO OTHER WILDLIFE

The GRBA restoration also appeared to benefit other wildlife species, although not all. In addition to the spike dace, Yellow-breasted Chats increased. We found no clear benefit to other bird species, however, probably because of variation in habitat needs among species. Killdeer declined because the increase in woody riparian meant a loss of their preferred cobble beds. Several of the other birds that showed no clear response require older, taller vegetation (Western Wood-Pewee, Bullock's Oriole), or cavities for nesting (Brown-crested Flycatcher, Lucy's Warbler). These species may benefit in the future when the new growth attains sufficient size. Other species (e.g., Common Yellowthroat, Red-winged Blackbird) are more closely associated with non-woody vegetation.

The two listed fish species in the GRBA have markedly different habitat needs than the Southwestern Willow Flycatcher. The fish require river reaches with riffles, while the flycatchers prefer slow water or backwaters (Probst 1999, Sogge and Marshall 2000). The oxbow created by the project offered suitable slow-water habitat for flycatchers adjacent to a river stretch suitable for the fishes.

In conclusion, Willow Flycatcher habitat was created by a combination of active management and natural events. The GRBA restoration project was initially undertaken to address a violation of the Clean Water Act. Rather than consider that goal as distinct from the goal of riparian restoration, we chose a more holistic approach to restore a functioning aquatic and riparian system, and thereby provide suitable habitats for an entire community of species. The results were not only an effective and economic stabilization of the eroding banks, but the creation of habitat for Southwestern Willow Flycatchers and other wildlife.

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MOVEMENTS AND HOME RANGE ESTIMATES OF FEMALE BROWN-HEADED COWBIRDS ALONG THE RIO GRANDE, NEW MEXICO

JUDDSON D. SECHRIST AND DARRELL D. AHLERS

Abstract. We studied daily and seasonal movements of female Brown-headed Cowbirds (*Molothrus ater*) at two riparian sites along the Rio Grande in central New Mexico in 1998 and 1999. One site was in close proximity (<2 km) to livestock grazing, while the other site was ungrazed. Forty-eight female cowbirds were captured, fitted with radio transmitters, and tracked over a 2-month period. Maximum daily movements averaged 1.9 km (±0.79 SD) in 1998 and 1.4 km (±0.54 SD) in 1999. Seasonal maximum movements averaged 5.3 km (±3.43 SD) in 1998 and 2.7 km (±0.83 SD) in 1999. Daily and seasonal movements did not differ between sites. Home ranges were also calculated using a fixed kernel home range estimator and the minimum convex polygon estimator. Home range sizes did not differ between sites. Female Brown-headed Cowbirds at our sites along the Rio Grande have smaller daily commuting distances and home ranges than other studies have previously shown. Since daily and seasonal movements did not differ between sites, the exclusion of livestock from Southwestern Willow Flycatcher (*Empidonax traillii extimus*) habitat may have limited beneficial effects within this system.

Key Words: Brown-headed Cowbird, *Empidonax traillii extimus*, home range, livestock, *Molothrus ater*, movements, New Mexico, radiotelemetry, Southwestern Willow Flycatcher.

The breeding ecology of Brown-headed Cowbirds (*Molothrus ater*) in relation to host species, especially State and Federal threatened and/or endangered species such as the Southwestern Willow Flycatcher (*Empidonax traillii extimus*), is often of special concern to researchers, land managers, and resource agencies in the southwestern United States (Rothstein et al. 1984, Friedman and Kiff 1985, Harris 1991, Sogge et al. 1997a; Ahlers and White 1998, 2000; Ahlers and Tisdale-Hein 2000, Ahlers et al. 2001, Rothstein et al. *this volume*). The cowbird's use of spatially differentiated breeding and feeding areas is well documented, but commuting distances are variable and appear to be site-specific (Raim 1978, Rothstein et al. 1984, Nickel 1992, Thompson 1994, Gates and Evans 1998, Curson et al. 2000, Goguen and Mathews 2001). The presence of livestock in riparian systems complicates the understanding of spatial relations because the abundance and distribution of Brown-headed Cowbirds is often influenced by the presence and distribution of livestock (Goguen and Mathews 1999, 2001).

It is believed that livestock grazing in and around riparian habitat may provide Brown-headed Cowbirds with greater opportunities to parasitize endangered species such as the Southwestern Willow Flycatcher by (1) providing greater access to nests, (2) improving foraging opportunities, and (3) establishing foraging areas closer to flycatcher nesting areas (U.S. Fish and Wildlife Service 2001, Rothstein et al. *this volume*). Brown-headed Cowbirds are highly mobile and can impact flycatcher nesting success even if livestock grazing is remote from flycatcher nesting habitat (Rothstein et al. 1984, U.S. Fish and Wildlife Service 2001). Site-specific movement and home range estimates for cowbirds are of value to resource managers because they provide insight into habitat utilization and livestock associations within the system. These data also provide the opportunity to aid in the recovery of endangered species, such as the Southwestern Willow Flycatcher, without causing unnecessary cultural and economic impacts (U.S. Fish and Wildlife Service 2001). The purposes of this paper are to: (1) quantify Brown-headed Cowbird movement in riparian areas with extensive anthropogenic activity and year-round grazing, and in riparian areas that are comparatively free of anthropogenic influence and grazed seasonally; and (2) provide preliminary home range estimates for cowbirds using both of these habitats. We describe daily and seasonal movement patterns, as well as home range estimates, of female Brown-headed Cowbirds along the Rio Grande, near Socorro, New Mexico.

METHODS

STUDY SITES

The study area includes riparian forest communities and adjacent flood plain along 100 km of the Rio Grande from San Acacia Diversion Dam to the delta of Elephant Butte Reservoir in New Mexico (Fig. 1). The study area was divided into two units based on land use.

The San Acacia Unit (SAU) extends from San Acacia Diversion Dam to the northern boundary of the Bosque del Apache National Wildlife Refuge. Riparian

FIGURE 1. Radiotelemetry study unit boundaries along the Rio Grande in central New Mexico, 1998–1999.

communities contain patches of cottonwood (*Populus* spp.), Goodding's willow (*Salix gooddingii*), and coyote willow (*Salix exigua*), but are dominated by non-native saltcedar (*Tamarisk* sp.). Upland areas east of the river support a creosotebush- (*Larrea tridentata*) mesquite (*Prosopis* sp.) complex. The flood plain to the west is predominantly irrigated small-grain agricultural lands and irrigated livestock pasture grazed year-round. Stocking rates for livestock are greater than surrounding upland areas due to the availability of water for irrigation. Brown-headed Cowbird feeding areas were well defined within the irrigated pastures, livestock feed lots, and other open areas.

The Elephant Butte Public Lands Unit (EBPLU) extends from the northern boundary of Elephant Butte Public Lands to the delta of Elephant Butte Reservoir. Southwestern Willow Flycatchers breed within this area, and this unit supports some of the largest patches of native riparian habitat along the Rio Grande; however, the majority of the historic flood plain is decadent saltcedar. Uplands on either side of the riparian corridor support a creosotebush-mesquite complex. This unit contains portions of three grazing allotments, although grazing was not permitted from 15 April to 1 August. Habitat features attractive to feeding Brown-headed Cowbirds were not well defined in or adjacent to this site; however, non-instrumented Brown-headed Cowbirds were often observed feeding along access and maintenance road right-of-ways, borrow sites, and other open areas scattered throughout the site.

TELEMETRY

We captured and outfitted 27 and 21 (in 1998 and 1999, respectively) female Brown-headed Cowbirds with 1.6-g backpack-style radio transmitters (Advanced Telemetry Systems [ATS], Isanti, MN) as described by Thompson (1994). Females fitted with the transmitters were captured within the respective study units between 28 May and 18 June in 1998, and 28 May and 1 July in 1999, and all were assumed to be breeding. Transmitters had a range of 0.8 km and a battery life of at least 60 d. Automatic scanning receivers with computer interfaces (ATS model R2100) were coupled with 3-lead antennas to receive signals from radio-tagged (instrumented) birds. Technicians conducted searches for instrumented females from a levee running parallel to the river and throughout the study area, from 31 May to 10 August in 1998, and 29 May to 2 August in 1999.

Temporally separated locations were initially collected from late-May to early-July in 1998, while later in the season, individuals were tracked continuously throughout the day. In 1999, we focused on tracking individual female cowbirds continuously throughout the daylight hours and breeding season. Detected signals were first located via compass bearing and Universal Transverse Mercator (UTM) coordinate recorded from a Garmin 12 global positioning system unit at the technician's location. Another UTM coordinate and bearing was taken 100–800 m from the first location. In 1998, these data were uploaded into a Geographic Information System (GIS) ArcView 3.2/Spatial Analyst database and intersection points plotted. In 1999, technicians input both bearings and UTM coordinates into a spreadsheet model on-site upon signal acquisition. The model determined if a signal location could be calculated based on the computed intersection of bearings. If a bird's location could not be computed, another position fix was acquired. Coordinate data were downloaded periodically into our GIS database. For each signal location, the time interval between respective bearings and UTM coordinates did not exceed 15 min, and was commonly less than 3 min. Technicians attempted to acquire at least four valid position locations/hr for each bird throughout the 16-hr daily tracking period. These locations were not considered independent of one another.

DATA ANALYSIS

Telemetry data were analyzed to determine daily and seasonal distance traveled, and home range characteristics. These movements were compiled on both an individual and sample population basis for each year. Individual mean maximum daily distances were calculated from the maximum straight line distances recorded for each day of tracking. A day consisted of at least ten coordinate locations with at least one location per hr for more than six hours beginning in the early morning. The sample population mean maximum daily distance was determined using individual mean maximum daily movements.

The individual maximum seasonal distance traveled was calculated as the greatest straight line distance between the two coordinate locations farthest away from one another over the course of the breeding season (≥21 days). The mean maximum seasonal distance of the sample population was calculated from individual maximum seasonal movements. Maximum seasonal distance was calculated for individuals tracked for a minimum of two days producing ten or more UTM-coordinate locations spanning the breeding season. Individuals provided data for one or both movement types based on our analysis criteria.

Home ranges were estimated using a GIS ArcView/Spatial Analyst program extension from the U.S. Geological Survey–Biological Resources Division, Alaska Biological Science Center (Hooge and Eichenlaub 1997). The minimum convex polygon (MCP; Mohr 1947, Stickel 1954, Jennrich and Turner 1969) and the fixed kernel home range (KHR; Worton 1989) estimators were used and compared. The KHR output for each individual provided home range area calculations for a 95-percent shapefile probability, with smoothing determined by ad hoc least-squares cross-validation (Silverman 1986). The MCP home range area estimate for each individual is based on a single shapefile theme selected for the entire data set. We chose to couple the 100-percent MCP to the 95-percent KHR to illustrate the centers of activity within each cowbird's home range and to provide a comparative perspective when analyzing the utilization distribution (Harris et al. 1990, Samuel and Fuller 1994, Seaman and Powell 1996, Hansteen et al. 1997).

Potential concerns associated with autocorrelated movement and home range data were addressed in the study design. Sampling methodology sought collection of location data over a minimum of a 6-hr period on a daily basis, and extended over a minimum of 21 days throughout the breeding season. Data collected over a sufficient time frame, with sufficient relocations, alleviate concerns associated with autocorrelation (Otis and White 1999, Seaman et al. 1999).

RESULTS

TELEMETRY

All 27 instrumented female Brown-headed Cowbirds were detected in 1998; however, seven did not provide usable data. Five individuals provided only seasonal movement data, and the remaining 15 were evaluated for both daily and seasonal movement. All 21 instrumented females were detected in 1999, but four did not provide usable data. Six individuals provided only daily movement data, and one provided only seasonal movement data. The remaining ten individuals provided both daily and seasonal data.

In 1998, individuals were tracked on average 7.6 days (±2.9 SD, range = 3–13) to obtain 26 locations (±13 SD, range = 9–57); in 1999, individuals were tracked on average 5.2 days (±2.3 SD, range = 1–9) to obtain a mean of 106 (±60 SD, range = 28–223) locations.

We conducted field trials to determine the ability of field technicians to locate instrumented birds. Field technicians triangulated the position of a known transmitter, and were determined to be able to consistently estimate actual transmitter locations within 200 m. All measurements calculated within our database were rounded to the nearest 100 m.

DAILY AND SEASONAL MOVEMENTS

Female Brown-headed Cowbirds moved a mean maximum daily distance of 1.9 km (±0.8 SD, range = 1.0–4.2, N = 15) in 1998, and traveled a mean maximum seasonal distance of 5.3 km (±3.4 SD, range = 2.1–13.0, N = 20; Table 1). The mean maximum daily distance traveled on the SAU was 2.0 km (±1.1 SD, N = 7), and 1.8 km (±0.5 SD, N = 8) on the EBPLU. Seasonally, eight individuals traveled a mean maximum distance of 4.7 km (±2.9 SD) on the SAU,

TABLE 1. MEAN MAXIMUM DAILY AND MEAN MAXIMUM SEASONAL MOVEMENTS OF INSTRUMENTED FEMALE COWBIRDS ON TWO STUDY AREAS ALONG THE RIO GRANDE, NM, IN 1998

Bird Number	Study Area[a]	Days Tracked	Number of Locations	Mean Maximum Daily Distance (km)[b]	Maximum Seasonal Distance (km)[b]
2	EBPLU	6	19		8.3
3	EBPLU	10	26	1.5	4.2
5	EBPLU	6	24	2.2	12.9
6	EBPLU	8	12		2.2
7	EBPLU	4	9		5.0
9	EBPLU	11	28	2.0	3.8
10	EBPLU	11	26	1.6	2.1
12	EBPLU	13	36	1.1	13.0
14	EBPLU	11	29		6.1
17	EBPLU	10	25	1.6	3.1
31	EBPLU	3	11	1.8	3.4
32	EBPLU	3	19	2.6	3.5
21	SAU	5	18	1.8	3.1
22	SAU	10	30	4.2	8.1
23	SAU	5	9		6.3
24	SAU	4	14	1.3	2.8
25	SAU	8	44	1.0	2.1
26	SAU	9	46	2.6	9.7
27	SAU	8	35	1.7	2.7
28	SAU	8	57	1.5	2.8
Mean ± SD				1.9 ± 7.9	5.3 ± 3.4

[a] EBPLU = Elephant Butte Public Lands Unit; SAU = San Acacia Unit.

[b] See METHODS for explanation of movement types.

while 12 individuals on the EBPLU exhibited a mean maximum seasonal distance of 5.6 km (±3.9 SD) in 1998.

Cowbirds in 1999 had a mean maximum daily distance of 1.4 km (±0.5 SD, range = 0.5–2.5, N = 16), and a mean maximum seasonal distance of 2.7 km (±0.8 SD, range = 1.6–3.7 km, N = 11; Table 2). Mean maximum daily distance traveled on the SAU was 1.2 km (±0.5 SD, N = 10), and 1.6 km (±0.6 SD, N = 6) on the EBPLU. Seven individuals traveled a mean maximum seasonal distance of 2.5 km (±0.8 SD)

TABLE 2. MEAN MAXIMUM DAILY AND MEAN MAXIMUM SEASONAL MOVEMENTS OF INSTRUMENTED FEMALE COWBIRDS ON TWO STUDY AREAS ALONG THE RIO GRANDE, NM, IN 1999

Bird Number	Study Area[a]	Days Tracked	Number of Locations	Mean Maximum Daily Distance (km)[b]	Maximum Seasonal Distance (km)[b]
2	EBPLU	4	103	0.9	
3	EBPLU	6	111	1.2	2.1
4	EBPLU	2	67	2.1	
6	EBPLU	7	125	2.5	3.7
7	EBPLU	7	164	1.5	3.7
10	EBPLU	6	83	1.3	3.1
1	SAU	5	161	1.6	1.9
12	SAU	2	38	0.8	
13	SAU	8	223	1.1	2.0
14	SAU	9	195	1.0	2.0
15	SAU	4	41		1.6
16	SAU	1	28	1.5	
17	SAU	8	79	0.5	3.7
18	SAU	6	192	1.5	3.4
19	SAU	4	33	0.6	
20	SAU	3	58	1.8	
21	SAU	6	106	1.8	2.7
Mean ± SD				1.4 ± 0.5	2.7 ± 0.8

[a] EBPLU = Elephant Butte Public Lands Unit; SAU = San Acacia Unit.

[b] See METHODS for explanation of movement types.

on the SAU, while four individuals on the EBPLU exhibited a mean maximum seasonal distance of 3.1 km (± 0.8 SD) in 1999.

We used a two-factor ANOVA (Type III sum of squares; Statgraphics Plus Ver 5.0) to detect the influence of study area (SAU and EBPLU) and year (1998 and 1999) on the dependent variables mean daily maximum distance and seasonal maximum distance traveled. Daily and seasonal distances traveled did not differ significantly between the two study areas ($P = 0.76$, $F = 0.09$, df = 1, 28 for mean daily maximum distance traveled; $P = 0.43$, $F = 0.63$, df = 1, 28 for seasonal maximum distance traveled). Distances traveled in 1998 were significantly greater than distances traveled in 1999 ($P = 0.04$, $F = 4.56$, df = 1, 28 for mean maximum daily; $P = 0.04$, $F = 4.63$, df = 1, 28 for maximum seasonal distance traveled). The interaction of study area and year did not have a significant effect on movement types.

Because the 1998 data were skewed in comparison to 1999, we compared medians of both movement types in different years using a rank sign test (Wilcoxon W). Median distances traveled in 1998 were also greater than distances traveled in 1999 ($P = 0.02$, $W = 64$ for daily movements; $P = 0.01$, $W = 48$ for seasonal movements). The distributions of the samples (Kolmogorov-Smirnov test) did not differ statistically between years ($P = 0.12$, K-S = 1.17, $D_N = 0.421$ for daily movement; $P = 0.06$, K-S = 1.33, $D_N = 0.5$ for seasonal movement).

Home Range

Eleven individuals provided data that spanned the entire 1999 breeding season and provided sufficient locations to permit home range analysis (mean locations per female = 135 ± 54 SD, range = 41–223; Table 3). There was no statistical difference in home range size between units for either estimator (two-sample comparison of means: KHR, $t = 1.02$, df = 3, 6, $P = 0.33$; MCP, $t = 1.66$, df = 3, 6, $P = 0.13$). Four individuals in the EBPLU exhibited mean KHR areas of 143 ha (±66 SD, range = 77–237). Seven individuals in the SAU exhibited mean KHR areas of 92 ha (±76 SD, range = 19–229). Individuals on the EBPLU exhibited a mean MCP of 249 ha (±40 SD, range = 186–286), while SAU individuals exhibited a mean MCP of 187 ha (±60 SD, range = 117–299). Schoener's ratio (Schoener 1981) was applied to the fixed kernel estimator to quantify the degree of autocorrelation within each female's home range; all 11 home range estimates were positively autocorrelated.

DISCUSSION

Local Movements, Home Range, and Livestock Associations

Female cowbirds' use of space reflects their parasitic breeding strategy and preference or requirement for specific foraging habitats (Rothstein et al. 1984), and this use varies with habitat occupied and resource availability (hosts, feeding areas, etc.) throughout the United States (Table 4). Individuals using riparian areas of the Rio Grande find host nests and meet their daily resource requirements in the same localized areas within a mean maximum daily distance of 1.4 to 1.9 km. Observations of movements in this system indicate smaller local travel patterns than those reported from other upland studies in the western United States (Rothstein et al. 1984, Curson et al. 2000, Goguen and Mathews 2001). A comparable study of spacing patterns of Brown-headed Cowbirds in riparian areas on the

TABLE 3. Kernel (KHR) and Minimum Convex Polygon (MCP) Home Range Estimators (in ha) for 11 Instrumented Female Cowbirds on Two Study Sites Along the Rio Grande, NM, in 1999

Bird	Site[a]	Locations	Home Range Estimator (ha)		Schoener's Ratio
			KHR—95% Prob.	MCP—100%	
3	EBPLU	111	173	186	0.172
6	EBPLU	125	237	280	0.423
7	EBPLU	164	77	286	0.735
10	EBPLU	83	85	244	1.051
1	SAU	161	26	166	1.355
13	SAU	223	19	146	1.110
14	SAU	195	34	138	1.546
15	SAU	41	47	117	1.101
17	SAU	79	163	246	0.313
18	SAU	192	125	299	0.145
21	SAU	106	229	197	0.441
Mean			110 ± 80	210 ± 64	

[a] EBPLU = Elephant Butte Public Lands Unit; SAU = San Acacia Unit.

TABLE 4. COMPARISONS OF BROWN-HEADED COWBIRD MOVEMENTS AND HOME RANGES

Sources	Geographic Area/Habitat Type	Maximum and/or Mean Commuting Distance (km)	Home Range Area (ha)
Curson et al. 2000	Colfax County, NM Short-grass prairie/coniferous forest	Maximum[a] = 20.6 $\bar{X}^{a,f} = 11.8$; N = 9 $\bar{X}^{a,h} = 19$; N = 3	N/A
Dufty 1982	Broome County, NY Deciduous forest/agricultural areas	N/A	$\bar{X}^{c,d} = 20.4$, N = 12
Gates and Evans 1998	Allegany County, MD Anthropogenic forest landscape	Maximum[a,f] = 6.14 $\bar{X} = 2.27 \pm 0.25$ SE, N = 35 Maximum[a,g] = 9.84 $\bar{X} = 2.96 \pm 0.43$ SE, N = 25 Maximum[a,h] = 4.91 $\bar{X} = 1.35 \pm 0.32$ SE, N = 20	$\bar{X}^{a,e} = 1592 \pm 287$ SE, N = 27 $\bar{X}^{a,j} = 31.6 \pm 2.2$ SE, N = 27
Goguen and Mathews 2001	Colfax County, NM Short-grass prairie/coniferous forest	Maximum[a] = 8.46 $\bar{X}^{a,k} = 1.94 \pm 0.22$ SE, N = 9; 3.14 ± 0.14 SE, N = 3 $\bar{X}^{a,l} = 1.47 \pm 0.16$ SE, N = 15; 2.51 ± 0.16 SE, N = 9	MCP $\bar{X}^{a,e,k} = 1154.9 \pm 276.3$ SE, N = 4 KHR $\bar{X}^{a,e,k} = 1184.8 \pm 273.9$ SE, N = 4 MCP $\bar{X}^{a,e,l} = 586.4 \pm 103.8$ SE, N = 16 KHR$\bar{X}^{a,e,l} = 634.0 \pm 91.5$ SE, N = 16
Nickel 1992	San Diego County, CA Riparian, native/exotic vegetation	Maximum[a] = 3.5, $\bar{X} = 2.2$, N = 13	$\bar{X}^{a,d} = 47.5 \pm 6.7$ SE, N = 10 $\bar{X}^{a,e} = 137.3 \pm 19.2$ SE, N = 10
Raim 1978	N/A	$\bar{X}^{c} = 1.5$, N = 60	N/A
Rothstein et al. 1984	Mono County, CA Eastern Sierra Nevada	Maximum[a] = 4.3, $\bar{X} = 3.5$, N = 5 Maximum[b] = 6.7, $\bar{X} = 3.9$, N = 7	$\bar{X}^{c,d} = 68$, N = 13 $\bar{X}^{c,e} = 442$, N = 13
Sechrist and Ahlers (this study)	Socorro County, NM Riparian, native/exotic vegetation	1998 Maximum[a,m] = 4.2 $\bar{X}^{n} = 1.9 \pm 0.79$ SD, N = 15 1999 Maximum[a,m] = 2.5 $\bar{X}^{n} = 1.4 \pm 0.54$, N = 16	MCP $\bar{X}^{a,e} = 210 \pm 64$ SD, N = 11 KHR $\bar{X}^{a,e} = 110 \pm 80$ SD, N = 11
Thompson 1994, Thompson and Dijak 2000	Union County, IL; Shannon, Reynolds, Boone and Carter Counties, MO Deciduous forest and cool season pasture/cropland	Maximum[a] = >10 $\bar{X}^{a,f} = 1.2 \pm 0.08$ SE, N = 86 $\bar{X}^{a,g} = 2.6 \pm 0.28$ SE, N = 70 $\bar{X}^{a,h} = 3.6 \pm 0.39$ SE, N = 56	Median[a,e,i] = 261 − 845, N = 84

[a] Female Brown-headed cowbirds.

[b] Male Brown-headed cowbirds.

[c] Male and female Brown-headed cowbirds.

[d] Area of non-feeding home range.

[e] Total home range area.

[f] Mean distances from breeding to feeding ranges.

[g] Mean distances from feeding ranges to roost.

[h] Mean distances from roost to breeding ranges.

[i] Non-normal distributions favoring median estimates.

[j] Estimate(s) of Core Range.

[k] Commuting distances/home range of cowbirds in ungrazed borders, <2 km from study area. Mean commuting distances given are before and after livestock removal.

[l] Commuting distance/home range of cowbirds on grazed study area. Mean commuting distances given are before and after livestock removal.

[m] Sample population mean for maximum seasonal distance traveled.

[n] Grand mean of sample population for maximum seasonal distance traveled.

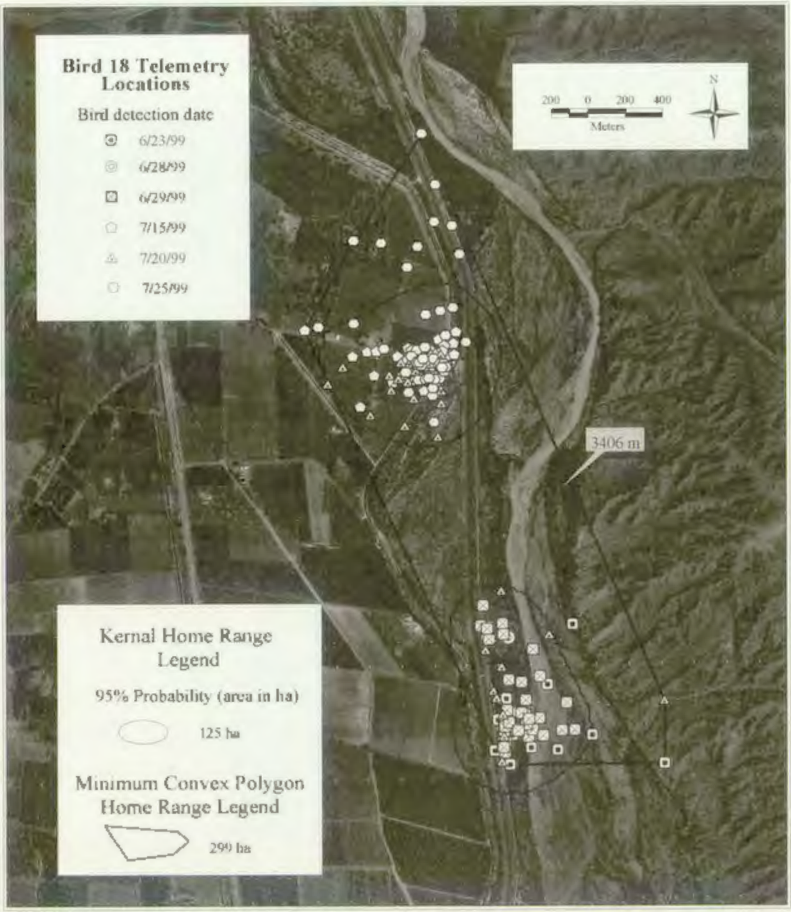

FIGURE 2. One-hundred percent minimum convex polygon and 95 percent kernel home range estimators for bird 18, illustrating centers of activity within the San Acacia Unit.

San Luis Rey River in California (Nickel 1992) reported that female commuting distances between breeding and feeding areas averaged 2.2 km, with a maximum distance traveled of 3.5 km (N = 10).

Our analyses of both daily and seasonal movement patterns revealed statistically significant differences between years, but not between sites. We attribute the variability between years to the increased effort devoted to tracking all instrumented birds as long and as often as possible in 1999. Our sampling methodology sought to incorporate rapid collection of location data on each individual over the course of an entire breeding season, and thus adequately describe daily and seasonal movement, as well as home ranges. We found that attempts to gather independent location data in 1998 often resulted in a loss of signal from instrumented birds (primarily due to signal attenuation in dense vegetation), and thus a loss of information. While home range estimates based on autocorrelated data have received criticism (Hansteen et al. 1997, Otis and White 1999) because they tend to underestimate home range sizes, other studies of highly mobile species (Andersen and Rongstad 1989, Reynolds and Laundre 1990, Ostro et al. 1999) have shown that autocorrelated data produce reliable home range estimates in comparison to statistically independent estimates.

The SAU supports extensive livestock grazing on irrigated pasture adjacent to riparian habitats used by potential host species. Goguen and Mathews (1999, 2001) and others (e.g., U.S. Fish and Wildlife Service 2001) believe the presence of livestock is a primary factor influencing cowbird distribution and abundance in the western United States; however, our movement data do not suggest livestock, anthropogenic food sources, and potential hosts in juxtaposition equate to shortened commuting distances in comparison to

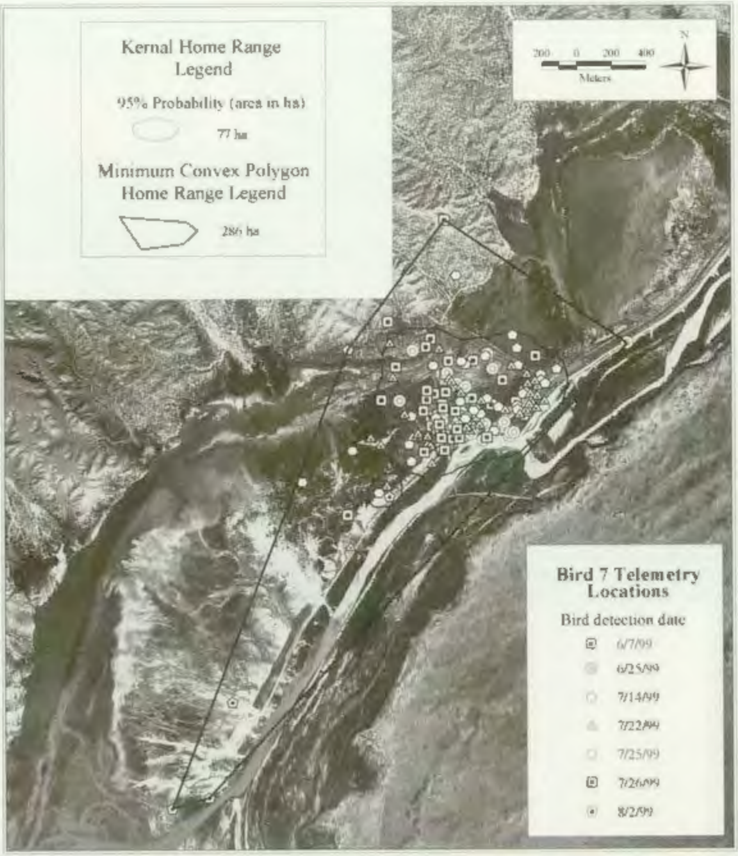

FIGURE 3. One-hundred percent minimum convex polygon and 95 percent kernel home range estimators for bird 7, illustrating a single center of activity within the Elephant Butte Public Lands Unit.

areas such as the EBPLU that are relatively free of anthropogenic influence.

There was no statistical difference between units in home range sizes with either estimator. Preliminary analysis of home range data indicates some females of the SAU such (such as bird 18; Fig. 2) exhibit multiple centers of activity and core ranges over the breeding season, while EBPLU females such as bird 7 (Fig. 3) appear to exhibit a defined center of activity. Further analysis of habitat utilization and core ranges of these birds is clearly warranted because (1) the relationship between livestock and Brown-headed Cowbirds remains unclear in this system, and (2) habitat features attractive to Brown-headed Cowbirds in the livestock-free EBPLU have yet to be identified. Cattle were not permitted on the EBPLU during the breeding season in either year, but cowbird captures remained consistent over a 4-year period (E. Best, unpubl. data). Cowbirds were also abundant on the Bosque del Apache National Wildlife Refuge where no grazing occurs (Tisdale-Hein and Knight *this volume*). Cowbirds are opportunistic, and if food resources are available, readily adapt to livestock-free environments (Rothstein et al. *this volume*). Tisdale-Hein and Knight (*this volume*) speculate that if food resources are adequate within the commuting distance of cowbirds, then the densities of potential hosts likely determine cowbird densities during morning hours regardless of whether sites are actively grazed or ungrazed. Thompson et al. (2000) reported a similar scenario in the midwestern United States; at local or habitat level scales, cowbird numbers were positively correlated with extent of edge and host density. The linear nature of riparian systems, especially in the xeric southwestern United States, suggests home ranges of cowbirds would be geographically constrained. Available data (Table 4) indicate that female Brown-headed Cowbirds in riparian areas of the western United States have smaller overall home ranges than their upland counterparts. For example, home ranges in the eastern Sierra Nevada (mean = 442 ha; Rothstein et al. 1984) and travel distances in the upland front range of New Mexico (mean = 19 km, N = 3; Curson et al. 2000) suggest some of the largest home ranges reported for breeding female cowbirds, compared to smaller values for cowbirds in riparian areas of Southern California (mean = 137 ha, N = 10; Nickel 1992) and New Mexico (range of means = 187–249 ha via MCP estimate; this study).

LIVESTOCK MANAGEMENT AND ENDANGERED SPECIES

The U.S. Fish and Wildlife Service (2001: Append. F, p. 15) implies that anthropogenic opportunities for cowbird feeding should be at least 7 km from the habitat of endangered species, (e.g., the Southwestern Willow Flycatcher) to effectively reduce brood parasitism. Livestock removal buffers in certain areas of Arizona already incorporate this distance (Goguen and Mathews 1999). It is further suggested that this distance may need to be increased in some instances to upwards of 14 km (e.g., Curson et al. 2000).

Our findings that cowbirds can occupy and apparently meet their ecological requirements in areas devoid of livestock, such as the EBPLU, indicate that livestock removal buffers may not achieve desired management goals in this system. Thus, some livestock exclusion areas established to reduce local cowbird population levels and, by extension, reduce parasitism of Southwestern Willow Flycatchers, may fail to accomplish either. The U.S. Fish and Wildlife Service (2001: Appendix G, p. 23) states that livestock should be excluded from Southwestern Willow Flycatcher sites "where the exclusion would result in the greatest ecological improvement and least economic loss." We concur with Rothstein et al. (*this volume*) that in order to achieve these goals, the relationship between cowbirds and nesting Southwestern Willow Flycatchers and/or flycatcher habitat should be evaluated on a site-specific basis.

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DENSITIES OF BROWN-HEADED COWBIRDS IN RIPARIAN AND RANGELAND AREAS, WITH AND WITHOUT CATTLE PRESENT, ALONG THE MIDDLE RIO GRANDE, NEW MEXICO

RINDA E. TISDALE-HEIN AND RICHARD L. KNIGHT

Abstract. We compared the densities of total Brown-headed Cowbirds (*Molothrus ater*), female cowbirds, and potential hosts during the morning hours on grazed and ungrazed riparian sites along the Rio Grande, New Mexico, in an attempt to evaluate the influence of the physical presence of cattle on these variables. In addition, we compared the densities of all cowbirds, female cowbirds, and potential hosts between morning and afternoon hours at riparian and rangeland sites, both with and without cattle present. We found no significant differences in total cowbird, female cowbird, or potential host densities during morning hours between riparian sites with and without cattle, indicating that the physical presence of cattle alone did not influence cowbird abundance or potential host abundance at our study sites. Cowbirds were absent from all of our riparian sites during the afternoon hours, indicating that habitat type and/or alternative feeding/congregation opportunities may have been more important in influencing cowbird densities during afternoon feeding periods than was the mere presence of cattle. Cowbird numbers in rangeland sites were low during both morning and afternoon periods, reflecting the low suitability of rangeland as cowbird breeding, and possibly feeding, habitat regardless of the presence of cattle. The lack of afternoon cowbird detections in both riparian and rangeland sites suggests that alternative feeding resources and/or congregation areas existed within the cowbird's commuting range. These findings have implications for current livestock management efforts to reduce cowbird parasitism of imperiled songbird species.

Key Words: abundance; Brown-headed Cowbird; cattle grazing; distribution; *Molothrus ater;* New Mexico; rangelands; riparian.

Brown-headed Cowbirds (*Molothrus ater*) exhibit a daily behavioral pattern that can influence their local densities during different diurnal periods (Rothstein et al. 1984, Thompson 1994, Goguen and Mathews 2000). Cowbirds commonly spend mornings engaged in breeding activities within riparian or woodland areas, and feed during afternoon hours in pastures or rangeland. Maximum distances reported for commuting between breeding and feeding areas are 12 km (Rothstein et al. 1984) to 15 km (Curson et al. 2000). However, in some situations where food is abundant within riparian areas, commuting distances may be much shorter. Anecdotal evidence suggests that cowbirds are commonly found feeding in the immediate vicinity of cattle during afternoon hours (Friedmann 1929, Mayfield 1965, Verner and Ritter 1983, Rothstein et al. 1984; Rothstein 1987, 1994). These observations have fostered an assumption that the presence (and therefore abundance) of cowbirds is dependent on the actual presence of cattle. This assumption has only recently been critically evaluated, with results varying from no apparent correlation (Goguen and Mathews 1998) to a seemingly direct association (Purcell and Verner 1999, Goguen and Mathews 2000, Curson et al. 2000).

The interpretation of relationships between cowbirds and cattle, and the effect of brood parasitism on some songbird populations, are influencing land management decisions (Rothstein et al. *this volume*) and igniting controversies regarding the movement and seasonal locations of cattle on public lands in the West. Management agencies have begun removing cattle from public lands where endangered songbirds are known to breed, based on the perception that they are removing feeding sites that attract cowbirds (Bureau of Land Management 1997, 1998). Recently, concern over the decline of the federally endangered Southwestern Willow Flycatcher (*Empidonax traillii extimus*; U.S. Fish and Wildlife Service 1995) in New Mexico has resulted in the curtailment of livestock grazing over extensive areas of public land (Bureau of Land Management 1997, 1998).

The primary objective of this study was to compare the morning densities of Brown-headed Cowbirds at riparian sites where cattle were present and similar sites where they were absent. If the physical presence of cattle is the most influential factor determining cowbird distribution and abundance, then cowbirds should be more abundant at sites with cattle present. We also compared female cowbird densities, because females are often the focus of cowbird management efforts (Beezley and Rieger 1987, Whitfield and Placer 1994, Eckrich et al. 1999). Finally, potential cowbird host densities were compared to better understand their role in cowbird abundance.

A secondary objective of this study was to further investigate cowbird diurnal movement patterns, and the effect of the presence of cattle on those patterns. We did this by comparing densities of all cowbirds and female cowbirds during morning and afternoon periods in riparian areas (cattle present and absent), and in rangeland sites (cattle present and absent). This was done to determine (1) if the presence of cattle in riparian areas influenced the afternoon feeding distribution of cowbirds, and (2) if the presence of cattle within the rangelands affected the number of cowbirds feeding there.

METHODS

The study area consisted of four riparian sites (two with cattle, two without) and four rangeland sites (two with cattle, two without) located on public and private lands along the Rio Grande in Socorro County (34°15′N, 106°30′W), New Mexico, at an elevation of 1350 to 1650 m (Fig. 1). We chose cattle-absent sites within cowbird commuting distance of cattle-present sites to allow us to isolate the effect of the presence of cattle from other factors that may influence cowbird abundance, such as distance to foraging areas. Sites without cattle (both riparian and rangeland) were located on the Sevilleta National Wildlife Refuge (NWR) and Bosque del Apache NWR, and had not supported livestock since 1939 and 1973, respectively. The distance to nearest active livestock grazing from the cattle-absent sites ranged from 0 km (at refuge boundaries) to 9.5 km (at center of point count route) for the Bosque del Apache NWR, and from 3 km (at north refuge boundary) to 4.5 km (at south refuge boundary) for the Sevilleta NWR. Study sites with cattle present included San Acacia North and San Acacia South (both riparian) managed by the Middle Rio Grande Conservancy District with a stock density of 0.10–0.15 cattle ha^{-1} during the study period, and two rangeland sites (Mulligan Gulch and Scott Ranch) managed by the U.S. Bureau of Land Management with a stock density of 0.02 cattle ha^{-1} during the summer of 1999.

We surveyed the songbird community at each site with either 5-min unlimited radius point counts (riparian sites) or line transects (rangeland sites) during morning and afternoon periods every two weeks during May–July 1999 (Tisdale-Hein 2001). The species and distance of each bird detected, as well as the sex of cowbirds, were recorded (Buckland et al. 1993). Counts included visual and aural detections. Point count route length and distance between stations on the riparian sites varied from 20 stations 250 m apart (Sevilleta NWR) to 25 stations either 760 or 800 m apart (Bosque del Apache NWR and both San Acacia sites, respectively). Line transects on the rangeland sites began at randomly selected points and extended 2300 m at 189 degrees from true north.

Point count and line transect data were analyzed using Program DISTANCE (Buckland et al. 1993, Thomas et al. 1998) to estimate the density of all cowbirds, female cowbirds, and potential host species on each site. Potential host species were defined as passerines that had been documented in the scientific literature as a cowbird host. Point count observations were truncated at 90 m. The half-normal/hermite polynomial and the uniform/cosine polynomial models were used in the analysis, with the half-normal/hermite polynomial model providing a better fit. We performed an unpaired two-tailed t-test on the average density of the two riparian sites with cattle and the average density of the two riparian sites without cattle, to determine if morning density estimates differed for all cowbirds, female cowbirds, and potential host species. Data were insufficient for statistical analysis of afternoon riparian point counts and rangeland line transects. The alpha level for all statistical tests was 0.05.

RESULTS

The riparian sites with and without cattle present did not differ significantly in morning densities of cowbirds, female cowbirds, or potential hosts. The average morning cowbird density was 1.8 ha^{-1} (± 0.4 SE) in the two riparian sites without cattle, and 1.2 ha^{-1} (± 0.3 SE) in the two riparian sites with cattle ($t = 1.1$, $df = 1$, $N = 2$, $P = 0.46$). The average density of female cowbirds during morning hours was 0.6 females ha^{-1} (± 0.2 SE) on the two cattle-absent riparian sites, and 0.3 females ha^{-1} (± 0.2 SE) at the two cattle-present sites ($t = 1.0$, $df = 1$, $N = 2$, $P = 0.33$). The average density of potential hosts was 5.9 ha^{-1} (± 1.3 SE) on the two riparian sites without cattle, and 3.7 ha^{-1} (± 0.5 SE) on the sites with cattle ($t = 1.6$, $df = 1$, $N = 2$, $P = 0.29$; Table 1).

Too few cowbirds were detected in the rangeland areas for statistical analysis. In contrast to the total of 603 cowbird detections recorded during the morning hours at riparian sites, only 43 cowbird detections were recorded during morning hours at rangeland sites. The average number of cowbirds detected per morning survey was the same (1.8) for rangeland sites with and without cattle present. No cowbirds were detected during afternoon surveys at either the riparian or rangeland sites.

Low densities of potential host species were detected on all rangeland sites. At the Sevilleta NWR and the Bosque del Apache NWR, we detected a total of four and five bird species, respectively; of these, only Mourning Dove (*Zenaida macroura)* and Black-throated Sparrow (*Amphispiza bilineata*) were potential cowbird hosts. Seven total avian species were detected at both the Milligan Gulch and the Scott Ranch allotments; of these, only Mourning Dove, Yellow-breasted Chat (*Icteria virens*), and Black-throated Sparrow were potential cowbird hosts. All detections of potential host species in the rangeland areas were infrequent, suggesting very low densities.

DISCUSSION

Discussions of declining songbird populations in the Western United States often include the

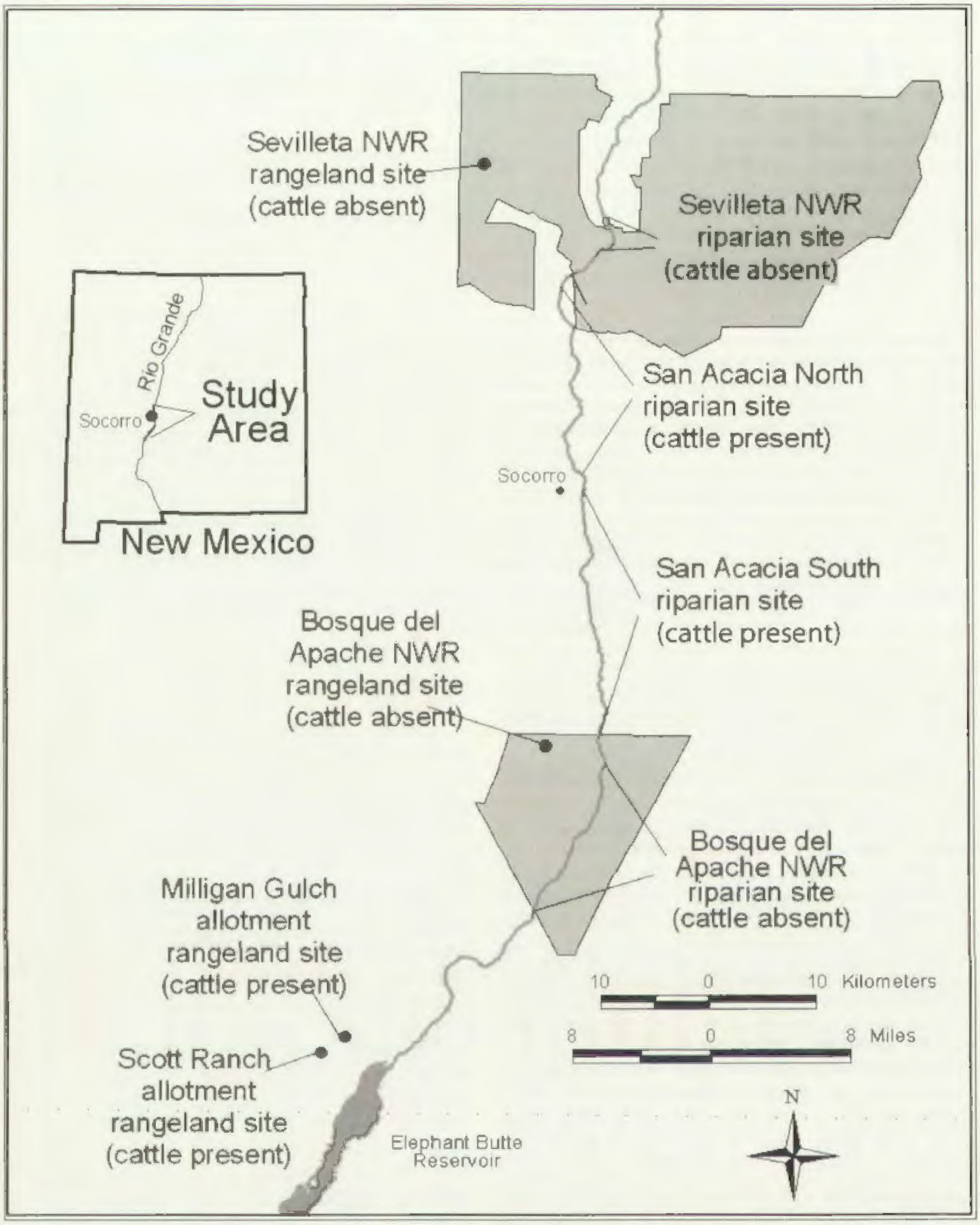

FIGURE 1. Brown-headed Cowbird study areas along the Rio Grande in New Mexico.

relationship between cowbird parasitism and the presence of cattle. Interpretation of this relationship varies, but in its simplest form is defined as one in which the presence of cattle is synonymous with the presence of cowbirds which is synonymous with negative impacts from brood parasitism. The anecdotal association between Brown-headed Cowbirds and livestock (Friedmann 1929, Mayfield 1965, Verner and Ritter 1983, Rothstein et al. 1984; Rothstein 1987, 1994) is undoubtedly the origin of such interpretations. Unfortunately, a management

TABLE 1. DENSITIES (NUMBER PER HA; COEFFICIENT OF VARIATION IN PARENTHESES) OF TOTAL COWBIRDS, FEMALE COWBIRDS, AND POTENTIAL HOSTS AT RIPARIAN SITES WITH AND WITHOUT CATTLE PRESENT, DURING MORNING HOURS

Cattle		All brown-headed cowbirds	Female brown-headed cowbirds	Potential hosts
Absent	Sevilleta NWR	2.2 (15.5%)	0.8 (22.9%)	7.2 (11.1%)
	Bosque NWR	1.4 (16.8%)	0.4 (24.8%)	4.7 (13.0%)
Present	San Acacia N	0.9 (22.3%)	0.2 (35.7%)	3.2 (14.3%)
	San Acacia S	1.5 (31.2%)	0.5 (25.0%)	4.2 (12.4%)

corollary is developing; removal of cattle is synonymous with removal of cowbirds and therefore a reduction or elimination of brood parasitism. This corollary is becoming incorporated into, or suggested as, management policy (removal of cattle) for areas supporting threatened songbird populations (Bureau of Land Management 1997, 1998; Goguen and Matthews 1999), including the Willow Flycatcher. We believe actions such as cattle removal designed to benefit cowbird host species are based on an incomplete understanding of cowbird behavior and ecology, a misconception of the relationship between livestock and cowbirds, and lack of local data on factors affecting cowbird distribution and impacts.

Our data illustrate the importance of first evaluating habitat at the landscape level when contemplating cowbird management strategies to aid songbird populations. For purposes of discussion, we narrowly consider cowbird habitat in terms of the presence of food and potential hosts. Cowbirds parasitize host nests in riparian areas during morning hours, and congregate in feeding areas during afternoon (Thompson 1994). We found no evidence that our riparian sites with cattle supported higher numbers of Brown-headed Cowbirds during morning hours than our similar riparian areas without cattle, indicating that the presence of cattle alone was not a good predictor of cowbird abundance. We speculate that if food resources are adequate within commuting distance of cowbirds, then the densities of potential hosts likely determine localized cowbird densities during morning hours regardless of whether cattle are present in, or absent from, the areas in which the cowbirds are parasitizing hosts nests. This hypothesis is supported by observations of D. Krueper (pers. comm.), who noted an 80% increase in cowbird numbers in response to extensive riparian habitat recovery and a subsequent 2- to 10-fold increase in songbirds following removal of cattle from sites on the San Pedro River in Arizona. Thus, presence of cattle may not be an attractant to cowbirds that are actively engaged in parasitism behavior.

The importance of habitat to cowbird behavior patterns is further illustrated by our surveys of rangeland sites. Few cowbirds were detected on rangeland sites during morning surveys regardless of grazing status, and none were recorded during afternoon surveys. These sites supported limited vegetation, low cattle densities, and low songbird densities. We believe the data reflect that the rangelands had limited habitat suitability for cowbirds in terms of food and host abundance, and further illustrate that the presence of cattle alone may have little influence on the presence of cowbirds, depending on other local and landscape factors. For example, the fact that we did not detect cowbirds during any of our afternoon surveys, in either riparian or rangeland sites, suggests that they fed elsewhere. Given that cowbirds have been documented foraging and congregating at bird feeders, campgrounds, agricultural fields, and other non-livestock areas (Rothstein et al. *this volume*), there are likely alternative (i.e., not associated with cattle) foraging opportunities within the commute distance of locally-breeding cowbirds. This is supported by research showing that cowbirds in the Middle Rio Grande region, and often elsewhere, generally find host nests and meet their daily resource needs within a relatively small local area requiring daily movements of approximately 2 km (Sechrist and Ahlers *this volume*).

Our findings have implications for the controversies surrounding cowbirds, grazing, and riparian bird management, but should be viewed with caution and interpreted with an understanding of their limitations. Random selection of survey sites was not possible in this study; therefore, external validity of the study, and consequently the ability to generalize to other areas, is limited. Replication was also limited, and low replication has been common in studies of the effects of cattle and/or grazing on riparian bird communities (Mosconi and Hutto 1982, Schulz and Leininger 1991, Ammon and Stacey 1997). The small number of sample sites and limited time scale (e.g., a single year) increase the possibility of committing a Type II error (not detecting an effect when there is one); the presence of cattle may influence the abundance of cowbirds, and our sample size may have been too small to detect the relationship. The limited spatial scale of our analysis may have influenced our results in a similar way, and it is possible that riparian sites more distant from cattle-present sites than was the case in our study may support a lower abundance of cowbirds than sites with or near cattle. Recent studies have found positive relationships between active livestock grazing and cowbird abundance (Goguen and Mathews 2000). However, based on apparent contradictory findings between this study and others, it is clear that results from cowbird impact and behavior studies should not be generalized, and more research is needed to identify specific factors influencing distribution and abundance of Brown-headed Cowbirds.

The results from our sites do not support the common belief that riparian sites with cattle support higher numbers of Brown-headed Cowbirds during morning hours than similar riparian areas without cattle. These results should generate discussion and ideas for expanded research to empirically determine the threshold of association between cowbirds and cattle in differing habitat types.

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