

NESTING SUCCESS OF THE YELLOW WARBLER IN A DISTURBED RIPARIAN FOREST IN COASTAL CALIFORNIA

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ABSTRACT: Widespread decline of Yellow Warbler populations in California has led to increased interest in their conservation and management. However, because the species is now rare throughout much of its historic range in the state, there is relatively little demographic information about it. Predation and Brown-headed Cowbird parasitism are cited as causing declines, but their effects are poorly quantified. To address this information need, in 2008 we investigated the reproductive biology of the Yellow Warbler along the Pajaro River in Santa Cruz and Monterey counties, California, where the species is still relatively abundant. We examined predation and parasitism pressures by monitoring nests and recording reproductive success. In this heavily disturbed area, the Yellow Warbler's nest success was very low (10%), revealing that one of the larger populations of this species remaining in the region may be threatened.

In California, the population of the Yellow Warbler (*Dendroica petechia*) has declined on a broad scale: according to the Breeding Bird Survey, an average of 1.1% yearly between 1966 and 2007 and 1.7% yearly between 1980 and 2007 (Sauer et al. 2008). Heath (2008) estimated that Yellow Warbler populations have decreased 40–80% and the species' breeding range in California has been reduced 20–40% in the last 65 years. As over much of the state, there is strong anecdotal evidence that the Yellow Warbler's breeding range has also contracted in Santa Cruz and Monterey counties along California's central coast over the last few decades (D. Suddjian pers. obs., Roberson and Tenney 1993).

Predation may be one factor in the Yellow Warbler's population declines in these counties. The reproductive success of birds breeding near suburbs and in human-altered uplands, such as those found in Santa Cruz and Monterey counties, can be lowered because predator densities and predation pressure are higher (Wilcove 1985, Andren 1992, Michaud et al. 2004). In naturally patchy western ecosystems, however, Tewksbury et al. (1998) and Cain et al. (2003) demonstrated predation on Yellow Warbler nests to be higher in forested landscapes than in those fragmented by agriculture, mainly because of predation of nests by mammals, predominantly squirrels.

Brood parasitism by the Brown-headed Cowbird (*Molothrus ater*) may also be an important factor in reducing reproductive success in Santa Cruz and Monterey counties. Agriculture and human habitation, interspersed with natural habitats, can attract cowbirds. Although commonly cited as a cause for Yellow Warbler population declines in the state (e.g., Gaines

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1974, Garrett and Dunn 1981), the role of brood parasitism has typically not been supported by recent data (Heath 2008). However, the rates and effects of parasitism were not quantified during the cowbird's initial invasion and exponential growth phase; these may have differed from those implied by these recent studies.

To better understand the causes for the declines of the Yellow Warbler population along the central coast of California, we measured the reproductive success, nest predation, and Brown-headed Cowbird parasitism on Yellow Warblers breeding along the Pajaro River.

METHODS

Study Area

We studied Yellow Warblers along the lower stretches (~16 km) of the Pajaro River, which forms the boundary between Santa Cruz and Monterey counties and is just south of the San Francisco Bay area. The Pajaro River corridor has been variously managed over the years, and riparian vegetation has been removed on multiple occasions. Nonetheless, prior to 1995, the river corridor supported a mostly continuous corridor of complex riparian forest of cottonwood and willow, making it one of the most significant such forests along the central California coast. In 1995, after a catastrophic flood in the Pajaro Valley, much of the riparian vegetation, including many of the mature trees that made up the canopy, was removed by bulldozers for flood control. Since then, portions of the woodland have been cut each year to control flooding, but extensive patches of Arroyo Willow (*Salix lasiolepis*) and Red Willow (*S. laevigata*) of varying age and height have been left in some areas. In addition to willows, the canopy vegetation along the Pajaro River is made up of Black Cottonwood (*Populus trichocarpa*) with lesser amounts of Box Elder (*Acer negundo*) and California Sycamore (*Platanus racemosa*). The understory, in addition to willow, is made up primarily of California Blackberry (*Rubus ursinus*), Western Poison-oak (*Toxicodendron diversilobum*), and noxious weeds such as Poison Hemlock (*Conium maculatum*), German Ivy (*Senecio mikanioides*), and Stinging Nettle (*Urtica dioica*).

Nest Searching and Monitoring

To evaluate reproductive success, we searched for nests from 25 April through 29 July 2008, following guidelines suggested by Martin and Guepel (1993). We selected the Pajaro River alone for our search for Yellow Warbler nests because of the species' abundance and concentration at this site and its paucity along other streams in the region. We monitored nests every 1–4 days until the young fledged or the nest failed (Ralph et al. 1993, Martin et al. 1997), using a digital camera mounted to the end of a telescoping aluminum pole to record the contents. We took care to minimize our effects on nest survival by not flagging nest trees but using a GPS unit to record the nests' coordinates. If necessary, we placed a distant flag and recorded the distance and bearing to the nest. We followed all other precautions recommended by Ralph et al. (1993) to avoid attracting predators and minimize disturbance.

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We considered a nest successful if it fledged at least one Yellow Warbler, even if the nest also fledged a cowbird, on the basis of visual or auditory detections of dependent young near an intact nest near the expected date of fledging. We considered a nest unsuccessful if all of the Yellow Warbler eggs or nestlings disappeared prior to the expected date of fledging, the nest was torn from its supporting branches, we found an adult dead on the nest midway through the nesting cycle, or the nest failed from some other cause such as eggs not hatching or the death of nestlings. We considered a nest parasitized if it contained a cowbird egg or nestling at any stage in the nesting cycle. We considered a nest to have failed from cowbird parasitism if only cowbird eggs or nestlings were present in the nest after we had observed Yellow Warbler eggs or young in it previously or if we noted only cowbird eggs or young in it through the entire time we monitored it. When feasible, we probed nests after the young fledged or the nest failed to search for buried cowbird eggs.

Reproductive Success

We calculated nest-survival rates by Mayfield's (1975) method with a standard error estimator (Johnson 1979). This approach to nest success minimizes the bias that results from nests being found at different stages of the nesting cycle. We calculated the probability of a nest's survival individually for each stage (laying, incubation, and nestling) and across an entire 25-day nesting cycle (4 days of egg laying, 11 of incubation, and 10 with nestlings; Lowther et al. 1999). For all nests, we started counting days of exposure when at least one Yellow Warbler egg or nestling was present. To calculate exposure days for nests with known fates, we used as the terminal date the midpoint between the date we last observed the nest active and the first date we observed the nest inactive; for nests with unknown fates, we used the date the nest was last known active to count exposure days (last-active B method in Manolis et al. 2000).

RESULTS

Daily Survival and Nest Success

We located and monitored 26 Yellow Warbler nests over the course of the breeding season. Timmer's surveys along the same section of river that year yielded 100–110 singing males, leading us to believe that we monitored the nests of approximately one quarter of the population. All nests were located in willows, four in Arroyo Willow and 22 in Red Willow. On the basis of the first egg laid, the earliest date of initiation of these nests was 3 May. Only 2 of the 26 nests (8%) nests were successful and fledged young. The daily survival rate for all stages of the cycle combined was 0.912 ± 0.019 (Table 1). The Mayfield (1975) estimate of overall nest success was 10.0%. There appeared to be little difference in nest success among the three stages, although daily survival rates were lower during laying than during the incubation and nestling periods (Table 1).

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Table 1 Daily Survival and Total Nest Success^a of Yellow Warblers Breeding along the Pajaro River, Santa Cruz and Monterey Counties, California, 2008

Period	Exposure days	Daily survival ^b	Nest success ^c
Laying	39	0.821 (0.061, 0.698–0.943)	0.453 (0.237–0.792)
Incubation	112.5	0.929 (0.024, 0.880–0.977)	0.444 (0.246–0.777)
Nestling	63.5	0.937 (0.030, 0.876–0.998)	0.522 (0.266–0.980)
All	216	0.912 (0.019, 0.874–0.950)	0.100 (0.035–0.276)

^aMayfield (1975).

^bStandard error and 95% confidence interval in parentheses.

^c95% confidence interval in parentheses.

Nest Outcomes: Predation

Predation directly caused 48% (11/23) of the failures of nests whose cause of failure we determined (Table 2). In fact, 83% (20/24) of all failed nests were eventually depredated. Depredation resulted in nests being left intact but empty, destroyed after being torn from the supporting branches, or intact but containing a dead adult. Of the 20 nests that were eventually depredated 11 were emptied but left intact, seven were destroyed, and two contained the remains of dead adults. Of the seven destroyed nests, all but one were depredated prior to the nestling stage, and five of the seven were not yet parasitized. No depredated nests were found destroyed past 12 June. Two nests were abandoned, and we did not determine whether parasitism had occurred at one nest because it was depredated before we identified its contents.

Table 2 Outcomes and Causes of Failure of Yellow Warbler Nests along the Pajaro River, Santa Cruz and Monterey Counties, California, 2008

	All nests	Parasitized nests	Unparasitized nests	Unknown
Outcome				
Total number of nests	26	14	11	1
Successful ^a	2	1	1	0
Unsuccessful	24	13	10	1
Percent successful	8%	7%	9%	0
Causes of failure				
Predation	12	3	8	1 ^c
Cowbird parasitism ^b	10	10	—	—
Abandonment (cause undetermined)	2	—	2	—

^aNests from which at least one Yellow Warbler fledged.

^bIncludes two nests fledging cowbirds and eight lost to predation subsequent to parasitism.

^cNest depredated before the contents were identified; not included in summary statistics because depredation was not definitively the cause of nest failure.

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Nest Outcomes: Brood Parasitism

Brown-headed Cowbirds parasitized 61% (14/23) of nests with known contents and were directly responsible for at least 43% (10/23) failures of nests whose cause of failure we determined. Of the 10 nests that failed because of cowbird parasitism, two fledged cowbird young and the remaining eight were depredated. We observed no instances of burial of cowbird eggs under nest material.

DISCUSSION

The Yellow Warblers we studied experienced very low reproductive success, due in part to high predation rates. Tewksbury et al. (1998) compared the productivity of Yellow Warbler nests in nonfragmented forest and fragmented agricultural areas in Montana and found that at the forested sites predation was high and parasitism was low whereas at the agricultural sites predation was low and parasitism was high. The net effect was equally low nesting success in both habitats. Similarly, in meadows containing shrubby willows in the northern Sierra Nevada, Cain et al. (2003) found that Yellow Warbler nests located farther from edges of coniferous forest experienced lower predation rates. In riparian woodland in coastal Marin County, California, just north of San Francisco Bay, Michaud et al. (2004) found high (73%) rates of predation of Wilson's Warbler nests, particularly near areas used by people. Along the Pajaro River, which is bordered mainly by agriculture and has no adjacent forested habitat and minimal adjacent residential areas, we anticipated that predation rates would be low. Nevertheless, they were similar to those recorded in Marin County and the Sierra Nevada. We believe that many of the nest predators were mammals because we observed few avian predators (e.g., corvids, hawks), but we did find tracks in the mud near depredated nests and occasionally branches supporting the nest broken. Interestingly, two adults were depredated in addition to eggs and nestlings. The loss of adult Yellow Warblers constitutes a larger problem because population trajectories are very sensitive to adults' survival. The levees and benches along the Pajaro River, which are cleared of woody vegetation and situated alongside narrow strips of riparian forest, may facilitate mammalian predators' access to nests.

Brown-headed Cowbird parasitism was another major factor in low reproductive success. Parasitism rates were predictably high because of the extensive agriculture along the river, and parasitism of a nest resulted in its failure in all cases but one. Interestingly, no nests were destroyed during depredation after 12 June, and most of those that were destroyed did not yet hold a cowbird egg. We suspect that the cowbirds also played a role in depredating and destroying the warblers' nests early in the season during egg laying, possibly accounting for the lower daily survival rates during laying. In other parts of its range, the Yellow Warbler has adopted anti-parasite strategies such as nest abandonment or burying cowbird eggs under another layer of nest material, sometimes producing multi-tiered nests if the nest is parasitized repeatedly (Clark and Robertson 1981, Lowther et al. 1999). On the east side of the Sierra Nevada Yellow Warblers regularly bury cowbird eggs (S. Heath pers. comm.). We observed no egg burial along the Pajaro

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River, and only two nests were abandoned (both prior to containing eggs). Perhaps coastal California populations are more susceptible to cowbird pressure because they have not coexisted with cowbirds for as long as inland populations. The first specific mention of the cowbird in Santa Cruz County was for 10 July 1955, a report of Song Sparrows (*Melospiza melodia*) feeding fledgling cowbirds in Soquel (*Audubon Field Notes* 9:402). We suspect they had arrived in the county a little earlier, but the late 1940s and early 1950s were a period of limited reporting, and the historical record from that time is rather thin.

Effectively recovering and managing declining populations of coastal Yellow Warblers will rely on high productivity and recruitment at sites like the Pajaro River. The problems of predation and brood parasitism are difficult to overcome. The habitat, as it is now, appears to be an ecological sink for this species. Altering the practice of vegetation thinning along the river could reduce the amount of abrupt edge and reduce predation pressure. Allowing the riparian woodland along the river to regenerate in a wider corridor may encourage the return of large carnivores, which would keep the populations of mesocarnivores such as raccoons, skunks, and opossums in check. Finally, controlling the population of Brown-headed Cowbirds by reducing areas where they feed or removing cowbirds with traps would likely bolster the recruitment of young into the breeding population. In southern California, a resurgence in numbers of the Yellow Warbler has coincided with trapping of cowbirds to benefit the Least Bell's Vireo (*Vireo bellii pusillus*; Unitt 2004).

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