PREDATOR ACTIVITY AND NEST SUCCESS OF WILLOW FLYCATCHERS AND YELLOW WARBLERS

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Abstract: Willow flycatchers (*Empidonax traillii*) and yellow warblers (*Dendroica petechia*) are riparian-dependent species that have declined throughout much of their former range in California, USA. These declines have been primarily associated with the loss of riparian breeding habitat, increases in brood parasitism, and increases in nest predation. We (1) identified potential nest predators using inactive yellow warbler nests; (2) determined the relationship of meadow wetness, meadow size, and amount of edge to predator activity; (3) determined the association between potential nest predator activity and nest success; and (4) determined how proximity to forest edge and isolated trees was related to nest success. We used automatic cameras to monitor inactive yellow warbler nests baited with zebra finch (*Taeniopygia guttata*) eggs to identify nest predators. We used track plates (mammalian), point counts (avian), and time-constrained searches (reptilian) to assess the activity of potential nest predators. We photographed short-tailed weasel (*Mustela erminea*), Douglas squirrel (*Tamiasciurus douglasii*), lodgepole chipmunk (*Tamias speciosus*), deer mouse (*Peromyscus maniculatus*), and unidentified chipmunks (*Tamias* spp.) depredating yellow warbler nests baited with finch eggs. The amount of meadow covered with water was negatively associated with the activity of chipmunks and Douglas squirrels. Meadow size was negatively associated with Douglas squirrel activity. The amount of edge was positively associated with the activity of Douglas squirrels, chipmunks, Steller's jays (*Cyanocitta stelleri*), and brown-headed cowbirds (*Molothrus ater*). Nest predation was the major cause of nest failure in our study. However, only short-tailed weasels, Douglas squirrels, Clark's nutcrackers (*Nucifraga columbiana*), Steller's jays, Cooper's hawks (*Accipiter cooperii*), and brown-headed cowbirds had activity indices that were negatively associated with nest success of either species. The distance to isolated trees was associated with willow flycatcher nest success, whereas the distance to both isolated trees and the forest edge was associated with yellow warbler nest success—nests located closer to isolated trees and the forest edge were more likely to be parasitized and/or depredated. Our results suggest that flooding portions of meadows may restrict meadow access to forest-edge-associated nest predators.

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Studies from the eastern and midwestern United States have found that rates of nest predation and brood parasitism are higher in fragmented than in unfragmented landscapes (Faaborg et al. 1995, Robinson et al. 1995*b*, Donovan et al. 1997), primarily due to higher nest predator and brood parasite abundances along edges in fragmented landscapes (Gates and Gysel 1978, Donovan et al. 1997, Winter et al. 2000). However, landscape fragmentation may not have the same influence on nest predation and brood parasitism rates in the naturally patchy landscapes of the western United States (Tewksbury et al. 1998, Sieving and Willson 1998). Differences in the effects of fragmentation between the eastern and western United States likely reflect differences in predator communities and natural levels of landscape heterogeneity (Tewksbury et al. 1998, Heske et al. 2001). Raccoons (*Procyon lotor*), Virginia opossums (*Didelphis virginiana*), stripped skunks (*Mephitis mephitis*), canids, snakes, and birds often are identified as major nest predators in the midwestern and eastern United States (Donovan et al. 1997, Winter et al. 2000). Conversely, forest predators, such as sciurid rodents (e.g., squirrels and chipmunks), corvids (e.g., Steller's jays), and accipiters (e.g., Cooper's hawks), have been identified as common nest predators in the western United States (Sieving and Willson 1998, Tewksbury et al. 1998, De Santo and Willson 2001, Liebezeit and George 2002).

The willow flycatcher and the yellow warbler are riparian-obligate species that have experienced declines in California. The willow flycatcher has been largely extirpated from the state and

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currently is restricted to a few isolated riparian meadow systems in the central Sierra Nevada and along the Kern, San Luis Rey, and Santa Margarita rivers in southern California (Harris et al. 1987, Unitt 1987, Sanders and Flett 1989). The yellow warbler also has declined throughout much of its range in California (Sauer et al. 2000). The yellow warbler is a species of special concern (California Department of Fish and Game 1992). These declines largely are due to the loss and degradation of riparian breeding habitat, increases in brood parasitism, and increases in nest predation (Harris et al. 1987, Sanders and Flett 1989, Desante and George 1994). The willow flycatcher was listed as endangered under the California Endangered Species Act in 1990 (California Department of Fish and Game 1999). The southwestern willow flycatcher (*E. t. extimus*) was listed as endangered in 1995 under the Federal Endangered Species Act (U.S. Fish and Wildlife Service 1995).

Montane meadows in the central Sierra Nevada are a small portion of the landscape and have a naturally patchy and fragmented distribution (Ratliff 1982, 1985). These meadows vary in size and shape and are defined largely by their hydrology (Ratliff 1982, 1985). Because habitat patch size, amount of edge, and the presence of standing water can influence predator communities, these landscape characteristics also may influence nest predation rates (Gates and Gysel 1978, Moller 1989, Picman et al. 1993, Robinson et al. 1995*b*, Donovan et al. 1997).

We investigated the relationship between meadow characteristics and the activity of common nest predator species, and the relationship between predator activity and nest success of willow flycatchers and yellow warblers in the central Sierra Nevada, California. Our objectives were to first identify potential nest predators of willow flycatchers and yellow warblers and then to determine (1) the relative effects of predation and nest parasitism on the reproductive success of each species; (2) the extent to which meadow size, perimeter to area ratio, and meadow wetness were associated with the activity of nest predators; (3) whether willow flycatcher and yellow warbler nest success was correlated with predator activity; and (4) whether the distance to the forest edge was associated with the probability of nest predation.

STUDY AREA

We monitored 12 meadows that were known to support breeding pairs of willow flycatchers. Given the limited distribution of willow flycatchers in the Sierra Nevada, we selected our study sites because they contained approximately 84% of the willow flycatcher territories located during 1997–1998 surveys of 104 meadows in the central Sierra Nevada (Bombay et al. 2002). Our study area encompassed the north-central Sierra Nevada Mountains, California (Fig. 1), which is characterized by mountainous topography that is divided by glacial and riverine valleys. The U.S. Forest Service manages most of the land within our study area, including the Tahoe National Forest, Lake Tahoe Basin Management Unit, and Toiyabe National Forest. The remaining land is managed by the California Department of Fish and Game or California State Parks, or is privately owned. Average daily summer (Jun–Aug) temperatures typically range from a low of 4 °C to a high of 26 °C. Late afternoon thundershowers are not uncommon, and summer precipitation averages 3.9 cm (National Oceanic and Atmospheric Administration 1999, 2000).

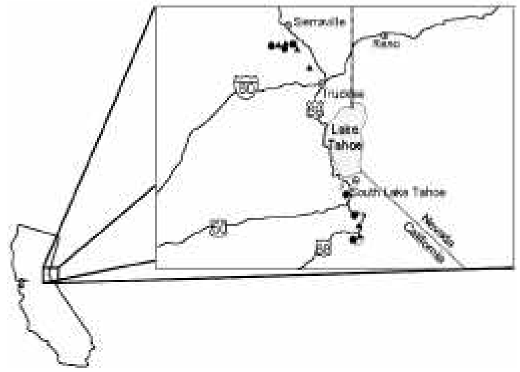

Fig. 1. Location of meadows monitored for willow flycatcher and yellow warbler nest success and nest predator activity during 1999 (▲) and 2000 (●), central Sierra Nevada, California, USA.

Study sites were wet montane meadows surrounded by lodgepole pine (*Pinus contorta*) forests and at elevations between 1,900 and 2,700 m. Meadows ranged in size from 4.6 to 167 ha (mean = 55.8 ± 15.6 ha). The herbaceous plant community of the meadows was dominated by sedges (*Carex* spp.), grasses, and rushes (*Juncus* spp.). The riparian shrub community was composed primarily of willows (*Salix* spp.), particularly Lemmon's willow (*S. lemmonii*) and Geyer's willow (*S. geyeriana*). Willow communities in the meadows often paralleled streams, but also were found scattered in clumps across the meadows. Some meadows also contained stands of mountain alder (*Alnus tenuifolia*) and quaking aspen (*Populus tremuloides*), usually along the meadow edge.

METHODS

We monitored nest success in 6 meadows each field season ($n = 12$). To increase our sample size, we monitored different meadows each year of our study. To determine which meadows were monitored each year, we listed the meadows in order from north to south and divided them into 2 groups. Beginning with the northernmost meadow, we selected every other meadow and placed them in group 1, the remaining meadows were placed in group 2. We used a coin toss to determine which group of 6 meadows was monitored in 1999. We monitored the remaining meadows in 2000 (Fig. 1).

Nest Location and Monitoring

We determined territory numbers and locations in each meadow using taped playback of male territorial songs and calls. We located nests by observing adult birds exhibiting breeding behaviors (Martin and Geupel 1993). When we found nests, we recorded the location and the number of eggs and or nestlings. We monitored yellow warbler nests every 3–4 days and willow flycatcher nests every 5–7 days until the nest failed or young fledged from the nest. Because of the endangered status of the willow flycatcher in California, we used a longer nest-monitoring interval in an attempt to minimize potential negative impacts due to nest-monitoring activity. We recorded the number of eggs and or nestlings and any evidence of nest predation or brood parasitism each time we checked a nest. Evidence of nest predation included missing eggs or missing nestlings too young to have fledged. We assumed that nest losses occurred at the midpoint between the discovery of the predation event and the date of the last nest observation. We calculated nest success using the Mayfield method (Mayfield 1961, 1975). We excluded from analysis nests that were abandoned before they were completely built and those that failed before clutch initiation was confirmed.

Predator Identification

We identified potential nest predators using automatic cameras at inactive yellow warbler nests. We did not attempt to identify nest predators at willow flycatcher nests because of the species' endangered status. Furthermore, because yellow warblers are a species of special concern in California (California Department of Fish and Game 1992), we did not use active nests for this portion of our study. Instead, we used yellow warbler nests that had successfully fledged young, been depredated, or were abandoned. For camera placement, we only considered yellow warbler nests located in (1) meadows also occupied by willow flycatchers, (2) the meadow rather than in the understory of the adjacent forest, and (3) willows. Based on visual assessment of nests that met these criteria, we selected a subset of 65 yellow warbler nests that had nest locations and vegetative concealment similar to that at willow flycatcher nests. Camera systems were comprised of an electronic camera, double-strand wire, and a micro-switch (Danielson et al. 1996, Cain 2001, York et al. 2001). We set up a camera system at the nest, placed zebra finch eggs inside the nest, and attached them to the micro-switch using monofilament line (Cain 2001). Removal of the eggs activated the camera. We monitored the nests with the camera systems for 12–14 days or until depredated.

Predator Activity Monitoring

Mammalian.—We established track-plate transects in each meadow to assess potential mammalian nest predator activity (Table 1; Heske et al. 1995 **NOT IN LIT CITED, SHOULD BE HESKE 1995?,** Winter et al. 2000). In each meadow, we established a baseline transect that paralleled the riparian shrub community. We placed track-plate transects at 200-m intervals along the baseline transect. Track-plate transects ran perpendicular to the baseline transect. The direction of the first transect was determined randomly, and subsequent transects were run in alternating directions. Each transect consisted of 4 track stations at 25-m intervals. Each track station consisted of 1 aluminum track plate (163 × 81.5 cm) covered with a mixture of carpenter's chalk and alcohol (Orloff et al. 1993, Cain 2001). We placed a piece of white contact paper on the center of the track plate. To protect the track plates from moisture, we constructed covers from surveyor's stakes and asphalt-soaked felt paper (Cain 2001). We sprayed quail eggs (*Coturnix coturnix*) with a mixture of egg and water and placed them on the contact paper.

We collected tracks weekly and monitored track plates for as long as nests were active in the meadow (Table 1). We identified tracks to the species level whenever possible, with the following exceptions. Due to the difficulty in differentiating chipmunk species based on tracks alone, we combined all chipmunk species and golden-mantled ground squirrels (*Spermophilus lateralis*). We combined all mouse (*Peromyscus* spp., *Reithrodontomys*

Table 1. Size (ha) of meadows, year monitored, duration of monitoring, and mammalian, avian, and reptilian nest predator survey effort, central Sierra Nevada, California, USA, 1999–2000.

Site (year monitored)	Meadow size (ha)	Duration of monitoring	No. of mammalian predator surveys (no. of track-plate transects)	No. of avian predator surveys (no. of survey points)	No of reptilian predator surveys (no. of survey points)
Perazzo Meadow (1999)	106	7 Jun–23 Aug	11 (12)	12 (8)	8 (6)
Little Truckee (1999)	102	9 Jun–23 Aug	11 (12)	12 (8)	8 (6)
Prosser Creek (1999)	90	14 Jun–24 Aug	10 (10)	12 (7)	8 (5)
Red Lake 1 (1999)	9	5 Jun–14 Aug	10 (3)	12 (3)	8 (2)
Saddle Meadow (1999)	18	7 Jun–9 Aug	9 (4)	9 (2)	6 (2)
Maxwell Creek (1999)	21	5 Jun–7 Aug	9 (3)	9 (2)	6 (2)
Webber Lake (2000)	167	2 Jun–18 Aug	11 (11)	12 (8)	8 (6)
Red Lake 2 (2000)	5	5 Jun–15 Aug	10 (3)	12 (2)	8 (2)
Little Truckee 3 (2000)	23	1 Jun–18 Aug	11 (5)	12 (3)	8 (3)
Little Perazzo (2000)	25	1 Jun–2 Aug	9 (5)	9 (3)	6 (3)
Grass Lake (2000)	98	5 Jun–15 Aug	10 (2)	12 (1)	8 (1)
Washoe Meadow (2000)	5	5 Jun–11 Jul	5 (3)	6 (2)	4 (2)

spp.) and vole (*Microtus* spp.) species into 1 group for the same reason.

We calculated an index of mammalian predator activity for all species or groups of species in each meadow. Because we were unable to determine whether >1 individual visited the track plate, we counted 1 detection/plate for each species observed (Heske 1995). We were also unable to determine whether some of the same individuals were visiting track plates each week. Therefore, for each meadow, we used the detections/plate for each species as an index of activity rather than an index of abundance.

Avian.—To assess avian nest predator and brood parasite activity in each meadow, we used modified point counts (Table 1; Tewksbury et al. 1998, Sieving and Willson 1998, De Santo and Willson 2001). We established point-count locations every 300 m along the baseline transect. We recorded only avian species that are known nest predators or brood parasites. We surveyed at each point for 14 min. We divided each survey into 7 2-min intervals and recorded the species and number of individuals seen or heard during the last 30 sec of every 2-min interval. Only individuals detected during the 30-sec period were recorded, and only 1 detection/individual was recorded for each 30-sec period.

To account for differences in the activity levels of the avian predators and brood parasites detected in the meadows, we did not attempt to avoid double-counting individual birds during subsequent 30-sec recording periods. Individual birds that had higher activity levels spent more time in the meadows and were more likely to be detected during >1 2-min interval. Therefore, an individual bird could have a maximum of 7 detections during a point count. We conducted point counts only during times of low to moderate winds and no precipitation. We surveyed the points in each meadow once during each diel time period: morning (dawn–1000 hr), midday (1100–1400 hr), and afternoon (1500 hr–dusk) every 14 days (Table 1). We calculated avian predator activity indices for each meadow in a manner similar to the method used for mammalian predator indices. However, avian predator surveys allowed for the detection of multiple individuals and multiple detections/individual of a species at each point.

Reptilian.—We assessed reptilian predator activity using time-constrained, visual-encounter surveys of randomly selected areas in the meadows (Corn and Bury 1990). At every other intersection of a track-plate transect and the baseline transect (400-m intervals), we selected a random distance between zero and 100 m. If this point was located outside the meadow, we selected another random distance. We located the starting points at the randomly selected distance from the baseline transect and in the opposite direction of the track-plate transect. Beginning at each starting point and radiating outward in a concentric pattern, we thoroughly searched as large an area in the meadow as possible within 45 min.

Snakes were the only reptilian predators in the meadows and were the focus of these searches. When we found a snake, we recorded the species and location. We searched the points in each meadow once during each of 2 daily periods: morning (0800–1200 hr), and afternoon (1200 hr–dusk) every 21 days (Table 1). Because of the differences in diurnal activity patterns of reptiles and birds, we defined daily time periods for reptile predator surveys differently than those used for avian predator and brood parasite surveys.

We calculated separate weekly activity indices for each species of mammalian, avian, and reptilian predator for each meadow by dividing the number of detections during a survey by the number of track plates or survey points in the meadow. This yielded the number of detections/plate (mammalian predators) or detections/point (avian and reptilian predators) as an index of predator activity for each species. We calculated an overall predator activity index at each meadow for each species by taking the mean of the weekly predator indices.

Meadow Wetness, Meadow Size, and Edge

Standing water in the nest area can affect predation rates by influencing the type and number of predator species present (Picman et al. 1993). To determine the percentage of standing water at each meadow, we made a visual estimate of the percent of standing water within a 50-m radius from each avian nest predator survey point. We estimated the percent of the meadow covered with water during each avian predator survey by averaging the estimates from all survey points. We calculated the overall mean percent of the meadow covered with water during the breeding season by averaging the mean values from all avian predator surveys. Meadow size and shape influences the amount of edge and potentially the activity of some nest predator species. We determined meadow size (ha) and the perimeter-area ratio (m:m^2) from aerial photos taken in 1996–1998 using ARCVIEW GIS (Environmental System Research Institute 2000).

Distance to Nearest Tree and Forest Edge

We measured the distance from nests to the nearest forest edge to examine how potentially different predator communities in different areas of the meadows affected willow flycatcher and yellow warbler nest success. We considered forest edge to be the transition in vegetation and hydrology between the meadow and the surrounding lodgepole pine forest. In some meadows, we found single lodgepole pine trees or small groups of trees (<10 trees) not associated with the forest edge. Because avian nest predators and brown-headed cowbirds may use these trees to forage or locate host nests (Lowther 1993, Rosenfield and Bielefeldt 1993), we also measured the distance from nests to the nearest tree.

Statistical Analyses

We used arcsine square-root transformation on nest-success data, percent of the meadow covered with water, and mammalian track-plate data (Zar 1996:282). Avian and reptilian predator data were transformed using the logarithmic transformation (Zar 1996:279). We attempted to increase the statistical power of the analyses and reduce the probability of committing a Type II error by conducting all statistical analyses with α set at 0.10 (Zar 1996:82, Steidl et al. 1997). All statistical analyses were preformed using SPSS 9.0 (1998).

Predator Activity.—We used 1-tailed partial correlation and Pearson correlation (Zar 1996:420) analyses to test the relationships between predator activity and nest success. We limited our analysis to predator species detected at an average of ≥10% of the surveys in each meadow. We conducted partial correlation analysis between predator activity and nest success while controlling for the meadow size effect. Partial correlation controls for the effect of meadow size by first performing a regression of predator activity on meadow size, then regressing nest success on meadow size. Pearson correlation of the residuals from these regressions represents the association between nest success and predator activity with the effect of meadow size removed (SPSS 1998). We used Pearson correlations to determine any relationships between predator activity, percent of meadow covered with water, meadow size, and perimeter-to-area ratio.

Distance to Nearest Tree and Forest Edge.—We used independent sample *t*-tests (Zar 1996:126) to determine whether differences existed in the mean distances to the nearest tree and forest edge between the nests of willow flycatchers and yellow warblers. We also used *t*-tests to determine if differences existed in the mean distance to the nearest tree and forest edge between successful and unsuccessful nests of each species.

RESULTS

Nest Success, Nest Predation, and Brood Parasitism

We detected breeding pairs of willow flycatchers at 8 of 12 meadows, and yellow warblers at 11 of 12 meadows. In 7 meadows, we detected both yellow warblers and willow flycatchers.

We located and monitored 49 willow flycatcher nests (mean = 6.1 ± 1.5 nests/meadow) and 78 yellow warbler nests (mean = 7.1 ± 1.5 nests/meadow). Seasonal Mayfield nest success (Table 2) var-

Table 2. Seasonal (Jun–Aug) Mayfield nest success for willow flycatchers and yellow warblers in montane meadows of the central Sierra Nevada, California, USA, 1999–2000.

Study site	Willow flycatcher Mayfield nest success (no. of nests)	Yellow warbler Mayfield nest success (no. of nests)
Perazzo Meadow	0.022 (5)	0.49 (11)
Little Truckee	0.28 (13)	0.32 (13)
Prosser Creek	0.40 (8)	0.40 (8)
Red Lake 1	0.0 (2)	0.45 (5)
Saddle Meadow	—[a]	0.33 (7)
Maxwell Creek	—	1.0 (1)
Webber Lake	0.61 (11)	0.69 (15)
Red Lake 2	0.74 (4)	0.0 (1)
Little Truckee 3	0.54 (4)	0.75 (7)
Little Perazzo	—	0.61 (9)
Grass Lake	0.46 (2)	—
Washoe Meadow	—	0.0 (1)
Overall mean nest success	0.37 ± 0.094	0.52 ± 0.091

[a] Species not present at site.

ied among meadows for both species and ranged from 2 to 74% for willow flycatchers and from zero to 100% for yellow warblers. Nest success for all meadows and both years combined was 37% for willow flycatchers and 52% for yellow warblers.

Nest predation was the leading cause of nest failure for both species (Table 3), accounting for 76% of willow flycatcher nest failures and 93% of yellow warbler nest failures. Two nests of each species were destroyed during egg laying, 10 willow flycatcher and 17 yellow warbler nests were destroyed during incubation, and 10 willow flycatcher and 18 yellow warbler nests were destroyed during the nestling stage. All depredated nests had the entire contents of the nest removed. Two percent (1 of 49 nests) of willow flycatcher nests and 9% (7 of 78 nests) of yellow warbler nests were parasitized by brown-headed cowbirds. Of these, 1 willow flycatcher nest and 1 yellow warbler nest were abandoned, 5 parasitized yellow warbler nests were subsequently depredated, and 1 yellow warbler nest produced only brown-headed cowbird young.

Predator Identification

Twenty of the nests we monitored with cameras were depredated; 14 predators were photographed. We photographed Douglas squirrels depredating 4 nests, a lodgepole chipmunk depredating 1 nest, unidentified chipmunk species depredating 5 nests, short-tailed weasels depredating 3 nests, and a deer mouse depredating 1 nest.

Table 3. Fate of willow flycatcher and yellow warbler nests in montane meadows of the central Sierra Nevada, California, USA, 1999–2000.

Nest site	Willow flycatcher	Yellow warbler
Successful (fledged ≥1 young)	20	38
Depredated	22	37[a]
Parasitized	1	7
Abandoned	4	0
Weather-related failure	2	1
Total nests	49	78

[a] Includes 5 nests that were also parasitized by the brown-headed cowbird.

Predator Activity, Meadow Wetness, Meadow Size, and Perimeter-to-Area Ratio

The activity of chipmunks ($r = -0.610$, $P = 0.035$) and Douglas squirrels ($r = -0.616$, $P = 0.033$) were negatively correlated with the mean percent of the meadow covered with standing water; the activity of both species declined with increasing meadow wetness (Fig. 2). An increase in the mean percent of the meadow covered with water from 5 to 17% corresponded with a decrease in activity from 17 to 1% of the track plates for chipmunks and from 26 to 1% for Douglas squirrels.

Douglas squirrel activity was negatively associated ($r = -0.501$, $P = 0.097$) with meadow size; activity indices for all other predator species were not associated with meadow size. Douglas squirrel ($r = 0.704$, $P = 0.011$), chipmunk ($r = 0.551$, $P = 0.063$), Steller's jay ($r = 0.533$, $P = 0.075$), and brown-headed cowbird ($r = 0.721$, $P = 0.008$) activ-

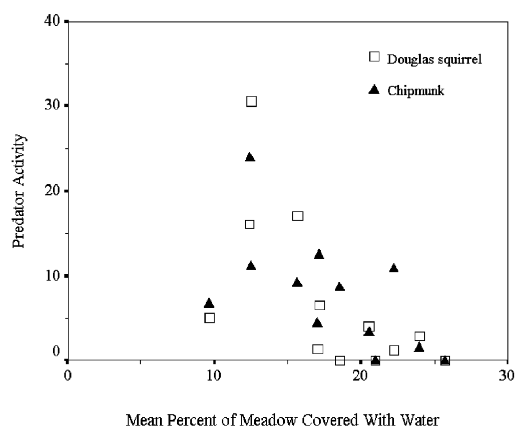

Fig. 2. Relationship between the arcsine transformed mean percent of the meadow covered with water and arcsine transformed chipmunk and Douglas squirrel activity, central Sierra Nevada, California, USA, 1999–2000.

Table 4. Predator species, number of meadows in which species was detected, and mean percent of surveys species detected in montane meadows (n = 12) of the central Sierra Nevada, California, 1999–2000.

Predator species	No. of meadows	Percent of surveys Mean	SD
Mouse group[a]	12	94	11.7
Chipmunk group[b]	10	45	32.6
Douglas squirrel	9	38	37.9
Short-tailed weasel	12	56	29.3
Long-tailed weasel (*Mustela frenata*)	9	22	19.5
Pine marten (*Martes americana*)	3	5	10.6
Mink (*Mustela vison*)	1	1	2.9
Striped skunk	2	5	18.5
Raccoon	1	1	3.2
Yellow-bellied marmot (*Marmota flaviventris*)	1	6	20.2
Western terrestrial garter snake (*Thamnophis elegans*)	10	34	28.3
Common garter snake (*T. sirtalis*)	5	8.5	12.5
Western aquatic garter snake (*T. couchii*)	6	23	31.2
Common raven (*Corvus corax*)	6	6	6.5
Clark's nutcracker	8	23	18.9
Steller's jay	12	44	27.0
Cooper's hawk	6	11	11.5
Red-tailed hawk (*Buteo jamaicensis*)	7	11	12.1
Brown-headed cowbird	10	21	18.7
Sharp-shinned hawk (*Accipter striatus*)	1	1	2.3
American kestrel (*Falco sparverius*)	4	5	7.7
Northern harrier (*Circus cyaneus*)	2	3	7.4

[a] Deer mouse, western harvest-mouse (*Reithrodontomys megalotis*), mountain vole (*Microtus montanus*), longtail vole (*M. longicaudus*).
[b] Allen's chipmunk (*Tamias senex*), lodgepole chipmunk (*T. speciosus*), yellow pine chipmunk (*T. amoenus*), Long-eared chipmunk (*T. quadrimaculatus*), golden-mantled ground squirrel (*Spermophilus lateralis*).

ity were positively correlated with the perimeter-to-area ratio.

Influence of Nest Predator and Brood Parasite Activity on Nest Success

Seventeen mammalian, 9 avian, and 3 reptilian species were detected at our study sites (Table 4). Of the potential nest predator species detected, 12 mammalian, 6 avian (5 predator and 1 brood parasite), and 2 reptilian species were detected on an average of ≥10% of the surveys in each meadow.

Five of the potential nest predator and brood parasite species had activity indices associated with overall willow flycatcher nest success. The activity indices of Douglas squirrels (pr = –0.847, P = 0.008), short-tailed weasels (pr = –0.648, P = 0.058), Clark's nutcrackers (pr = –0.586, P = 0.083), Cooper's hawks (pr = –0.709, P = 0.037), and brown-headed cowbirds (pr = –0.724, P = 0.033) all were negatively associated with willow flycatcher nest success.

Three potential nest predator and brood parasite species had activity indices negatively associated with overall yellow warbler nest success. Yellow warbler nest success was negatively associated with the activity indices of Douglas squirrels (pr = –0.600, P = 0.033), Steller's jays (pr = –0.462, P = 0.090), and brown-headed cowbirds (pr = –0.629, P = 0.026).

Distance to Nearest Tree and Forest Edge

The distance from successful and unsuccessful willow flycatcher nests to the forest edge was not significantly different (t_{47} = 1.483, P = 0.145). Successful willow flycatcher nests were an average of 56 m farther from the nearest tree than were unsuccessful nests (t_{47} = 1.948, P = 0.057; Table 5).

Successful yellow warbler nests were an average of 26 m farther from the forest edge than unsuccessful nests (t_{76} = 1.823, P = 0.072). Successful yellow warbler nests were an average of 29 m farther from the nearest tree than were unsuccessful nests (t_{76} = 2.088, P = 0.040; Table 5).

Yellow warbler nests were on average 26 m closer to the forest edge (t_{125} = 1.849, P = 0.067) and 27 m closer to the nearest tree than willow flycatcher nests (t_{125} = 1.841, P = 0.068). The mean distance between nests (both species) parasitized by brown-headed cowbirds and the nearest tree was 30 m (SE = 5.03, n = 8). All parasitized nests were within 55 m of a tree and 88% were within 30 m of a tree. The mean distance between nests (both species) parasitized by brown-headed cowbirds and the forest edge was 47 m (SE = 3.1, n = 8); 88% (7 of 8) of all parasitized nests were within 55 m of the forest edge.

DISCUSSION

Nest success of willow flycatchers and yellow warblers was associated with a subset of the mammalian and avian predators and brood parasites detected at study sites. Douglas squirrel, Steller's jay, and brown-headed cowbird activity was negatively associated with nest success of both willow flycatchers and yellow warblers, and short-tailed weasel, Cooper's hawk, and Clark's nutcracker activity had a negative association with willow flycatcher nest success.

Differences in the location of willow flycatcher and yellow warbler nests in relation to isolated trees and the forest edge likely influenced expo-

Table 5. Mean distance (m) from successful and unsuccessful willow flycatcher and yellow warbler nests to the forest edge and to the nearest tree, central Sierra Nevada, California, USA, 1999–2000.

	Distance to forest edge (m)							Distance to the nearest tree (m)						
	Successful nests			Unsuccessful nests				Successful nests			Unsuccessful nests			
	Mean	SE	*n*	Mean	SE	*n*	*P*	Mean	SE	*n*	Mean	SE	*n*	*P*
Willow flycatcher	139.0	25.6	20	98.5	14.3	29	0.145	123.5	27.5	20	67.1	14.8	29	0.057
Yellow warbler	102.3	11.9	38	76.0	8.3	40	0.072	78.0	12.9	38	49.3	5.32	40	0.046

sure to predators. Cooper's hawks, Steller's jays, Clark's nutcrackers, and brown-headed cowbirds may use isloated trees, and nests closer to these trees may more likely be depredated or parasitized (Lowther 1993, Rosenfield and Bielefeldt 1993, Bombay et al. 2002). Because yellow warbler nests tended to be closer to the forest edge than willow flycatcher nests, yellow warbler nest success may be more sensitive to the activity of forest-edge-associated predators and brood parasites (i.e., Douglas squirrel, chipmunk, brown-headed cowbird, and Steller's jays), particularly at meadows with more edge (Lowther 1993, Best et al. 1994, Gannon and Forbes 1995, Greene et al. 1998, Steele 1999). Furthermore, Douglas squirrel and chipmunk activity declined sharply with increasing meadow wetness. Therefore, nests located far from the forest edge and those surrounded by standing water may be less vulnerable to predation from Douglas squirrels and chipmunks than nests in dry areas or near the forest edge.

The relationship between nest success and proximity to the forest edge was not consistent between species. Many willow flycatcher nests may have been located too far from forest edges to be influenced by the increased predator activity. Johnson and Temple (1990) and Burger et al. (1994) reported that nests of grassland birds experienced higher predation rates <45 and <60 m from a wooded edge, respectively. Similarly, Paton (1994) suggested that increased predation near edges is typically found <50 m from a forest edge. Therefore, willow flycatchers nesting in larger meadows with less edge may be less likely influenced by forest-edge-associated predators.

However, because short-tailed weasels forage throughout the meadow (King 1983, Fagerstone 1987), distance from nests to the forest edge probably had little influence on nest predation by weasels. In addition, weasels in open areas may concentrate their activity near shrubs, which act as protective cover (Musgrove 1951, King 1983, Fagerstone 1987, Sheffield and Thomas 1997). Therefore, not only are weasels active at all distances from meadow edge, but their need for protective cover may place them in close proximity to the willows used as nest sites by willow flycatchers and yellow warblers.

Our predator-identification results support our predator-activity indices, suggesting that Douglas squirrels and short-tailed weasels are depredating nests in these meadows. By using natural nests, we avoided some biases commonly associated with the construction and placement of artificial nests (Major and Kendal 1996). However, only mammalian predators were photographed at camera-monitored nests. Because nests were inactive during monitoring, the lack of activity and noise at the nests may have made detection by avian predators less likely (Martin 1992, Martin et al. 1996). This potential bias may be alleviated with the use of video cameras to monitor active willow flycatcher and yellow warbler nests to identify nest predators.

Nest predation caused the failure of 10 times as many nests as brood parasitism and severe weather combined. Nest predation rates we observed for the willow flycatcher and yellow warbler are at the high end of the range of rates observed for both species (Goossen and Sealy 1982, McCabe 1991, Whitfield et al. 1999, Ortega and Ortega 2000).

Preliminary analyses of data collected over the past 6 years (1997–2002) as part of an ongoing demography study of this population of willow flycatchers indicate that this population likely is declining. These analyses have found that the population has a fecundity rate (number of fledglings per adult female) that is below the minimum needed to maintain or increase the current population size, juvenile recruitment in 1 year is highly correlated with the number of young fledged the previous year, and nest predation has been the leading cause of nest failure each year (Robinson et al. 1993, 1995*a*, *b*; M. L. Morrison, U.S. Forest Service, unpublished data). Therefore, we believe that nest predation is the major factor determining nest success of these populations of willow flycatchers and yellow warblers and may be high enough to influence their abundance in the central Sierra Nevada.

Brood parasitism by brown-headed cowbirds was not a factor in the failure of a significant number of nests in our study. Observed brood parasitism rates for willow flycatchers and yellow warblers in our study were well below the parasitism rates found in other studies of both species (Sedgwick and Knopf 1988, Burgham and Picman 1989, Whitfield and Sogge 1999, Ortega and Ortega 2000). Compared to other populations, brood parasitism appears to have a minimal impact on the reproductive success of willow flycatchers and yellow warblers at our study sites. The negative association we found between brown-headed cowbird activity and willow flycatcher and yellow warbler nest success appears contradictory to the low parasitism rates we observed. However, meadows with high brown-headed cowbird activity had more edge and high activity of other forest-edge-associated species, such as Douglas squirrels, chipmunks, and Steller's jays. Furthermore, parasitism of willow flycatcher and yellow warbler nests in these meadows appears to be largely compensatory in nature, since most of the parasitized nests were subsequently depredated.

Small sample sizes often are inherent to studies of endangered species. As a result of the endangered status of the willow flycatcher in California, a potential limitation of our study is the small sample size of nests and meadows. Small population size of willow flycatcher in the central Sierra Nevada limited the number of nests available for monitoring, and logistical constraints limited the number of meadows we could effectively monitor each year. Although we monitored all willow flycatcher territories and most yellow warbler territories in each meadow, and we believe that we subsequently monitored >75% of nests in these meadows, the number of meadows monitored ultimately limited our sample size.

MANAGEMENT IMPLICATIONS

Our results suggest that limiting access of nest predators to meadows, and thus to willow flycatcher and yellow warbler nests, could increase nest success. Actively flooding meadows and/or restoring water tables to historic levels by using water tending trucks or diversions to fill existing oxbows and depressions may limit access and decrease nest predation by forest-edge-associated predators (Clay 1984, Zeedyk et al. 1996). In some meadows, flooding the portion of the meadow nearest the riparian deciduous shrubs and the forest edge may be all that is necessary. By ensuring that meadows stay wet throughout the breeding season, managers may be able to limit meadow access to some nest predators and reduce nest predation. Future studies that compare nest success of willow flycatchers and yellow warblers and predator activity in unflooded and actively flooded meadows would be useful to determine the efficacy of using this method to limit predator access and increase nest success for these species. Increasing water tables to historic levels in these meadows may also enhance survival and recruitment of riparian shrubs. The establishment of riparian vegetation in suitable areas may be an option for increasing the amount of breeding habitat for willow flycatchers and yellow warblers. While not a current management activity in these meadows, restoration of riparian vegetation has been a successful management option for other riparian-dependent species (Kus 1998). However, our results suggest that nests were more successful when located farther from, rather than closer to, the forest edge and isolated trees. Management activities involving the establishment of willows should occur at suitable locations at least 100–150 m from the forest edge.

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LITERATURE CITED

Best, T. L., R. G. Clawson, and J. A. Clawson. 1994. Tamias speciosus. Mammalian Species 478:1–9.

Bombay, H. L., M. L. Morrison, and L. S. Hall. 2002. Scale perspectives in habitat selection and reproductive success for willow flycatchers (*Empidonax traillii*) in the central Sierra Nevada, California. *In* M. K. Sogge, B. E. Kus, M. J.Whitfield, and S. J. Sferra, editors. Ecology and conservation of the willow flycatcher. Studies in Avian Biology No. 26. In press. **UPDATE?**

Burger, L. D., L. W. Burger, and J. Faaborg. 1994. Effects of prairie fragmentation on predation on artificial nests. Journal of Wildlife Management 58:249–254.

Burgham, M. C. J., and J. Picman. 1989. Effects of brown-headed cowbirds on the evolution of yellow warbler anti-parasite strategies. Animal Behavior 38:298–308.

Cain, J. W. 2001. Nest success of yellow warblers (*Dendroica petechia*) and willow flycatchers (*Empidonax traillii*) in relation to predator activity in montane meadows of the central Sierra Nevada, California. Thesis, California State University, Sacramento, California, USA.

California Department of Fish and Game. 1992. Bird species of special concern. Unpublished list, July

1992. California Department of Fish and Game, Sacramento, California, USA.

———. 1999. State and federally listed endangered and threatened animals of California. California Department of Fish and Game. Sacramento, California, USA.

CLAY, D. H. 1984. High mountain meadow restoration. Pages 477–479 *in* R. E. Warner and K. M. Hendrix, editors. California riparian systems, ecology, conservation, and productive management. University of California Press, Berkeley, California, USA.

CORN, P. S., AND R. B. BURY. 1990. Sampling methods for terrestrial amphibians and reptiles. Pages 1–34 *in* A. B. Carey and L. F. Ruggiero, editors. Wildlife-habitat relationships: sampling procedures for Pacific Northwest vertebrates. U.S. Forest Service General Technical Report PNW-256.

DANIELSON, W. R., R. M. DEGRAAF, AND T. K. FULLER. 1996. An inexpensive automatic camera system for wildlife research. Journal of Field Ornithology 67:414–421.

DE SANTO, T. L., AND M. F. WILLSON. 2001. Predator abundance and predation of artificial nests in natural and anthropogenic coniferous forest edges in southeast Alaska. Journal of Field Ornithology 72:136–149.

DESANTE, D. F., AND T. L. GEORGE. 1994. Population trends in the landbirds of western North America. Pages 173–190 *in* J. R. Jehl, Jr. and N. K. Johnson, editors. A century of avifaunal change in western North America. Studies in Avian Biology 15.

DONOVAN, T. M., P. W. JONES, E. M. ANNAND, AND F. R. THOMPSON, III. 1997. Variation in local-scale edge effects: mechanisms and landscape context. Ecology 78:2064–2075.

ENVIRONMENTAL SYSTEM RESEARCH INSTITUTE (ESRI). 2000. ARCVIEW 3.2. ESRI, Redlands, California, USA.

FAABORG, J., M. BRITTINGHAM, T. DONOVAN, AND J. BLAKE. 1995. Habitat fragmentation in the temperate zone. Pages 357–380 *in* T. E. Martin and D. M. Finch, editors. Ecology and management of Neotropical migratory birds. Oxford University Press, New York, New York, USA.

FAGERSTONE, K. A. 1987. Black-footed ferret, long-tailed weasel, short-tailed weasel and least weasel. Pages 548–573 *in* M. Novak, J. A. Baker, M. E. Obbard, and B. Mallock, editors. Wild furbearer management and conservation in North America. Ontario Trappers Association under auspices of the Ontario Ministry of Natural Resources. Ontario, Canada.

Gannon, W. L., and R. B. Forbes. 1995. *Tamias senex.* Mammalian Species 502:1–6.

GATES, J. E., AND L. W. GYSEL. 1978. Avian nest dispersion and fledging success in field-forest ecotones. Ecology 59:871–883.

GOOSSEN, J. P., AND S. G. SEALY. 1982. Production of young in a dense nesting population of yellow warblers, *Dendroica petechia*, in Manitoba. Canadian-Field Naturalist 96:189–199

GREENE, E., W. DAVISON, AND V. R. MUEHTER. 1998. Steller's jay. The birds of North America 343. The Academy of Natural Sciences, Philadelphia, Pennsylvania, USA, and the American Ornithologists Union, Washington, D.C., USA.

HARRIS, J. H., S. D. SANDERS, AND M. A. FLETT. 1987. Willow flycatcher surveys in the Sierra Nevada. Western Birds 18:27–36.

HESKE, E. J. 1995. Mammal abundances on forest-farm edges versus forest interiors in southern Illinois: is there an edge effect? Journal of Mammalogy 76:562–568.

———, S. K. ROBINSON, AND J. D. BRAWN. 2001. Nest predation and Neotropical migrant songbirds: piecing together the fragments. Wildlife Society Bulletin 29:52–61.

JOHNSON, R. G., AND S. A. TEMPLE. 1990. Nest predation and brood parasitism of tallgrass prairie birds. Journal of Wildlife Management 54:106–111.

KING, C. M. 1983. Mustela erminea. Mammalian Species 195:1–8.

KUS, B. E. 1998. Use of restored riparian habitat by endangered least Bell's vireo (*Vireo bellii pusillus*). Restoration Ecology 6:75–82.

LIEBEZEIT, J. R., AND T. L. GEORGE. 2002. Nest predators, nest-site selection, and nesting success of the dusky flycatcher in a managed ponderosa pine forest. Condor 104:507–517.

LOWTHER, P. E. 1993. Brown-headed cowbird. The birds of North America 47. The Academy of Natural Sciences, Philadelphia, Pennsylvania, USA, and the American Ornithologists Union, Washington, D.C., USA.

MAJOR, R. E., AND C. E. KENDAL. 1993. The contribution of artificial nest experiments to understanding avian reproductive success: a review of methods and conclusions. Ibis 138:298–307.

MARTIN, T. E. 1992. Breeding productivity considerations: what are the appropriate habitat features for management? Pages 455–473 *in* J. M. Hagen and D. W. Johnston, editors. Ecology and conservation of Neotropical migrant landbirds. Smithsonian Institution Press, Washington, D.C., USA.

———, I. J. BALL, AND J. TEWKSBURY. 1996. Environmental perturbations and the rates of nest predation in birds. Transactions of the 61st North American Wildlife and Natural Resources Conference 43–49.

———, AND G. R. GEUPEL. 1993. Nest-monitoring plots: methods for locating nests and monitoring success. Journal of Field Ornithology 64:507–519.

MAYFIELD, H. F. 1961. Nest success calculated from exposure. Wilson Bulletin 73:255–261.

———. 1975. Suggestions for calculating nest success. Wilson Bulletin 97:456–466.

MCCABE, R. A. 1991. The little green bird: ecology of the willow flycatcher. Rusty Rock Press, Madison, Wisconsin, USA.

MOLLER, A. P. 1989. Nest site selection across field-woodland ecotones: the effect of nest predation. Oikos 56:240–246.

MUSGROVE, B. F. 1951. Weasel foraging patterns in the Robinson Lake area, Idaho. Murrelet 32:8–11.

NATIONAL OCEANIC AND ATMOSPHERIC ADMINISTRATION. 1999. Climatological data annual summary, California. National Climate Data Center, Ashville, North Carolina, USA.

———. 2000. Climatological data annual summary, California. National Climate Data Center, Ashville, North Carolina, USA.

ORLOFF, S. G., A. W. FLANNERY, AND K. C. BELT. 1993. Identification of San Joaquin kit fox (*Vulpes macrotis mutica*) tracks on aluminum tracking plates. California Fish and Game 79:45–53.

ORTEGA, J. C., AND C. P. ORTEGA. 2000. Effects of brown-headed cowbirds and predators on the nesting success of yellow warblers in southwest Colorado. Journal of Field Ornithology 71:516–524.

PATON, P. W. 1994. The effect of edge on avian nest success: how strong is the evidence? Conservation Biology 8:17–26.

PICMAN J., M. L. MILKS, AND M. LEPTICH. 1993. Patterns of predation on passerine nests in marshes: effects of water depth and distance from edge. Auk 110:89–94.

RATLIFF, R. D. 1982. A meadow site classification for the Sierra Nevada, California. U.S. Forest Service General Technical Report PSW-60.

———. 1985. Meadows in the Sierra Nevada of California: state of knowledge. U.S. Forest Service General Technical Report PSW-84.

ROBINSON, S. K., J. A. GRYZBOWSKI, S. I. ROTHSTEIN, M. C. BRITTINGHAM, L. J. PETIT, AND F. R. THOMPSON, III. 1993. Management implications of cowbird parasitization on Neotropical migrant songbirds. Pages 93–102 *in* D. M. Finch and P. W. Strangel, editors. Status and management of Neotropical migratory birds. U.S. Forest Service General Technical Report RM-229.

———, S. I. ROTHSTEIN, M. C. BRITTINGHAM, L. J. PETIT, AND J. A. GRYZBOWSKI. 1995*a*. Ecology of cowbirds and their impact on host populations. Pages 428–460 *in* T. E. Martin and D. M. Finch, editors. Ecology and management of Neotropical migratory birds. Oxford University Press, New York, New York, USA.

———, F. R. THOMPSON, III, T. M. DONOVAN, D. R. WHITEHEAD, AND J. FAABORG. 1995*b*. Regional forest fragmentation and the nesting success of migratory birds. Science 267:1987–1990.

ROSENFIELD, R. N., AND J. BIELEFELDT. 1993. Cooper's hawk. The birds of North America 75. The Academy of Natural Sciences, Philadelphia, Pennsylvania, USA, and the American Ornithologists Union, Washington D.C., USA.

SANDERS, S. D., AND M. A. FLETT. 1989. Montane riparian habitat and willow flycatchers: threats to a sensitive environment and species. Pages 262–266 *in* D. L. Abell, technical coordinator. Proceedings of the California Riparian Systems Conference: Protection, Management, and Restoration for the 1990s. U.S. Forest Service General Technical Report PSW-110.

SAUER, J. R., J. E. HINES, I. THOMAS, J. FALLON, AND G. GOUGH. 2000. The North American Breeding Bird Survey, results and analysis 1966–1999. Version 98.1. U.S. Geological Survey Patuxent Wildlife Research Center, Laurel, Maryland, USA. (http://www.mbr.nbs.gov/bbs/bbs.html)

SEDGWICK, J. A., AND F. L. KNOPF. 1988. A high incidence of brown-headed cowbird parasitism of willow flycatchers. Condor 90:253–256.

SHEFFIELD, S. R., AND H. H. THOMAS. 1997. Mustela frenata. Mammalian Species 570:1–9.

SIEVING, K. E., AND M. F. WILLSON. 1998. Nest predation and avian species diversity in northwestern forest understory. Ecology 79:2391–2402.

SPSS. 1998. SPSS Graduate Pack 9.0 for Windows. SPSS, Chicago, Illinois, USA.

STEELE, M. A. 1999. Tamiasciurus douglasii. Mammalian Species 630:1–8.

STEIDL, R. J., J. P. HAYES, AND E. SCHAUBER. 1997. Statistical power analysis in wildlife research. Journal of Wildlife Management 61:270–279.

TEWKSBURY, J. J., S. J. HEJL, AND T. E. MARTIN. 1998. Breeding productivity does not decline with increasing fragmentation in a western landscape. Ecology 79:2890–2903.

UNITT, P. 1987. *Empidonax traillii extimus*: an endangered subspecies. Western Birds 18:137–162.

U.S. Fish and Wildlife Service. 1995. Final rule determining endangered status for the southwestern willow flycatcher. Federal Register 60:10694 (February 27, 1995).

WHITFIELD, M. J., AND M. K. SOGGE. 1999. Range-wide impact of brown-headed cowbird parasitism on the southwestern willow flycatcher (*Empidonax traillii extimus*). Pages 182–190 *in* M. L. Morrison, L. S. Hall, S. K. Robinson, S. I. Rothstein, D. C. Hahn, and T. D. Rich, editors. Research and management of the brown-headed cowbird in western landscapes. Studies in Avian Biology No. 18.

———, K. M. ENOS, AND S. P. ROWE. 1999. Is cowbird trapping effective for managing populations of the endangered southwestern willow flycatcher? Pages 260–266 *in* M. L. Morrison, L. S. Hall, S. K. Robinson, S. I. Rothstein, D. C. Hahn, and T. D. Rich, editors. Research and management of the brown-headed cowbird in western landscapes. Studies in Avian Biology No. 18.

WINTER, M., D. H. JOHNSON, AND J. FAABORG. 2000. Evidence for edge effects on multiple levels in tallgrass prairie. Condor 102:256–266.

YORK, E. C., T. L. MORUZZI, T. K. FULLER, J. F. ORGAN, R. M. SAUVAJOT, AND R. M. DEGRAAF. 2001. Description and evaluation of a remote camera and triggering system to monitor carnivores. Wildlife Society Bulletin 29:1228–1237.

ZAR, J. H. 1996. Biostatistical analysis. Third edition. Prentice-Hall, Inc., Upper Saddle River, New Jersey, USA.

ZEEDYK, B., B. ROMERO, AND S. K. ALBERT. 1996. Using simple structures for flow dispersion in wet meadow restoration. Pages 258–259 *in* D. W. Shaw and D. M. Finch, editors. Desired future conditions for southwestern riparian ecosystems: bringing interests and concerns together. U.S. Forest Service General Technical Report RM-272.

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