

Influence of Mammal Activity on Nesting Success of Passerines

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Abstract

For many avian species, predation is the leading cause of nest failure. However, relationships between predator abundance and nest predation often differ across spatial scales. We examined the relationship between environmental characteristics in meadows and mammalian predator activity, the relationship between predator activity at 2 spatial scales, and the probability of nest predation of willow flycatchers (*Empidonax traillii*), dusky flycatchers (*Empidonax oberholseri*), and yellow warblers (*Dendroica petechia*) in the central Sierra Nevada Mountains, California, USA. Environmental characteristics associated with the detection of nest predators varied depending on species. Douglas's squirrel (*Tamiasciurus douglasii*) and chipmunks (*Tamias spp.*) were associated with characteristics common along edges of meadows; short-tailed weasels (*Mustela erminea*) were associated with willows, whereas mice (*Peromyscus maniculatus*, *Reithrodontomys megalotis*, and *Microtus spp.*) and long-tailed weasels (*Mustela frenata*) were distributed throughout the meadows. The probability of predation of willow and dusky flycatcher nests increased with increasing short-tailed weasel activity, and the probability of predation of yellow warbler nests increased with increasing activity of chipmunks and short-tailed weasels. Variation in the occurrence of predator species in different areas of the meadows likely influences the probability of nest predation by each species and the nesting success of birds. Identifying factors that influence the distribution and abundance of common nest predators will likely be integral to the development of conservation efforts to increase the reproductive success of some bird species. (JOURNAL OF WILDLIFE MANAGEMENT 70(2):522–531; 2006)

Key words

California, *Dendroica petechia*, *Empidonax oberholseri*, *Empidonax traillii*, mammalian predator activity, montane meadows, neotropical migrants, nest predation, Sierra Nevada.

For many passerine species, nest predation is the most common cause of nest failure (Martin 1992). Birds nesting in areas with high abundances and activity of nest predators often have a high probability of nest predation (Andren 1992, Tewksbury et al. 1998, Cain et al. 2003). However, the relationships between predator abundance or activity and nest predation vary across spatial scales (Heske et al. 2001, Chalfoun et al. 2002). Environmental characteristics at local and regional spatial scales can influence predator abundance, activity, and the probability of nest predation (Donovan et al. 1997, Sieving and Willson 1998, Tewksbury et al. 1998, Dijak and Thompson 2000, Chalfoun et al. 2002). Differences between the eastern and western United States in relationships between predator abundance and nest predation rates may reflect differences in natural and anthropogenic levels of landscape heterogeneity, land use patterns (e.g., agricultural areas vs. forested areas), and predator communities (Donovan et al. 1997, Tewksbury et al. 1998, Dijak and Thompson 2000, Heske et al. 2001). At local spatial scales, variation in habitat features (e.g., vegetation associations, ecotones, successional stages, and presence of water or coarse woody debris) can influence the distribution and abundance of potential nest predators (Simms 1979, Andersen et al. 1980, Wilson and Carey 1996, Cain et al. 2003).

Because management efforts are often implemented at local or site-specific spatial scales, the design of effective conservation efforts requires knowledge of the identity and autecology of locally important nest predators, particularly factors that influence their distribution and abundance (Paton 1994, Heske et al. 2001, Chalfoun et al. 2002). Habitat features at the local scale can influence the distribution and abundance of nest predators and the probability of nest predation, knowledge of which habitat characteristics are associated with which nest predator species will be important in the development of site-specific management actions designed to reduce local nest predation rates (Martin 1992, Heske et al. 2001).

The willow flycatcher and the yellow warbler are riparian-obligate species that have experienced declines in California (Sauer et al. 2004). Willow flycatchers have been largely extirpated from the state and are currently restricted to a few isolated riparian meadow systems in the Cascade and Sierra Nevada ranges and along the Kern, San Luis Rey, and Santa Margarita rivers in southern California (Harris et al. 1987, Sanders and Flett 1989). The dusky flycatcher is not a riparian-obligate species, but riparian areas may be important breeding areas for this species in some regions (Cain and Morrison 2003). Dusky flycatcher populations are increasing in California, possibly because they may benefit from silvicultural practices that create forest openings (Sedgwick 1993, Sauer et al. 2004).

The decline of willow flycatchers and yellow warblers in California, like most declines of riparian-dependent species, is largely due to the loss of riparian breeding habitat and increases in brood parasitism (Harris et al. 1987, Sanders and Flett 1989,

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DeSante and George 1994). Although the role of nest predation in these population declines is unclear, preliminary analysis of data from an ongoing demography study indicates that willow flycatchers are declining in the central Sierra Nevada Mountains, California, USA (Loffland et al., 2003; Annual report and preliminary demographic analysis for willow flycatcher monitoring in the central Sierra Nevada, U.S. Forest Service, unpublished report). This preliminary data also indicated that nest predation is the leading cause of nest failure, and in most years of the study, juvenile recruitment was associated with the previous summer's fledging success; years with high fledging success were frequently followed by years with high juvenile recruitment. By limiting the number of fledglings produced each year, nest predation may be limiting the recovery of this population.

Our objectives were to determine whether environmental characteristics within meadows were associated with the probability of detection of common mammalian nest predators and to determine whether the probability of nest predation of willow flycatcher, dusky flycatcher, and yellow warbler nests was related to mammalian predator activity in the nest area. Knowledge of these factors can be used to identify areas of the meadows where predator removal or exclusion methods and vegetation management will likely have the largest impact on nest success.

Study Area

Our study area encompassed the north-central Sierra Nevada Mountains, California, USA. We monitored 12 meadows that supported breeding pairs of willow flycatchers. We selected sites that contained approximately 84% of the willow flycatcher territories that were located during 1997–1998 surveys of 104 meadows in the central Sierra Nevada Mountains (Bombay et al. 2003). The region was characterized by mountainous topography that was divided by glacial and riverine valleys. The majority of lands located within the study area were managed by the U.S. Forest Service including the Tahoe National Forest, Lake Tahoe Basin Management Unit, and Humboldt–Toiyabe National Forest. The remaining lands were managed by the California Department of Fish and Game and the California Department of Parks and Recreation, or they were privately owned. Average daily summer (Jun–Aug) temperatures typically ranged from 4 to 26°C. Late-afternoon thundershowers were common, and summer precipitation averaged 3.9 cm (National Oceanic and Atmospheric Administration 1999, 2000).

Study sites were wet montane meadows at elevations of 1,900 to 2,700 m, surrounded by lodgepole pine (*Pinus contorta*) forests. Meadows ranged in size from 4.6 to 167.0 ha ($\bar{X} = 55.8 \pm 15.6$ [SD] 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, particularly Lemmon's willow (*Salix lemmonii*) and Geyer's willow (*S. geyeriana*). Willow communities in the meadows often paralleled streams but were also found scattered in clumps across meadows. Big sagebrush (*Artemisia tridentata*) was present in drier portions of some 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 and predator activity in 6 meadows each breeding season (May–Aug), totaling 12 meadows over 2 breeding seasons. To determine which meadows were monitored each year, we listed the meadows in order from north to south and selected every other meadow for group 1; we placed the remaining meadows in group 2. We used a coin toss to determine which group of 6 meadows was monitored in 1999, and the other 6 were monitored in 2000.

Nest Location and Monitoring

We determined territory locations in each meadow by broadcasting male territorial songs and calls. We located nests by following adult birds exhibiting breeding behaviors (Martin and Geupel 1993). For each nest found, we recorded the number of eggs or nestlings. We monitored yellow warbler and dusky flycatcher nests every 3–4 days and willow flycatcher nests every 5–7 days, recording the number of eggs and nestlings and any evidence of nest predation or brood parasitism until the nest failed or young fledged from the nest. Because the willow flycatcher is listed as endangered under the California Endangered Species Act, we used a longer nest-monitoring interval to reduce potential negative impacts caused by observers. Evidence of nest predation included missing eggs or missing nestlings that were too young to have fledged. We classified nest fate as successful, depredated, parasitized, parasitized and depredated, abandoned, weather-related failure, or unknown. We considered nests successful if ≥ 1 nestling fledged. We considered the date of fledging or predation to be the midpoint between the penultimate and ultimate nest check. We excluded nests from analyses that were abandoned before they were completely built, failed before clutch initiation was confirmed, or failed for reasons other than predation. We recorded the location of all nests using a Trimble Pathfinder Pro-XR Global Positioning System (GPS) (Trimble Navigation Ltd., Sunnyvale, California) and measured the distance between each nest and the nearest forest edge.

Mammalian Predator Activity

We established track-plate transects in each meadow to assess the activity of potential mammalian nest predators (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 and perpendicular to the baseline transect. The direction of the first track-plate transect was determined randomly and subsequent track-plate transects were run in alternating directions. Each track-plate transect consisted of 4 track stations at 25-m intervals (Fig. 1). 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 (27 × 23 cm) 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). To bait potential nest predators, we sprayed quail eggs (*Coturnix coturnix*) with a mixture of egg and water, and placed 1 egg on the contact paper of each track plate.

We collected contact paper from each track plate weekly and replaced contact paper and quail eggs. We monitored track plates

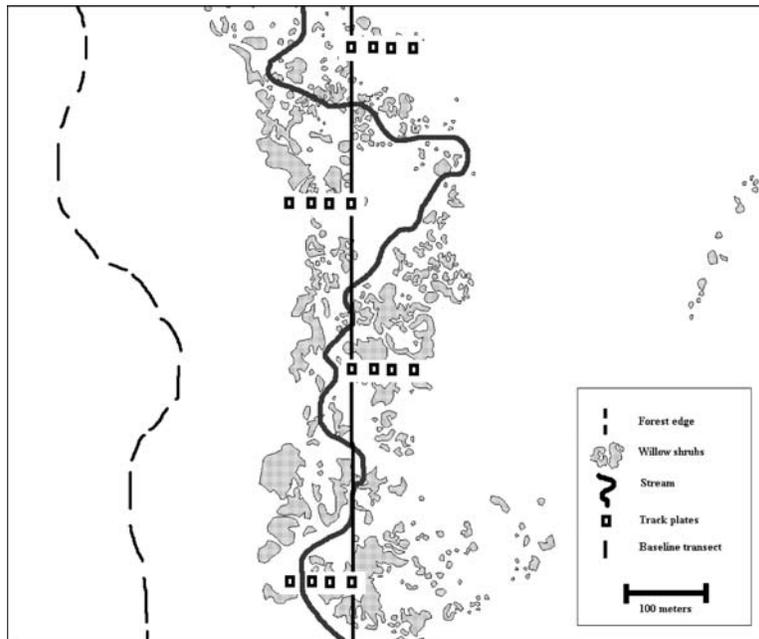


Figure 1. Typical arrangement of track-plate transects and track-plate locations used to monitor nest predator activity in montane meadows of the central Sierra Nevada Mountains, California, USA, 1999–2000.

in each meadow for as long as nests of the 3 avian species were active in that meadow. We identified tracks to the species level whenever possible with the following exceptions: 1) Because of the difficulty in differentiating chipmunk species based on tracks, we combined Allen’s chipmunk (*Tamias senex*), lodgepole chipmunk (*T. speciosus*), yellow pine chipmunk (*T. amoenus*), long-eared chipmunk (*T. quadrimaculatus*), and golden-mantled ground squirrel (*Spermophilus lateralis*); and 2) we also combined deer mouse (*Peromyscus maniculatus*), western harvest-mouse (*Reithrodontomys megalotis*), montane vole (*Microtus montanus*), and long-tailed vole (*M. longicaudus*) into a single group.

We calculated an index of predator activity for all species or groups of species for each track plate. Because we were unable to determine >1 individual of a species visited a track plate, we counted 1 detection/plate/week for each species detected (Hesse 1995). We were also unable to determine whether some of the same individuals visited track plates each week. Hence, we used the ratio of the number of detections per species to the number of weeks monitored as an index of activity for each track plate, rather than an index of abundance for each species.

Meadow Characteristics of Track-Plate Locations

We mapped the location of track plates using a Trimble GPS. We used ARCVIEW Geographic Information System (GIS) 3.2 (Environmental System Research Institute, Inc. Redlands, California) to digitize the perimeter of each meadow using orthographic aerial photos taken in 1996–1998 and imported the track-plate locations into ARCVIEW GIS. We then measured the distance between each track-plate location and the nearest forest edge using ARCVIEW GIS.

We recorded the substrate of the track-plate location as grass or bare ground and classified each track-plate location as wet or dry. We classified track-plate locations as wet if the soil at the track-plate location was moist to the touch at the midpoint of the field

season. We recorded the presence or absence of willows, sagebrush, conifers, and coarse woody debris within a 3-m radius of each track plate, and we recorded whether willows or conifers formed a canopy above each track plate.

Nest Selection and Predator Activity

We used ARCVIEW GIS to create and overlay coverage of the track plate and nest site locations. To examine whether nest fate was associated with the amount of predator activity in the area surrounding the nest, we compared predator activity in the area surrounding successful and depredated nests. Because the home-range sizes of the potential nest predators in our study area varied from <1 ha (e.g., deer mouse) to >10 ha (e.g., short-tailed weasel), we examined predator activity using 2 spatial scales: 100-m radius and 200-m radius surrounding each nest. For each predator species, we calculated overall activity index within the areas surrounding each nest by averaging the activity indices of all track plates located within 100 and 200 m of each nest. In further analyses, we only included nests that were successful or depredated and that were located ≤200 m of a track-plate transect.

Statistical Analyses

We performed all statistical analyses using SAS 9.1.3 (SAS Institute, Cary, North Carolina). To determine whether the probability of detection for each predator species was associated with the environmental characteristics at the track-plate location, we developed 20 a priori models that represented the varying environmental characteristics in different areas of the meadows (Table 1). We then used PROC LOGISTIC in SAS to model the probability that a species was detected for each a priori model. To determine whether the probability of predation was associated with the activity of each predator species, we created 12 a priori models that represented the potential variation in predator assemblages in different areas of the meadows (Table 2). Because

Table 1. Model number and structure of the 20 a priori models relating the probability of detection of nest predator species^a in montane meadows of the central Sierra Nevada Mountains, California, USA, 1999–2000.

Model number	Model structure ^b
1	WILLOW
2	WILLOW + CANW
3	WILLOW + DIST
4	WILLOW + DIST + MOIST
5	DIST
6	DIST + MOIST
7	DIST + SAGE
8	DIST + MOIST + SAGE
9	DIST + MOIST + SAGE + WILLOW
10	DIST + MOIST + SAGE + WILLOW + LOG
11	DIST + MOIST + SAGE + WILLOW + LOG + SUB
12	DIST + MOIST + SAGE + WILLOW + LOG + SUB + PINE
13	DIST + MOIST + SAGE + WILLOW + LOG + SUB + PINE + CANP
14	DIST + MOIST + SAGE + WILLOW + LOG + SUB + PINE + CANP + CANW
15	SUB + SAGE + DIST
16	SUB + SAGE + DIST + CANP
17	CANP + SUB + DIST + LOG + MOIST
18	CANP + SUB + DIST + LOG + MOIST + CANW
19	SAGE
20	SAGE + DIST + CANP

^a Mouse group (deer mouse, western harvest-mouse, montane vole, and long-tailed vole), chipmunk group (Allen’s chipmunk, lodgepole chipmunk, yellow pine chipmunk, long-eared chipmunk, and golden-mantled ground squirrel), Douglas’s squirrel, short-tailed weasel, and long-tailed weasel.

^bVariable notation: WILLOW = willow \leq 3 m from track plate (present/absent); CANW = canopy-forming willows above track plate (present/absent); DIST = distance to forest edge (m); MOIST = moisture of track plate location (wet/dry); SAGE = sagebrush \leq 3 m of track plate (present/absent); LOG = coarse wood debris \leq 3 m of track plate (present/absent); SUB = substrate (grass/bare ground) of track-plate location; PINE = conifers \leq 3 m from track plate (present/absent); CANP = canopy-forming conifers above track plate (present/absent).

nests were found during different stages of the nesting cycle and were not monitored for the same duration, we used the Mayfield logistic regression procedure described by Hazler (2004). We used PROC LOGISTIC in SAS with events/trials syntax to model the probability of predation for each of the 12 a priori models. We used an information-theoretic approach to select the most parsimonious model using Akaike’s Information Criterion (AIC_c) corrected for small sample sizes (Burnham and Anderson 2002). We used AIC_c to select our best model and considered models with Δ AIC_c values <2.0 to be competing models. To account for model-selection uncertainty, we calculated model-averaged parameter estimates (\pm SE) and 95% confidence intervals for variables in the competing models using multimodel averaging following Burnham and Anderson (2002). For ease of interpretation, we calculated odds ratios by exponentiating the model-averaged parameter estimates and 95% confidence intervals (Hosmer and Lemeshow 2000). The odds ratio indicates how much more or less likely it is for the outcome (i.e., detection or predation) to occur with a 1-unit change in the explanatory variable (Hosmer and Lemeshow 2000). Changes in explanatory variables with odds ratio confidence intervals that did not include 1.0 were considered to result in a change in the likelihood of the outcome of interest (i.e., detection or predation), whereas changes

Table 2. Model number and structure of the 12 a priori models relating the probability of nest predation of willow flycatcher, dusky flycatcher, and yellow warbler nests to nest predator activity and distance to forest edge in montane meadows of the central Sierra Nevada Mountains, California, USA 1999–2000.

Model number	Model structure ^a
1	TAMIA + TADO + PEMA + DIST
2	TAMIA + TADO + PEMA
3	TAMIA + TADO + MUER + MUFR + DIST
4	TAMIA + TADO + MUER + MUFR
5	TAMI + TADO + DIST
6	TAMI + TADO
7	MUER + PEMA + TAMI + MUFR + TADO + DIST
8	MUER + PEMA + TAMI + MUFR + TADO
9	MUER + MUFR + PEMA + DIST
10	MUER + MUFR + PEMA
11	MUER + MUFR + DIST
12	MUER + MUFR

^a Variable notation: TAMIA = chipmunk group; TADO = Douglas’s squirrel; PEMA = mouse group; MUER = short-tailed weasel; MUFR = long-tailed weasel; DIST = distance from nest to forest edge.

in variables with odds ratio confidence intervals that included 1.0 were concluded not to affect the likelihood of the outcome of interest.

Results

We monitored 32 dusky flycatcher, 41 willow flycatcher, and 76 yellow warbler nests. Of the nests ≤ 100 m from a track-plate transect, 50% of dusky flycatcher, 64% of willow flycatcher, and 47% of yellow warbler nests were depredated. Of the nests ≤ 200 m from a track-plate transect, 53% of dusky flycatcher, 61% of willow flycatcher, and 47% of yellow warbler nests were depredated.

Mammal species detected on $\geq 10\%$ of track-plate surveys included Douglas’s squirrel, short-tailed weasel, long-tailed weasel, and individuals from the mouse and chipmunk groups. Mink (*Mustela vison*), pine marten (*Martes americana*), striped skunk (*Mephitis mephitis*), raccoon (*Procyon lotor*), and yellow-bellied marmot (*Marmota flaviventris*), were each detected on an average of $\leq 10\%$ of surveys and were excluded from analysis.

Meadow Characteristics of Track-Plate Locations and Predator Activity

There were no individual models that best described the probability of detection for any of the predator species. There were 4 competing models that described the probability of detection for species in the mouse group (Table 3). These models included distance to forest edge, presence of sagebrush within 3 m of track plate, and moisture of track-plate location. However, odds ratios calculated from model-averaged parameter estimates all had 95% confidence intervals that included 1.0, providing little evidence that the probability of detection was associated with these variables (Table 4). There were 2 competing models that described the probability of detection of species in the chipmunk group, both of which included substrate of track-plate location, sagebrush within 3 m of track plate, and distance to forest edge as covariates and the highest ranking model also included conifers that formed a canopy over track plates (Table 3). The probability of detection of chipmunks decreased by 96% (i.e., odds ratio = 0.039) when there was a grass substrate and decreased by 2% with

Table 3. Five highest-ranking a priori models for the detection of each predator species or group of species relative to environmental characteristics^a in montane meadows of the central Sierra Nevada Mountains, California, USA 1999 – 2000. Maximized log-likelihoods, number of parameters (k), Akaike's Information Criterion adjusted for small sample size (AIC_c), ΔAIC_c, and Akaike weights. Models ranked according to AIC_c from best to worst approximating model.

Model	Log likelihood	k	AIC _c	ΔAIC _c	AIC _c weight
Mouse group ^b					
DIST	-81.25	3	87.25	0.0	0.321
DIST + SAGE	-80.07	4	88.07	0.82	0.213
SAGE	-82.71	3	88.71	1.46	0.155
DIST + MOIST	-80.96	4	88.96	1.71	0.137
DIST + MOIST + SAGE	-79.90	5	89.90	2.65	0.085
Chipmunk group ^c					
SUB + SAGE + DIST + CANP	-146.77	6	158.77	0.0	0.489
SUB + SAGE + DIST	-149.11	5	159.11	0.34	0.413
DIST + MOIST + SAGE + WILLOW + LOG + SUB + PINE	-146.12	9	164.12	5.35	0.034
DIST + MOIST + SAGE + WILLOW + LOG + SUB	-148.59	8	164.59	5.82	0.027
DIST + MOIST + SAGE + WILLOW + LOG + SUB + PINE + CANP + CANW	-143.23	11	165.23	6.46	0.019
Douglas' squirrel					
CANP + SUB + DIST + LOG + MOIST + CANW	-119.81	8	135.81	0.0	0.591
CANP + SUB + DIST + LOG + MOIST	-123.73	7	137.73	1.93	0.226
DIST + MOIST + SAGE + WILLOW + LOG + SUB + PINE	-122.56	9	140.56	4.75	0.055
DIST + MOIST + SAGE + WILLOW + LOG + SUB + PINE + CANP + CANW	-118.74	11	140.74	4.93	0.050
DIST + MOIST + SAGE + WILLOW + LOG + SUB + PINE + CANP	-121.49	10	141.49	5.68	0.034
Short-tailed weasel					
WILLOW + DIST	-325.34	4	333.34	0.0	0.290
WILLOW + DIST + MOIST	-323.55	5	333.55	0.21	0.261
WILLOW	-328.48	3	334.48	1.13	0.164
DIST + MOIST + SAGE + WILLOW + LOG + SUB + PINE + CANP + CANW	-317.57	11	339.57	6.23	0.010
DIST + MOIST + SAGE + WILLOW + LOG + SUB + PINE + CANP	-317.80	10	337.80	4.46	0.030
Long-tailed weasel					
SAGE	-190.89	3	196.99	0	0.414
SAGE + DIST	-190.73	4	198.89	1.91	0.159
DIST + MOIST + SAGE + WILLOW + LOG	-187.78	7	201.78	4.89	0.021
DIST + MOIST + SAGE + WILLOW	-190.21	6	202.21	5.32	0.017
DIST + MOIST + SAGE + WILLOW + LOG + SUB + PINE	-185.46	9	203.46	6.56	0.009

^a Variable notation as in Table 1.

^b Deer mouse, western harvest-mouse, montane vole, and long-tailed vole.

^c Allen's chipmunk, lodgepole chipmunk, yellow pine chipmunk, long-eared chipmunk, and golden-mantled ground squirrel.

every 1-m increase in distance to forest edge (Table 4). Probability of detection of species in the chipmunk group was 18 times higher on track plates located ≤3 m from sagebrush and 35% higher on track plates that were located under a canopy of conifers.

There were 2 competing models describing the probability of detection of Douglas's squirrels (Table 3). Both models included the substrate and moisture at the track-plate location, distance to forest edge, presence of coarse woody debris, and the presence of canopy forming conifers above track plates; the highest ranking model also included the presence of a canopy composed of willows at track-plate locations. Odds ratios for the presence of canopy-forming conifers and willows and the substrate at the track-plate location included 1.0, providing little evidence that the probability of detection of Douglas's squirrels changed with changes in these variables. The probability of detection of Douglas's squirrels was 20 times higher on track plates located ≤3 m from coarse woody debris, 77% lower in wet locations than in dry locations, and decreased by 2% with each 1-m increase in distance from the forest edge (Table 4).

There were 3 competing models that described the probability of detection of short-tailed weasels, which included the presence of willows within 3 m of track plates, distance to forest edge, and moisture of track-plate locations (Table 3). Only the odds ratios for the presence of willow within 3 m of track plates did not include 1.0; the probability of detection of short-tailed weasels was

approximately 1.3 times higher on track plates near willows than those without willows within 3 m (Table 4).

There were 2 competing models that described the probability of detection of long-tailed weasels; the highest-ranking model included only the presence of sagebrush as a covariate, and the competing model included both the presence of sagebrush and distance to forest edge. However, the 95% confidence intervals for odds ratio of both covariates included 1.0, indicating that the probability of detection did not change with changes in these variables (Table 4).

Nest Success and Predator Activity

Individual nests of all 3 avian species had different numbers of track plates within 100 m and 200 m. However, the predator activity indices around the nests of all 3 bird species were not correlated with the number of track plates present, either at the 100- or 200-m spatial scale (all Pearson $r \leq 0.16$, all $P \geq 0.05$).

Willow flycatchers.—There was not an individual model with enough support to suggest that it was the single best model describing the probability of predation for willow flycatcher nests in relation to predator activity within 100 m of the nests (Table 5). There were 2 competing models describing the probability of predation for willow flycatcher nests and predator activity within 100 m of the nests, both included short-tailed and long-tailed weasel activity, and the second highest-ranking model also

Table 4. Model-averaged logistic regression coefficient estimates, standard errors, odds ratios, and 95% confidence intervals for variables included in best-approximating models for the probability of detection of nest predator species relative to environmental characteristics^a in montane meadows of the central Sierra Nevada Mountains, California, USA 1999–2000.

Environmental variable	Model averaged coefficient		Odds ratio	95% Confidence interval	
	Estimate	SE		Lower CL	Upper CL
Mouse group ^b					
Sage	3.370	15.867	29.080	9.1×10^{-13}	9.3×10^{14}
Dist	0.007	0.005	1.010	0.990	1.020
Moist	-0.977	0.204	0.907	0.608	1.354
Chipmunk group ^c					
SUB	-3.245	1.116	0.039	0.004	0.347
SAGE	2.890	0.784	17.996	3.872	89.641
Dist	-0.017	0.005	0.983	0.974	0.993
CANP	0.303	1.534	1.354	0.067	27.361
Douglas's squirrel					
CANP	2.241	3.881	9.401	0.005	18.142
CANW	0.662	0.352	1.938	0.971	3.866
LOG	3.027	1.208	20.546	1.925	219.254
Dist	-0.015	0.004	0.985	0.976	0.994
Moist	-1.487	0.586	0.226	0.071	0.712
SUB	-1.366	0.813	0.255	0.052	1.254
Short-tailed weasel					
WILLOW	0.827	0.276	2.287	1.333	3.926
Dist	0.002	0.001	1.002	0.999	1.006
Moist	0.008	0.005	1.008	0.998	1.017
Long-tailed weasel					
Dist	0.001	0.002	1.001	0.997	1.005
SAGE	1.249	0.650	3.473	0.971	12.423

^a Variable notation as in Table 1.

^b Deer mouse, western harvest-mouse, mountain vole, and long-tailed vole.

^c Allen's chipmunk, lodgepole chipmunk, yellow pine chipmunk, long-eared chipmunk, and golden-mantled ground squirrel.

included activity of species in the mouse group (Table 5). However, the 95% confidence intervals for long-tailed weasel and species in the mouse group included 1.0 (Table 6). The probability of nest predation increased 6% with every 1% increase in short-tailed weasel activity within 100 m of willow flycatcher nests. The same 2 models were also competing models describing the

probability of predation for willow flycatcher nests and predator activity within 200 m of the nests (Table 7). Again, odds ratios for both long-tailed weasels and species in the mouse group both included 1.0. However, the probability of predation of willow flycatcher nests increased by 7% with every 1% increase in short-tailed weasel activity within 200 m of nests (Table 8).

Table 5. Five highest-ranking a priori models for the probability of predation relative to the activity of nest predators ≤ 100 m of willow flycatcher, dusky flycatcher, and yellow warbler nests in montane meadows of the central Sierra Nevada Mountains, California, USA, 1999–2000. Maximized log-likelihoods, number of parameters (k), Akaike's Information Criterion adjusted for small sample size (AIC_c), ΔAIC_c , and Akaike weights. Models ranked according to AIC_c from best- to worst-approximating model.

Model ^a	Log likelihood	k	AIC_c	ΔAIC_c	AIC_c weight
Willow flycatcher					
MUER + MUFR	-135.78	4	145.78	0.0	0.445
MUER + MUFR + PEMA	-134.18	5	147.33	1.56	0.204
MUER + MUFR + DIST	-135.78	5	148.93	3.16	0.092
MUER + MUFR + PEMA + DIST	-132.78	6	149.44	3.67	0.071
TAMI + TADO	-139.56	4	149.56	3.79	0.067
Dusky flycatcher					
MUER + MUFR	-85.43	4	96.10	0.0	0.517
MUER + MUFR + PEMA	-83.89	5	98.18	2.07	0.183
MUER + MUFR + DIST	-83.97	5	98.25	2.15	0.176
MUER + MUFR + PEMA + DIST	-81.49	6	99.95	3.85	0.076
TAMIA + TADO + MUER + MUFR	-84.16	6	102.63	6.52	0.020
Yellow warbler					
TAMIA + TADO + PEMA	-246.59	5	257.81	0.0	0.378
TAMI + TADO	-250.08	4	258.88	1.06	0.222
TAMIA + TADO + PEMA + DIST	-246.53	6	260.28	2.47	0.110
TAMI + TADO + DIST	-249.68	5	260.90	3.09	0.081
MUER + PEMA + TAMI + MUFR + TADO	-244.94	7	261.33	3.51	0.065

^a Variable notation as in Table 2.

Table 6. Mean predator-activity indices (\pm SD), model-averaged logistic regression coefficient estimates, standard errors, odds ratios, and 95% confidence intervals for variables included in best-approximating models for the probability of nest predation relative to predator activity ≤ 100 m from willow flycatcher ($n = 25$), dusky flycatcher ($n = 20$), and yellow warbler ($n = 58$) nests in montane meadows of the central Sierra Nevada Mountains, California, USA, 1999–2000.

Predator species ^a	Successful nests		Depredated nests		Model averaged coefficient		95% Confidence interval		Odds ratio
	Mean	SD	Mean	SD	Estimate	SE	Lower CL	Upper CL	
Willow flycatcher									
PEMA	0.547	0.283	0.346	0.056	-0.006	0.222	0.994	0.984	1.003
MUER	0.037	0.043	0.121	0.083	0.053	0.025	1.055	1.004	1.108
MUFR	0.0 ^b		0.020	0.011	0.394	0.210	1.480	0.982	2.237
Dusky Flycatcher									
PEMA	0.345	0.196	0.346	0.191	0.009	0.007	1.011	0.995	1.020
MUER	0.020	0.022	0.095	0.078	0.133	0.050	1.140	1.040	1.250
MUFR	0.011	0.020	0.021	0.018	0.288	0.166	1.330	0.964	1.850
DIST	57.810	35.017	30.430	28.470	-0.005	0.004	0.995	0.988	1.001
Yellow warbler									
PEMA	0.471	0.039	0.396	0.196	-0.019	0.011	0.982	0.962	1.001
TAMIA	0.020	0.039	0.076	0.013	0.058	0.024	1.060	1.012	1.111
TADO	0.017	0.048	0.026	0.064	-0.044	0.055	0.957	0.859	1.066

^a Variable notation as in Table 2.

^b Long-tailed weasels not detected on track plates ≤ 100 m of successful willow flycatcher nests.

Dusky flycatchers.—The model describing the probability of predation for dusky flycatcher nests with the lowest AIC_c value included short-tailed weasel and long-tailed weasel activity within 100-m of the nest, this model had 2.8 times more support than the second highest-ranking model, which included species in the mouse group in addition to the 2 weasel species (Table 5) and 2.9 times more support than the third highest-ranking model, which included the distance to the forest edge in addition to the weasel species. The probability of nest predation increased 14% with every 1% increase in short-tailed weasel activity within 100 m of the nests; however, the odds ratios for the distance to the forest edge and activity of long-tailed weasels and species in the mouse group included 1.0 (Table 6). There were 3 competing models describing the probability of predation and predator activity

within 200 m of dusky flycatcher nests (Table 7). The 2 highest ranking models had approximately equal support. The highest-ranking model included the distance to the forest edge and the activity of species in the chipmunk group and Douglas’s squirrels as covariates, whereas the second highest-ranking model included distance to the forest edge in addition to the activity of both short-tailed and long-tailed weasels as covariates; the third highest-ranking model included only the activity of the 2 weasel species. Of the 5 covariates included in the 3 competing models, only short-tailed weasel activity had an odds ratio with 95% confidence intervals that did not include 1.0. The probability of predation of dusky flycatcher nests increased 10% with every 1% increase in short-tailed weasel activity within 200 m of the nests (Table 8).

Table 7. Five highest-ranking a priori models for the probability of predation relative to the activity of nest predators ≤ 200 m of willow flycatcher, dusky flycatcher, and yellow warbler nests in montane meadows of the central Sierra Nevada Mountains, California, USA, 1999–2000. Maximized log-likelihoods, number of parameters (k), Akaike’s Information Criterion adjusted for small sample size (AIC_c), Δ AIC_c, and Akaike weights. Models ranked according to AIC_c from best- to worst-approximating model.

Model ^a	Log likelihood	k	AIC _c	Δ AIC _c	AIC _c weight
Willow flycatcher					
muer + mufr	-213.79	4	222.90	0.0	0.340
muer + mufr + pema	-212.14	5	223.85	0.95	0.231
muer + mufr + dist	-212.74	3	225.49	2.58	0.102
muer + mufr + pema + dist	-213.77	5	226.61	3.70	0.058
tami + tado + dist	-212.13	6	226.92	4.02	0.052
Dusky flycatcher					
TAMI + TADO + dist	-146.88	3	153.74	0.0	0.351
MUER + MUFR + dist	-141.66	5	153.97	0.23	0.312
MUER + MUFR	-145.97	4	155.46	1.72	0.148
muer + mufr + pema + dist	-141.66	6	157.02	3.28	0.068
muer + mufr + pema	-145.18	5	157.49	3.75	0.054
Yellow warbler nest					
TAMI + TADO + dist	-343.51	3	349.84	0.0	0.424
MUER + MUFR	-343.33	4	351.89	2.05	0.152
TAMI + TADO	-343.98	4	352.55	2.70	0.110
muer + mufr + pema	-341.69	5	352.55	2.71	0.110
muer + mufr + pema + dist	-341.14	6	354.36	4.52	0.044

^a Variable notation as in Table 2.

Table 8. Mean predator-activity indices (\pm SD), model-averaged logistic regression coefficient estimates, standard errors, odds ratios, and 95% confidence intervals for variables included in best-approximating models for the probability of nest predation relative to predator activity ≤ 200 m from willow flycatcher ($n = 41$), dusky flycatcher ($n = 32$), and yellow warbler ($n = 76$) nests in montane meadows of the central Sierra Nevada Mountains, California, USA, 1999–2000.

Predator species ^a	Successful nests		Depredated nests		Model averaged parameter			95% Confidence interval	
	Mean	SD	Mean	SD	Estimate	SE	Odds ratio	Lower CL	Upper CL
Willow flycatcher									
PEMA	0.295	0.352	0.238	0.237	-0.005	0.004	0.996	0.989	1.002
MUER	0.029	0.034	0.021	0.049	0.650	0.028	1.067	1.011	1.127
MUFR	0.003	0.009	0.077	0.055	0.037	0.034	1.037	0.971	1.109
Dusky Flycatcher									
TAMIA	0.132	0.152	0.115	0.145	-0.002	0.008	0.998	0.981	1.014
TADO	0.022	0.057	0.018	0.041	0.008	0.024	1.008	0.962	1.055
MUER	0.038	0.034	0.051	0.041	0.091	0.041	1.096	1.011	1.188
MUFR	0.015	0.023	0.018	0.041	0.134	0.085	1.144	0.968	1.351
DIST	44.88	33.04	30.52	24.66	-0.015	0.009	0.985	0.968	1.002
Yellow warbler									
TAMIA	0.105	0.187	0.160	0.200	0.047	0.005	1.048	1.039	1.057
TADO	0.021	0.047	0.022	0.051	-0.020	0.024	0.980	0.934	1.028
MUER	0.031	0.021	0.076	0.037	0.019	0.009	1.019	1.001	1.038
MUFR	0.011	0.017	0.023	0.042	0.019	0.251	1.019	0.622	1.668
DIST	107.64	81.87	84.32	58.40	-0.002	0.001	0.997	0.995	1.001

^a Variable notation as in Table 2.

Yellow warblers.—There were 2 competing models describing the probability of predation in relation to predator activity within 100 m of yellow warbler nests (Table 5). Both models included the activity of species in the chipmunk group and Douglas’s squirrels, and the highest-ranking model also included the activity of species in the mouse group. Only chipmunk activity had an odds ratio with 95% confidence intervals that did not include 1.0; the probability of predation of yellow warbler nests increased by 6% with every 1% increase in chipmunk activity within 100 m of the nests (Table 6). The model with the lowest AIC_c that described the probability of predation in relation to predator activity within 200 m of yellow warbler nests included the distance to forest edge and activity of both Douglas’s squirrels and species in the chipmunk group as covariates and the second highest-ranking model included short-tailed and long-tailed weasel activity as covariates (Table 7). However, distance to forest edge and Douglas’s squirrel and long-tailed weasel activity had odds ratios with confidence intervals that did not include 1.0 (Table 8). The probability of predation increased by 5% for every 1% increase in activity of species in the chipmunk group and increased by 2% with every 1% increase in short-tailed weasel activity.

Discussion

Variation in the distribution and activity of mammalian predator species in different areas of the meadows likely influences the probability of nest predation by each species and the nesting success of birds. The autecology of the potential mammalian nest predators in montane meadows influences the spatial variation in their occurrence. Environmental characteristics associated with the detection of potential mammalian nest predators depended on predator species. Douglas’s squirrel and chipmunks were most strongly associated with environmental characteristics (e.g., distance to forest edge, dry areas, presence of sagebrush, conifers, and coarse woody debris) common along edges of meadows, whereas detection of short-tailed weasels was associated with the presence of willow, which occurred throughout the meadows.

However, the probability of detection of other species (e.g., mice and long-tailed weasels) could not be explained in relation to the environmental characteristics we measured and may be due to the distribution of these species throughout the meadows.

The distribution of nest predators can influence the probability of nest predation. Sciurid rodents are typically associated with the forest interiors and edges of montane meadows (Andersen et al. 1980, Steele 1999). Nests located in areas near the forest edge, or in small meadows with a large perimeter to area ratio may be more likely to be depredated by chipmunks and squirrels (Smith and Andersen 1982, Cain et al. 2003). We found that the activity of chipmunks was associated with the probability of nest predation of yellow warblers but not willow flycatchers. Yellow warblers in these meadows tend to nest closer to the meadow edge than willow flycatchers, likely increasing the risk of predation by these predators (Cain et al. 2003). Conversely, the distribution of short-tailed weasels is generally associated with riparian areas, grassy-shrublands, and early successional communities with a high shrub-cover component that provides protective cover (Musgrove 1951, King 1983, Sheffield and Thomas 1997). In our study, short-tailed weasels occurred throughout the meadow, particularly in areas near willow shrubs. The detection of short-tailed weasels throughout the meadows and their use of willows as protective cover likely exposed all 3 bird species to predation risk from short-tailed weasels and may explain the association observed between short-tailed weasel activity and the nest success of yellow warblers, dusky flycatchers, and willow flycatchers. Similarly, thirteen-lined ground squirrels (*Spermophilus tridecemlineatus*) use shrubs as protective cover from raptors resulting in higher predation rates of McCown’s longspur (*Calcarius mccownii*) nests near shrubs than in nests farther away from shrubs (With 1994).

We did not find any major differences in the relationships between predator activity and the probability of nest predation when comparing the activity indices within 100 and 200 m of the nest. Short-tailed weasels were consistently included in the highest-ranking models, suggesting that they may be important

predators at these sites. Chipmunks may also be important predators; however, they were only included in the competing models for yellow warblers. These results are similar to the associations found when predator activity and nest success were compared at the intermeadow spatial scale (Cain et al. 2003). We acknowledge that high activity of a specific nest predator near nests does not necessarily mean that this species is responsible for depredating the nests (Peterson et al. 2004). However, the fact that chipmunks and short-tailed weasels were also 2 of the most commonly photographed species depredating yellow warbler nests in these meadows supports our predator activity results (Cain et al. 2003).

Population growth rates of passerines are largely determined by adult survival, juvenile recruitment, and fecundity. Of these factors, management opportunities may be greatest for influencing juvenile recruitment. Studies indicate that juvenile recruitment is highly associated with the previous summer's fledging success (Ricklefs 1992, Sherry and Holmes 1992, 1995). Furthermore, increases in the success of first nest attempts would likely have the largest impact on juvenile recruitment, given that first nest attempts of these species typically have larger clutch sizes than subsequent nesting attempts and birds that fledge earlier in the breeding season often have higher survival rates than those fledging later in the breeding season (Sedgwick 1993, Brown and Roland 2002).

Raccoons, Virginia opossums (*Didelphis virginiana*), striped skunks, and snakes are major nest predators in the eastern and midwestern United States (Donovan et al. 1997, Winter et al. 2000). In contrast, nest predation rates in the forested areas of the western United States are often related to the abundance and activity of forest predators (i.e., chipmunks, tree squirrels, corvids; Sieving and Willson 1998, Tewksbury et al. 1998, De Santo and Willson 2001, Liebezeit and George 2002). Knowledge of the autecology of the local nest predators will be essential to the

development of local conservation efforts to increase the nest success of some species. Determination of factors that influence the distribution and abundance of nest predators will likely be integral to the development of management plans for neotropical migratory birds (Heske et al. 2001, Calfoun et al. 2002).

Management Implications

We recommend that removal or exclusion efforts focused on short-tailed weasels and chipmunks be used to increase nest success and suggest that our results can be used to identify areas where these efforts are likely to have the most impact on predator species associated with the predation of willow flycatcher, dusky flycatcher, and yellow warbler nests in these meadows. For example, the removal or exclusion of chipmunks could focus on areas near willow shrubs that are near forest edge with bare ground, coarse woody debris, and sagebrush. Also, because the activity of chipmunks decreases with increasing meadow wetness (Cain et al. 2003), we recommend that managers use active flooding or restoration of water tables to limit meadow access for these predators. Finally, we suggest that our results may help identify areas where vegetation restoration efforts will be most beneficial to neotropical migrants and minimize the establishment of new willow shrubs in areas where nests would be more vulnerable to predation (Kus 1998, Bombay et al. 2003).

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