RESEARCH ARTICLE

Response of medium- and large-sized terrestrial fauna to corridor restoration along the middle Sacramento River

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A fundamental challenge in restoration ecology is to understand when species are expected to colonize newly created habitat. Determining this is important for assessing progress toward restoration goals and, more generally, for gaining insight into ecosystem functioning and dynamics. We studied this question as it relates to mid- to large-sized terrestrial fauna in restored riparian habitats at the Sacramento River National Wildlife Refuge, in northern California. We used camera traps to document use of 16 riparian corridor sites of varying restoration age. Comparisons of species richness (diversity) and visitation frequency (activity) were made across different-aged sites. We found that predator diversity and activity levels tended to be higher in restored forests than in remnant forests, and that they tended to be highest in young restored forests. This trend persisted when data from variable sampling periods were pooled, although significant differences occurred more often in wet and cold sampling periods. The trend did not always hold for the animal community at large (consisting of both predator and non-predator species). We conclude that restoration age affects predator diversity and activity levels in restored and remnant floodplain forests, and that predator communities can establish soon after restoration. Our results suggest that restoring natural river processes that promote habitat regeneration may benefit mid- to large-sized terrestrial predators that appear to mostly use early successional habitat.

Key words: floodplain, habitat use, mammals, predators, remnant, richness, riparian, succession

Implications for Practice

- Riparian corridor restoration can support medium- and large-sized mammalian predators along the middle Sacramento River by promoting the formation of early successional habitats, be it through active planting efforts, or through the restoration of river processes that naturally give rise to young habitat types.
- Because mature riparian forests appear to be used frequently by some species (e.g. black-tailed deer and wild turkeys), efforts should be made to protect this habitat type.

Introduction

Riparian corridor restoration can be vital to wildlife conservation in fragmented landscapes. Often associated with high biodiversity (Naiman et al. 1993), riparian corridors promote the connectivity necessary for interpatch movement (Gillies & St. Clair 2008), migration (Dingle et al. 2005; Walter et al. 2011), and dispersal (Clements et al. 2011).

It is assumed that restored corridors that closely resemble intact natural habitats will have high levels of use by wildlife, but more needs to be learned about the specific factors that influence colonization and use. The available literature offers valuable insights to guide corridor restoration. For example, wide corridors are used by more native species and have higher species richness than narrow corridors (Hilty & Merenlender 2004). Furthermore, species richness rises with corridor proximity to continuous forest (Downes et al. 1997). Importantly, several studies have shown that different-aged Sacramento River riparian restoration sites were favored by different organisms, such that species composition changed as the sites matured (Gardali et al. 2006; Golet et al. 2008; Williams 2010). Thus, some animals appear to require several years following riparian corridor restoration before habitat develops sufficiently to support them. Once habitat requirements are sufficiently met, wildlife may use corridors not only as movement routes but also for permanent residence (Downes et al. 1997). [Correction added on 15 December 2015, after first online publication: The

second sentence of this paragraph has been changed from "The available literature offers valuable insights into guide corridor restoration." to "The available literature offers valuable insights to guide corridor restoration."]

Although patterns of use vary, many mammalian species have been shown to use restored riparian corridors (Doherty & Grubb 2002; for review, see Noss & Daly 2006). Highly mobile mammalian top predators fare poorly in fragmented habitats (Crooks 2002), and are more likely to use corridors consisting of riparian habitats than anthropogenic landscapes (Hilty & Merenlender 2004; Shepherd & Whittington 2006).

Despite riparian corridors' presumed value to terrestrial fauna, few studies have examined how the mid- to large-sized members of this group respond to corridor restoration over time. The Sacramento River National Wildlife Refuge (SRNWR), with its suite of different-aged restoration sites, provides an opportune setting for just such an investigation. Here, 25 years of restoration work along California's largest river have led to the formation of riparian habitat that may serve a variety of functions—ranging from permanent home to stepping stone corridor—for highly mobile terrestrial species. However, the effects that this restoration work has had on mid- to large-sized terrestrial fauna have never been assessed. Previous studies in the area offer a basis to draw upon, having focused on smaller wildlife (land birds, insects, and small mammals) and vegetation (Alpert et al. 1999; Holl & Crone 2004; Golet et al. 2007, 2008, 2011, 2013a; McClain et al. 2011). These studies highlighted the importance of assessing restoration results across time or in reference to old or remnant habitat, because results may vary as habitats mature.

Our study supplements current knowledge of corridor ecology by characterizing medium- and large-sized terrestrial fauna's use of remnant and restored habitats. More specifically, it describes how species richness and visitation frequency in a riparian corridor are influenced by restoration age. Primarily, we analyze habitat use by mammalian predators; however, we also include prey species for which sufficient data are available. This provides information on species diversity and activity in habitats of different ages, which may be used to guide future restoration efforts.

Methods

Study Area

The Sacramento River once meandered freely through California's Central Valley, providing habitat for rich terrestrial and aquatic wildlife communities (USFWS 2005). In the mid-1800s, much of the diverse habitats were converted to agriculture and development (Katibah 1984). Today, approximately 5% of the Central Valley's historical riparian habitat remains (Warner & Hendrix 1985). Efforts to recover natural habitats and ecosystem processes along the Middle Sacramento River, where 10% of the area's historical wetland and riparian habitat can still be found (USFWS 2005), led to the initiation of riparian restoration and the formation of the SRNWR in

1989. For information on the restoration efforts, see Alpert et al. (1999) and Golet et al. (2013a).

The SRNWR consists of 28 units (USFWS 2015), from 11.3 to 465 ha in size (USFWS 2015), located discontinuously along 81 river miles (130 km) of the Middle Sacramento River, between the towns of Red Bluff and Colusa. These units contain mosaics of remnant and restored habitats, including mixed riparian, cottonwood, and valley oak riparian forests and woodlands; elderberry savanna, grasslands, sand and gravel bars, wetlands, scrub, and agriculture (USFWS 2005). The topography is generally flat, although remnant habitats tend to occur in somewhat lower elevation areas susceptible to flooding (a factor that rendered these areas unsuitable for conversion to agriculture). The region occurs in a Mediterranean climate, characterized by hot, dry, summers, followed by mild, variably wet winters (USFWS 2005). Cooler and warmer periods also differ in wildlife phenology and behavioral trends. Many mammal species native to the area have a tendency toward dispersal and movement during the cooler months, and breeding and/or rearing in the warmer months (Chapman & Feldhamer 1982).

Site Selection

We classified SRNWR habitats into three age treatments: young (restored in 2003–2007), old (restored in 1991–2000), and remnant (intact habitat that arose by natural means). A 3-year age gap was established between the thresholds that defined the upper age limit of old restoration and the lower age limit of young restoration to increase the functional habitat differences among age categories. We deemed 3 years to be sufficient based on visual inspections of the study areas, in which we observed notable differences in vegetation growth and canopy structure that we expected might influence wildlife use patterns. Young restoration contained less upper canopy, but more understory and diversity than did old restoration, in part because more herbaceous vegetation was added to restoration design over time (Gardali et al. 2006). Golet et al. (2008) list species planted at SRNWR restoration sites. Remnant forests had a less complex canopy structure than restored forests, and were characterized by upper canopy cover and sparse understory. Although the composition of habitat types varied across study sites such that overlap occurred, this habitat heterogeneity is typical in lowland alluvial floodplains where soils are often highly variable (Gallardo 2003). We standardized our comparisons across all three treatment groups by sampling only in native riparian forests. These forests included Fremont's cottonwood (*Populus fremonti*), valley oak (*Quercus lobata*), and feral hybridized black walnut (*Juglans hindsii* ×), intermixed with shrubs and herbs.

Sampling occurred along an approximately 100-km section of the Sacramento River (Fig. 1). Sample site selection occurred opportunistically, targeting areas characterized by riparian forest cover, flood safety, minimal human use, and relatively easy researcher accessibility. Within these areas, cameras were placed at sites that were sufficiently open to allow for movement of multiple animals at one time. One camera was placed at each site near animal sign (e.g. tracks, scat, and scratch
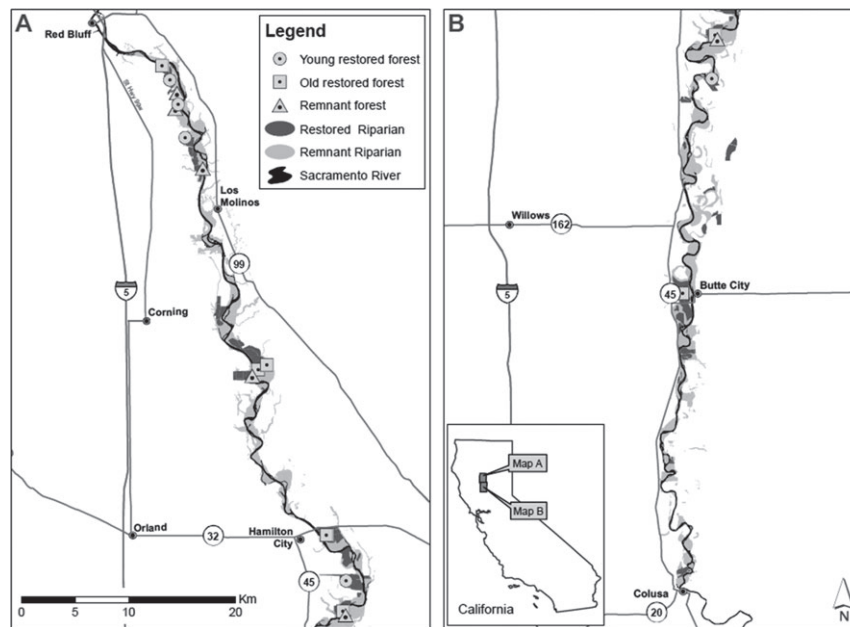
Figure 1. Sampling site locations in the SRNWR. Inset map shows the location of the northern (A) and southern (B) maps within California. The two southernmost sites in (A) appear as the two northernmost sites in (B), for geographic reference.

marks), to maximize detection. Sites were selected to span a variety of restoration ages within the prescribed age treatments and to provide wide coverage of the SRNWR, with an average distance of 5.34 km (SD = 7.05) between sites. All sites occurred within the 100-year floodplain; all restored sites were subject to restoration strategies associated with The Nature Conservancy's Sacramento River Project, including prioritization of flood-prone areas that contain and/or border remnant riparian habitat, revegetation with local ecotypes of indigenous flora, and restoration of natural river processes (USFWS 2005; Golet et al. 2008).

Initially, 18 sample sites (six sites per age treatment) were established; however, one site was discontinued because of the loss of a camera and another site was dropped due to excessive human presence, reducing the final number of sites to 16 (5 young, 6 old, and 5 remnant) (Fig. 1).

Data Collection

The study spanned both cool (31 December–8 March) and warm (23 May–5 July) time periods over two consecutive years (2010–2012). We used three types of camera traps to detect mammals: Bushnell Trophy Cam (Bushnell Outdoor Products, Inc., Overland Park, KS, U.S.A.), Moultrie Game Spy I45 (EBSCO Industries, Inc., Alabaster, AL, U.S.A.), and Wildview EZ-Cam (Stealth Cam, LLC, Grand Prairie, TX, U.S.A.). Although differences exist in these cameras' battery life and available modes, an independent scouting camera review source found their trigger times to be similar (ChasinGame 2009*a*, 2009*b*, 2010). The Wildview EZ-Cam battery life was lower than the other cameras and necessitated more frequent visits to camera sites for battery replacement. We minimized the

potential effect of human presence on animal visits to camera sites by applying scent eliminators to our clothes, shoes, and skin. Aside from these extra trips, all cameras were visited for general maintenance every 1–1.5 months. We attempted to keep cameras in position continuously throughout the study; however, individual duration of camera function varied due to battery shortage, camera malfunction, camera theft, and the need to remove some cameras from the field during floods and periods of high human presence associated with episodic public use (e.g. spring wild turkey [*Meleagris gallopavo*] hunting season).

We mounted cameras approximately 2.1 m off the ground on trees. Preliminary work showed that heights greater than 2.4 m hindered motion detector performance; heights less than 1.8 m reduced the cameras' field of view. Upon completion of camera trap setup, we applied Caven's "Gusto" scent lure (Minnesota Trapline Products, Pennock, MN, U.S.A.) mixed with tuna to a tree or large bush near each camera, to enhance trap effectiveness (Gompper et al. 2006; Barea-Azcon et al. 2007).

Data Analysis

We counted the number of species, as well as the number of visits made by each species, at each camera site. Visitation events were defined as one or several consecutive photos of a single animal species, in which photos are taken less than 1 hour apart from each other. Thus, each visitation event began at least 1 hour after a prior visitation event, and ended at least 1 hour before the next visitation event. This 1-hour interval is commonly accepted in camera trap studies to differentiate between separate visitation events by our focal species (J. Perrine 2011, California Polytechnic State University, personal communication), although preliminary data examination showed that visitation

Table 1. Cumulative animal detections per camera site over two sampling years. Due to potential differences in cameras' ability to detect smaller animals, we include only wildlife equivalent to or greater than skunks in height. Sites are listed under the names of the SRNWR units in which they were located. [a]Species analyzed separately because together they accounted for 99.5% of visitations.

| | | Cumulative Detections | | | | | | | | |
| | | Predators | | | | | | Other | | |
Sampling Site	Year Restored	Raccoon[a]	Coyote[a]	Bobcat[a]	Skunk	Puma	Stray Cat	Deer[a]	Turkey[a]	Pig
Young restoration										
Capay	2007	4	6	2				40		
Dead Man's Reach	2007	6	4	2				86		
La Barranca (north)	2006	9	16	6		1		116	1	
La Barranca (south)	2006	1	6		2			57	16	
Ohm	2003	27	10	4			1	82	15	
Total		47	42	14	2	1	1	381	32	
Old restoration										
Sul Norte	2000	14	10					31	35	
Pine Creek	1999	3	4	1				22	1	
Rio Vista (southwest)	1999	7	4					141		1
La Barranca	1997	2	2		1			82	1	
Rio Vista (southeast)	1993	41	2	4				43	2	
Phelan Island	1991							68	29	
Total		67	22	5	1			387	68	1
Remnant										
Flynn	N/A		1	1				26	179	
La Barranca	N/A	10	1		1			85	31	
Mooney	N/A		2	1	1			15	5	
Phelan Island	N/A		1					101	25	
Rio Vista	N/A							92		
Total		10	5	2	2			319	240	
Grand total		124	69	21	5	1	1	1,087	340	1

criteria as short as 15 minutes would have yielded essentially identical results. When visitation events involved more than one individual of a given species, we recorded the maximum number of individuals detected per visitation event.

We analyzed separately the species richness and visitation frequency of (1) all wild animals and (2) predators (Table 1). We examined only animals equivalent to or greater than striped skunks (*Mephitis mephitis*) in height, because the cameras we used may have differed in their ability to detect shorter animals.

To examine the potential effects of annual variation in weather conditions on our results, we analyzed data from (1) the cumulative dataset, (2) each sampling year separately, (3) all cooler months pooled together, and (4) all warmer months pooled together. This allowed us to account for the effects of a dry period that occurred during our second sampling year. Total precipitation, measured 30 days prior to the onset of sampling year and ending on the last sampling day, was 487 mm for the first year of our study and 268 mm for the second (Western Regional Climate Center 2013).

We transformed variables with non-normal distributions to satisfy requirements of normality (Table S1, Supporting Information). We then used one-way analysis of covariance (ANCOVA) to compare species richness and visitation frequency across restoration ages, with "age" (years since planting) as a fixed effect and "camera days" as a covariate. Our covariate controlled for sampling effort, that is the amount of time that each camera operated in the field. However, we found no effects (Table 2) of the covariate on our dependent variables

and therefore omitted this factor from further analyses. When ANCOVA tests showed significant differences between age categories, we used Sidak's multiple comparison probabilities to determine which specific age categories differed from one another.

When transformed data did not meet ANCOVA assumptions, we used one-way analysis of variance (ANOVA), and controlled for sampling effort by dividing each data entry by camera days (Table S1). When ANOVA tests showed significant differences, we used post hoc Tukey–Kramer tests to determine which specific forest age categories differed from one another.

Predators' warm season species richness and visitation data, and their visitation data in the entire first sampling year could not be normalized. For these datasets, we used Kruskal–Wallis tests to compare species-richness-to-camera-day ratios and visitation-frequency-to-camera-day ratios for individual animals in our forest age treatment groups. When Kruskal–Wallis tests showed significant differences in these ratios among treatments, we used Mann–Whitney *U*-tests between pairs of age groups with a Bonferroni correction to determine which specific age categories differed from one another.

For species with larger datasets (Table 1), we used the same methods as discussed above to compare species-specific cumulative visitation frequencies across forest age classes. We also examined these species for interactions that might account for community-level habitat use patterns. In this part of the analysis, we distinguished raccoons (*Procyon lotor*) as mesopredators, separate from the larger predator

Table 2. Main effects ($\alpha = 0.05$) of the fixed factor (forest age) and—if ANCOVA was conducted—covariate (camera days) on species richness and visitation frequency, after all necessary data transformations were applied.

| | | *Main Effects,* p | | |
| | *Species Richness* | | *Visitation Frequency* | |
	Forest Age	*Camera Days*	*Forest Age*	*Camera Days*
Cumulative data				
All species	0.14		0.06	0.30
Predators	0.04		0.09	0.12
Wet year data				
All species	0.02	0.58	0.37	0.77
Predators	0.01		0.03	
Dry year data				
All species	0.51	0.67	0.13	0.27
Predators	0.35	0.58	0.09	0.62
All cool season data				
All species	0.05	0.20	0.65	0.36
Predators	0.03	0.46	0.07	0.69
All warm season data				
All species	0.28		0.97	0.47
Predators	0.19		0.24	

community. We used Spearman's rank correlation analysis to examine whether or not the cumulative visitation frequencies (corrected for sampling effort) of any predator–predator, predator–mesopredator, or predator–prey species combinations were correlated. To account for potential additive effects of more than one predator species on mesopredators and prey, we compared black-tailed deer (*Odocoileus hemionus columbianus*) and turkey visitation to predator community-level visitation, and raccoon visitation to predator community visitation.

Results

We documented 1,960 animal visitations from a total of 5,810 animal photographs over 2,641 camera days. Of the 1,960 visitations, 1,649 were made by wild animals large enough in size to be included in our analyses. These animals consisted of non-predators, including 65.9% black-tailed deer (*Odocoileus hemionus columbianus*), 20.6% wild turkeys (*Meleagris gallopavo*), and 0.1% wild pigs (*Sus scrofa*), and predators, including 7.5% raccoons (*Procyon lotor*), 4.2% coyotes (*Canis latrans*), 1.3% bobcats (*Felis rufus*), 0.3% striped skunks (*Mephitis mephitis*), 0.1% pumas (*Puma concolor*), and 0.1% feral cats (*F. catus*) (Fig. 2). Thus, in our analyses, five of the nine species detected accounted for 99.5% of total animal visitations; bobcats, coyotes, and raccoons accounted for 96.8% of the predator visitations (Table 1). Within each forest age group, relative animal detection varied across sites (Table S2), in large part due to differences in camera days that were accounted for in the analysis.

Cumulative Results

Predator species richness was 1.9 times higher in young forests than in remnant forests (ANOVA: $F_{[2,13]} = 4.15$, $p = 0.040$)

(Fig. 3). In contrast, total animal species richness did not differ significantly across forest age groups (ANOVA: $F_{[2,13]} = 2.33$, $p = 0.136$). Visitation frequency did not vary significantly with forest age for predators (ANCOVA: $F_{[2,12]} = 3.04$, $p = 0.086$) or for the larger animal community (ANCOVA: $F_{[2,12]} = 0.064$, $p = 0.938$) (Fig. 4).

Wet Year (31 December 2010–5 July 2011)

In the wet year, the species richness of predators (ANOVA: $F_{[2,12]} = 8.26$, $p = 0.006$), and the larger animal community (ANCOVA: $F_{[2,11]} = 5.63$, $p = 0.021$) was higher in young forests than in remnant forests. Furthermore, predator species richness in young forests was 1.6 times higher than in old forests. Predators were also 18.1 times more likely to visit young forests than remnant forests (Kruskal–Wallis test: $\chi_2^2 = 7.07$, $p = 0.029$). Forest age had no significant effect on the visitation frequency of the animal community at large (ANCOVA: $F_{[2,11]} = 1.08$, $p = 0.372$).

Dry Year (31 December 2011–5 July 2012)

In the dry year, we detected no significant effects of forest age on the species richness of predators (ANCOVA: $F_{[2,12]} = 1.16$, $p = 0.347$) or the larger animal community (ANCOVA: $F_{[2,12]} = 0.712$, $p = 0.510$). Similarly, no effect of forest age on visitation frequency was detected in predators (ANCOVA: $F_{[2,12]} = 3.03$, $p = 0.086$) or the larger animal community (ANCOVA: $F_{[2,12]} = 2.44$, $p = 0.129$).

Cooler Sampling Periods (31 December–8 March)

During cooler periods, predator species richness was 2.1 times higher in young restored forests than in remnant forests (ANCOVA: $F_{[2,12]} = 4.98$, $p = 0.027$). The species richness of the larger animal community also tended to fall with forest age (ANCOVA: $F_{[2,12]} = 3.88$, $p = 0.050$), although Sidak post hoc comparisons identified no clear difference in species richness between any two forest age categories. On the other hand, visitation frequency did not change with forest age for either predators (ANCOVA: $F_{[2,12]} = 3.46$, $p = 0.065$) or the animal community at large (ANCOVA: $F_{[2,12]} = 0.46$, $p = 0.645$).

Warmer Sampling Periods (23 May–5 July)

During warmer periods, we detected no significant effect of forest age on the species richness of predators (Kruskal–Wallis test: $\chi_2^2 = 3.37$, $p = 0.186$) and the larger animal community (ANOVA: $F_{[2,13]} = 1.41$, $p = 0.280$) or on their respective visitation frequencies (for predators: Kruskal–Wallis test: $\chi_2^2 = 1.47$, $p = 0.480$; for all species, ANCOVA: $F_{[2,12]} = 0.03$, $p = 0.970$).

Individual Species' Visitation

Coyotes visited young restored forests 8.75 times more than remnant forests (Kruskal–Wallis test: $\chi_2^2 = 8.75$, $p = 0.013$). Forest age was not a significant predictor of visitation frequency for bobcats (Kruskal–Wallis test: $\chi_2^2 = 4.26$, $p = 0.119$), raccoons (Kruskal–Wallis test: $\chi_2^2 = 4.60$, $p = 0.100$), turkeys

Figure 2. Terrestrial fauna repeatedly documented at camera sites. Row 1 (left to right): bobcat (*Felis rufus*) and striped skunk (*Mephitis mephitis*). Row 2: raccoon (*Procyon lotor*) and black-tailed deer (*Odocoileus hemionus columbianus*). Row 3: coyote (*Canis latrans*) and wild turkey (*Meleagris gallopavo*).

(Kruskal–Wallis test: $\chi_2^2 = 2.41$, $p = 0.299$), and deer (ANOVA: $F_{[2,13]} = 0.354$, $p = 0.708$), despite predator species' apparent tendency to visit restored sites more than remnant sites, and turkeys' tendency to increase visitation with forest age (Table 1).

Correlations in Visitation Frequency

We found strong, positive correlations between the visitation frequencies of raccoons and coyotes (Spearman's test: $r_s(14) = 0$ 0.684, $p = 0$ 0.003), and between bobcats and coyotes (Spearman's test: $r_s(14) = 0.498$, $p = 0.049$). No other significant correlations between species–species and species–community visitation frequencies were detected.

Discussion

Our results suggest that, along the Sacramento River, forest age influences riparian habitat use for medium- to large-sized terrestrial fauna. Studies of other wildlife taxa (Gardali et al. 2006; Golet et al. 2007; Williams 2010) support our findings. Mammalian predators' visitation frequency and species richness tended to be higher in restored than in remnant forests. Furthermore, predator visitation and species richness tended to be higher in young restored forests than in old restored forests. These trends persisted even when data from variable seasons and climatic conditions were pooled, although they were more often significant in the wet year and in cooler months. Previous studies on the Sacramento River verify that the extent to which species richness differs between restored and remnant sites changes with season (Golet et al. 2011). High predator activity at restored and especially young sites was driven in large part by coyotes, likely due to their higher detection frequency. Nonetheless, members of the predator community with lower detection frequency generally followed the same trend on a non-significant level. In the terrestrial fauna community at large (including both predator and non-predator species), species richness patterns followed those of predators; lack of pattern in visitation frequency may have resulted from high numbers of deer detections in all forest age classes and high numbers of turkey detections in mature forests, especially at one remnant site.
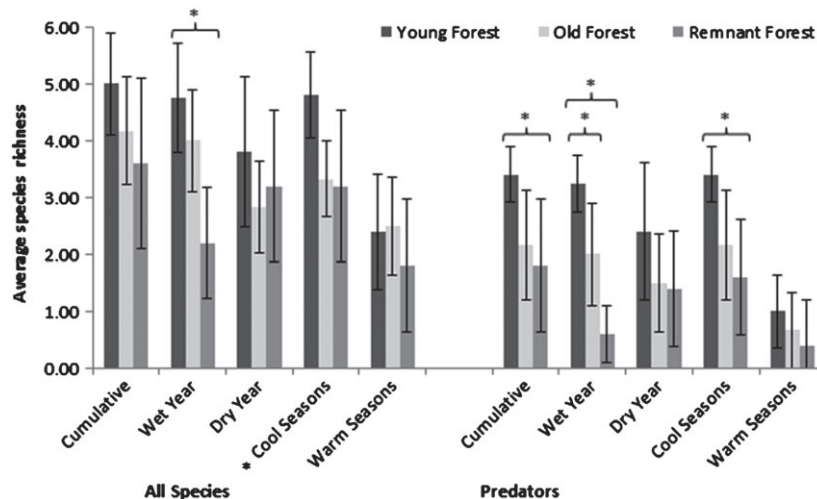
Figure 3. Average species richness for predators and all animals detected in three forest age treatments, at different sampling times. Error bars represent ±2SE. Averages and error bars are based on raw data; asterisks (*) mark significant differences ($p < 0.05$) based on transformed data. An asterisk on the horizontal axis indicates a significant effect of forest age, but that Sidak comparisons identified no clear difference between any two forest age categories.
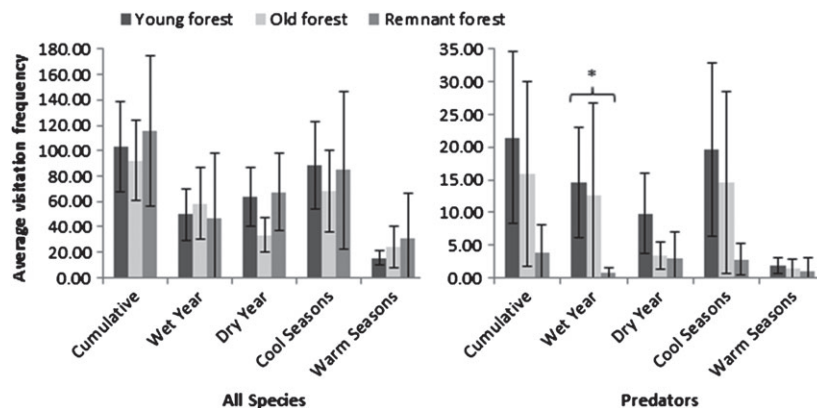

Figure 4. Average visitation frequency for predators and all animals detected in three forest age treatments, at different sampling times. Error bars represent ±2 SE. Averages and error bars are based on raw data; asterisks (*) mark significant differences ($p < 0.05$) based on transformed data.

Species-specific habitat preferences among predators may explain why species diversity and predator activity at SRNWR tended to be higher in restored and especially young forests. Although all predators in our study are habitat generalists (Ingles 1965; Verts & Carraway 1998; Jameson & Peeters 2004), even generalists display some level of preference. Bobcats (Ingles 1965; Litvaitis et al. 1986; Verts & Carraway 1998) and pumas (Dickson et al. 2005; Laundré & Loxterman 2007; Kertson et al. 2011) tend to favor brush, dense understory, and edge. Skunks (Ingles 1965; Verts & Carraway 1998; Bixler & Gittleman 2000) and coyotes (Litvaitis & Shaw 1980; Holzman et al. 1992; Jameson & Peeters 2004) typically prefer young or edge-like habitat with open canopies and brush, whereas raccoons opt for ready access to trees and water (Ingles 1965; Verts & Carraway 1998; Henner et al. 2004). In our study sites, predators' habitat preferences were apparently best satisfied by young forests, where edge-like environments, early successional stages, complex vegetation structure, and associated prey, such as California voles (*Microtus californicus*) (Golet et al.

2013*b*), abound. Although raccoons were less often observed in young restored sites than in old restored sites (possibly indicating selection for mature trees), this tendency was not significant and remained in accordance with our general finding that the predator community is more active in restored forests than in remnant forests. Thus, species-specific habitat choices contribute to community-level habitat use patterns [Correction added on 15 December 2015, after first online publication: Reference citation of Golet et al. 2013*b* has been changed from "(2013Golet et al. 2013*b*)" to "(Golet et al. 2013*b*)."].

Species interactions may also affect habitat use. Interestingly, there were no negative correlations in visitation frequencies between species to suggest the effects of mesopredator release (Ritchie & Johnson 2009) or predator avoidance (Sih 1984; Ritchie & Johnson 2009). For example, we found no significant negative correlation between turkey and predator visitation, despite coyotes', bobcats', raccoons', and skunks' reputation for preying on turkeys or their eggs (Thogmartin & Schaeffer 2000; Dreibelbis et al. 2008). Similarly, deer presence did not correlate

negatively with other predators, and remained generally even across all forest age categories (Derugin 2013). Those correlations that we detected were all positive. Raccoon and coyote visitation correlated highly, indicating as has been suggested by others (Gehrt & Clark 2003; Gehrt & Prange 2007), that mesopredator release is not always a major driver of their spatial distributions. Low detection did not allow us to analyze the interactions between all top predators (e.g. pumas) and mesopredators (e.g. skunks). We did not document any foxes, despite sampling in an area thought to be inhabited by both gray fox (*Urocyon cinereoargenteus*) and the Sacramento Valley red fox (*Vulpes vulpes* ssp. nov.; Sacks et al. 2010). Fox populations may be restricted by coyotes in the specific areas that we studied, as has been shown elsewhere (Harrison et al. 1989; Fedriani et al. 2000; Thompson & Gese 2007). The extent to which mesopredator release impacts habitat use patterns on the Sacramento River warrants further investigation. Further research is also needed to evaluate how interactions involving species that we did not document affect habitat use at SRNWR, e.g. the degree to which flood-induced declines and subsequent recovery of varying small mammal populations (Golet et al. 2013b) affect their predators' habitat choices. This interaction may explain predators' more pronounced presence at young habitats relative to the somewhat lower-elevation (i.e. flood prone) remnant habitats during rainy months [Correction added on 15 December 2015, after first online publication: Reference citation of Golet et al. 2013b has been changed from "(2013Golet et al. 2013b)" to "(Golet et al. 2013b)."].

Our study provides clear evidence that riparian corridor restoration along the Sacramento River benefits medium- and large-sized mammalian predators; these benefits are observed soon after restoration. Predators appear to respond positively to restored riparian forest sites. Remnant sites receive less use by predators, yet are frequented by common prey species (deer and turkey). Thus, both young and remnant habitats are needed to support the complement of mid- to large-sized terrestrial fauna documented at SRNWR. Further research needs include characterization of wildlife's habitat preferences based on differences in habitat availability, detection probabilities, and other factors. We suggest that management emphasize the restoration of natural river processes, such as meander migration and overbank flooding, to continuously provide conditions for new habitats and create landscape heterogeneity. The magnitude and potential of restoration along the middle Sacramento River are thrilling—a valley once stripped of its wildlands is now bisected by an increasingly continuous corridor of riparian habitat, one utilized by the very animals that so often symbolize wilderness in our minds [Correction added on 15 December 2015, after first online publication: The word "to" was removed from the fifth sentence of this paragraph, "Further research needs 'to' include characterization of wildlife's habitat preferences based on differences in habitat availability, detection probabilities, and other factors," and the word "emphasizes" has been changed to "emphasize" in the sixth sentence of this paragraph, "We suggest that management 'emphasizes' the restoration of natural river processes, such as meander migration and overbank flooding, … "].

LITERATURE CITED

Alpert P, Griggs FT, Peterson DR (1999) Riparian forest restoration along large rivers: initial results from the Sacramento River Project. Restoration Ecology 7:360–368

Barea-Azcon JM, Virgos E, Ballesteros-Duperon E, Moleon M, Chirosa M (2007) Surveying carnivores at large spatial scales: a comparison of four broad-applied methods. Biodiversity and Conservation 16:1213–1230

Bixler A, Gittleman JL (2000) Variation in home range and use of habitat in the striped skunk (*Mephitis mephitis*). Journal of Zoology 251:525–533

Chapman JA, Feldhamer GA (eds) (1982) Wild mammals of North America: biology, management, economics. The Johns Hopkins University Press, Baltimore, Maryland

ChasinGame (2009a) Moultrie I45 4mp MFH-DGS-I45 IR flash review. http://www.chasingame.com/index.php?id=114 (accessed 22 Apr 2013)

ChasinGame (2009b) Wildview EZ cam STC-TGLBC1 1.3mp white flash review. http://www.chasingame.com/index.php?id=106 (accessed 22 Apr 2013)

ChasinGame (2010) Bushnell Trophy Cam XLT review. http://www.chasingame.com/index.php?id=140 (accessed 22 Apr 2013)

Clements GM, Hygnstrom SE, Gilsdorf JM, Baasch DM, Clements MJ, Vercauteren KC (2011) Movements of white-tailed deer in riparian habitat: implications for infectious diseases. Journal of Wildlife Management 75:1436–1442

Crooks KR (2002) Relative sensitivities of mammalian carnivores to habitat fragmentation. Conservation Biology 16:488–502

Derugin VVD (2013) Response of mammalian predators to corridor restoration along the Middle Sacramento River. MS thesis. San Francisco State University, San Francisco, California

Dickson BG, Jenness JS, Beier P (2005) Influence of vegetation, topography, and roads on cougar movements in southern California. Journal of Wildlife Management 69:264–276

Dingle H, Zalucki MP, Rochester WA, Armijo-Prewitt T (2005) Distribution of the monarch butterfly, *Danaus plexippus* (L.) (Lepidoptera: Nymphalidae), in western North America. Biological Journal of the Linnean Society 85:491–500

Doherty PF, Grubb TC (2002) Survivorship of permanent-resident birds in a fragmented forested landscape. Ecology 83:844–857

Downes SJ, Handasyde KA, Elgar MA (1997) The use of corridors by mammals in fragmented Australian eucalypt forests. Conservation Biology 11:718–726

Dreibelbis JZ, Melton KB, Aguirre R, Collier BA, Hardin J, Silvy NJ, Peterson MJ (2008) Predation of Rio Grande wild turkey nests on the Edwards Plateau, Texas. The Wilson Journal of Ornithology 120:906–910

Fedriani JM, Fuller TK, Sauvajot RM, York EC (2000) Competition and intraguild predation among three sympatric carnivores. Oecologia 125:258–270

Gallardo A (2003) Spatial variability of soil properties in a floodplain forest in Northwest Spain. Ecosystems 6:564–576

Gardali T, Holmes AL, Small SL, Nur N, Geupel GR, Golet GH (2006) Abundance patterns of landbirds in restored and remnant riparian forests on the Sacramento River, California, U.S.A. Restoration Ecology 14:391–403

Gehrt SD, Clark WR (2003) Raccoons, coyotes, and reflections on the mesopredator release hypothesis. Wildlife Society Bulletin 31:836–842

Gehrt SD, Prange S (2007) Interference competition between coyotes and raccoons: a test of the mesopredator release hypothesis. Behavioral Ecology 18:204–214

Gillies CS, St. Clair CC (2008) Riparian corridors enhance movement of a forest specialist bird in fragmented tropical forest. Proceedings of the National Academy of Sciences of the United States of America 105:19774–19779

Golet GH, Bogiatto RJ, Hunt JW, Koenig D, Werner G (2007) Effects of riparian restoration on abundances of small mammal agricultural pest species (California). Ecological Restoration 25:136–137

Golet GH, Brown DL, Carlson M, Gardali T, Henderson A, Holl KD, et al. (2013*a*) Successes, failures and suggested future directions for ecosystem restoration of the Middle Sacramento River, California. San Francisco Estuary and Watershed Science 11:1–29. http://www.escholarship.org/uc/item/0db0t6j1 (accessed 25 Jun 2014)

Golet GH, Gardali T, Howell CA, Hunt J, Luster RA, Rainey W, Roberts MD, Silveira J, Swagerty H, Williams N (2008) Wildlife response to riparian restoration on the Sacramento River. San Francisco Estuary and Watershed Science 6:1–26. http://www.escholarship.org/uc/item/4z17h9qm (accessed 29 Jun 2009)

Golet GH, Gardali T, Hunt J, Koenig D, Williams N (2011) Temporal and taxonomic variability in response of fauna to riparian restoration. Restoration Ecology 19:126–135

Golet GH, Hunt JW, Koenig D (2013*b*) Decline and recovery of small mammals after flooding: implications for pest management and floodplain community dynamics. River Research and Applications 29:183–194

Gompper ME, Kays RW, Ray JC, LaPoint SC, Bogan DA, Cryan JR (2006) A comparison of noninvasive techniques to survey carnivore communities in northeastern North America. Wildlife Society Bulletin 39:1142–1151

Harrison DJ, Bissonette JA, Sherburne JA (1989) Spatial relationships between coyotes and red foxes in eastern Maine. Journal of Wildlife Management 53:181–185

Henner CM, Chamberlain MJ, Leopold BD, Burger LW Jr (2004) A multi-resolution assessment of raccoon den selection. Journal of Wildlife Management 68:179–187

Hilty JA, Merenlender AM (2004) Use of riparian corridors and vineyards by mammalian predators in northern California. Conservation Biology 18:126–135

Holl KD, Crone EE (2004) Local vs. landscape factors affecting restoration of riparian understory plants. Journal of Applied Ecology 41:922–933

Holzman S, Conroy MJ, Pickering J (1992) Home range, movements, and habitat use of coyotes in southcentral Georgia. Journal of Wildlife Management 56:139–146

Ingles LG (1965) Mammals of the Pacific States: California, Oregon, and Washington. Stanford University Press, Stanford, California

Jameson EW Jr, Peeters HJ (2004) California mammals. University of California Press, Berkeley

Katibah EF (1984) A brief history of riparian forests in the Central Valley of California. Pages 2–22. In: Warner RE, Hendrix KM (eds) California riparian systems: ecology, conservation, and productive management. University of California Press, London, United Kingdom

Kertson BN, Spencer RD, Marzluff JM, Hepinstall-Cymerman J, Grue CE (2011) Cougar space use and movements in the wildland-urban landscape of western Washington. Ecological Applications 8:2866–2881

Laundré JW, Loxterman J (2007) Impact of edge habitat on summer home range size in female pumas. American Midland Naturalist 157:221–229

Litvaitis JA, Shaw JH (1980) Coyote movements, habitat use and food habits in Southwestern Oklahoma. Journal of Wildlife Management 44:62–68

Litvaitis JA, Sherburne JA, Bissonette JA (1986) Bobcat habitat use and home range size in relation to prey density. Journal of Wildlife Management 50:110–117

McClain CD, Holl KD, Wood DM (2011) Successional models as guides for restoration of riparian forest understory. Restoration Ecology 19:280–289

Naiman RJ, Decamps H, Pollock M (1993) The role of riparian corridors in maintaining regional biodiversity. Ecological Applications 3:209–212

Noss RF, Daly KM (2006) Incorporating connectivity into broad-scale conservation planning. Pages 587–619. In: Crooks KR, Sanjayan M (eds) Connectivity conservation. Cambridge University Press, New York

Ritchie EG, Johnson CM (2009) Predator interactions, mesopredator release and biodiversity conservation. Ecology Letters 12:982–998

Sacks BN, Wittmer HU, Statham MJ (2010) The Native Sacramento Valley red fox. Report to the California Department of Fish and Game, May 30, 2010, 49pp

Shepherd B, Whittington J (2006) Response of wolves to corridor restoration and human use management. Ecology and Society 11:1. http://www.ecologyandsociety.org/vol11/iss2/art1 (accessed 12 Jun 2009)

Sih A (1984) The behavioral response race between predator and prey. The American Naturalist 123:143–150

Thogmartin WE, Schaeffer BA (2000) Landscape attributes associated with mortality events of wild turkeys in Arkansas. Wildlife Society Bulletin 28:865–874

Thompson CM, Gese EM (2007) Food webs and intraguild predation: community interactions of native mesocarnivore. Ecology 88:334–346

U.S. Fish and Wildlife Service (2005) Sacramento River National Wildlife Refuge final comprehensive conservation plan. California/Nevada Refuge Planning Office/Sacramento National Wildlife Refuge Complex, Sacramento, California/Willows, California

U. S. Fish and Wildlife Service (2015) 2015 Annual habitat management plan: Sacramento River National Wildlife Refuge. Sacramento National Wildlife Refuge Complex, Willows, California

Verts BJ, Carraway LN (1998) Land mammals of Oregon. University of California Press, Berkeley

Walter WD, Baasch DM, Hygnstrom SE, Trindle BD, Tyre AJ, Millspaugh JJ, Frost CJ, Boner JR, VerCauteren KC (2011) Space use of sympatric deer in a riparian ecosystem in an area where chronic wasting disease is endemic. Wildlife Biology 17:191–209

Warner RE, Hendrix KM (1985) Riparian resources of the Central Valley and California desert: final draft. The Resources Agency, Department of Fish & Game, Sacramento, California

Western Regional Climate Center (2013) Remote automated weather station: station monthly summary for Corning, California. http://www.raws.dri.edu/cgi-bin/rawMAIN.pl?caCCRN (accessed 22 Apr 2013)

Williams NM (2010) Restoration of nontarget species: bee communities and pollination function in riparian forests. Restoration Ecology 19:450–459

Supporting Information

The following information may be found in the online version of this article:

Table S1. Transformations applied to datasets. CD, camera days; K, largest possible value + 1; Pred, predator; Spp, species; SR, species richness; TopPred, top predator.
Table S2. Percent of cumulative animal detections per camera site over two sampling years.