The Condor 103:491–501
© The Cooper Ornithological Society 2001

REPRODUCTIVE SUCCESS OF LEWIS'S WOODPECKER IN BURNED PINE AND COTTONWOOD RIPARIAN FORESTS

VICTORIA A. SAAB[1,3] AND KERRI T. VIERLING[2,4]

[1]*USDA Forest Service, Rocky Mountain Research Station, 316 E. Myrtle Street, Boise, ID 83702*
[2]*Department of EPO Biology, University of Colorado, Boulder, CO 80309*

Abstract. Lewis's Woodpecker (*Melanerpes lewis*) has been characterized as a ''burn specialist'' because of its preference for nesting within burned pine forests. No prior study, however, has demonstrated the relative importance of crown-burned forests to this woodpecker species by examining its reproductive success in different forest types. We studied breeding Lewis's Woodpeckers in cottonwood (*Populus fremontii*) riparian forest patches of Colorado and crown-burned ponderosa pine (*Pinus ponderosa*) forests of Idaho to compare their reproductive success, productivity, and potential source-sink status in the two forest types. Daily nest survival rates were significantly lower in cottonwood compared to burned pine forests. Nesting success was 46% ($n = 65$) in cottonwood forests and 78% ($n = 283$) in burned pine forests. Proportion of nests destroyed by predators was significantly higher in cottonwood forests (34%) compared to burned pine forests (16%). We consistently found crown-burned forests to be potential source habitat, whereas cottonwood riparian sites were more often concluded to be potential sink habitat. Cottonwood riparian forests were surrounded primarily by an agricultural landscape where the composition and abundance of nest predators was likely very different than the predator assemblage occupying a large-scale burn in a relatively natural landscape. Conversion of riparian and adjacent grassland landscapes to agriculture and prevention of wildfire in ponderosa pine forests have likely reduced nesting habitat for this species. Prescribed understory fire is the prevailing management tool for restoring ponderosa pine ecosystems. Conditions created by crown fire may be equally important in maintaining ponderosa pine systems and conserving nesting habitat for the Lewis's Woodpecker.

Key words: crown-burned forests, Lewis's woodpecker, Melanerpes lewis, *nest success,* Pinus ponderosa, Populus fremontii, *source-sink habitats.*

Éxito Reproductivo de *Melanerpes lewis* en Bosques de Pinos Quemados y Bosques Ribereños de *Populus fremontii*

Resumen. *Melanerpes lewis* ha sido caracterizado como un ''especialista de quemas'' porque prefiere anidar en áreas de pinos maduros quemados. Sin embargo, ningún estudio anterior ha demostrado la importancia relativa de los bosques de árboles con copas quemadas para este carpintero examinando su éxito reproductivo en diferentes tipos de bosques. Estudiamos *M. lewis* reproductivos en parches de bosques ribereños de *Populus fremontii* en Colorado y bosques de *Pinus ponderosa* con las copas quemadas en Idaho para comparar su éxito reproductivo, productividad y la condición potencial de fuente-sumidero de los dos tipos de bosques. Las tasas diarias de supervivencia de los nidos fueron significativamente más bajas en los bosques de *Populus fremontii* que en las áreas de pinos maduros quemados. El éxito de los nidos fue de 46% ($n = 65$) en los bosques de *Populus fremontii* y 78% ($n = 283$) en los bosques de pinos quemados. La proporción de nidos destruídos por depredadores fue signicativamente más alta en los bosques de *Populus fremontii* (34%) que los bosques de pinos quemados (16%). Encontramos consistentemente que las áreas de pinos con las copas quemadas son potencialmente hábitats fuente mientras que los bosques de *Populus fremontii* fueron considerados como sumideros potenciales con mayor frecuencia. Los bosques de *Populus fremontii* estaban rodeados principalmente por un paisaje agrícola donde la composición y la abundancia de los depredadores de nidos eran probablemente muy diferentes de las de un área quemada de gran escala en medio de un paisaje natural. La conversión de paisajes ribereños y de pastizales a áreas agrícolas y la prevención de fuegos naturales en los bosques de *P. ponderosa* probablemente ha reducido el habitat de anidación de esta especie. El manejo de fuegos planificados en el sotobosque es la técnica más utilizada para reestablecer los ecosistemas de *P. ponderosa.* Las condiciones creadas por el fuego en

Manuscript received 13 September 2000; accepted 27 April 2001.
[3] E-mail: vsaab@fs.fed.us
[4] Present address: South Dakota School of Mines and Technology, Department of Chemistry and Chemical Engineering, Rapid City, SD 57701.

las copas de los árboles podían ser igualmente importante para mantener los sistemas de *P. ponderosa,* incluyendo la conservación de los hábitats de anidación de *M. lewis.*

INTRODUCTION

Populations of Lewis's Woodpecker (*Melanerpes lewis*), found in open woodlands throughout western North America, have been declining at both regional and local scales (Tobalske 1997). During 1966–1994, Breeding Bird Survey data for the U.S. indicated a significant negative trend in relative abundance per year ($-3.4 \pm 3.0\%$ [95% CI]; $P < 0.05$, $n = 55$ routes; Tobalske 1997). Possible explanations for these declines include losses of suitable habitat, increased mortality due to pesticides, and competition for nest holes. Unlike most picids, Lewis's Woodpeckers are primarily aerial flycatchers during the breeding season. Ponderosa pine (*Pinus ponderosa*) forests and riparian woodlands dominated by cottonwoods (*Populus* spp.) have been identified as the most important nesting habitats for Lewis's Woodpecker (Tobalske 1997). Open stands of ponderosa pine and burned, partially logged pine forests are particularly valuable nesting habitat (Tobalske 1997, Saab and Dudley 1998). In fact, Lewis's Woodpeckers have been characterized as ''burn specialists'' because of their preference for nesting in snags within burned pine forests (Bock 1970, Raphael and White 1984, Tobalske 1997, Linder and Anderson 1998). This species is thought to favor burned forests not only because of snag abundance, but also because of the relatively open canopy that allows for shrub development and associated arthropod prey (Bock 1970), good visibility and perch sites for foraging (Linder and Anderson 1998), and space for foraging maneuvers (Saab and Dudley 1998).

The breeding distribution of the Lewis's Woodpecker closely follows the range of ponderosa pine (Fig. 1). This species may have evolved in open ponderosa pine systems, which were historically maintained by frequent, low-severity fire (Agee 1993). Practices of fire exclusion, selective timber harvest, and livestock grazing since Euro-American settlement have disrupted the natural process of fire in ponderosa pine systems and subsequently altered the composition and structure of these forests (Shinneman and Baker 1997). Western riparian habitats are considered the most degraded ecosystems in western North America and have suffered losses due to water management practices, livestock grazing, and agricultural and urban development (Ohmart 1994, Noss et al. 1995, Saab et al.

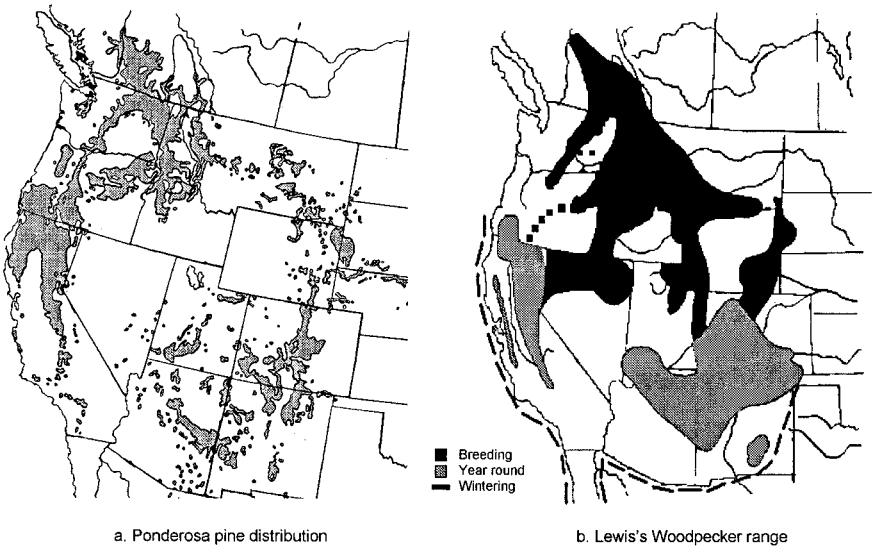

FIGURE 1. (a) Distribution of ponderosa pine (Little 1971), and (b) range of Lewis's Woodpecker (Tobalske 1997) in North America. The dark squares represent local breeding sites in Washington and Oregon. The species winters irregularly south and west to the dashed line.

1995). These ecological changes in ponderosa pine and cottonwood riparian forests have likely reduced or degraded conditions for Lewis's Woodpecker. Thus, the loss of suitable habitat is a plausible hypothesis for population declines of this woodpecker species.

Several studies have documented the presence or absence of nesting birds in burned forests (Bock 1970, Raphael and White 1984, Block and Brennan 1987, Linder and Anderson 1998) and open riparian woodlands (Bock 1970, Vierling 1997). No study, however, has demonstrated the relative importance of crown-burned forests to Lewis's Woodpeckers by examining their demography in different forest types. Yet this information is required to identify habitat features that are necessary for the long-term persistence of Lewis's Woodpecker. The purpose of this study was to compare reproductive success and productivity of Lewis's Woodpecker breeding in cottonwood riparian habitats of Colorado and crown-burned ponderosa pine forests of Idaho, and to use demographic parameters to evaluate the potential source or sink status of the two habitats.

Our comparison may be problematic because the two forest types we studied are inherently different in vegetation composition, structure, and other microhabitat features. Comparing different fire conditions in ponderosa pine forests would be the best test for determining if high-severity, crown fire within this forest type creates source habitat for Lewis's Woodpecker. We located few nests in unburned pine forests and have not had the opportunity to study these woodpeckers in surface-burned forests. Here, our objective is to compare population demographics between two important nesting habitats for Lewis's Woodpecker, cottonwood riparian forest patches and crown-burned ponderosa pine forests.

METHODS

STUDY AREAS

The burned habitat was located in ponderosa pine forests of southwestern Idaho (43°35′N, 115°42′W). We studied nesting woodpeckers in two burns separated by 0–20 km. Most nests (90%) were monitored during 1994–1997 within an 89 159-ha burn created in August 1992 by a high-severity, stand-replacing wildfire (Idaho Foothills study site, Table 1). Half of the standing dead trees (snags) >23 cm diameter breast height (dbh) at this site were removed (salvage-logged) during the first year after the fire (Saab and Dudley 1998). The other 10% of nests were monitored during 1995–1997 within a 12 467-ha burn created in August 1994 by a mixed-severity, patchy wildfire (Star Gulch study site, Table 1). Elevation ranged from 1130 m to 2300 m. Ninebark (*Physocarpus malvaceus*) and mountain balm (*Ceanothus velutinus*) were the most abundant understory shrubs. Trees and snags were often patchily distributed within the burned landscapes and interspersed with large openings of shrubs. Most standing trees were snags, due to the severity of the fires. Nest trees (n = 256) averaged 46.7 ± 1.2 cm (SE) dbh, whereas the mean diameter of non-nest random trees (n = 256) was 21.0 ± 0.8 cm.

TABLE 1. Percentages of land classes within and surrounding (within a 1-km radius) study sites surveyed in burned pine forest of Idaho and cottonwood forest patches of Colorado. Area surveyed by study site is reported in parentheses.

	Idaho Foothills (1271 ha)	Idaho Star Gulch (949 ha)	Colorado Foothills (423 ha)	Colorado Plains (2123 ha)
Agriculture	0	0	15	76
Forest	79[a]	95[a]	85[b]	<3[b]
Grassland	0	0	0	10
Residential	0	0	0	10
Shrubland	21	5	0	0
Water/wetland	0	0	0	<2

[a] Burned ponderosa pine-Douglas-fir (*Pseudotsuga menziesii*) forest.
[b] Unburned ponderosa pine and cottonwood forests.

We studied nesting woodpeckers at two unburned cottonwood riparian sites in central Colorado during 1992 and 1993. One site consisted of cottonwood riparian patches on the plains of the Arkansas River Valley (38°05′N, 103°45′W, elevation 1285 m) in an area of 2123 ha that was intensively farmed or grazed by livestock (Colorado Plains study site, Table 1). Nest trees occurred on the edges of the riparian zone in small cottonwood forest patches consisting primarily of broadleaf cottonwoods (*Populus fremontii*). Diameters (dbh) of nest trees (n = 47) in both study sites averaged 112.6 ± 0.9 cm (SE), while the mean of non-nest random trees (n = 47) was 63.6 ± 1.1 cm (SE) (Vierling 1997). Shrubs were absent near the cottonwood

groves, primarily due to the agricultural nature of the landscape. The second study site was near the foothills of the Wet Mountains (38°05′N, 104°58′W, elevation 1939 m) with moderate livestock grazing (Colorado Foothills study site, Table 1). The shrub layer was virtually nonexistent, presumably because of livestock grazing pressures. Nest trees were primarily broadleaf cottonwoods (Vierling 1997). Additionally, we conducted extensive nest searches in unburned ponderosa pine forests over an area of 6000 ha to the west of the foothills study area during 1992 and 1993. Only one pair of Lewis's Woodpeckers was found nesting in the pines, so we were unable to include any data from the unburned pine forests. Thus, our nesting data comparisons are in cottonwood forests of Colorado and high-intensity, burned ponderosa pine forests of Idaho.

Landscape composition, including a 1-km radius surrounding each of the study sites, was markedly different in the two study areas (Table 1). Land and vegetation classes were derived from Landsat Thematic Mapper images. Agriculture dominated the Colorado Plains landscape, while ponderosa pine forest and some agriculture surrounded the Colorado Foothills study site. The Idaho landscapes were composed entirely of coniferous forest and shrubland.

NEST AND VEGETATION MONITORING

In Idaho, we conducted a complete census of occupied nests using belt transects (0.4 × 1.0 km) during mid-May through June in an area that averaged 2220 ha each year from 1994–1997. In Colorado, we conducted a complete census of 2546 ha in plains/cottonwood habitat during 1992 and 1993.

We monitored nests every 3–4 days until fledging or failure. All nests were monitored by viewing woodpeckers and their behavior at the cavity entrance. We classified nest failures as depredated (based on adult behavior, loss of nestlings, or predator signs on nest trees), weather related, or unknown. A nest was considered successful if parents were observed feeding young near the time of fledging (80% of average fledging age, or 24 days old) or if fledged young were observed near the nest. Productivity data (number of fledglings per nest) were recorded near or shortly after the time of fledging. Although some young woodpeckers were observed close to the nest cavity for 2–3 days after fledging, we likely underestimated productivity for both populations because the time interval between our nest visits was 3–4 days.

Shrub densities were estimated in the Idaho study area, because we assumed that shrubs provided substrate for arthropod prey of Lewis's Woodpeckers (Bock 1970, Linder and Anderson 1998). In Idaho, densities were estimated at 90 random stations located at least 250 m apart. Each random station encompassed four, 5-m-radius circular plots for a total of 360 circular plots. Shrub stem (>2–8 cm diameter) densities were recorded in each circular plot and averaged for each of 90 random stations. In Colorado, shrubs were rare and stem densities were estimated visually.

DATA ANALYSIS AND SOURCE-SINK EVALUATION

Nest success was calculated using Johnson's (1979) method (modified from Mayfield 1961, 1975) to correct for biases attributable to unequal periods of nest observation and to include the standard error of the success estimator (Table 2). We assumed that nesting success and nest failure were constant throughout the breeding season. Differences in nesting survival rates among years and between study areas were examined using program CONTRAST (Hines and Sauer 1989), which uses a chi-square statistic to test for homogeneity of survival rates by creating a linear contrast of rate estimates (Sauer and Williams 1989). A chi-square analysis of a contingency table (Zar 1984) was used to test for differences in proportion of nests destroyed by predators between the two study areas. We assumed no weather-related differences in years because of the large spatial separation in the study areas. Differences in daily nest survival and predation rates were considered significant at $P < 0.05$. Means are presented ± SE.

Estimation of source and sink status requires both reproductive information and mortality data from juveniles and adults. In a closed breeding population, population size will not change whenever adult mortality is balanced by juvenile recruitment. This relationship was expressed as an equation by Donovan et al. (1995):

$$1 - \text{adult survivorship} = (\text{mean number female fledglings per female per year}) \times (\text{juvenile survivorship}).$$

TABLE 2. Nesting success ± 2 SE, mean daily nest survival ± SE, and mean number of young per successful nest ± SE of Lewis's Woodpecker in burned ponderosa pine forests of Idaho and cottonwood riparian habitats of Colorado. Number of nests per study site is reported in parentheses.

Variable	Burned ponderosa pine—Idaho			Cottonwood riparian—Colorado		
	Foothills (256)	Star Gulch (27)	Total (283)	Foothills (19)	Plains (46)	Total (65)
Overall nesting success	0.77 ± 0.06	0.84 ± 0.15	0.78 ± 0.06	0.25 ± 0.13	0.56 ± 0.14	0.46 ± 0.11
Daily survival rate	0.995 ± 0.001	0.997 ± 0.002	0.995 ± 0.001	0.973 ± 0.007	0.987 ± 0.003	0.985 ± 0.003
Young per successful nest	1.73 ± 0.05	2.16 ± 0.17	1.78 ± 0.05	2.0 ± 0	1.6 ± 0.15	1.7 ± 0.14

If recruitment rates of young (mean number of female fledglings per female per year × juvenile survivorship) into a closed breeding population do not compensate for the rate of adult mortality (1 − adult survivorship), then the population is likely a sink. Alternatively, if recruitment rates of young exceed the adult mortality rate, then the population is potentially a source (Pulliam 1988). A rearrangement of the above equation can be used to evaluate source and sink habitats and to determine if a population will replace itself (Donovan et al. 1995):

$$\frac{(1 - \text{adult survivorship})}{\text{juvenile survivorship}} = \text{mean number female fledglings per female per year.}$$

We considered the population to be a potential sink if the annual productivity (number female offspring per female adult) was less than adult mortality (1 − adult survival) divided by juvenile survival. Conversely, if productivity was greater than adult mortality (1 − adult survival) divided by juvenile survival, we considered the population a likely source.

In order to calculate the mean number of female offspring produced per female per year, we considered data on (1) the mean number of female offspring produced (total number of fledglings × 0.5) per successful nest, (2) habitat-specific reproductive success, and (3) the number of nests successful in fledging at least one young (Donovan et al. 1995). Number of renests was not incorporated. Lewis's Woodpeckers raise only one brood per year (Tobalske 1997), and we assumed that females did not renest after failed first attempts.

Renests were never observed at Colorado sites, and <6% of all Idaho nests could have been renests. Most nests failed late in the breeding season during the nestling stage and their nesting cycle is relatively long (average of 52 days for 283 nests in Idaho). Only 15 of 283 nests failed with sufficient time to renest, i.e., with at least 52 days remaining in the nesting season (based on their average departure date from the Idaho study area). Renesting in *Melanerpes* occurs in those species with more southerly breeding ranges, where a longer nesting season (Koenig et al. 1995, Husak and Maxwell 1998, Smith et al. 2000) allows more time for renesting than that available for Lewis's Woodpeckers.

We calculated the proportion of nests that were successful, quantified the mean number of female young produced per adult female per successful nest, and used these values to calculate the total number of female young produced by all adult females throughout the breeding season (Donovan et al. 1995). For example, using reproductive success and productivity estimates from the Idaho data, where nesting success was 77%, 77 of 100 nests would succeed in fledging at least one young and 23 females would produce no young. The successful nests produced an average of 1.78 young per nest or, assuming a 50:50 sex ratio, 0.89 female fledglings per successful nest. Assuming one brood and no renests in this example, 68.88 female fledglings would be produced per 100 adult females (or 0.69 female fledglings per female per year). To calculate standard errors and 95% confidence intervals for the mean number of female fledglings per female per year, we used the method of moments estimator for the variance of a product (Mood and Graybill 1974).

TABLE 3. Number of Lewis's Woodpecker female fledglings per female per year necessary to offset adult mortality given a specific juvenile survival rate, based on a range of survival and mortality estimates of other melanerpine species.

Juvenile survival	Adult survival			
	Lowest (0.59)[1]	Med 1 (0.62)[2]	Med 2 (0.68)[3]	Highest (0.75)[4]
Lowest (0.35)[5]	1.17	1.08	0.91	0.71
Mean (0.46)[6]	0.89	0.83	0.70	0.54
Highest (0.57)[7]	0.72	0.67	0.56	0.44

[1] Acorn Woodpecker (Stacey and Taper 1992).
[2] Red-headed Woodpecker (Martin 1995).
[3] Red-bellied Woodpecker (Karr et al. 1990, Martin 1995).
[4] Acorn Woodpecker (Koenig and Mumme 1987).
[5] Acorn Woodpecker (Stacey and Taper 1992).
[6] Average of lowest and highest juvenile survival values.
[7] Acorn Woodpecker (Koenig and Mumme 1987).

We had no data on adult or juvenile survival rates of Lewis's Woodpeckers in either study area, so we used a range of survival estimates from the literature to perform a simple modeling exercise for evaluating the potential source or sink status of the two habitats. Estimates of annual adult survival reported for *Melanerpes* include 62% for Red-headed Woodpecker (*M. erythrocephalus*; Martin 1995), 59% (Stacey and Taper 1992) to 75% (Koenig and Mumme 1987) for Acorn Woodpecker (*M. formicivorus*), and 68% for Red-bellied Woodpecker (*M. carolinus*; Karr et al. 1990, Martin 1995). We assumed for both study areas that adult survival rates for Lewis's Woodpecker were within this range of values (0.59–0.75). We used the four values (minimum: 0.59; medium 1: 0.62; medium 2: 0.68; and maximum: 0.75) of these adult survival rates to evaluate the potential sink or source status in the two habitats studied (Table 3).

The only published juvenile survivorship data that we could find for a melanerpine species were for Acorn Woodpecker. We recognize that life history differences between Acorn and Lewis's woodpeckers could be problematic for this analysis. Acorn Woodpecker is a cooperatively breeding, permanently resident, *k*-selected species, whereas Lewis's Woodpecker is an opportunistic, *r*-selected species and likely to have lower juvenile survivorship than Acorn Woodpeckers. Estimates of juvenile survivorship for Acorn Woodpecker range from 35% (Stacey and Taper 1992) to 57% (Koenig and Mumme 1987), with an average of 46%. We used the minimum, maximum, and average of these juvenile survival rates to evaluate the potential sink or source status of the two populations studied (Table 3).

The range of productivity values necessary to offset adult mortality was computed (Table 3), and possible sources, under a conservative, best-case scenario (using the highest juvenile and adult survival rates), were defined as those sites where at least 0.44 female fledglings per female per year were produced. Conversely, sites that produced fewer than 0.44 female fledglings per female per year were considered potential sinks.

RESULTS

NESTS AND VEGETATION

We monitored 283 nests from 1994–1997 in Idaho, and 65 nests in Colorado during 1992–1993 (Table 2). Point estimates of nesting densities were four times greater in burned pine forests compared to cottonwood habitats (0.4 vs. 0.1 nests per 10 ha in Idaho and Colorado, respectively), although measures of precision could not be calculated. Shrub stem densities (stem sizes 2–8 cm) were nearly seven times higher in the two-year-old burned forests of Idaho compared to cottonwood riparian patches of Colorado (>30 000 vs. <4000 stems per hectare).

Daily nest survival rates were not statistically different among years in burned forests or between years in cottonwood forest patches (χ^2 test, $P > 0.2$ in all cases). We therefore pooled data across years (Table 2). We assumed nesting success in Colorado populations remained similar in the years that Idaho data were collected. Daily nest survival rates were not equal between cottonwood sites in Colorado ($\chi^2_1 = 4.0$, $P = 0.05$; Table 2), whereas nest survival rates did not differ statistically between burned pine sites in Idaho ($\chi^2_1 = 0.8$, $P = 0.37$; Table 2). Therefore, we pooled data for the two study sites in burned forests for separate comparisons of nest success with each of the cottonwood study sites (Table 2).

Overall, nest success in the burned forests was 78%, whereas nest success in cottonwood forest patches averaged 46%. Daily nest survival rates differed between burned forests of Idaho and the two cottonwood study sites in Colorado ($\chi^2_2 = 14.1$, $P = 0.001$; Table 2). Proportion of nests

TABLE 4. Mean number of Lewis's Woodpecker female fledglings per female per year (95% CI) produced in burned ponderosa pine forest of Idaho and cottonwood riparian habitats of Colorado. Based on best-case survivorship estimates from the literature, productivity values above 0.44 female fledglings per female per year are potential sources (boldface).

Year	Burned ponderosa pine—Idaho		Cottonwood riparian—Colorado	
	Foothills	Star Gulch	Foothills	Plains
1992	—	—	0.14 (–0.89–1.16)	0.37 (–0.10–0.84)
1993	—	—	0.31 (–0.42–1.04)	**0.47** (0.11–0.82)
1994	**0.90** (0.65–1.15)	—	—	—
1995	**0.63** (0.49–0.77)	—	—	—
1996	**0.63** (0.44–0.82)	**0.92** (0.62–1.22)	—	—
1997	**0.61** (0.34–0.88)	**0.91** (0.51–1.30)	—	—
All years by site	**0.67** (0.57–0.77)	**0.91** (0.60–1.22)	0.25 (–0.35–0.84)	**0.45** (0.16–0.73)
All years by habitat	**0.69** (0.59–0.78)		0.38 (0.11–0.64)	

destroyed by predators was significantly lower in burned pine forests (44 of 283, 16%) compared to cottonwood riparian patches (22 of 65, 34%; $\chi^2_1 = 11.5$, $P = 0.001$).

Predation was the major cause of nest failure in both study areas. Most (44 of 49, 90%) nest failures in burned forests of Idaho were attributed to predation. Other failures (5 of 49, 10%) were weather related or due to unknown causes. In Colorado cottonwood forests, nest failures were attributed to predation (22 of 28, 79%), inclement weather (5 of 28, 18%), and one nest usurpation by European Starling (*Sturnus vulgaris*; Vierling 1998).

Potential nest predators differed in the two study areas. Predators observed in or near nest cavities in burned forests of Idaho included black bears (*Ursus americanus*), weasels (*Mustela* spp.) and chipmunks (*Tamias* spp.). In cottonwood riparian forest patches, common nest predators viewed in the study sites were bullsnake (*Pituophis melanoleucus sayi*), common raccoon (*Procyon lotor*), fox squirrel (*Sciurus niger*), red squirrel (*Tamiasciurus hudsonicus*), Abert's squirrel (*Sciurus aberti*), and Black-billed Magpie (*Pica hudsonia*).

SOURCE-SINK ANALYSIS

Burned forests in Idaho supported the highest levels of reproductive success and productivity (Table 2), and consistently appeared as potential source habitats compared to riparian sites of Colorado (Table 4). The 95% CI around the pooled data for riparian sites ranged from 0.11–0.64, whereas the confidence interval around the pooled data for burned forests ranged from 0.59–0.78. Therefore, the upper end of the confidence interval for the pooled riparian data set overlapped minimally with the lower end of the confidence interval for the pooled burned forest data. This suggests that the burned forests were more likely to function as population sources than were riparian forest patches.

DISCUSSION

Open ponderosa pine forests and cottonwood riparian woodlands have been recognized as the principal nesting habitats of Lewis's Woodpecker (Tobalske 1997). Yet we observed significant differences in woodpecker demographics in these two habitats. Lewis's Woodpecker experienced higher levels of reproductive success and productivity in crown-burned ponderosa pine forests compared to cottonwood riparian forest patches.

Both of these habitats have been dramatically reduced and altered since the turn of the twentieth century. Some western states have lost more than 90% of their historic riparian and ponderosa pine habitats (Ohmart 1994, Noss et al. 1995). Causes of these declines in deciduous riparian habitats are due primarily to dams, water management practices, livestock grazing, and agricultural development (Rood and Heinze-Milne 1989, Ohmart 1994, Noss et al. 1995, Saab et al. 1995). Ponderosa pine forests have been extensively altered by timber harvest, domestic livestock grazing, and change in historic fire regime from frequent understory burns to rare stand-replacing fires (Agee 1993, Arno 1996, Shinneman and Baker 1997, Veblen et al. 2000). Our data are likely representative of the current conditions for Lewis's Woodpecker in these two types of habitats.

Nest success was primarily influenced by predation, which differed between burned pine and cottonwood forests. The differences could have been caused by several factors, including landscape context, colonization by predators, and forest structure. Cottonwood forests were surrounded by an agricultural landscape with residential development in the Colorado Plains study site, and by unburned pine forest with agriculture in the Colorado Foothills site. Burned forests of Idaho were situated in a relatively natural forested landscape. Human-commensal predators (e.g., raccoons, magpies, and fox squirrels) and the apparency of the riparian zone in an agricultural matrix likely attracted predators to cottonwood forests (Hoffman and Gottschang 1977, Laubhan and Fredrickson 1997, Saab 1999). While we did not quantify distribution and abundance of nest predators, we did note that commonly detected predators (raccoons, tree squirrels, and snakes) in riparian forests were rarely, if ever, observed in burned pine forests. Possible nest predators that are common in western Idaho include gopher snakes (*Pituophis melanoleucus*; Nussbaum et al. 1983), and tree squirrels (*Tamiasciurus hudsonicus* and *Glaucomys sabrinus*; Zeveloff 1988). No gopher snakes and less than 20 tree squirrels were observed at our burned study sites, although these potential nest predators were regularly seen in adjacent, unburned pine forests.

Influences of fire on predator colonization likely have profound effects on the source-sink status of burned habitats. Recolonization of snakes and tree squirrels into habitats affected by large-scale disturbances (including wildfire) may take several years (Gashwiler 1970, Lillywhite 1977, MacMahon et al. 1989); thus lower rates of nest predation would be expected in recently burned forests compared with unburned cottonwood and coniferous forests.

Nest success and landscape context differed between the cottonwood study sites in Colorado. Nest success was lower in the predominantly forested landscape than in the fragmented, agricultural landscape. While this finding is consistent with that reported for cottonwood forests in western Montana (Tewksbury et al. 1998), it contrasts with studies from the midwestern United States that suggest predation rates increase with increasing amounts of agriculture (Donovan et al. 1995, Robinson et al. 1995). In cottonwood forests of western Montana, the most abundant nest predator was the red squirrel; their densities were highest in forested landscapes and declined with increasingly fragmented, agricultural landscapes (Tewksbury et al. 1998). A similar process may have operated within our Colorado study area.

Differences in vegetation structure and composition between the two forest types also cannot be discounted as important influences on predator assemblages, arthropod prey, and subsequently, nesting success. While nesting substrate in cottonwood forests of Colorado did not appear to be limiting (Vierling 1997), understory shrub cover was virtually nonexistent. This likely decreased food availability by reducing substrate for arthropod prey compared to burned forests in Idaho.

Postfire habitats and subsequent insect outbreaks are known to attract cavity-nesting birds (Blackford 1955, Koplin 1969, Lowe et al. 1978, Raphael et al. 1987, Kotliar et al., in press), especially in the first few years following tree death. Vegetation regrowth after wildfire generally results in rapid increases in arthropod populations (Horst 1970, Best 1979, Many 1984), attracting aerial and ground insectivores (Lowe et al. 1978, Apfelbaum and Haney 1981). These postfire characteristics and an open canopy are apparently highly suitable nesting and foraging habitat for Lewis's Woodpecker (Bock 1970, Galen 1989, Tobalske 1997, Linder and Anderson 1998). In our study, conditions created by stand-replacing wildfire in ponderosa pine forests more often appeared to be potential source than sink habitat, whereas cottonwood forests in an agricultural and unburned pine landscape were more frequently concluded to be sink habitat. It is unknown whether riparian forests in another context could be source habitat, e.g., cottonwood forests surrounded by a matrix of native vegetation in the absence of agriculture. In addition, we do not know if stand-replacing conditions could be more productive habitat relative to unburned ponderosa pine forests with decades of fire exclusion. Nesting Lewis's Woodpeckers, however, appear to be relatively rare in unburned pine habitat of Idaho (VAS, unpubl. data) and Colorado (Vierling 1998).

The availability of suitable nesting habitat in ponderosa pine forests of Colorado has apparently declined for Lewis's woodpecker (Vierling 1998). Despite extensive nest searches along the Colorado Front Range, no nests were found in

unburned ponderosa pine forests. Historically, Lewis's woodpeckers were common in ponderosa pine forests (Warren 1910, Betts 1913), but the only ponderosa pine tree used in the Colorado study area was located within a riparian zone. Ponderosa pine forests of the Colorado Front Range have been altered by fire exclusion practices and logging (Veblen and Lorenz 1991, Veblen et al. 2000). Pine forests have higher tree densities of smaller diameters compared to historical conditions (Veblen and Lorenz 1991), which has evidently reduced breeding habitat for Lewis's Woodpecker (Vierling 1997). In addition, alterations in the forest structure have eliminated many natural openings and large, decayed trees that are typical of foraging and nesting habitat, respectively (Vierling 1997).

Large-scale burned forests may play a critical role in providing ephemeral source habitats for Lewis's Woodpecker. Lewis's Woodpecker populations may be sustained by a patchwork of burned forests, much like that suggested for Black-backed Woodpeckers (Hutto 1995). Although ponderosa pine forests of the western United States were typically maintained by frequent low-severity surface fires (equilibrium dynamics), recent evidence indicates that large, stand-replacing crown fires (nonequilibrim dynamics) occurred historically on an infrequent but regular basis (Shinneman and Baker 1997, Brown et al. 1999, Veblen et al. 2000). The nonequilibrium perspective suggests that temporal and spatial variation in the natural disturbance regime may create a changing mosaic of patch types, which influences the distribution of species (Sprugel 1991). Historically, a patchwork of both low-intensity ground fires and stand-replacing wildfires throughout the range of ponderosa pine (Shinneman and Baker 1997, Veblen et al. 2000), and concomitantly the range of the Lewis's Woodpecker (Fig. 1), may have created a network of source habitats for this woodpecker. Prescribed understory fire is the prevailing management tool for restoring ponderosa pine ecosystems (e.g., Agee 1998, Swetnam et al. 1999). Conditions created by stand-replacing crown fire may be equally important in maintaining ponderosa pine systems (Shinneman and Baker 1997) and conserving nesting habitat for the Lewis's Woodpecker.

ACKNOWLEDGMENTS

We thank Carl Bock, Craig Groves, Dick Hutto, Therese Donovan, and Bret Tobalske for critical reviews of an earlier version of the manuscript. David Dobkin, Larkin Powell, Barny Dunning, and Hugh Powell offered helpful suggestions for improving the manuscript. Field assistance in Idaho was provided by Jon Dudley, Dan Shaw, Holiday Sloan, Jennifer Chambers, Gary Vos, Danielle Bruno, Christa Braun, Lottie Hufford, David Wageman, Steve Breth, Suzanne DiGiacomo, Colette Buchholtz, Janine Schroeder, Jim Johnson, and Josh Bevan. Larry Donohoo provided logistical support and assistance with study design in Idaho. Dave Turner and Jon Dudley assisted with data analysis. U.S. Department Agriculture, Forest Service, Rocky Mountain Research Station was the primary source of funding for the Idaho work with additional help from other units of the Forest Service, including the Intermountain Region, Pacific Northwest Region, and Boise National Forest, especially the Mountain Home District. The University of Colorado, Department of EPO Biology and the University Museum supplied office space and logistical support for work conducted in Idaho and Colorado. We thank the U.S. Department of Interior Fish and Wildlife Service nongame migratory bird program and the U.S. Department of Education, Patricia Roberts Harris Fellowship for financial assistance in Colorado.

LITERATURE CITED

AGEE, J. K. 1993. Fire ecology of Pacific Northwest forests. Island Press, Washington, DC.

AGEE, J. K. 1998. The landscape ecology of western forest fire regimes. Northwest Science 72:24–34.

APFELBAUM, S., AND A. HANEY. 1981. Bird populations before and after wildfire in a Great Lakes pine forest. Condor 83:347–354.

ARNO, S. F. 1996. The concept: restoring ecological structure and process in ponderosa pine forests, p. 37–38. *In* C. C. Hardy and S. F. Arno [EDS.], The use of fire in forest restoration. U.S.D.A. Forest Service General Technical Report INT-GTR-341, Ogden, UT.

BEST, L. B. 1979. Effects of fire on a Field Sparrow population. American Midland Naturalist 101: 434–442.

BETTS, N. D. 1913. Birds of Boulder County. University of Colorado Press, Boulder, CO.

BLACKFORD, J. L. 1955. Woodpecker concentration in a burned forest. Condor 57:28–30.

BLOCK, W. M., AND L. A. BRENNAN. 1987. Characteristics of Lewis' Woodpecker on the Modoc Plateau, California. Western Birds 18:209–212.

BOCK, C. E. 1970. The ecology and behavior of the Lewis woodpecker. University of California Publication, Zoology 92:1–100.

BROWN, P. M., M. R. KAUFMANN, AND W. E. SHEPPERD. 1999. Long-term, landscape patterns of past fire events in a montane ponderosa pine forest of central Colorado. Landscape Ecology 14:513–532.

DONOVAN, T. M., F. R. THOMPSON, J. FAABORG, AND P. R. PROBST. 1995. Reproductive success of migratory birds in habitat sources and sinks. Conservation Biology 9:1380–1395.

GALEN, C. 1989. A preliminary assessment of the status of the Lewis's Woodpecker in Wasco County, Oregon. Oregon Department of Fish and Game,

Nongame Wildlife Program, Technical Report 88-3-1, Portland, OR.

GASHWILER, J. S. 1970. Plant and animal changes on a clearcut in west-central Oregon. Ecology 51: 1018–1026.

HINES, J. E., AND J. R. SAUER. 1989. CONTRAST program for the analysis of several survival or recovery rate estimates. Patuxent Wildlife Research Center, U.S. Fish and Wildlife Service, Laurel, MD.

HOFFMAN, C. O., AND J. L. GOTTSCHANG. 1977. Numbers, distribution, and movements of a racoon population in a suburban residential community. Journal of Mammalogy 58:623–636.

HORST, G. A. 1970. The effects of controlled burning on arthropod density and biomass in relation to Bobwhite Quail brood habitat on a right-of-way. Tall Timbers Conference on Ecological Animal Control by Habitat Management No. 2:173–183.

HUSAK, M. S., AND T. C. MAXWELL. 1998. Golden-fronted Woodpecker (*Melanerpes aurifrons*). *In* A. Poole and F. Gill [EDS.], The birds of North America, No. 373. The Birds of North America, Inc. Philadelphia, PA.

HUTTO, R. L. 1995. Composition of bird communities following stand-replacement fires in Northern Rocky Mountain (U.S.A.) conifer forests. Conservation Biology 9:1041–1058.

JOHNSON, D. H. 1979. Estimating nest success: the Mayfield method and an alternative. Auk 96:651–661.

KARR, J. R., J. D. NICHOLS, K. KLIMKIEWICZ, AND J. D. BRAWN. 1990. Survival rates of birds of tropical and temperate forests: will the dogma survive? American Naturalist 136:277–291.

KOENIG, W. D., AND R. L. MUMME. 1987. Population ecology of the cooperatively breeding Acorn Woodpecker. Princeton University Press, Princeton, NJ.

KOENIG, W. D., P. B. STACEY, M. T. STANBACK, AND R. L. MUMME. 1995. Acorn Woodpecker (*Melanerpes formicivorus*). *In* A. Poole and F. Gill [EDS.], The birds of North America, No. 194. The Academy of Natural Sciences Philadelphia, and The American Ornithologists' Union, Washington, DC.

KOPLIN, J. R. 1969. The numerical response of woodpeckers to insect prey in a subalpine forest in Colorado. Condor 71:436–438.

KOTLIAR, N. B., S. J. HEJL, R. L. HUTTO, V. A. SAAB, C. P. MELCHER, AND M. E. MCFADZEN. In press. Effects of wildfire and post-fire salvage logging on avian communities in conifer-dominated forests of the western United States. Studies in Avian Biology.

LAUBHAN, M. K., AND L. H. FREDRICKSON. 1997. Wetlands of the Great Plains: habitat characteristics and vertebrate aggregations, p. 20–48. *In* F. L. Knopf and F. B. Samson [EDS.], Ecology and conservation of Great Plains vertebrates. Ecological Studies 125, Springer-Verlag, New York.

LILLYWHITE, H. B. 1977. Animal responses to fire and fuel management in chaparral, p. 368–373. *In* H. A. Mooney and C. E. Conrad [EDS.], Proceedings of the symposium on the environmental consequences of fire and fuel management in Mediterranean ecosystems. U.S.D.A. Forest Service General Technical Report WO-3, Washington, DC.

LINDER, K. A., AND S. H. ANDERSON. 1998. Nesting habitat of Lewis' Woodpeckers in southeastern Wyoming. Journal of Field Ornithology 69:109–116.

LITTLE, E. L., JR. 1971. Atlas of United States trees, vol. 1: conifers and important hardwoods. USDA Forest Service Miscellaneous Publication 1146, Washington, DC.

LOWE, P. O., P. F. FOLLIOTT, J. H. DIETERICH, AND D. R. PATTON. 1978. Determining potential wildlife benefits from wildfire in Arizona ponderosa pine forests. U.S.D.A. Forest Service General Technical Report RM-52, Fort Collins, CO.

MACMAHON, J. A., R. R. PARMENTER, K. A. JOHNSON, AND C. M. CRISAEFULLI. 1989. Small mammal recolonization on the Mount St. Helens volcano: 1980–1987. American Midland Naturalist 122: 365–387.

MANY, D. E. 1984. Factors influencing the use of winter-burnt grassland by foraging Bald Ibises (*Geronticus calvus*). South African Journal of Zoology 19:12–15.

MARTIN, T. E. 1995. Avian life history evolution in relation to nest sites, nest predation, and food. Ecological Monographs 65:101–127.

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

MAYFIELD, H. F. 1975. Suggestions for calculating nest success. Wilson Bulletin 87:456–466.

MOOD, A. M., AND F. A. GRAYBILL. 1974. Introduction to the theory of statistics. McGraw-Hill, New York.

NOSS, R. F, E. T. LAROE III, AND J. M. SCOTT. 1995. Endangered ecosystems of the United States: a preliminary assessment of loss and degradation. USDI National Biological Service Biology Report 28, Washington, DC.

NUSSBAUM, R. A., E. D. BRODIE, AND R. M. STORM. 1983. Amphibians and reptiles of the Pacific Northwest. University of Idaho Press, Moscow, ID.

OHMART, R. D. 1994. The effects of human-induced changes on the avifauna of western riparian habitats. Studies in Avian Biology 15:272–285.

PULLIAM, R. H. 1988. Sources, sinks, and population regulation. American Naturalist 132:652–661.

RAPHAEL, M. G., AND M. WHITE. 1984. Use of snags by cavity-nesting birds in the Sierra Nevada. Wildlife Monographs 86:1–66.

RAPHAEL, M. G., M. L. MORRISON, AND M. P. YODER-WILLIAMS. 1987. Breeding bird populations during twenty-five years of postfire succession in the Sierra Nevada. Condor 89:614–626.

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

ROOD, S. B., AND S. HEINZE-MILNE. 1989. Abrupt downstream forest decline following river dam-

ming in southern Alberta. Canadian Journal of Botany 67:1744–1749.

SAAB, V. A. 1999. Importance of spatial scale to habitat use by breeding birds in riparian forests: a hierarchical analysis. Ecological Applications 9:135–151.

SAAB, V. A., AND J. G. DUDLEY. 1998. Responses of cavity-nesting birds to stand-replacement fire and salvage logging in ponderosa pine/Douglas-fir forests of southwestern Idaho. U.S.D.A. Forest Service Research Paper RMRS-RP-11, Ogden, UT.

SAAB, V. A., C. E. BOCK, T. D. RICH, AND D. S. DOBKIN. 1995. Livestock grazing effects in western North America, p. 311–353. *In* T. E. Martin and D. M. Finch [EDS.], Ecology and management of Neotropical migratory birds: a synthesis and review of critical issues. Oxford University Press, New York.

SAUER, J. R., AND B. K. WILLIAMS. 1989. Generalized procedures for testing hypotheses about survival or recovery rates. Journal of Wildlife Management 53:137–142.

SHINNEMAN, D. J., AND W. L. BAKER. 1997. Nonequilibrium dynamics between catastrophic disturbances and old-growth forests in ponderosa pine landscapes of the Black Hills. Conservation Biology 11:1276–1288.

SMITH, K. G., J. H. WITHGOTT, AND P. G. RODEWALD. 2000. Red-headed Woodpecker (*Melanerpes erythrocephalus*). *In* A. Poole and F. Gill [EDS.], The birds of North America, No. 518. The Birds of North America, Inc., Philadelphia, PA.

SPRUGEL, D. G. 1991. Disturbance, equilibrium, and environmental variability: what is 'natural' vegetation in a changing environment? Biological Conservation 58:1–18.

STACEY, P. B., AND M. TAPER. 1992. Environmental variation and the persistence of small populations. Ecological Applications 2:18–29.

SWETNAM, T. W., C. D. ALLEN, AND J. L. BETANCOURT. 1999. Applied historical ecology: using the past to manage for the future. Ecological Applications 9:1189–1206.

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.

TOBALSKE, B. W. 1997. Lewis' Woodpecker (*Melanerpes lewis*). *In* A. Poole and F. Gill [EDS.], The birds of North America, No. 284. The Academy of Natural Sciences, Philadelphia, and The American Ornithologists' Union, Washington DC.

VEBLEN, T., AND D. C. LORENZ. 1991. The Colorado front range: a century of ecological change. University of Utah Press, Salt Lake City, UT.

VEBLEN, T. T., T. KITZBERGER, AND J. DONNEGAN. 2000. Climatic and human influences on fire regimes in ponderosa pine forests in the Colorado Front Range. Ecological Applications 10:1178–1195.

VIERLING, K. T. 1997. Habitat selection of Lewis's Woodpeckers in southeastern Colorado. Wilson Bulletin 109:121–130.

VIERLING, K. T. 1998. Interactions between European Starling and Lewis's Woodpeckers at nest cavities. Journal of Field Ornithology 69:376–379.

WARREN, E. R. 1910. Some central Colorado bird notes. Condor 12:23–29.

ZAR, J. H. 1984. Biostatistical analysis. Prentice-Hall, Inc. Englewood Cliffs, NJ.

ZEVELOFF, S. I. 1988. Mammals of the Intermountain West. University of Utah Press, Salt Lake City, UT.