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Andreas Leidolf
Utah State University, Logan, UT, andreasleidolf@msn.com

Ronald J. Ryel
Utah State University, Logan, UT, ron.ryel@usu.edu

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AVIAN RESPONSE TO FROST-DAMAGED ASPEN IN NORTHERN UTAH

Andreas Leidolf[1,2] and Ronald J. Ryel[1]

ABSTRACT.—In early May 2007, northern Utah mountains experienced a period of prolonged warmer-than-normal temperatures, followed by a frost that killed or damaged much of the first-flush quaking aspen (*Populus tremuloides*) foliage. We assessed the effects of this transitory disturbance on the aspen bird species assemblage by comparing breeding bird survey data collected in the Bear River Mountain Range, Utah, USA, in 2005 and 2006 (predisturbance) to data from 2007 (postdisturbance). Whereas bird total abundance, species richness, and species diversity did not differ significantly among years, there were significant year-by–frost damage severity interactions, with plots with low levels of frost damage having significantly higher total abundance, richness, and diversity. Based on these results, we concluded that (1) at the landscape scale, the postdisturbance avian species assemblage was essentially identical to the predisturbance assemblage both in terms of number of individuals and species, and (2) there was a pronounced shift in the spatial distribution of birds at the stand scale, with most individuals favoring stands with low levels of frost damage over those with intermediate and high levels of frost damage. Thus, aspen stands with little or no frost damage served as refugia for birds displaced from highly impacted sites, thereby buffering any adverse effects on the avian community as a whole, at least in the short term. However, with severe climatic events predicted to become more frequent, cumulative effects of successive frost-induced defoliations on long-term avian productivity and survival may be more severe.

RESUMEN.—A comienzos de mayo de 2007, las montañas del norte de Utah experimentaron un período prolongado de temperaturas más cálidas que lo normal, seguido de una helada que mató o dañó a gran parte del follaje del álamo *Populus tremuloides.* Evaluamos los efectos de esta perturbación transitoria en el ensamble de las especies de aves del álamo al comparar los datos del monitoreo de aves en etapa de reproducción, recopilados en la cadena montañosa Bear River en Utah, Estados Unidos, durante 2005 y 2006 (previo a la perturbación) con los datos de 2007 (después de la perturbación). Mientras que la abundancia total de aves, la riqueza y diversidad de las especies no difirieron significativamente entre años, hubo interacciones significativas entre los años y la severidad de los daños producidos por la helada: las parcelas con niveles bajos de daños producidos por la helada tuvieron una abundancia total, riqueza y diversidad significativamente mayores. Con base en estos resultados, concluimos que: (1) a escala del paisaje, el ensamble de aves después de la perturbación fue esencialmente idéntico al ensamble previo a la perturbación, en términos de la cantidad de individuos y especies; (2) hubo un cambio pronunciado en la distribución espacial de las aves a escala del microhábitat: la mayoría de los individuos prefirieron sitios con niveles bajos de daños producidos por la helada, con respecto a sitios con niveles intermedios y elevados de daños. Por lo tanto, los álamos, con poco o sin ningún daño producido por la helada, sirvieron de refugio para las aves desplazadas de los sitios muy impactados. De este modo, redujeron cualquier efecto adverso en la comunidad aviar en su conjunto, al menos en el corto plazo. Sin embargo, con los severos eventos climáticos que se predice que serán más frecuentes, los efectos acumulativos de las defoliaciones provocadas por heladas sucesivas sobre la productividad de las aves a largo plazo y sobre su supervivencia podrían ser más severos.

Quaking aspen (*Populus tremuloides*) is the most widespread tree species in North America (Little 1971). Although the majority of aspen is found in the boreal zone of Canada and the northeastern United States, it is also a prominent element in montane landscapes of the western United States, covering as many as 2.5 million ha in the central and southern Rocky Mountains. The role of disturbance in aspen ecology and management is a subject of much interest and debate, in large part because of the widespread loss of aspen evident across much of the western United States (Kay 1997, Bartos and Campbell 1998) and the hypothesized negative response to climatic changes (Hogg et al. 2002, Rehfeldt et al. 2009). In the West, when associated with conifers, quaking aspen is generally considered a seral species, and reductions in the frequency of stand-replacing fires may affect its long-term persistence on the landscape (Jones and DeByle 1985, Brown and DeByle 1987, Rogers 2002). Pure stands of aspen also occur, and regeneration has been severely reduced in many areas (Kay and Bartos 2000, Ripple and Larsen 2000, Kaye et al. 2005, Rogers et al. 2010).

[1]Department of Wildland Resources and the Ecology Center, Utah State University, 5230 Old Main Hill, Logan, UT 84322-5230.
[2]E-mail: andreasleidolf@msn.com

The effects of drought on aspen are well understood (Frey et al. 2004); however, studies of the effects of extreme temperatures are more limited. Premature leaf flush in response to early, warm spring conditions is well documented in quaking aspen (Korstian 1921, Cayford et al. 1959, Fairweather et al. 2008). At the same time, quaking aspen shows the greatest sensitivity to frost damage among a range of tree species in both montane (Korstian 1921) and boreal (Cayford et al. 1959) settings. With extreme climatic conditions likely to increase in the future (Easterling et al. 2000, Bell et al. 2004, Solomon et al. 2007), large-scale frost-induced defoliation and subsequent mortality of quaking aspen may become more frequent and widespread.

One common effect of any vegetation change is a shift in wildlife occupancy and utilization. This shift is particularly evident for birds, which can be useful ecological indicators (Bibby 1999, Canterbury et al. 2000, Nuttle et al. 2003; but see Chambers 2008). The effects of large, stand-replacing disturbance events on avian populations are well understood (e.g., Smith and Petit 1988, Brawn et al. 2001, Saab and Powell 2005), but studies of such transitory disturbances as defoliation events are less common. What little information is available regarding the effects of forest defoliation on birds is limited to studies of insect defoliation, primarily gypsy moth, *Lymantria dispar* (e.g., DeGraaf 1987, Bell and Whitmore 2000, Gale et al. 2001); to our knowledge, there are no published accounts of avian response to frost-induced defoliation of forest habitat.

In May 2007, following an early leaf-out in response to warmer-than-average temperatures, a large proportion of montane aspen trees across northern Utah suffered varying levels of leaf damage and defoliation (Currit and St. Clair 2010). Because this event coincided with the arrival in northern Utah of many bird species from their wintering grounds at lower latitudes and elevations (Fig. 1, Dixon 1995), we used this opportunity to examine the influence of this transitory disturbance on the breeding bird species assemblage. Our objective was to assess the effects of level of frost damage to quaking aspen trees on relevant avian community summary statistics. To do so, we proposed a framework of avian response encompassing 3 potential courses of action: (1) birds abandon the affected landscape and attempt to establish a breeding territory in a different geographic area or habitat type unaffected by the disturbance; (2) birds remain in the affected landscape by adjusting to the modified habitat, a response that is well documented in the literature (Emlen 1970, Lyon and Marzluff 1985, DeGraaf 1987); or (3) birds resettle locally by choosing a territory within the affected landscape and habitat type that has been minimally impacted by the disturbance. There is anecdotal evidence in the literature that supports such a response: for example, Clark (1935) observed "territory crowding" in undisturbed habitats after fire in California chaparral.

We conducted our research at Deseret Land and Livestock (DLL, 41°22′49.00″N, 111°27′46.35″W), located in the Bear River Mountain Range of northern Utah, USA, approximately 145 km northeast of Salt Lake City. DLL occupies approximately 90,000 ha in Rich, Weber, and Morgan counties at an elevation ranging from 1890 m to 2650 m. It is bordered by the Ogden Ranger District of the Wasatch–Cache National Forest (WCNF) to the west, the Utah–Wyoming state line to the east, and Utah SR-16 and Interstate 80 to the north and south, respectively. DLL is in the Middle Rocky Mountains physiographic province, bounded by the Wyoming Basin to the east, the Colorado Plateau to the south, and the Basin and Range physiographic province to the west. The lower elevations at DLL are dominated by sagebrush (*Artemisia* spp.) steppe, which accounts for 30% of overall land cover (National Audubon Society 2009); vegetation at the higher elevations below treeline consists of a mosaic of quaking aspen stands and conifer forest, interspersed with big sagebrush (*Artemisia tridentata* var. *vaseyana*) meadows. Pure aspen stands are typically mature (>100 years) and relatively small, rarely occupying more than 50 ha.

In May 2007, warmer-than-average temperatures during the period 7–21 May (Fig. 1), combined with a smaller-than-average snowpack, produced a roughly one month earlier snowmelt at DLL (LaMalfa and Ryel 2008, St. Clair et al. 2009). This event precipitated an earlier leaf flush in much of the montane aspen, possibly in response to increased soil temperature. When daily minimum temperatures subsequently dropped to –5 °C on 23 May (Fig. 1), a large proportion of aspen trees

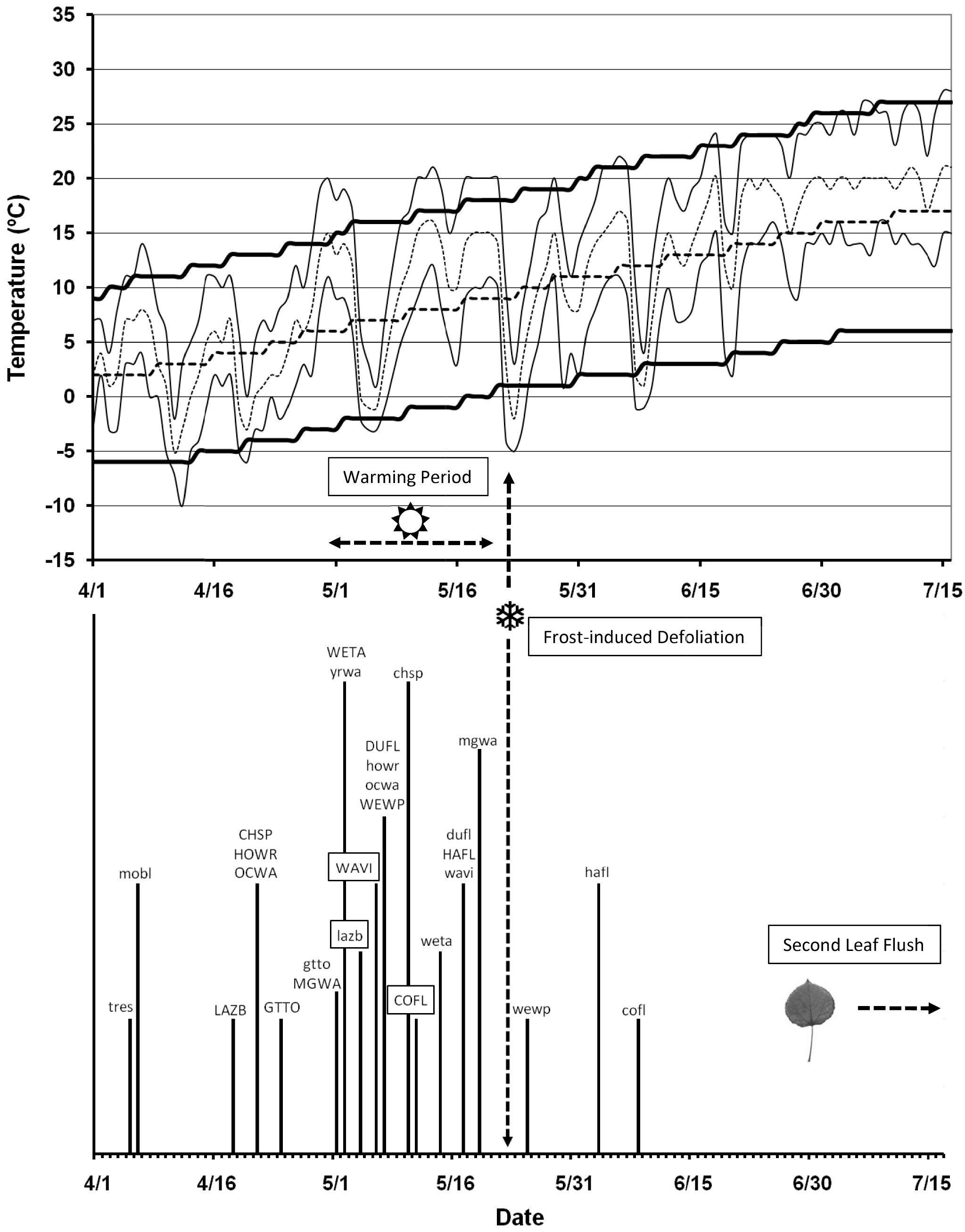

Fig. 1. Timeline of weather events at Deseret Land and Livestock (DLL), Utah, USA, during spring 2007 vis-à-vis arrival dates of migratory birds. Above are daily minimum/maximum (—) and average (- - -) temperatures (°C) for 1 April–15 July 2007; thin lines represent 2007 readings from Lightning Ridge NRCS SNOTEL site (41°21′00″N, 111°29′00″W); thick lines indicate daily 1971–2000 station normals from Woodruff, Utah, USA (41°31′30″N, 111°08′58″W, National Climatic Data Center 2001). Below are earliest recorded (capitals) and average (lowercase) arrival dates of migratory birds (Dixon 1995) in nearby Cache County, Utah. Bird Banding Laboratory species alpha codes were used (available from: http://www.pwrc.usgs.gov/BBl/manual/sname.htm): CHSP – Chipping Sparrow, COFL – Cordilleran Flycatcher, DUFL – Dusky Flycatcher, GTTO – Green-tailed Towhee, HAFL – Hammond's Flycatcher, HOWR – House Wren, LAZB – Lazuli Bunting, MGWA – MacGillivray's Warbler, MOBL – Mountain Bluebird, OCWA – Orange-crowned Warbler, TRES – Tree Swallow, WAVI – Warbling Vireo, WETA – Western Tanager, WEWP – Western Wood-Pewee, YRWA – Yellow-rumped Warbler.

suffered varying levels of leaf damage and defoliation. Approximately 5 weeks later, in early July, aspen trees at DLL that had lost all or part of their first-flush canopy produced a second flush of leaves, resulting in a landscape mosaic of aspen stands with varying levels of canopy cover.

We monitored avian abundance in montane aspen in conjunction with a breeding bird survey at DLL during 2005–2006 (predisturbance) and 2007 (postdisturbance), using 42 permanent 50-m radius (0.785 ha) circular plots established along transects at 320-m (0.2 mi) intervals. Because transects were laid out at the forest stand scale, a small number of plots were located on adjacent national forest land, where stands of interest straddled the boundary between DLL and WCNF. Our survey protocol followed standards recommended by Ralph et al. (1993, 1995). All plots were comparable with respect to topography (ridgelines or plateaus with nearly level topography) and elevation (range 2495.7–2585.9 m, $\bar{x}$ = 2533.2 m, SD = 23.8 m), and they supported nearly identical vegetation communities dominated by mature quaking aspen. The same plots were visited once each year in early to mid-July by the same single observer. Counts typically began at 06:00 (MST) and were completed by 10:30. We did not conduct fieldwork under rainy or extremely windy conditions. Counts began immediately when an observer reached a plot and were conducted for 5 min, All birds seen or heard were recorded and data subtallied by minute. Individuals flushed by the observer approaching or leaving the plot within 50 m of plot center were counted as being inside the plot. In 2007, we assigned each survey plot a level of frost damage by visual inspection of first- and second-flush foliage on aspen trees throughout the plot (methodology of St. Clair et al. 2009): low (majority of trees having maintained first-flush leaves), intermediate (majority of trees having lost first-flush leaves, with full secondary leaf flush from surviving leaf buds evident), and severe (majority of trees having lost first-flush leaves, with patchy secondary leaf flush). Of the 42 survey plots, we scored 10 as having low frost damage, 19 as having intermediate frost damage, and 13 as having severe frost damage. Frost effects occurred at the scale of individual stands (single dominant clone; i.e., damage was related to genetic rather than geographic variation—St. Clair et al. 2009), resulting in an interspersion of frost damage level among plots.

We compared bird total abundance, species richness (S), Shannon–Weaver species diversity (H'; Shannon 1948, Shannon and Weaver 1949), and Shannon–Weaver species evenness (J'; Shannon 1948, Shannon and Weaver 1949) among levels of frost damage and years. We used a generalized linear mixed model of a 2-way factorial in a split-plot design, with frost damage level as the whole-plot factor and year as the split-plot factor. As appropriate, we used Tukey's Studentized Range Test ($P <$ 0.050) to separate means while controlling type I experimental error (Day and Quinn 1989). All computations were performed using the procedure GLIMMIX in SAS/STAT® software, Version 9.1.3, of the SAS System for Windows. Because the point-count methodology of Ralph et al. (1993, 1995) is most suited for passerines, we excluded all nonpasserines from the analysis.

Over the study period, we observed 37 bird species, of which 28 were passerines (Appendix). Although not all bird species were observed in each year, both the number of passerine species and the number of bird species observed were fairly consistent over the 3-year period, varying by 0% and 5%, respectively. With the exception of Northern Flicker (*Colaptes auratus*), all bird species observed in all 3 years were passerines (Appendix). Species with the highest abundance across years were, in descending order, White-crowned Sparrow (*Zonotrichia leucophrys*), Dark-eyed Junco (*Junco hyemalis*), and Warbling Vireo (*Vireo gilvus*).

Point estimates of passerine total abundance, S, and H' increased from 2005 to 2007 (Table 1); however, differences among years were not significant ($P \geq 0.050$). J' decreased significantly from 2005 to 2007 ($P < 0.001$; Table 1), with bird species less evenly distributed among sample plots in 2007 than in either 2005 or 2006. In 2007, passerine total abundance, S, and H' differed significantly among plots assigned different levels of frost damage (Figs. 2A–C). Aspen plots that had sustained low levels of frost damage had significantly higher total abundance (7.30, SE = 0.77) than plots with either intermediate (4.63, SE = 56) or severe (2.62, SE = 0.67) levels of frost damage (Fig. 2A); significantly higher S (4.80, SE = 0.48) than plots with either intermediate

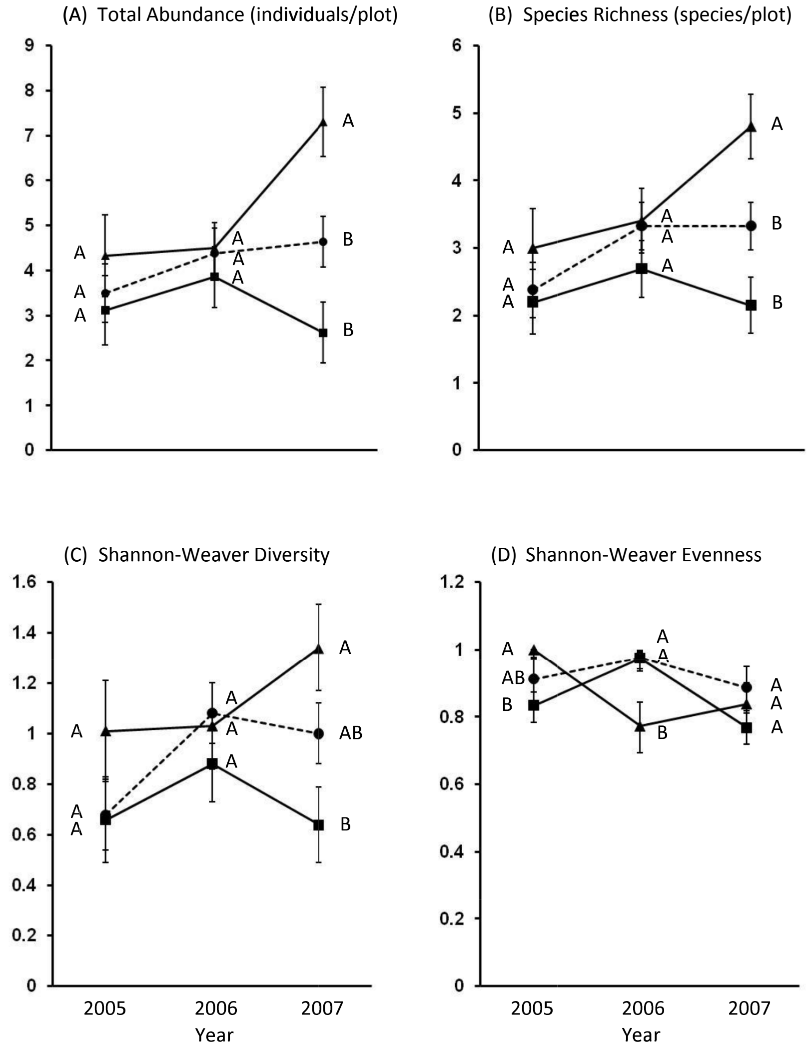

Fig. 2. (A) Total abundance (individuals/plot); (B) species richness (species/plot); (C) Shannon–Weaver species diversity (H', Shannon 1948, Shannon and Weaver 1949); and (D) Shannon–Weaver species evenness (J', Shannon 1948, Shannon and Weaver 1949) of the bird species assemblage in montane aspen at Deseret Land and Livestock, Utah, USA, during summer 2005–2007. Means are shown for 3 levels of frost damage: low (—▲—), intermediate (- - ● - -), and severe (—■—). Means in a column sharing a letter are not significantly different ($P \geq 0.050$) among levels of frost damage (Tukey's Studentized Range Test). Error bars represent one standard error around the mean.

(3.32, SE = 0.35) or severe (2.15, SE = 0.42) levels of frost damage (Fig. 2B); and significantly higher H' (1.34, SE = 0.17) than plots with severe frost damage (0.64, SE = 0.15; Fig. 2C). J' did not differ significantly among aspen plots with different levels of frost damage in 2007, although significant differences had been observed in 2005 and 2006 (Fig. 2D).

Our study found no significant changes at the landscape scale in the bird species assemblage of montane aspen at DLL over the 3-year monitoring period as measured by avian total abundance, S, and H' and no significant changes in these parameters from the pre- to the postdisturbance period (Table 1). However, we observed significant differences in total abundance, S, and H' in the year 2007 among sample plots having experienced different levels of frost damage: all 3 parameters increased with decreasing level of frost damage

TABLE 1. Avian community summary statistics of passerines (Passeriformes) in montane aspen at Deseret Land and Livestock, Utah, USA, during summer 2005–2007.

	2005		2006		2007			
	Mean	SE	Mean	SE	Mean	SE	$F_{2,67}$	P[a]
Total abundance (individuals per plot)	3.65	0.45	4.24	0.39	4.85	0.39	2.14	0.126
Species richness (species per plot, S)	2.52	0.28	3.14	0.24	3.42	0.24	2.97	0.058
Species diversity (H')[b]	0.78	0.10	1.00	0.08	1.00	0.08	1.70	0.190
Species evenness (J')[b]	0.93 A[c]	0.03	0.92 A	0.03	0.83 B	0.03	12.71	<0.001

[a]Probability of a greater F (df = 2, 67) for H_0: mean value for parameter of interest does not differ among years.
[b]Shannon (1948), Shannon and Weaver (1949).
[c]Means sharing a letter are not significantly different ($P \geq 0.050$) among years according to Tukey's Studentized Range Test.

severity (Fig. 2A–C). This result suggests that frost-induced defoliation affected how birds distributed themselves across the landscape at the stand scale, with greater use of stands with low frost damage severity over those with intermediate or high levels of frost damage. During the predisturbance years of 2005 and 2006, no such differences were found. Thus, whereas the range of frost damage severity among aspen stands was almost certainly linked to genetic differences affecting such phenotypic traits as timing of leaf flush or susceptibility to frost damage (St. Clair et al. 2009), these underlying factors do not appear to have influenced bird distribution during the predisturbance years of 2005 and 2006.

A significant decrease in J' from the pre- to the postdisturbance period (Table 1) is the only metric that suggests a change at the landscape scale in the avian community at DLL in response to frost-induced defoliation. It is possible that some species were simply more successful at quickly adjusting to a modification of their breeding habitat, causing them to numerically dominate the species assemblage to a greater degree than during the predisturbance years. Similarly, large numbers of individuals of species with lesser adaptive capabilities leaving the site could have also resulted in lower evenness. For example, 2 of the most numerically dominant species at DLL, White-crowned Sparrow and Warbling Vireo, had greatly reduced abundance in stands with severe frost damage. Two other common species, Western Wood-Pewee (*Contopus sordidulus*) and MacGillivray's Warbler (*Oporornis tolmiei*), were completely absent from these stands. Finally, a lower J' in 2007 may have been driven, in part, by a greater dominance of a few highly plastic, generalist species able to successfully establish territories in stands most impacted by the frost defoliation event. To wit, we observed the lowest J' of any group of plots in any year on plots with high levels of frost damage in the postdisturbance year of 2007 (Fig. 2D).

The observed avian response to frost-induced defoliation at DLL most closely fits our hypothesis of local resettlement within the affected landscape into habitat patches least impacted by the disturbance (Clark 1935). This outcome seems intuitive when considering that, at the time of the disturbance, the majority of species were probably already on site or within the general geographic area. To wit, only 3 species, Western Wood-Pewee, Hammond's Flycatcher (*Empidonax hammondii*), and Cordilleran Flycatcher (*Empidonax occidentalis*), have average arrival dates after May 23, and even these species all have earliest documented arrival dates that precede the defoliation event (Dixon 1995; Fig. 1). Even stands with severe frost damage were not completely abandoned by birds. This may be because some individuals had already progressed too far into their breeding cycle to relocate (Emlen 1970). Another possibility is that the changed habitat conditions in the most impacted aspen stands actually created more favorable conditions for certain species (Leidolf et al. 2007). For example, both American Robin (*Turdus migratorius*) and Yellow-rumped Warbler (*Dendroica coronata*) were more abundant in aspen stands with severe frost damage than in stands with either low or moderate frost damage. Finally, it is possible that birds in these stands were simply unable to successfully compete for territories in less severely impacted stands and were left with no other choice but to remain.

This study has shown that even transitory disturbances can have significant effects on the bird species assemblage of montane aspen. At the same time, our results suggest the importance of landscape-level genetic diversity of montane aspen for buffering the temporal dynamics of avian populations by providing refugia of unaffected habitat for birds impacted by extreme weather events. If such events increase in frequency due to climate changes in the future, the long-term effects of successive frost-induced defoliations on avian populations may be more severe. To this end, future research is needed on the effects of frost-induced defoliation on avian productivity and recruitment, as well as overwinter survival of adult birds, both in affected stands and in unaffected refuge stands experiencing temporarily increased bird densities.

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APPENDIX. Mean abundance of 37 bird species in montane aspen stands at Deseret Land and Livestock, Utah, USA, during summer 2005–2007.

Common name (scientific name)[a]	Mean abundance (individuals/plot) ± SE[b]		
	2005	2006	2007
American Kestrel (*Falco sparverius*)	0.06 ± 0.04	0.02 ± 0.02	—
American Robin (*Turdus migratorius*)	0.19 ± 0.09	0.33 ± 0.11	0.14 ± 0.06
American Three-toed Woodpecker (*Picoides dorsalis*)	0.03 ± 0.03	—	—
Black-billed Magpie (*Pica hudsonia*)	0.23 ± 0.20	—	—
Black-capped Chickadee (*Poecile atricapillus*)	0.19 ± 0.13	0.02 ± 0.02	0.26 ± 0.11
Brown-headed Cowbird (*Molothrus ater*)	0.06 ± 0.06	—	—
Cassin's Finch (*Carpodacus cassinii*)	—	—	0.02 ± 0.02
Cedar Waxwing (*Bombycilla cedrorum*)	—	—	0.05 ± 0.05
Chipping Sparrow (*Spizella passerina*)	0.16 ± 0.08	—	0.05 ± 0.03
Clark's Nutcracker (*Nucifraga columbiana*)	0.03 ± 0.03	—	—
Common Raven (*Corvus corax*)	—	0.05 ± 0.05	—
Cordilleran Flycatcher (*Empidonax occidentalis*)	—	0.02 ± 0.02	—
Dark-eyed Junco (*Junco hyemalis*)	0.84 ± 0.19	0.60 ± 0.14	0.90 ± 0.17
Downy Woodpecker (*Picoides pubescens*)	—	—	0.14 ± 0.05
Dusky Flycatcher (*Empidonax oberholseri*)	0.06 ± 0.04	0.10 ± 0.06	0.36 ± 0.07
Green-tailed Towhee (*Pipilo chlorurus*)	0.06 ± 0.04	0.17 ± 0.07	0.10 ± 0.05
Hairy Woodpecker (*Picoides villosus*)	—	—	0.02 ± 0.02
Hammond's Flycatcher (*Empidonax hammondii*)	0.03 ± 0.03	—	—
House Finch (*Carpodacus mexicanus*)	—	0.05 ± 0.05	—
House Wren (*Troglodytes aedon*)	0.26 ± 0.08	0.26 ± 0.08	0.29 ± 0.08
Lazuli Bunting (*Passerina amoena*)	—	0.40 ± 0.10	—
MacGillivray's Warbler (*Oporornis tolmiei*)	0.06 ± 0.04	0.19 ± 0.06	0.14 ± 0.06
Mountain Bluebird (*Sialia currucoides*)	0.03 ± 0.03	0.12 ± 0.07	0.07 ± 0.07
Mountain Chickadee (*Poecile gambeli*)	0.03 ± 0.03	—	—
Mourning Dove (*Zenaida macroura*)	—	0.02 ± 0.02	—
Northern Flicker (*Colaptes auratus*)	0.16 ± 0.07	0.07 ± 0.04	0.19 ± 0.09
Orange-crowned Warbler (*Vermivora celata*)	—	—	0.02 ± 0.02
Red-naped Sapsucker (*Sphyrapicus nuchalis*)	—	0.02 ± 0.02	0.14 ± 0.08
Red-tailed Hawk (*Buteo jamaicensis*)	0.03 ± 0.03	—	—
Ruby-crowned Kinglet (*Regulus calendula*)	—	0.10 ± 0.05	—
Tree Swallow (*Tachycineta bicolor*)	—	—	0.12 ± 0.08
Warbling Vireo (*Vireo gilvus*)	0.29 ± 0.12	0.40 ± 0.09	0.62 ± 0.11
Western Tanager (*Piranga ludoviciana*)	—	0.02 ± 0.02	0.02 ± 0.02
Western Wood-Pewee (*Contopus sordidulus*)	0.16 ± 0.07	0.19 ± 0.07	0.43 ± 0.10
White-crowned Sparrow (*Zonotrichia leucophrys*)	1.06 ± 0.21	1.05 ± 0.16	0.95 ± 0.17
Williamson's Sapsucker (*Sphyrapicus thyroideus*)	0.03 ± 0.03	—	—
Yellow-rumped Warbler (*Dendroica coronata*)	0.10 ± 0.05	0.17 ± 0.08	0.21 ± 0.06

[a]American Ornithologists' Union (1998)
[b]Based on a survey of 42 permanent 50-m radius (0.785-ha) circular plots