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RESEARCH ARTICLE

Spatial variation in songbird demographic trends from a regional network of banding stations in the Pacific Northwest

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ABSTRACT

Many North American landbird populations have declined in recent decades, including those that occupy Western forest habitats. Long-term monitoring of abundance and vital rates allows us to detect species and habitats of concern, and to identify potential management actions. Here, we analyze capture data from a regional network of 10 banding sites in the Klamath-Siskiyou Bioregion, USA, to examine demographic trends for 12 Western forest bird species from 2002 to 2013. Adult abundance declined significantly in some breeding populations of Audubon's Yellow-rumped Warbler (*Setophaga coronata auduboni*) and Purple Finch (*Haemorhous purpureus*), and near-significantly in Oregon Dark-eyed Junco (*Junco hyemalis oreganus*). We observed significant declines in productivity of the Purple Finch and Spotted Towhee (*Pipilo maculatus*). Black-headed Grosbeaks (*Pheucticus melanocephalus*) and Yellow-breasted Chats (*Icteria virens*) increased significantly in adult abundance, but with variation among sites. Productivity in one year was positively correlated with adult abundance in the following year for only one species, suggesting that local productivity may not be the proximate demographic cause of population change. Trends in adult abundance were generally heterogeneous across the landscape, while trends in productivity were more consistent among sites. Ten of 12 bird species exhibited similar or more positive trends in the Klamath-Siskiyou Bioregion than in the larger Pacific Northwest region as measured by Breeding Bird Survey data. Data from long-term banding sites that include productivity indices and breeding status of adults can provide important supplementary information to other long-term monitoring data and help to generate hypotheses regarding proximate demographic causes of local population trends. Future studies using regional networks of banding sites may begin to elucidate source–sink dynamics and the scale at which they operate, a topic with implications for species conservation.

Keywords: abundance, banding, Breeding Bird Survey, long-term monitoring, mist netting, population trends, productivity, Western birds

Variación espacial en las tendencias demográficas de aves canoras a partir de una red regional de estaciones de anillado en el Noroeste del Pacífico

RESUMEN

Muchas poblaciones de aves terrestres de América del Norte han disminuido a lo largo de las últimas décadas, incluyendo aquellas que ocupan hábitats boscosos del Oeste. El monitoreo de largo plazo de las abundancias y las tasas vitales nos permite detectar especies y hábitats de interés, e identificar potenciales acciones de manejo. Aquí, analizamos datos de captura de una red regional de 10 sitios de anillado en la Biorregión de Klamath–Siskiyou para examinar las tendencias demográficas de 12 especies de aves de bosque del Oeste desde 2002 a 2013. La abundancia de los adultos disminuyó significativamente en algunas poblaciones reproductivas de *Setophaga coronata auduboni* y *Haemorhous purpureus*, y casi significativamente en *Junco hyemalis oreganus*. Observamos disminuciones significativas de productividad en *H. purpureus* y *Pipilo maculatus*. *Pheucticus melanocephalus* e *Icteria virens* aumentaron significativamente en abundancia de adultos, pero con variaciones entre sitios. La productividad en un año estuvo correlacionada positivamente con la abundancia de adultos en el año siguiente solo para una especie, sugiriendo que la productividad local podría no ser la causa demográfica inmediata del cambio poblacional. Las tendencias en abundancia de adultos fueron generalmente heterogéneas a través del paisaje, mientras que las tendencias en productividad fueron más consistentes entre sitios. Diez de las 12 especies de aves mostraron tendencias similares o más positivas en la Biorregión de Klamath–Siskiyou que en la región más amplia del Noroeste del Pacífico medidas con datos del Muestreo Reproductivo de Aves. Los datos de largo plazo de los sitios de anillado que incluyen índices de productividad y estatus reproductivo de adultos pueden brindar información suplementaria importante a otros datos de monitoreo de largo plazo y pueden ayudar a generar hipótesis sobre las causas demográficas inmediatas de las tendencias poblacionales locales. Los estudios futuros que usen redes regionales de sitios de anillado podrían comenzar a dilucidar las dinámicas de fuente-sumidero y la escala a la cual operan, un tema con implicancias para la conservación de las especies.

Palabras clave: abundancia, anillado, aves del Oeste, monitoreo de largo plazo, Muestreo Reproductivo de Aves, productividad, redes de niebla, North American Bird Breeding Survey, tendencias poblacionales

INTRODUCTION

Populations of many landbirds are declining throughout North America (Robbins et al. 1989, Pyle et al. 1994, Ballard et al. 2003, Sauer and Link 2011, Sauer et al. 2013, Ralston et al. 2015). The population index for birds of Western forest habitats, based on 39 obligate breeding species, has declined nearly 20% since 1968 (NABCI 2014). With a few prominent exceptions (e.g., Smith et al. 2006, Holmes 2011), the proximate demographic mechanisms driving avian population trends remain relatively unknown. Effective conservation and management of avian populations requires information about which populations are declining and the potential causes of such declines. Long-term monitoring of abundance and vital rates such as productivity can be used to identify species and/or populations of conservation concern, as well as potentially which portion of the annual cycle is most limiting (DeSante et al. 2001, Saracco et al. 2008). Examining trends from monitoring provides a wealth of baseline data, an opportunity to recognize changes in abundance or phenology, and a way to monitor the effects of persistent environmental change such as habitat conversion, fire suppression, and global climate change (Porzig et al. 2011). The Breeding Bird Survey (BBS) is one of the most important large-scale monitoring efforts. Started in 1966, the BBS is a continental-scale survey of breeding birds in North America, carried out by volunteer observers, and intended to track population change (Sauer et al. 2017b). The long-term data collected through this effort have made major contributions to species assessments and conservation plans at regional and national scales (Rosenberg et al. 2017). However, constant effort mist netting stations operated during the breeding season can provide information about bird populations within a more specific geography than large-scale monitoring programs such as the BBS, providing valuable supplementary data at finer spatial scales (Temple and Wiens 1989, Porzig et al. 2011). Understanding variation in local trends can help land managers to identify and implement local or regional conservation actions. Data from banding stations also provide more detailed information, such as breeding status, which is useful for understanding demographic patterns by reducing noise in the data introduced by migrants, floaters, and other nonterritorial individuals.

Although monitoring long-term population trends is useful for identifying species or populations of conservation concern, abundance estimates may not provide the data needed for targeting management efforts (Saracco et al. 2008). Information on adult abundance alone may be misleading, as in the case of an ecological sink (Pulliam 1988) or trap (reviewed by Robertson and Hutto 2006). Subordinate individuals may be abundant in poor-quality habitat, yet experience low reproductive success or survival and thus fail to contribute to population growth (Van Horne 1983). Therefore, understanding demographic rates that directly influence population growth, such as productivity (often measured by the capture rate of young birds, or the ratio of young birds captured to adults), is important. Species can also exhibit declines despite the availability of high-quality breeding habitat, because limiting factors on the nonbreeding grounds may also affect breeding season abundance (Peach et al. 1991, Szép 1995, Wilson et al. 2011) and reproductive success (Norris et al. 2004, Saino et al. 2004, Rockwell et al. 2012) of migratory bird species. Linking local productivity to abundance trends may provide insight into the proximate demographic causes underlying population change. For example, while variation in adult abundance accompanied by variation in productivity in the prior year is consistent with the hypothesis that local breeding habitat is the primary driver of trends, if these parameters are unrelated, other factors may be more important (e.g., DeSante et al. 2001, Holmes 2011). Constant effort mist netting provides information on productivity that can aid the development of hypotheses regarding causes of population change.

In addition, a regional network of constant effort mist netting sites can further elucidate spatial and temporal variation in indices of abundance and productivity. We can investigate whether bird populations at multiple banding stations exhibit differing trends, or whether the larger region as a whole is influenced by broad-scale limiting factors. If adult abundance reflects processes operating within local landscapes (e.g., local habitat quality, productivity, and recruitment), then we might expect to observe spatial variation in trends across a regional network of banding stations. If abundance varies over time but not space (i.e. multiple banding stations in the same region tend to have similar trends), then we might suspect large-scale environmental impacts such as climate change, widespread habitat loss, forest management practices, or conditions across the nonbreeding grounds to be driving population change. Comparing trends among multiple banding stations in one region may provide more insight than examining local patterns in isolation.

Here, we analyze long-term population trends for breeding adults of 12 Western forest bird species, using data collected at 10 constant effort monitoring stations (hereafter referred to as banding sites) in the Klamath-Siskiyou Bioregion of southern Oregon and northern California, USA, from 2002 to 2013. We took advantage of a unique opportunity to compare population trends at multiple banding sites within a regional network, and examined changes in abundance and productivity over time as a first step toward understanding potential demographic causes of population trends. We used capture rates of locally breeding birds as an index of adult abundance. To determine whether there was spatial variation in abundance trends at a regional scale, we tested models that allowed each site in our network to have either a distinct slope or the same slope across sites. We also used hatch-year capture rates to assess trends in productivity and to evaluate the potential influence of local reproductive success on adult abundance in the following year. Finally, to interpret our results in a broader regional context, we compared trends from our study sites with those derived from Breeding Bird Survey data from the portion of the Northern Pacific Rainforest Bird Conservation Region within California, Oregon, and Washington, USA (Figure 1).

METHODS

Study Sites

The Klamath-Siskiyou Bioregion of southern Oregon and northern California comprises 17.5 million hectares from the central Pacific coast east to the Great Basin. The confluence of several mountain ranges has created a complex geology and climate (Mitchell 1976), with corresponding diversity in habitat types, plants, and wildlife, including birds (e.g., Whittaker 1960, Trail et al. 1997, DellaSala et al. 1999, Strittholt and DellaSala 2001). High-ranking priority conservation areas for birds are concentrated in the Klamath and Siskiyou mountains (Veloz et al. 2015).

Klamath Bird Observatory has operated 10 banding sites in this region from 2002 to 2013 (Figure 1). Antelope Creek in Klamath National Forest (ANT1), Johnson Creek in Bureau of Land Management Lakeview District (JOHN), both in the Cascades Range, and Oregon Caves National Monument (ORCA) in the Klamath Range are high-elevation riparian sites (1,500–1,700 m) dominated by gray alder (*Alnus incana*) and a variety of willows (*Salix* spp.), nested within a mature mixed-conifer forest matrix. Sevenmile Guard Station (7MIL), Rocky Point Cabin (CABN), Odessa Creek Campground (ODES), and Wood River Wetland (WOOD) are midelevation riparian sites (1,200m–1,300 m) on the shores, waterways, and wetlands around Upper Klamath Lake, Oregon. The 7MIL and CABN sites are dominated by willows within a mature mixed-conifer forest matrix, and the WOOD site is characterized by poplars and cottonwoods (*Poplus* spp.) and willows surrounded by marsh wetland, pastures, and human dwellings. Frain Ranch Campground–Topsy Grade (TOPS), Wildlife Images (WIIM), and Willow Wind (WIWI) are lower-elevation riparian sites (<1,000 m) along Klamath River, Rogue River, and Bear Creek, respectively. The TOPS site is situated in an area dominated by willows and Oregon ash (*Fraxinus latifolia*) close to the river and mixed oak–hardwood and ponderosa pine (*Pinus ponderosa*) forest farther from the river. The WIIM site is dominated by nonnative Himalayan blackberry (*Rubus armeniacus*) and willows surrounded by mixed hardwood forest. The WIWI site is characterized by a mix of Himalayan blackberry, poplar, cottonwood, and willows surrounded by former pasture and human dwellings.

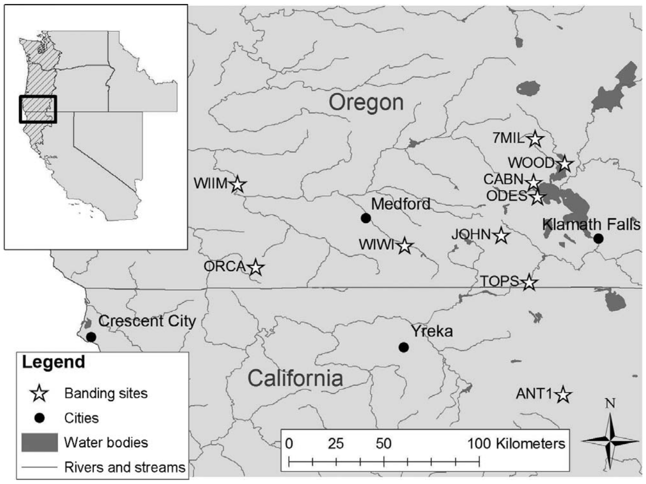

FIGURE 1. Ten constant effort mist netting sites located within the Klamath-Siskiyou Bioregion of southern Oregon and northern California, USA. The inset map shows the location of the study area inside the black square and the region of Breeding Bird Survey (BBS) analysis in hashed lines (Bird Conservation Region 5 = Northern Pacific Rainforest; California, Oregon, and Washington only).

Study Species

We chose 12 songbird species for analysis based primarily on their abundance at the study sites (i.e. those with the largest sample sizes for analysis) and their inclusion in regional avian conservation plans. Eight of the selected study species are Neotropical migrants that breed in this region in the spring and summer months. They include the Yellow-breasted Chat (*Icteria virens*), Orange-crowned Warbler (*Oreothlypis celata*), Nashville Warbler (*Oreothlypis ruficapilla*), MacGillivray's Warbler (*Geothlypis tolmiei*), Yellow Warbler (*Setophaga petechia*), Audubon's Yellow-rumped Warbler (*Setophaga coronata auduboni*), Western Tanager (*Piranga ludoviciana*), and Black-headed Grosbeak (*Pheucticus melanocephalus*). The Purple Finch (*Haemorhous purpureus*), Spotted Towhee (*Pipilo maculatus*), Song Sparrow (*Melospiza melodia*), and Oregon Dark-eyed Junco (*Junco hyemalis oreganus*) are year-round residents of this area, although there is evidence that Oregon Dark-eyed Juncos and Song Sparrows undergo short-distance seasonal movements, such that the breeding and overwintering populations in a given area are not necessarily composed of the same individual birds (J. Alexander and R. Frey personal observation), which may be true for the other resident species as well.

All of these bird species are either of regional conservation concern or considered important indicator species of coniferous or riparian habitats in the western United States. Focal species are birds that are representative of certain desired habitat attributes, such that conservation of these species should benefit many other birds that use those habitats (Chase and Geupel 2005), whereas priority species are of concern because of declining population trends. Our 12 study species are all focal and/or priority species in either the Partners in Flight (PIF) lowlands and valley bird conservation plan for Oregon (Altman 2000), the riparian plan for California (RHJV 2004), or the coniferous forest bird conservation plans for Oregon–Washington (Altman and Alexander 2012) or California (CalPIF 2002).

Field Methods

Sampling consisted of constant effort mist netting using a standardized protocol (Ralph et al. 1993, Stephens et al. 2010), with nets placed in the same locations at each site throughout the duration of the study. Banding at each site began at the onset of the songbird breeding season (between early May and early June, with the exact date determined by elevation and snow cover), with one site operated year-round (WIWI). Efforts continued through postbreeding dispersal and fall migration until mid- or late October. Visits were scheduled once in each 10-day cycle beginning May 1 through late August, and once in each 7-day cycle thereafter (except for the CABN site, which was visited 3 times in each 7-day cycle, and the WIIM site, which was visited once each 3-day cycle beginning September 1). The ANT1 site was not operated until early July in 2006 due to a road closure. In 2007, ANT1 was operated just once over a single 2-day visit, so this site–year combination was excluded from analysis.

At each site, a mist net array of 10–12 nets was situated within vegetative cover. During each site visit, nets were opened 15 min before local sunrise and operated for 5 hr (6 hr at WIIM), weather conditions permitting. Captured birds were aged and sexed when possible using standard methods (Pyle 1997), checked for breeding condition (i.e. cloacal protuberances and brood patches), marked with individually numbered aluminum leg bands, and released. We grouped netting efforts into 10-day periods beginning on January 1, and numbered these periods using the ordinal date of the center of each period (5 = January 1–10, 15 = January 11–20, etc., ending with 355 = December 17–26).

Defining Local Breeding Populations

For migratory species, a consistent problem in the analysis of mist netting data is that not all individuals that are captured are local breeders (e.g., Johnson and Geupel 1996, Nur et al. 1999). To limit our analyses to the local breeding populations of interest, we included only adults captured within species- and site-specific breeding season windows. The windows began with the first 10-day period in which 5% of total adults captured had well-developed brood patches (i.e. fully vascularized or wrinkled), and continued up to and including the last 10-day period in which 5% of total adults captured retained well-developed brood patches. We used total adult captures rather than total female captures as the denominator in this percentage, because for some species sex cannot be determined by plumage once breeding condition subsides (e.g., Song Sparrow). Within the breeding window, only those adults in high breeding condition—defined as a medium to large cloacal protuberance (males) or a fully vascularized or wrinkled brood patch (females)—were counted.

We used the capture rate of hatch-year birds (young born in the current breeding season) as an index of local productivity. Such indices are often positively correlated with measures of known local nest success derived using other methods such as nest-searching or by estimating changes in population size and survival rates (Nur and Geupel 1993, Bart et al. 1999, Dunn and Ralph 2004). To limit the productivity index to hatch-year birds fledged locally, we used the same site- and species-specific breeding season windows that we used for adults. Within these windows, we only counted captured young with >50% juvenal plumage and/or 0% to trace levels of skull pneumatization. This allowed us to exclude, to the best of our ability, captures of fall transient hatch-year birds dispersing away from their natal sites by restricting the capture window to the period when females at a given site still showed evidence of brooding young. Additionally, hatch-year birds that have only trace (or less) skull pneumatization should be only a few days to a few weeks postfledging. We acknowledge that these methods likely resulted in a different sampling area for adult and juvenile captures. The scale of the local populations for which we measured trends was not just the few hectares containing the banding site, but rather the surrounding landscape. The sampling area can be defined as the area around the banding sites with a radius determined by how far adult and hatch-year birds will travel within a few days to 2–3 weeks postbreeding or postfledging.

Statistical Analysis

We used annual capture totals for adults and young that fit our definitions of 'local' (outlined above) to estimate trends in adult and hatch-year abundance for the 12 study species. To account for varying effort at each study site and in different years, we calculated net-hours for adults (sum of all net-hours within site- and species-specific breeding season windows) and hatch-year individuals (sum of net-hours within the same windows, except excluding any 10-day time periods that occurred before the first hatch-year captures of the season were recorded). Results are presented as the yearly change in capture rates, with one observation for each species per study site per year. Sites were eliminated for a given species in the adult analysis if fewer than 10 individuals were captured at that site, and eliminated in the hatch-year analysis if fewer than 10 individuals were captured or if insufficient adults were captured there in breeding condition (implying that that species rarely breeds in that location). Thus, for a given species, between 3 and 9 banding sites were included in the analyses of adult and/or hatch-year trends.

Numbers of adult or hatch-year captures for each species were generally zero-inflated and Poisson-distributed, as is common for count data, and models fit with normal error distributions were deemed inappropriate. There was evidence of overdispersion (dispersion parameter > 1.5) for nearly all species, so we fitted quasi-Poisson models in all analyses to avoid falsely inflating significance (Zuur et al. 2009). We used generalized linear models (GLMs) to analyze trends, including the number of annual captures of adult or hatch-year birds as the dependent variable, Year and Site as independent variables, and the log of Net-hours as an offset. We also assessed whether models that included an interaction term (Year * Site), which allowed each banding site to differ in slope, provided a better fit to the data than models with a single slope for all sites. We evaluated the interaction by comparing full (with the interaction term) and reduced (without the interaction term) models with analysis-of-deviance F-tests with one degree of freedom. Results are given as slope estimates with 95% confidence intervals. We also used quasi-Poisson models to investigate potential demographic causes of trends by assessing the effect of hatch-year capture rates in one year (year n) on adult capture rates in the following year (year $n + 1$), including Site as an additional independent variable.

We calculated BBS trends for the portion of the Northern Pacific Rainforest Bird Conservation region located within California, Oregon, and Washington (Figure 1) for the study period (2002–2013). The BBS measures an index of adult abundance during the breeding season, and BBS trends are calculated from the ratio of annual indices for the first and last years of the interval of interest (Sauer et al. 2017a). Results were generated from online analysis tools and are based on hierarchical models for population change, as described by Sauer and Link (2011). The BBS online tools analyze Yellow-rumped Warbler (*Setophaga coronata*) and Dark-eyed Junco (*Junco hyemalis*) only at the species level, but nearly all of the individuals present in our region during the breeding season represent the easily diagnosable Audubon's Yellow-rumped Warbler (*S. c. auduboni*) and Oregon Dark-eyed Junco (*J. h. oreganus*) subspecies.

RESULTS

We gathered data from ~70,000 net-hours during 1,362 visits to 10 banding sites from 2002 to 2013. The beginning of the breeding season capture window fell between March 22 (earliest for resident Song Sparrows and Spotted Towhees) and June 30 (latest for Orange-crowned Warblers and Purple Finches at high-elevation sites). Date of first capture for hatch-year birds fell between May 21 (earliest for Song Sparrows) and July 20 (latest for Western Tanagers), depending on species and site. The end of the breeding season capture window fell between July 9 (earliest for Nashville Warblers) and September 7 (latest for Black-headed Grosbeaks and Western Tanagers), depending on species and site.

Analysis of data from constant effort mist netting in the Klamath-Siskiyou Bioregion revealed significant or near-significant negative trends in adult breeding populations from 2002 to 2013 for 3 of 12 species examined, and a significant increase for 2 species (Table 1). The Purple Finch exhibited the steepest decline, at an annual rate of –5.7% (95% CI: –9.3% to –2.4%), but breeding adults were present in substantial numbers at only 3 of our sites (Figure 2). Audubon's Yellow-rumped Warblers also decreased significantly overall (–4.8% per year; 95% CI: –8.5% to –1.4%), but with significant spatial variation in the slope of the trend, and 7MIL was the only site where adult captures increased (Figure 2). Oregon Dark-eyed Juncos declined at a near-significant rate (–2.5% per year; 95% CI: –5.0% to 0.1%) that was consistent across sites. Yellow-breasted Chat (7.3% per year; 95% CI: 1.4% to 12.9%) and Black-headed Grosbeak (4.0% per year; 95% CI: 0.4% to 7.5%) populations increased significantly overall, though individual sites showed increasing, decreasing, and stable population trends (Table 1, Figure 2). The remaining species showed no significant population change across all banding sites.

For the majority of species analyzed (8 of 12), the interaction term (Year * Site) that allowed slopes to vary by banding site significantly or near-significantly improved the explanatory power of the model. Therefore, with the

TABLE 1. Local and regional trends for 12 study species in the Klamath-Siskiyou Bioregion presented as annual percent change in adult and hatch-year breeding season capture rates at 10 banding sites in southern Oregon and northern California, USA ('Adult trend' and 'HY trend'). 'Year * Site' columns give *F*-values from analysis-of-deviance tests showing whether adding this interaction term to the adult and hatch-year trend models significantly improved the fit. 'HY–Adult' column gives the relationship between hatch-year abundance in year *n* and adult abundance in year $n + 1$ (in percent change per unit increase). Northern Pacific Rainforest region Breeding Bird Survey trends are presented as the ratio of annual adult abundance indices for the first and last years of the study interval ('BBS trend'; Sauer et al. 2017a). Significant ($P < 0.05$) results are in bold font, and near-significant ($0.05 < P < 0.10$) results are in italic font. *P*-values are not available for BBS trends; bold font indicates that 95% confidence intervals do not overlap zero. BBS data measure trends at the species level only (i.e. Yellow-rumped Warbler and Dark-eyed Junco).

	Adult trend					HY trend					HY–Adult		BBS trend
Common name	% annual change	*P*	Year * Site	*P*	*n*	% annual change	*P*	Year * Site	*P*	*n*	% change per unit	*P*	ratio of indices
Purple Finch	**−5.71**	**0.002**	0.70	0.50	657	**−6.62**	**0.02**	0.83	0.45	454	0.21	0.46	−1.12
Spotted Towhee	1.60	0.53	**5.12**	**0.004**	140	**−5.71**	**0.005**	0.80	0.50	384	−0.04	0.96	−0.80
Song Sparrow	−0.02	0.99	1.68	0.11	1,334	*−2.83*	*0.06*	**3.20**	**0.003**	2,319	0.11	0.22	**−2.11**
Oregon Dark-eyed Junco	*−2.46*	*0.06*	0.58	0.75	599	−2.27	0.25	1.08	0.38	1,224	0.04	0.77	**−1.38**
Yellow-breasted Chat	**7.34**	**0.02**	*2.75*	*0.08*	153	−3.45	0.23	1.52	0.46	111	0.28	0.89	−0.99
Orange-crowned Warbler	4.86	0.16	0.48	0.85	86	1.86	0.45	0.78	0.59	959	−0.10	0.69	**−2.20**
Nashville Warbler	−1.53	0.55	**2.25**	**0.05**	277	−1.18	0.78	0.84	0.51	445	0.34	0.15	−1.04
MacGillivray's Warbler	0.75	0.58	**2.44**	**0.03**	519	−1.28	0.53	0.58	0.75	338	0.69	0.15	**−2.46**
Yellow Warbler	2.04	0.22	**2.89**	**0.01**	567	−2.86	0.36	0.34	0.80	310	*0.51*	*0.07*	−1.28
Audubon's Yellow-rumped Warbler	**−4.82**	**0.008**	**2.73**	**0.02**	426	−6.31	0.10	0.59	0.71	335	−0.10	0.93	0.92
Western Tanager	−0.61	0.71	**2.63**	**0.03**	465	−4.58	0.13	0.45	0.81	346	−0.02	0.94	0.66
Black-headed Grosbeak	**3.98**	**0.03**	**3.07**	**0.007**	439	0.82	0.71	0.96	0.45	306	−0.15	0.84	**1.24**

exception of the remaining 4 species (Purple Finch, Song Sparrow, Oregon Dark-eyed Junco, and Orange-crowned Warbler), most adult abundance trends varied by site (Table 1, Figure 2). However, when separated by site, few species–site combinations had significant trends (Figure 2), although power was reduced due to the smaller sample sizes.

Productivity, as measured by capture rates of hatch-year birds, declined significantly or near-significantly in the Klamath-Siskiyou Bioregion during the study period for 3 of 12 species, although 1 of these species' trends varied by site (Table 1, Figure 3). The declines in productivity that we observed included species in which the adult population also experienced a decline (Purple Finch productivity: –6.6% per year, 95% CI: –12.2% to –1.4%), as well as species in which the adult population remained relatively stable (Song Sparrow productivity: –2.8% per year, 95% CI: –5.8% to 0.2%; and Spotted Towhee productivity: –5.7% per year, 95% CI: –9.7% to –2.0%). No species showed a significant increase in productivity (Table 1). Models of hatch-year capture rates were improved by including the Year * Site interaction term for only one species (Song Sparrow: $F = 3.20$, $P = 0.003$), so most species' productivity trends were well represented by a single slope for all sites (Table 1).

Adult abundance in year n was significantly or near-significantly positively correlated with productivity in the previous year (year $n - 1$) for only 1 of 12 species (Yellow Warbler: $t = 0.51$, $P = 0.07$; Table 1). The adult population of Yellow Warblers tended to increase in years following those with a high capture rate of hatch-year birds, but for most species these parameters were not related (Table 1).

In BBS data from the Northern Pacific Rainforest Bird Conservation Region (California, Oregon, and Washington), 4 of 12 Western forest birds exhibited significant negative population trends from 2002 to 2013 (MacGillivray's Warbler, Orange-crowned Warbler, Song Sparrow, and Oregon Dark-eyed Junco; Table 1). One species, the Black-headed Grosbeak, increased significantly in abundance (Table 1). There was no relationship between trends derived from our banding data and trends derived from BBS data across this larger geographic region ($R^2 = –0.09$, $P = 0.79$; Figure 4). Ten of 12 study species exhibited similar or more positive trends in the Klamath-Siskiyou Bioregion than in the Northern Pacific Rainforest Bird Conservation Region as a whole (Table 1).

DISCUSSION

During 12 years of constant effort mist netting in the Klamath-Siskiyou Bioregion, we documented significant declines in some adult breeding populations of Purple Finch and Audubon's Yellow-rumped Warbler, and near-significant declines in Oregon Dark-eyed Junco populations. The Purple Finch additionally experienced concurrent decreases in productivity across this same region, as did other species with relatively stable adult populations (Song Sparrow, Spotted Towhee). Adult breeding popula-

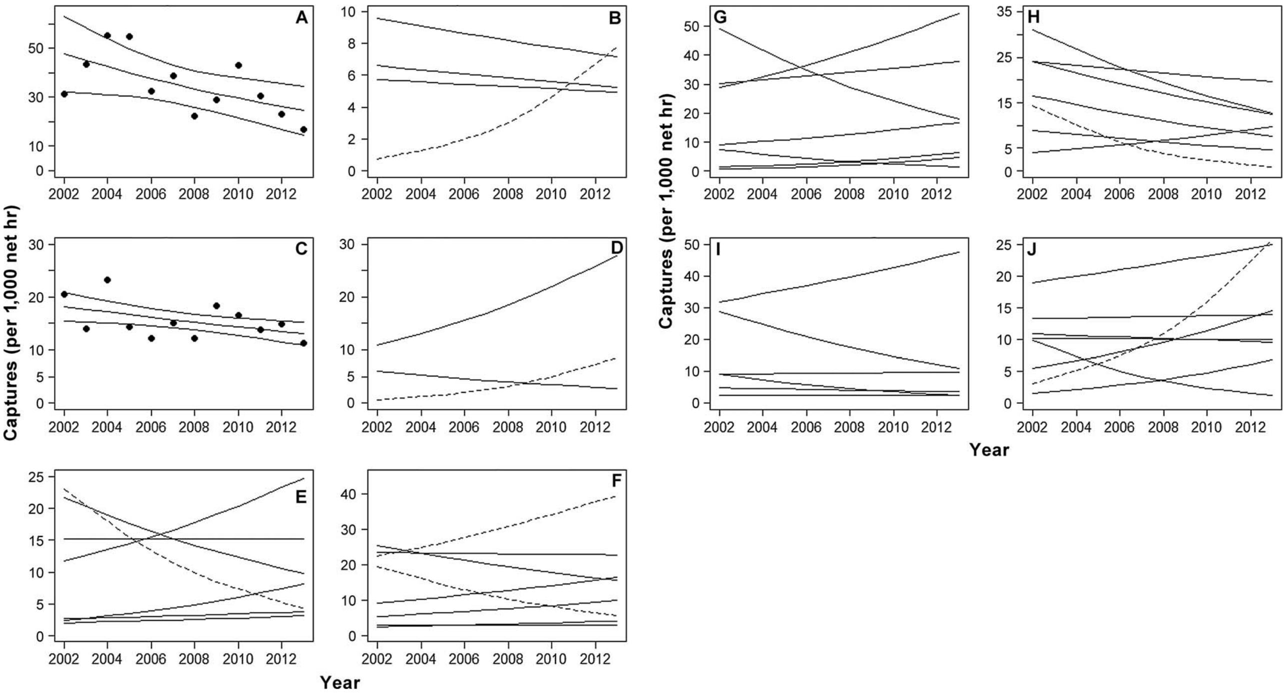

FIGURE 2. Trends in abundance (capture rates of breeding adult birds per 1,000 net-hours) for bird species in the Klamath-Siskiyou Bioregion, USA, from 2002 to 2013. When overall trends are significant ($P < 0.05$) or near-significant ($P < 0.10$), raw means are displayed by data points and fitted lines ± 1 SE are from quasi-Poisson models including effects of Year and Site. When slopes vary by site (significant or near-significant Site * Year interaction), fitted lines from quasi-Poisson models each represent an individual banding site, and sites with significant individual slopes ($P < 0.05$) are indicated by dashed lines. Only species with significant or near-significant overall trends or site effects are shown. (**A**) Purple Finch, (**B**) Spotted Towhee, (**C**) Oregon Dark-eyed Junco, (**D**) Yellow-breasted Chat, (**E**) Nashville Warbler, (**F**) MacGillivray's Warbler, (**G**) Yellow Warbler, (**H**) Audubon's Yellow-rumped Warbler, (**I**) Western Tanager, and (**J**) Black-headed Grosbeak.

tions of Yellow-breasted Chat and Black-headed Grosbeak increased significantly over the study period, though with some among-site variation. We further took advantage of a unique opportunity to compare demographic trends at multiple banding sites within a regional network, and found that, while trends in adult abundance for most species varied significantly across our regional network (sites 8–170 km apart), trends in productivity for nearly all species were similar across the landscape.

All 3 species for which we found evidence of decline are common species considered to be important indicators of healthy coniferous forest habitats in the western United States (CalPIF 2002, Altman and Alexander 2012). Adult Purple Finch declined at the 3 sites for which we had sufficient sample sizes, including the one at which they were most abundant (TOPS), and also showed a significant overall decline in productivity. We were unable to find additional studies that analyzed Purple Finch trends over the same time period, but fall migrants of this species on the California coast declined significantly from 1979 to 1999 (Ballard et al. 2003). Purple Finches prefer ponderosa pine forests with oak trees in the subcanopy (Altman and Alexander 2012) and midsuccessional forests with a closed canopy dominated by conifers (Altman and Hagar 2007). Purple Finch declines in Oregon have been attributed to habitat loss as a result of forest clearance and increased competition with growing House Finch (*Haemorhous mexicanus*) populations (Vroman 2003). Causes of declines in adult and hatch-year captures at our study sites are unknown and warrant further investigation. These data support the current conservation status of this species as a U.S. Fish and Wildlife Service (USFWS) bird of conservation concern for Bird Conservation Region 5 (Northern Pacific Rainforest region; USFWS 2008), and one with a higher regional concern score in the Partners in Flight species assessment database (PIF 2017). While adult Audubon's Yellow-rumped Warbler trends varied across the banding sites in our study area, all but one site (7MIL) had negative slope estimates. We are unsure why the 7MIL site was an exception; while there has been extensive forest thinning within 16 km of the banding station, the banding site itself is located in relatively mature, stable forest, as are our other sites where Audubon's Yellow-rumped Warblers are captured in large numbers. We also recorded a near-significant overall decline in Oregon Dark-eyed Juncos, corresponding to a significant population decline in large-scale BBS data

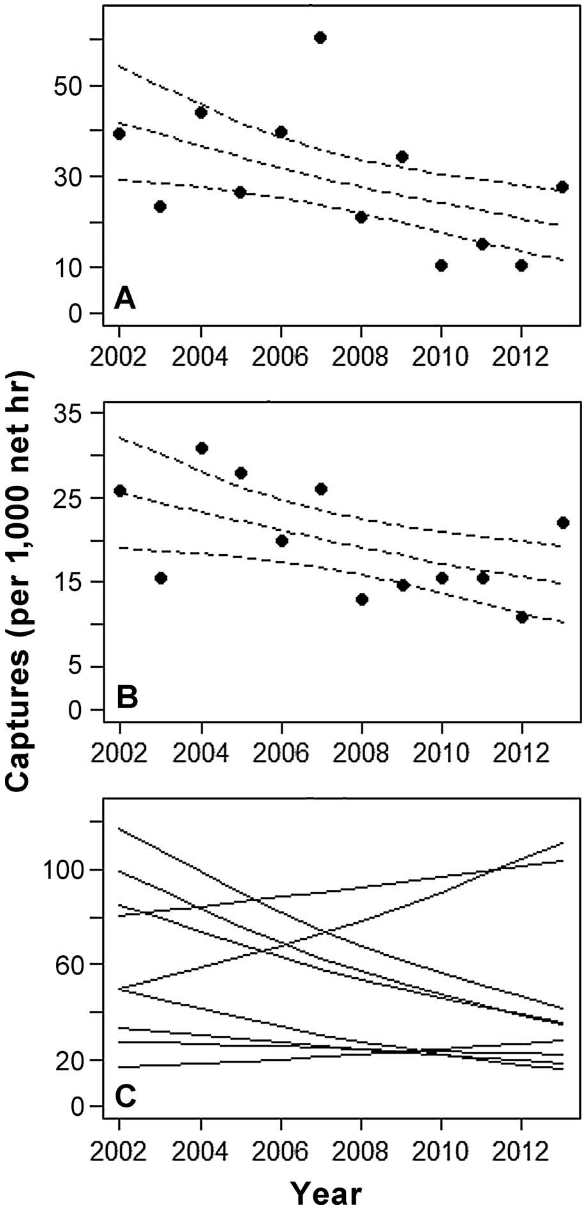

FIGURE 3. Trends in productivity (capture rates of hatch-year birds per 1,000 net-hours) for bird species in the Klamath-Siskiyou Bioregion, USA, from 2002 to 2013. When overall trends are significant ($P < 0.05$), raw means are displayed by data points and fitted lines ± 1 SE are from quasi-Poisson models including effects of Year and Site. When slopes vary by site (significant Site * Year interaction), fitted lines from quasi-Poisson models each represent an individual banding site, and sites with significant individual slopes ($P < 0.05$) are indicated by dashed fitted lines. Only species with significant or near-significant overall trends or site effects are shown. (**A**) Purple Finch, (**B**) Spotted Towhee, and (**C**) Song Sparrow.

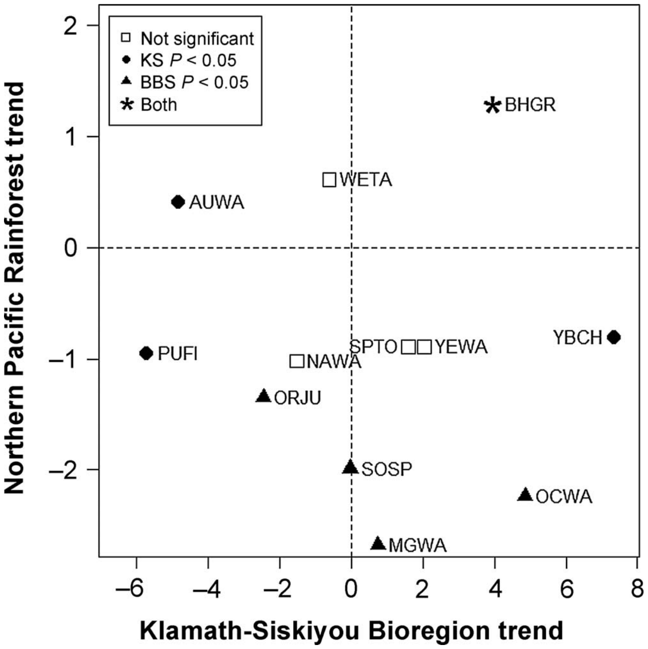

FIGURE 4. Correspondence between adult abundance trends in the Northern Pacific Rainforest region derived from Breeding Bird Survey (BBS) data and in the Klamath-Siskiyou Bioregion derived from capture data at banding sites, 2002–2013. BBS trends are measured as the ratio of annual abundance indices for the first and last years of the study interval (Sauer et al. 2017a). Klamath-Siskiyou Bioregion trends are presented as the annual percent change in abundance. Species in the lower left and upper right quadrants have matching trend directions from both data sources, while those in the lower right and upper left show opposite patterns. Symbols display whether species' trends are significant ($P < 0.05$) in BBS data, Klamath-Siskiyou Bioregion data, both datasets, or neither dataset. Species abbreviations: AUWA = Audubon's Yellow-rumped Warbler, BHGR = Black-headed Grosbeak, MGWA = MacGillivray's Warbler, NAWA = Nashville Warbler, OCWA = Orange-crowned Warbler, ORJU = Oregon Dark-eyed Junco, PUFI = Purple Finch, SOSP = Song Sparrow, SPTO = Spotted Towhee, WETA = Western Tanager, YBCH = Yellow-breasted Chat, YEWA = Yellow Warbler.

over the same time period, suggesting a similar trend in the Klamath-Siskiyou Bioregion as in the entire Pacific Northwest. Neither the Oregon Dark-eyed Junco nor the Audubon's Yellow-rumped Warbler is considered a regional or national species of conservation concern, although the junco has a Highly Vulnerable regional population trend score in the Partners in Flight species assessment database (PIF 2017). The Purple Finch and Audubon's Yellow-rumped Warbler were the only 2 study species for which we found significant declines unique to the Klamath-Siskiyou Bioregion (i.e. not found at the larger geographic scale). Coniferous forests in this region are dynamic, as fire suppression, timber harvest, insect outbreaks, and natural succession continuously change forest structure and composition across the landscape (e.g., Hessburg et al. 2000, Haugo et al. 2015). All 3 species depend on coniferous forest habitats, so determining local management alternatives or forest restoration techniques that benefit this habitat type may be important.

In contrast, both Yellow-breasted Chat and Black-headed Grosbeak adults significantly increased in abundance in the Klamath-Siskiyou Bioregion, although trends varied by site. Chats increased at 2 of 3 sites, and grosbeaks at 5 of 8 sites. Both species exhibited strong increases at WIIM, a site with relatively mature riparian forest and a dense shrub layer that includes Himalayan blackberry. The Yellow-breasted Chat and Black-headed Grosbeak are both important indicators of riparian habitats (RHJV 2004). The Yellow-breasted Chat is additionally listed as a state species of special concern in California (Comrack 2008), and a critically sensitive species (ODFW 2016) and conservation strategy species (ODFW 2005) in Oregon, but the population in our local bioregion appears to be increasing. Riparian areas in the western U.S. have been subjected to substantial anthropogenic impacts over the last several decades and now cover only a fraction of their former range (Altman 2000, Rich et al. 2004), but riparian zones surrounding our banding sites have largely remained intact.

Any habitat changes that did occur at our banding sites could have caused variation in capture rates that was unrelated to actual population change (Remsen and Good 1996); however, vegetation at banding sites remained fairly constant at all but one station (WIWI) for the duration of our study (J. Alexander and R. Frey personal observation). The WIWI site underwent extensive riparian restoration during the study period, including planting of native shrubs and large-scale removal of nonnative yellow star-thistle (*Centaurea solstitialis*) and Himalayan blackberry (except for a 25-m buffer around our net sites), followed by additional native shrub planting. These vegetation changes appeared to have inconsistent effects on the shrub-nesting birds in our study. Restoration actions may have contributed to the site-specific decline in Yellow-breasted Chats, as well as declines in chat and Spotted Towhee productivity, as shrub density, important for nesting habitat, was temporarily reduced. However, Spotted Towhee adult populations and Song Sparrow (another shrub-nesting bird) productivity increased over the same time period at this site. In many cases, the trends at WIWI for shrub-nesting species were in contrast to the general trends found at other sites, so the site-specific differences at WIWI might have been a consequence of restoration, although the mechanism is not clear.

Positive correlation between productivity in one year and adult abundance in the following year is consistent with the hypothesis that a population may be limited by reproductive success on the breeding grounds. However, we documented a positive relationship between productivity in one year and adult abundance in the next for only one species (Yellow Warbler). For the other 11 species, productivity and subsequent adult abundance were unrelated, consistent with the hypothesis that local productivity is not a proximate demographic cause of population change. This result contrasts with those of numerous previous studies of songbirds in both the eastern and western U.S. that detected a 1-yr time lag in the relationship between local productivity and adult abundance, e.g., Prairie Warbler (*Setophaga discolor*; Nolan 1978), American Redstart (*Setophaga ruticilla*; Sherry and Holmes 1992), Swainson's Thrush (*Catharus ustulatus*; Johnson and Geupel 1996), Wilson's Warbler (*Cardellina pusilla*; Chase et al. 1997), and Black-throated Blue Warbler (*Setophaga caerulescens*; Sillett et al. 2000). We did not find a similar pattern, which may indicate the true lack of a relationship, but there are alternative explanations. Several of the studies cited above examined new breeder abundance (i.e. second-year birds), which may be a stronger test of hatch-year recruitment into the breeding population in year $n + 1$. It is also possible that our index of local productivity (hatch-year abundance in year n) sampled a different, perhaps larger, geographic region than our index of breeding adults. Still, the consistent productivity trends that we observed across the 10 banding sites for most species in our study should have reduced any dilution of the relationship between productivity and subsequent adult abundance caused by the unknown scale of natal dispersal. Even our resident study species, which tend to have shorter natal dispersal distances than migrants (Paradis et al. 1998, Sutherland et al. 2000), did not demonstrate a relationship between productivity and adult abundance. In some years, such as 2009 and 2013, we captured an unusually large number of hatch-year individuals of many species, suggesting that regional conditions in those years were particularly good for reproduction of many bird species. However, years with high productivity were not necessarily followed by years of unusually high adult abundance, suggesting that limiting factors may occur between fledging and subsequent recruitment into the adult breeding population.

We demonstrated that trends in breeding adult abundance can vary even within the relatively small regional network sampled by our banding sites. This observation is consistent with the hypothesis that local breeding ground factors may be important for regulating populations of local breeding adults. If large-scale factors such as climate change, habitat loss, forest management practices, or conditions on the wintering grounds were regulating bird populations, then we might expect more consistent trends across multiple banding sites in the same region. This study was not designed to explicitly test which portion of the life cycle is most limiting for these bird populations, but the fact that we found spatial variation in adult abundance trends and little evidence of a relationship between productivity and adult abundance provides equivocal evidence of an important effect of local conditions on population regulation that warrants further study. Additional full life cycle analyses will be needed to determine which portion of the annual cycle is most limiting for Western forest bird species and the necessary management strategies to reverse declines.

Contrary to several previous studies that have found concordance between regional BBS trends and trends derived from local mist netting captures (Hagan et al. 1992, Hussell et al. 1992, Pyle et al. 1994, Ballard et al. 2003, Lloyd-Evans and Atwood 2004), we observed very little correlation. There are inherent difficulties in comparing results from 2 very different survey methods at different geographic scales (e.g., roadside bias of BBS, Keller and Fuller 1995; or conflicting trends in BBS routes across a wider region obscuring the relationship, Lloyd-Evans and Atwood 2004). However, we expected BBS trends to be more likely to align with trends derived from local mist netting captures for species with similar trends among all banding sites in our network (those that were well represented by a single slope). We found little support for this hypothesis; of the 4 species with a single trend across sites, only Oregon Dark-eyed Junco trends matched those derived from BBS data. In fact, we found that many populations (e.g., Song Sparrow, Orange-crowned Warbler, and MacGillivray's Warbler; Table 1) were stable or increasing in the Klamath-Siskiyou Bioregion despite declines or stable trends in the Northern Pacific Rainforest Bird Conservation Region as a whole, emphasizing the value of the Klamath-Siskiyou Bioregion for bird populations. The 2 prominent exceptions were the Purple Finch and Audubon's Yellow-rumped Warbler. Both are common species that are important indicators of the health of coniferous forest habitats, but are declining in our bioregion and may warrant additional conservation actions. While we did not find evidence in this study for local productivity being an important driver of population change, we encourage future studies to explore proximate demographic causes in more detail. Long-term monitoring data from banding sites that include data on breeding status and productivity provide an important supplement to the data obtained through large-scale monitoring programs (Saracco et al. 2008, Porzig et al. 2011).

Future research using regional networks of monitoring sites could provide opportunities to better understand source–sink dynamics. For instance, because adult birds are typically considered highly philopatric (e.g., Greenwood and Harvey 1982, Holmes and Sherry 1992), natal dispersal distances will often determine distances between interacting sites of population sources and population sinks. A few previous studies have found correlations in the abundance of passerine birds from one year to the next in areas 2–100 km apart, which is evidence of source–sink dynamics at this spatial scale (Winkler et al. 2005, Tittler et al. 2006, McKim-Louder et al. 2013). However, the geographic scales at which source–sink dynamics operate in avian ecology remain poorly understood. These data will be critical to shedding light on metapopulation dynamics, gene flow, and the scale at which populations are demographically connected, with important implications for identifying conservation actions needed to preserve population processes.

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