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Socio-Ecological Systems

Using culturally significant birds to guide the timing of prescribed fires in the Klamath Siskiyou Bioregion

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Abstract

Historically, wildfire and tribal burning practices played important roles in shaping ecosystems throughout the Klamath Siskiyou Bioregion of northern California and southern Oregon. Over the past several decades, there has been increased interest in the application of fire for forest management through the implementation of prescribed fires within habitats that are used by a diversity of migrant and resident land birds. While many bird species may benefit from habitat enhancements associated with wildfires, cultural burning, and prescribed fire, individuals may face direct or indirect harm. In this study, we analyzed the timing of breeding and molting in 11 species of culturally significant land birds across five ecologically distinct regions of northern California and southern Oregon to explore the potential timeframes that these bird species may be vulnerable to wildland fires (wildfire, prescribed fire, or cultural burning). We estimated that these selected species adhered to a breeding season from April 21 to August 23 and a molting season from June 30 to October 7 based on bird capture data collected between 1992 and 2014. Within these date ranges, we found that breeding and molting seasons of resident and migratory bird species varied temporally and spatially throughout our study region. Given this variability, spring fires that occur prior to April 21 and fall fires that occur after October 7 may reduce the potential for direct and indirect negative impacts on these culturally significant birds across the region. This timing corresponds with some Indigenous ecocultural burning practices that are aligned with traditionally observed environmental cues relating to patterns of biological phenology, weather, and astronomy. We detail the timing of breeding and molting seasons more specific to regions and species, and estimate 75%, 50%, and 25% quartiles for each season to allow for greater flexibility in planning the timing of prescribed fires and cultural burning, or regarding the potential implications of wildfires. The results of our study may serve as an additional resource for tribal members and cultural practitioners (when examined within the context of Indigenous Traditional Ecological

Knowledge) and forest and wildland fire managers to promote stable populations of culturally significant bird species within fire-dependent forest systems.

KEYWORDS
bird, breed, Indigenous people, Klamath Siskiyou Bioregion, molt, wildland fire

INTRODUCTION

Indigenous peoples have lived along the northern Pacific coast for millennia where they integrate burning as an ecological process into cultural stewardship practices (Boyd, 2022; Matson & Coupland, 1995). Historical Indigenous fire use ultimately shaped forest physiognomy while contemporary use of low-intensity fire in cultural burns remains an important stewardship practice among coastal tribes in Oregon and California, as exemplified by the Klamath River Prescribed Fire Training Exchange, Indigenous Peoples' Burning Network, Cultural Fire Management Council, and others (Buono, 2020; Crawford et al., 2015; Long et al., 2018; Walsh et al., 2015). These tribal burning practices are important because they promote food security while maintaining resilient ecosystems (Lake & Long, 2014; Long et al., 2018). For example, the maintenance of open-canopy oaks (*Quercus* spp.) through cultural burning provides traditional sources of food, thereby advancing cultural restoration while preserving traditional fire knowledge (Anderson, 2007; Huffman, 2013). Also, low-intensity fires diminish conifer recruitment while promoting oak savanna landscapes, one of the most imperiled habitats throughout the Klamath Siskiyou Bioregion of southern Oregon and northern California (Altman & Stephens, 2012). Forest landscapes in the Klamath Siskiyou Bioregion have been shaped by both wildfire (Taylor & Skinner, 1998) and tribal burning practices (Lake, 2013; Pullen, 1996) and host numerous culturally significant bird species. Some bird species have recently experienced population declines attributed to habitat degradation associated with fire suppression and industrial scale-timber management, among other factors (Table 1; Altman, 2011; Sauer et al., 2017). The absence of naturally occurring fire and Indigenous burning has altered the habitat and composition of bird communities in comparison to similar areas where fire has not been excluded (Marshall, 1963).

Similar to other regions globally (Whitehead et al., 2003), birds in the Klamath Siskiyou Bioregion have long been an integral part of tribal lifeways, Indigenous traditional ecological knowledge (ITEK), and cultural values, serving as indicators for ecological phenomena, habitat quality, and environmental and seasonal changes (Appendix S1: Table S1; Anderson, 2005; Kroeber & Gifford, 1980). For example, patterns of avian lifecycle phenology have been captured in traditional stories that link seasonal bird behavior with tribal use of different habitats and species. Birds are also commonly used in spiritual regalia and ceremonies (Gleeson et al., 2012; Riedler et al., 2012), and are revered, highly sought after, and considered sacred by tribes throughout northern California and southern Oregon (Long et al., 2018). Further, avian species of cultural importance represent a set of beliefs or "character" traits that form avian traditional knowledge, where some species are the focus of story-teaching lessons and ethics of stewardship or used for regalia and food (Anderson, 2005).

One aspect of tribal values for birds is as an indicator to assure human responsibility is at the forefront in limiting the impact of human fire use and stewardship practices on the reproductive rights in nature. The importance of birds to regional tribal philosophies led to a belief system that among some tribes includes the practice of prohibiting larger landscape burning that would negatively affect birds in the spring and early summer during mating, reproduction, or nesting (Long et al., 2020, see also Mistry et al., 2016 for South American tropical savannas). Because many bird species have co-evolved with and benefit from fire and cultural burning, the time of their nesting can be used by cultural practitioners as an indicator for when to cease burning at larger spatial scales (see Karuk Tribe, 2019:77, fig. 3.8). Among the belief systems of some Karuk tribal community members and as the current policy of the Karuk Tribe (residing in the mid-Klamath River and western Klamath Mountain regions of northern California), cultural burning is not conducted when the Pleiades star cluster disappears and should stop when certain birds indicate it is time to do so, only to start when other indicators present themselves. During this time, fire is only used in the context of heating and cooking (William Tripp citing Karuk ITEK, personal communication). "The appearance of Pleiades in the night sky denotes the time for cultural burning … This knowledge gained from attending to the land over generations is inscribed in ceremonies and prayers" (Karuk Tribe, 2019:58). Additionally, birds may be used as indicator species to

TABLE 1 Bird species of cultural significance to tribes captured in mist nets in northern California and southern Oregon, 1992–2014.

Common name	Scientific name	BBS trend	BBS cred.[a]	Total captures
Residents				
Mountain Quail	*Oreortyx pictus*	−1.62	1	15
California Quail	*Callipepla californica*	0.56	1	159
Cooper's Hawk	*Accipiter cooperii*	2.06	3	2
Western Screech-Owl	*Otus kennicottii*	2.02	3	32
Northern Pygmy-Owl	*Glaucidium gnoma*	1.85	3	6
Northern Saw-whet Owl	*Aegolius acadicus*	[b]	...	7
Belted Kingfisher	*Ceryle alcyon*	−0.57	2	11
Acorn Woodpecker	*Melanerpes formicivorus*	0.65	1	8
Red-breasted Sapsucker	*Sphyrapicus ruber*	3.05	1	474
Downy Woodpecker	*Dryobates pubescens*	−1.20	1	392
Hairy Woodpecker	*Dryobates villosus*	0.72	1	123
White-headed Woodpecker	*Dryobates albolarvatus*	−1.44	2	7
Northern Flicker	*Colaptes auratus*	−0.65	1	133
Pileated Woodpecker	*Dryocopus pileatus*	1.06	2	3
Steller's Jay	*Cyanocitta stelleri*	−0.10	1	318
California Scrub-Jay	*Aphelocoma californica*	1.16	1	179
Pacific Wren	*Troglodytes pacificus*	−0.72	1	361
American Dipper	*Cinclus mexicanus*	1.26	3	11
Golden-crowned Kinglet	*Regulus satrapa*	−1.64	1	197
Western Bluebird	*Sialia mexicana*	−3.51	1	13
Mountain Bluebird	*Sialia currucoides*	−5.35	3	2
American Robin	***Turdus migratorius***	**−0.52**	**1**	**1636**
Varied Thrush	*Ixoreus naevius*	−2.76	1	195
Evening Grosbeak	*Coccothraustes vespertinus*	2.56	1	1
Pine Siskin	*Spinus pinus*	−1.22	1	518
Lesser Goldfinch	*Spinus psaltria*	−1.51	1	405
American Goldfinch	***Spinus tristis***	**−2.26**	**1**	**1758**
Spotted Towhee	***Pipilo maculatus***	**−0.23**	**1**	**2745**
Dark-eyed Junco	***Junco hyemalis***	**−1.29**	**1**	**3915**
Red-winged Blackbird	*Agelaius phoeniceus*	−1.69	1	31
Yellow-rumped Warbler	***Setophaga coronata***	**−0.42**[c]	**1**	**1559**
Migrants				
Black-chinned Hummingbird	*Archilocus alexandri*	[b]	...	1
Anna's Hummingbird	*Calypte anna*	8.17	2	182
Rufous Hummingbird	*Selasphorus rufus*	−2.56	1	560
Allen's Hummingbird	*Selasphorus sasin*	−3.79	1	869
Calliope Hummingbird	*Stellula calliope*	7.39	3	27
Tree Swallow	*Tachycineta bicolor*	−2.19	1	206
Violet-green Swallow	*Tachycineta thalassina*	−0.64	1	110
Barn Swallow	*Hirundo rustica*	−2.84	1	645
Ruby-crowned Kinglet	*Regulus calendula*	0.04	2	633
Northern Mockingbird	*Mimus polyglottos*	0.10	3	1

(Continues)

TABLE 1 (Continued)

Common name	Scientific name	BBS trend	BBS cred.[a]	Total captures
Cedar Waxwing	*Bombycilla cedrorum*	−1.91	1	460
Yellow-breasted Chat	***Icteria virens***	**0.41**	**1**	**2814**
Bullock's Oriole	*Icterus bullockii*	−1.43	2	469
Orange-crowned Warbler	***Oreothlypis celata***	**−1.09**	**1**	**1763**
Nashville Warbler	*Oreothlypis ruficapilla*	−1.90	1	692
MacGillivray's Warbler	***Geothlypis tolmiei***	**−2.04**	**1**	**3957**
Common Yellowthroat	*Geothlypis trichas*	0.24	1	93
Yellow Warbler	***Setophaga petechia***	**−1.67**	**1**	**2806**
Townsend's Warbler	*Setophaga townsendi*	0.37	1	18
Hermit Warbler	*Setophaga occidentalis*	−0.37	1	461
Wilson's Warbler	***Cardellina pusilla***	**−1.36**	**1**	**3250**
Western Tanager	*Piranga ludoviciana*	1.99	1	827
Black-headed Grosbeak	***Pheucticus melanocephalus***	**0.70**	**1**	**2080**
Lazuli Bunting	*Passerina amoena*	−0.20	1	426
Grand total				38,566

Note: Breeding Bird Survey population trends (BBS trend) between 2005 and 2015 for North American Bird Conservation Region 5 (Northern Pacific Rainforest [NABCI, 2020]) are shown as yearly percent change with BBS credibility category (BBS cred.; Sauer et al., 2017). BBS credibility categories incorporate the potential for problems with population change estimates due to small sample sizes, low relative abundances on survey routes, imprecise trends, and missing data. Species are grouped by migratory status: residents (i.e., nonmigrants) and migrants. Total captures is the number of adults captured in mist nets. Species in boldface were selected for further analyses.

[a] BBS credibility category: (1) highest credibility: reflects data with moderate abundance on routes, at least 14 samples in the long term, and of moderate precision; (2) moderate credibility: reflects data with a deficiency with regional abundance, small sample size, or imprecise estimate; (3) lowest credibility: reflects data with an important deficiency with very low abundance, very small samples, or very imprecise.

[b] No data.

[c] Both subspecies.

guide burns at microscales, within specific vegetation communities, such as savannah oak stands (Altman & Stephens, 2012: fig. 2). Tribal fires during certain culturally determined timeframes are applied in relatively small areas for vegetation management, such as clearing brush, maintaining meadows, and enhancing the production of basketry materials, heating, and cooking (Anderson & Moratto, 1996; Lake, 2013), whereas at other times, fire is used across larger spatial scales. Timing of cultural burns is often guided by specific environmental cues that suggest optimal conditions for fire initiation (Anderson & Moratto, 1996; Lake et al., 2010). Such cues relate to tribal belief systems that birds are omens or messengers from the Creator, and as such are teachers to humans regarding culturally appropriate conduct for stewardship activities, such as the timing (within seasons) and specificity (habitat type/vegetation) that guides cultural burning considerations. However, birds are not the only indicator for when fire is or is not used. For example, the Karuk Tribe traditionally sets the World Renewal Ceremony fires on certain mountains during certain phases of the lunar cycle in late summer and early fall (Karuk Tribe, 2010; William Tripp citing Karuk ITEK, personal communication).

By contrast, Euro-American colonization and subsequent US fire policies in the early 1900s led to forest management characterized by fire suppression as "the first measure necessary for the successful practice of forestry" (Graves, 1910:7), often leading to vegetation and habitat changes as the result of excluding all fires (including cultural burning). In drier western forests where frequent fires previously occurred from both natural and Indigenous sources, fire suppression led to increased shrub and tree densities contributing to excessive fuel accumulations (Knight et al., 2020, 2022; Ryan et al., 2013) or changes in successional patterns and increased levels of surface fuels (Parsons & DeBenedetti, 1979). Where ecotones occurred, such as in open oak savannas and woodlands near coniferous forests (Altman & Stephens, 2012) or juniper/prairie ecotones in the midwestern United States (DeSantis et al., 2011), reduction in fires allowed woody vegetation, generally fire-intolerant species such as Douglas fir or junipers, to encroach and create closed forests, thereby diminishing open grasslands (see Knight et al., 2020, 2021, 2022). Skinner (1995), documenting forest mosaic changes after 40 years of fire suppression between 1944 and 1985, reported that forest openings in northern California mixed-conifer forests were fewer and smaller. Similarly, the western Klamath Mountains in northern California have more contiguous landscape biomass–vegetation now as a result of fire exclusion (Knight et al., 2021).

Early in the 1930s, forest managers in the southeastern United States recognized the ecological benefits of prescribed fire for the maintenance of upland game habitat. Other regions of the United States were slower to promote this land management technique (Ryan et al., 2013; Stephens & Ruth, 2005), but over the past two decades, it has quickly become a tool used by forest managers, with the number of prescribed fires set in the United States by federal and state agencies increasing from 14,000 fires in 1998 totaling 355,000 hectares to over 450,000 fires totaling over 2.4 million hectares in 2018 (National Interagency Fire Center, 2019). The greatest proportion of the reported increase in prescribed fire was on tribal lands, as tribes seek to re-introduce intentional fire on the landscape (Kolden, 2019). Recognizing that fire played an integral role in shaping ecosystems along the northern Pacific coast (Huff et al., 2005), state and federal agencies are integrating prescribed fire into forest management plans in the western United States to reduce fuel loads, restore ecosystems, and enhance forest structure to a desired condition (Agee, 2007; Huff et al., 2005; Long et al., 2017; Ryan et al., 2013). At the same time, tribes are both conducting prescribed fires with partners and seeking to reinstitute cultural burns, working with agencies and other fire use entities to reduce barriers to implementation (Clark et al., 2022; Karuk Tribe, 2010; Long et al., 2018; Senos et al., 2006).

It has been asserted that cultural burning should not be categorized with western Colonial prescribed fire (Clark et al., 2022) and a prescribed fire may or may not have cultural objectives. It is important to note and distinguish the difference between cultural burning and prescribed fire. Clark et al. (2022:3) state “Both [involve] the act of setting fire to a specific landscape to achieve a desired outcome, including fuel reduction and wildlife habitat improvement. However, cultural burning and prescribed fire are distinct concepts and are often conducted by different groups for different purposes. Prescribed fire is implemented based on a ‘prescription’ derived from models to determine conditions for burning. Especially when state [or federal] agencies are involved, prescribed fire typically includes the production of a burn plan, smoke management plan, and completion of environmental impact analysis. Cultural burning is typically less formal and is integrative of holistic knowledge of place to guide the timing and implementation of burning activities. Cultural burning implies the purposeful use of fire by a cultural group … for a variety of purposes and outcomes.”

In the Klamath Siskiyou Bioregion, as well as across the United States and other regions of the world, there is heightened interest in evaluating the use of prescribed fire by government agencies and local organizations (e.g., USDA Forest Service and Fire Safe Councils) for fuels and fire risk reduction. Wildland fires are potentially detrimental to birds, several of which are culturally significant indicators in the tribal belief systems about the ethical uses of fire (Long et al., 2020). Conversely, wildland fire may also provide benefits to birds (Bagne & Purcell, 2011; Saab & Powell, 2005; Stephens et al., 2019). By contrast, our objective in this study—which is a collaborative partnership among tribal/Indigenous, agency, academics, and nongovernmental organizations (NGOs)—is to provide sound science to inform management and address emergent challenges and to formulate a better understanding of the potential effects of wildland fires on land birds. The intent is not to “validate” tribal knowledge or belief systems, but rather to explore the implications of those concerns which have been raised by tribes and forest and wildland fire managers in our study region, or other Indigenous peoples globally (Mistry et al., 2016; Whitehead et al., 2003). Cultural concerns and ITEK relating to birds and other indicators may help to inform prescribed fire and cultural burning practitioners and may result in limiting impacts to birds of both cultural importance and conservation concern.

Currently, state and federal agencies, tribes, and other cooperative burn entities (i.e., NGOs) determine the best times for setting these fires based primarily on air quality regulations, authorized versus potential burn days, fire personnel and resource availability, as well as environmental, biophysical, or ecological variables such as fuels treatment history, fuel loading, temperature, humidity, wind, time of day, and seasonal restrictions (e.g., limited operating periods) for sensitive wildlife species (Knapp et al., 2009; Quinn-Davidson & Varner, 2012; Ryan et al., 2013). Thus, prescribed fires are increasingly being conducted in the spring to early summer and mid-to-late fall in the western United States when “controlled” burns (prescribed fires) are less likely to exceed intended severities and extents and fire personnel are more available when not engaged in fire suppression or wildfire management. As a result, many prescribed fires in northern California and southern Oregon are implemented during times when fire would have historically been likely excluded by some tribes (e.g., late spring/early summer), such as those tribal community members who hold such beliefs among the Karuk Tribe (Karuk Tribe, 2010).

However, there are also some examples where federal agencies are aligning their collaborative burning efforts with Indigenous indicators (see USDA Forest Service, 2018). Recent studies of low-to-mid elevation forests show a low historical presence of fire scars in earlywood, which would also suggest that Indigenous burning practices limited the extent of spring to mid-summer burns, especially those of higher severity that would cause tree scarring (Knight et al., 2022).

The timing of contemporary prescribed fires may coincide with breeding or molting in land birds, which are energetically taxing and vulnerable phases of the avian lifecycle, and not often considered in fire planning (Huff et al., 2005; Knapp et al., 2009, but see Ryan et al., 2013). Fires during the nesting season may reduce populations more than burning in other seasons (Lyon et al., 2000). Direct effects of fire on birds during the breeding season include destruction of active nests and mortality of young or adults (though adults can generally escape fires; Bagne & Purcell, 2009; Knapp et al., 2009). Besides direct effects, in the short-term food resources and cover for some species may become scarce depending on the scale and severity of the burn (Lyon et al., 2000), while long-term consequences include the displacement of some species while other species may take advantage of new post-fire resources (Huff & Smith, 2000; Knapp et al., 2009). Bird nest site selection, territory establishment, and nesting success can also be directly and negatively affected by fire (Lyon et al., 2000). Ground-dwelling birds may be affected by fires of any severity while canopy-dwelling birds may not be as affected by understory, lower intensity burns (Lyon et al., 2000).

Fires occurring during the prebasic (fall) molt—an energetically taxing period when adult birds completely replace their feathers—could directly endanger individuals, particularly during periods of heavy molt when a bird's capacity to fly is diminished and they become less capable of escaping fire (Swaddle & Witter, 1997). Fire can also indirectly affect birds by reducing arthropod and fruit availability during the prebasic molt when birds rely on abundant food resources. Yet, the magnitude of the impact to a bird's diet may vary by habitat quality. For example, while some food resources may decrease post-fire, others may not be impacted or may increase, including fire-adapted shrubs such as manzanita (e.g., sticky leaf manzanita, *Arctostaphylos viscida*) (Fryer, 2015) and select arthropod species, which may be attracted to fire (Huff & Smith, 2000).

The energetic demands during molt are substantially greater compared to daily maintenance needs at a time when disruption in food availability during burns could put additional metabolic stress on birds. Murphy and Taruscio (1995) reported that the daily increase in whole-body protein synthesis in molting White-crowned Sparrows (*Zonotrichia leucophrys*) equaled at least a 3.5-fold increase over daily synthesis by non-molting sparrows. Similarly, Murphy and King (1992) calculated a daily energy cost for peak molt equal to 58% of basal metabolic rate in addition to daily energy costs. Heise and Rimmer (2000) reported that during late molt stages, Gray Catbirds (*Dumetella carolinensis*) increased their foraging, which coincided with significant increases in fat stores.

To balance the ecological benefits, sociocultural values, and management objectives of prescribed fires and cultural burning with the inevitable complexities of implementation, we synthesized data from long-term scientific bird monitoring to inform the planning and timing of fire use that better informs the potential of fire-related impacts to those land bird species that are an important part of the cultural heritage of local tribes (Appendix S1: Table S1). According to the Karuk Tribe (2019:60), "burn timing follows a gradient that tracks the reproductive lifecycles of season and elevational migrant species … [and] the nesting of birds. William Tripp describes how the Karuk practice of careful observation is critical to this process: 'When the birds come back and nest it is time to move upriver or upslope with your burning.' Fire management occurs working uphill in the Spring along this gradient of reproductive timing [for resident and migratory land birds]."

There are reasons to consider, from an Indigenous tribal perspective, that our study species may serve as bioindicators for other bird species which may be more susceptible to fires and potentially vulnerable to environmental or climatic impacts (Long et al., 2020). Examples of bioindicator species correlations are well established in existing western scientific research and monitoring (Chase & Geupel, 2005; Stephens et al., 2019), but not well addressed by Indigenous peoples (Long et al., 2020, see also Karuk Tribe, 2019). For example, Saab and Powell (2005), in compiling results from multiple studies of the effects of fire (wildfire and prescribed fires) on birds, reported similarities within avian foraging and nesting guilds. Aerial, ground, and bark insectivores were positively influenced by fire, whereas foliage gleaners were negatively influenced. Additionally, they reported that species with closed nests were more positively influenced by fire than those with open-cup nests, and ground and canopy nesters more positively influenced than shrub nesters.

In this study, we summarize the timing of breeding and molting for 11 culturally significant land bird species that regularly occur in five ecologically distinct regions in the Klamath Siskiyou Bioregion of northern California and southern Oregon. Our estimates of breeding and molting seasonality were derived from a long-term bird banding dataset from the Klamath Bird Monitoring Network (Alexander, 2011), at the center of which is the long-standing investment in avian research by the US Forest Service Pacific Southwest Research Station in cooperation with Klamath Bird Observatory. The aim of our analysis is to provide tribes and forest and wildland fire managers with the best available science to support efforts to better understand the potential impacts of the timing of fire use on culturally significant bird species.

MATERIALS AND METHODS

We conducted our study in the Klamath Siskiyou Bioregion of southern Oregon and northern California (Figure 1) as described by Alexander et al. (2017). We operated 96 bird banding stations between 1992 and 2014, each station operating from 2 to 22 years (Table 2). Data were collected by multiple cooperators as part of the Klamath Bird Monitoring Network (Alexander, 2011). Stations were operated from May through October. From May through August (breeding season), stations were scheduled once every 10-day period and from September through October (fall migration season), stations were scheduled at least once per week (Ralph et al., 1993; Stephens et al., 2010). Each station had 8–15 net sites that were opened 15 min prior to sunrise and operated for 5–6 h during each sampling day. Banding stations were typically placed in a water-associated or meadow riparian zone to maximize bird capture rate. We grouped stations into five "regions," defined by elevation and proximity to one another, thus reflecting similar habitats (Figure 1, Table 2). Captured individuals were aged and sexed following Pyle (1997). Banding methods followed Ralph et al. (1993). We followed US Federal Regulations as outlined by the USGS Bird Banding Laboratory (BBL) (2019b) and its attached documentation for obtaining and maintaining ethical use of Federal Bird Banding and Marking Permits (permits 09082 and 22834). We also adhered to the "Ethics and Responsibilities of Bird Banders" (BBL, 2019a). Our methods for capturing and processing land birds were approved by Humboldt State University's Institute for Animal Care and Use Committee. The preliminary results and framing of culturally significant birds were presented to the Karuk Resource Advisory Board (KRAB), with additional review of content from William Tripp and Colleen Rossier of the Karuk Tribe's Department of Natural Resources.

We compiled a list of culturally significant species ($n = 55$) derived from tribal ITEK holders (reviewed and amended by KRAB, November 2019) and ethnographic information of northwestern California and southwestern Oregon tribal uses of birds for food, regalia, and cultural teachings (see Table 1 for scientific names). From this list, we selected study species that had more than 1000 individuals captured ($n = 11$) for subsequent analyses which resulted in an adequate number of captures in at least two season-region data subsets for an individual species analyses (see details below on data subset requirements for analyses). The 11 species selected were 5 residents (American Robin, American Goldfinch, Spotted Towhee, Dark-eyed Junco, and Yellow-rumped Warbler) and 6 migrants (Yellow-breasted Chat, Orange-crowned Warbler, MacGillivray's Warbler, Yellow Warbler, Wilson's Warbler, and Black-headed Grosbeak), which occur in a variety of habitats across the study area.

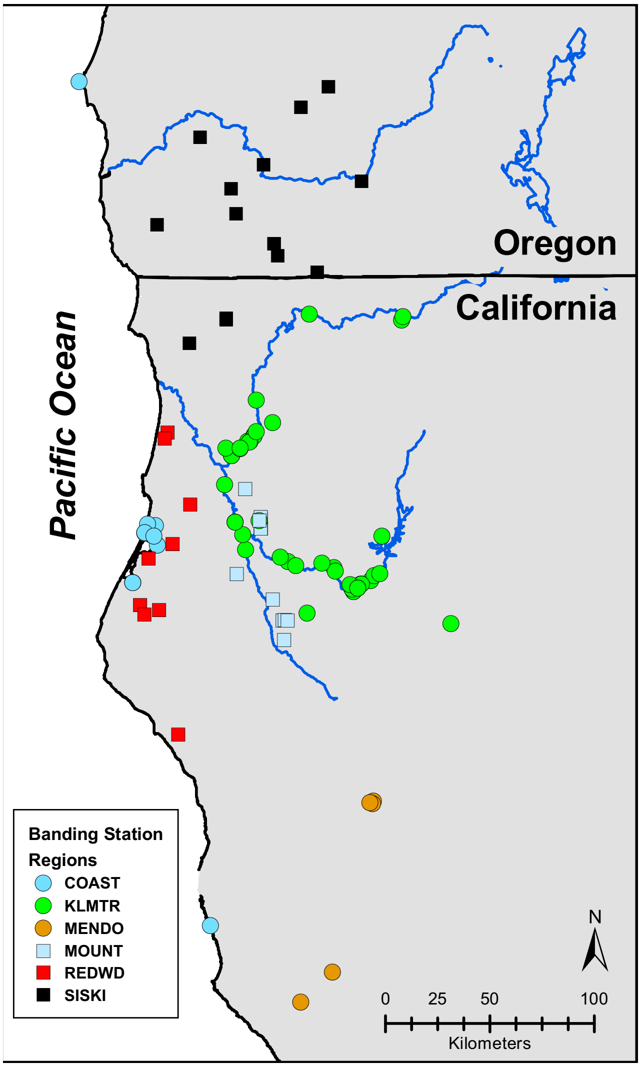

FIGURE 1 Map of the Klamath Siskiyou Bioregion study area in northern California and southern Oregon showing locations and regional designations of 92 banding stations where adult birds were captured. Region abbreviations are: COAST, Coast; KLMTR, Klamath-Trinity; MENDO, Mendocino; MOUNT, Mountain; REDWD, Redwood; SISKI, Siskiyou.

TABLE 2 List of six “regions” with code, name, and number of banding stations resulting from grouping similar banding stations based on proximity to one another, similar elevations, and distance inland from the Pacific Ocean, thus reflecting similar environmental conditions.

Region code	Region name	No. stations	Elevation (m) Min.	Elevation (m) Max.	Elevation (m) Mean	Distance inland (km) Min.	Distance inland (km) Max.	Distance inland (km) Mean
COAST	Coast	11	2	79	11	0.4	8.3	3.4
KLMTR	Klamath-Trinity	42	79	869	347	34.0	151.5	77.2
MENDO	Mendocino	5	291	1954	1249	24.8	81.3	62.4
MOUNT	Mountain	15	513	1364	1176	45.7	80.0	61.8
REDWD	Redwood	8	10	315	62	4.5	112.1	29.1
SISKI	Siskiyou	15	249	1495	750	7.0	141.0	62.3
	Total	96						

Note: Minimum, maximum, and mean values of elevation and distance inland for stations are shown for each region.

For each species, we calculated the total number of adult birds and total numbers of breeding or molting adults per 10-day period, beginning with the start of sampling Period 1 on May 1 (first period of data collection for many of our stations) and ending with Period 19 on November 7. Breeding birds were defined as adults with a smooth, vascularized, or wrinkled brood patch (indicating egg incubation in females), or a medium, large, or bulbous cloacal protuberance (indicating breeding in males). Molting birds were defined as adults undergoing the annual prebasic molt (when worn flight feathers are replaced with new ones) as characterized by the observation of symmetrical flight feather molt. We then calculated the percent of total breeding or molting birds per period, for all species combined and individual species, by all regions combined and individual region. For our calculations, we assumed that during the breeding season both breeding and nonbreeding adults generally had a similar likelihood of being captured. Similarly, we assumed that during the molting season both molting and non-molting adults had a similar likelihood of being captured.

From each data subset, we calculated two second-order polynomial equations in program R using the linear model function (R Core Team, 2018), one for breeding birds and the second for molting birds, which represented the distribution of breeding or molting individuals over time (Figure 2; Appendix S1: Table S2). Response variables were percent breeding and molting birds, respectively, while the explanatory variable was a 10-day sampling period. We used only those data subsets with at least 100 individuals and 10-day periods where >5% of adults showed breeding or molting condition in order to smooth subsequent curves. This method allowed us to estimate breeding season start dates and molting season end dates that occurred outside our sampling period.

We calculated the area under the curve (AUC) for each of the two polynomial equations (calculated above) using SAS software’s Proc Expand (SAS, 2012). Since the calculated equation represents the estimated total distribution of breeding or molting individuals over time, including estimates for time periods outside our data collection, the AUC value represents an estimate of 100% of the individuals in the distribution and can be used to calculate the percentage of a subset of the population within a selected time interval. To generate the breeding season data for this calculation, we estimated the percent of adults (y) exhibiting breeding characteristics by 5-day periods (x) from each equation; the shorter time spans (compared to the 10-day period for data collection) allowed for greater precision in estimating the percentage of breeding population during a selected time interval. Proc Expand used these incremental (x, y) pairs to compute the approximate AUC using cubic spline interpolation and the trapezoid rule. The resulting AUC value represented 100% of the estimated breeding season duration (e.g., Figure 3). We then estimated the AUC for 25%, 50%, and 75% of the breeding season duration (Figure 3). To do this, we trimmed the calculated equation curve from the edges in a symmetric fashion from both ends of the curve in increments of 5-day periods and calculated a new AUC with Proc Expand for an estimate of the percentage of the full season’s AUC for that time span. This was repeated until we had estimated time spans for 25%, 50%, and 75% of the breeding season duration. This process was repeated for molting birds to estimate the AUC for 25%, 50%, 75%, and 100% of the molting season duration (Figure 3).

We considered 50% of the seasonal distribution to be the “core” of the season and use this quartile value in our results and discussion. In a few instances, we found the estimates for the beginning of breeding season

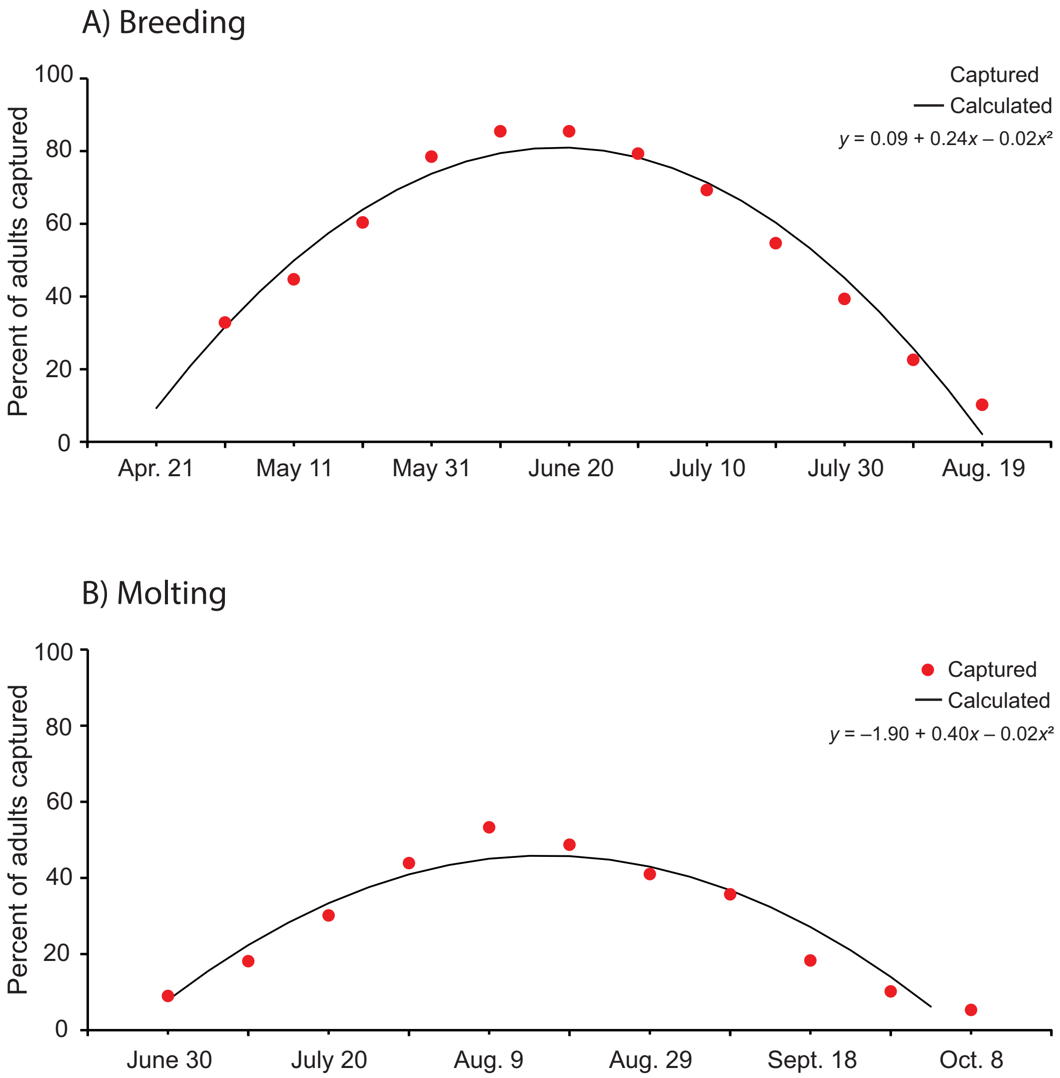

FIGURE 2 Percent of adult birds captured in (A) breeding and (B) molting condition over time in the Klamath Siskiyou Bioregion by 10-day sampling periods, all regions and all culturally significant bird species combined. Dots designate the actual percentage of captured birds by 10-day period showing signs of breeding or molting and the estimated polynomial equations (line and equation in upper right). Dates are the first day of the 10-day sampling period.

(100% of range) to be outside the reported ranges for certain species' arrival dates to the study area. These early estimates for breeding season dates were heavily influenced by the lack of data prior to May 1, particularly for those species which were already well into breeding seasonality at the start of the monitoring season, such as American Robin, Black-headed Grosbeak, and Spotted Towhee (Figure 4).

To test the assumptions of goodness of fit for using a second-order polynomial as a model, we calculated the adjusted R^2 value for each calculated model (Appendix S1: Table S2). About 80% of the models had adjusted R^2 values >0.70, suggesting good fit. To test additional assumptions of the data, we plotted histograms of the residuals for each model, most of which showed a normal distribution and evaluated plots of fitted versus residuals values for each model to assess assumptions of homogeneity (Appendix S1: Table S2).

Despite low adjusted R^2 values (<0.70) for three of our study species, we decided to report these species to demonstrate the wide variation in breeding and molting seasons between species and regions in this study.

RESULTS

A total of 38,566 adults of 55 culturally significant bird species were captured in northern California and southern Oregon from 1992 to 2014 (Table 1). We recorded a higher percentage of adults with signs of breeding (85% on June 10) than those undergoing molt (53% on August 9) (Figure 2).

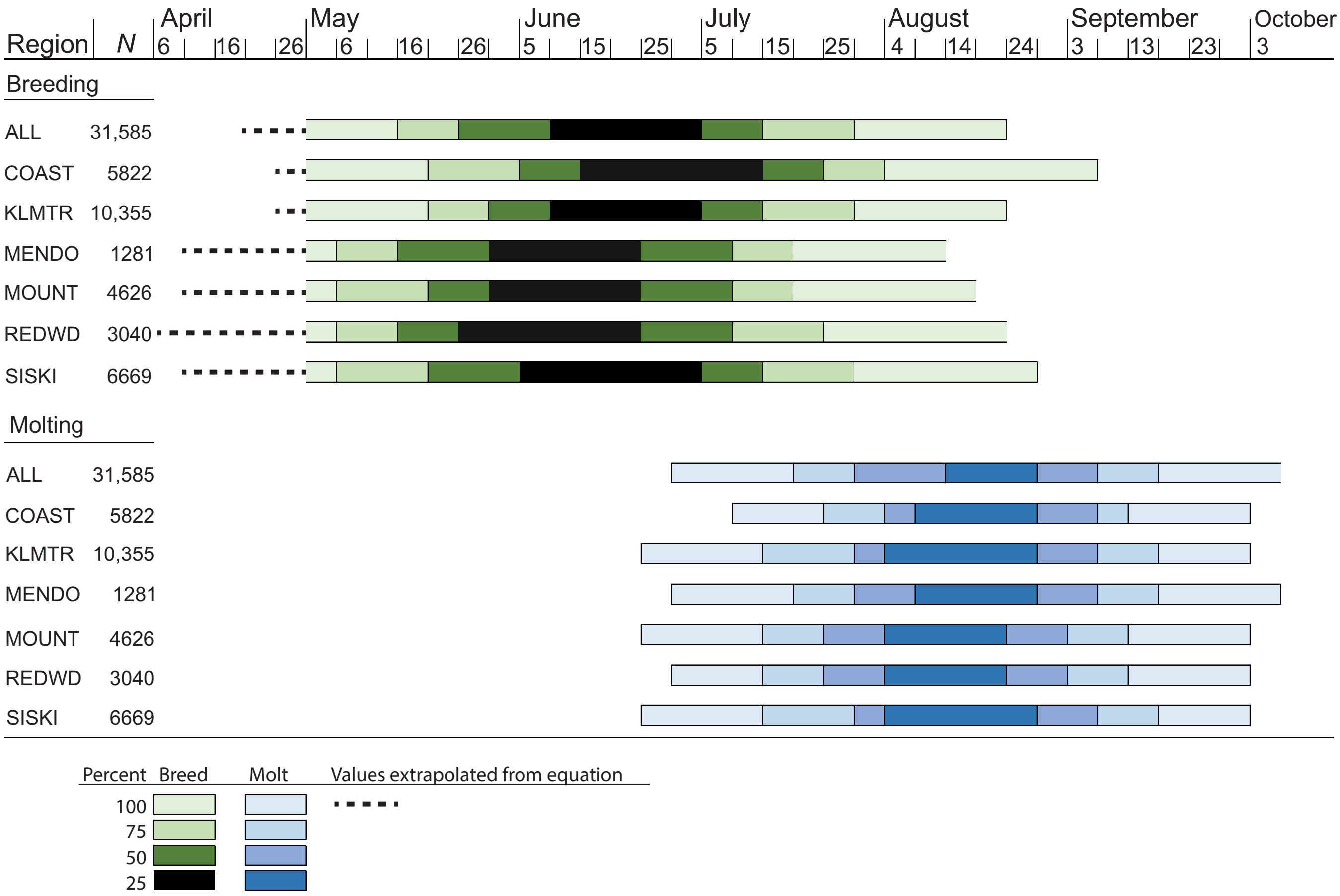

FIGURE 3 Breeding and molting season begin and end date estimates by 5-day periods for all regions combined and by each region, using all culturally significant birds combined. Gradations of fill indicate the percentage of the calculated area under the curve. Dates are the first day of the 5-day period. *N* is the number of individuals captured and used to estimate the polynomial equation. Region abbreviations are: ALL, all regions combined; COAST, Coast; KLMTR, Klamath-Trinity; MENDO, Mendocino; MOUNT, Mountain; REDWD, Redwood; SISKI, Siskiyou.

We combined all captures of culturally significant species to assess general patterns of breeding and molting seasonality and determine timeframes with the greatest potential for negative impacts across the 11 most abundant culturally significant bird species.

Breeding season

We estimated that the breeding season of the most abundant culturally significant bird species occurred from April 21 to August 23 (Figure 3). We found 75% of the estimated breeding season occurred from May 16 to July 29, the core 50% from May 26 to July 14, and 25% from June 10 to July 4.

Regional estimates for the beginning of the full breeding season ranged from April 6 in REDWD to April 26 in COAST and KLMTR (a difference of 20 days; Figure 3). The end of the breeding season ranged from August 13 in MENDO to September 7 in COAST (a difference of 25 days). The shortest breeding duration was 120 days for KLMTR while the longest duration was 140 days for REDWD. The beginning of the core breeding season ranged from May 16 (MENDO and REDWD) to June 5 (COAST) (a difference of 20 days), with the end of the season ranging from July 9 (MENDO, MOUNT, and REDWD) to July 24 (COAST) (a difference of 15 days).

Individual species showed a wider range in estimated breeding seasons. For example, beginning of breeding season ranged from March 17 for Black-headed Grosbeak to May 1 for Wilson's Warbler (a difference of 45 days; Figure 5A). The end of the breeding season ranged from August 8 for Wilson's Warbler to September 7 for American Goldfinch and American Robin (a difference of 30 days). Yellow-breasted Chat had the shortest breeding duration of 60 days, American Robin and Spotted Towhee had the longest breeding duration of 95 days each (Table 3). The difference in breeding season start

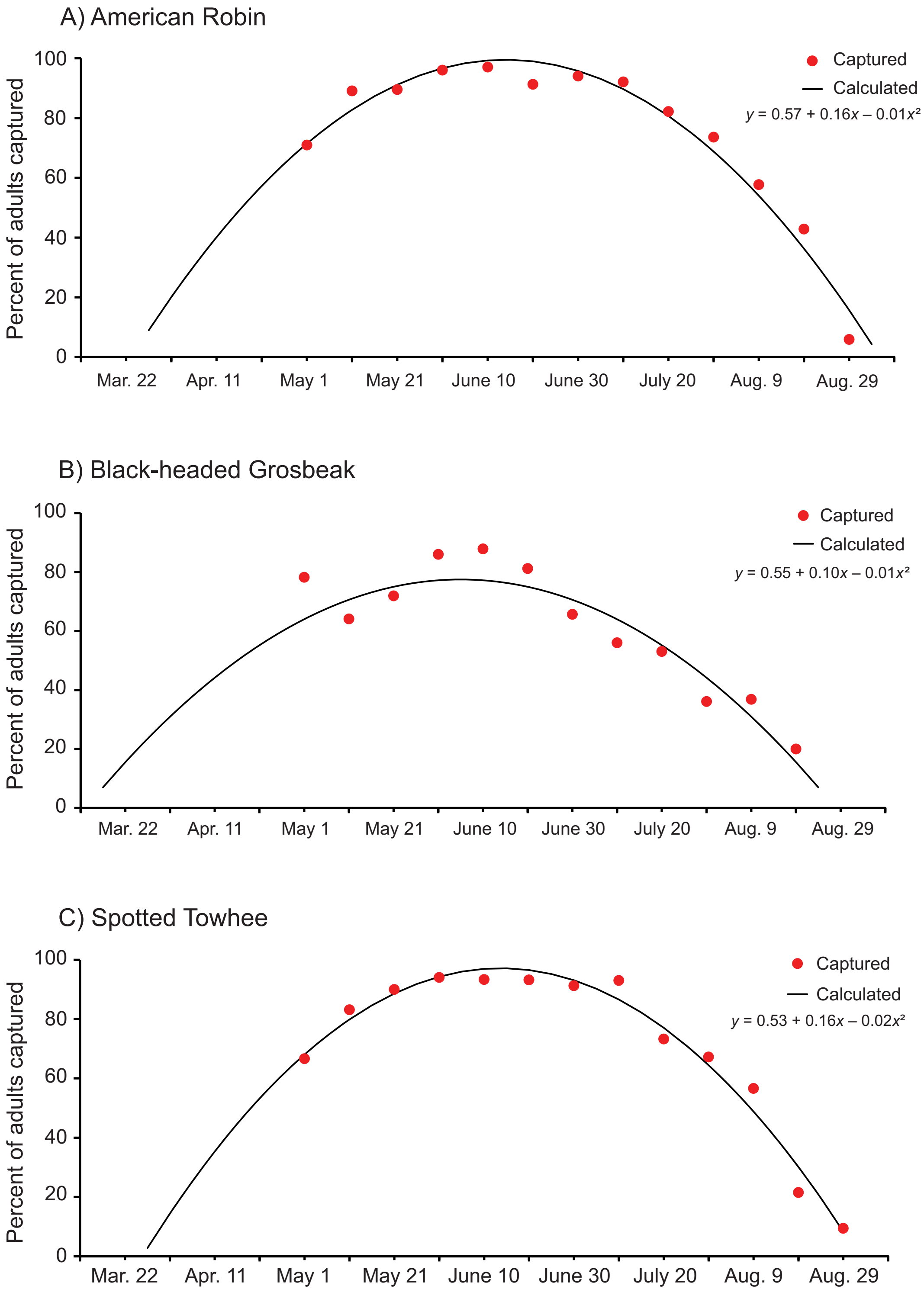

FIGURE 4 Percent of adult birds breeding throughout the season in the Klamath Siskiyou Bioregion by 10-day periods, all regions combined, for three species with early estimated breeding start dates. Dots designate the actual percentage of captured birds by 10-day period showing signs of breeding and the estimated polynomial equations (line and equation in upper right). Dates are the first day of the 10-day sampling period.

dates between species was less variable when considering the season core (Figure 5A). Core breeding start dates ranged from May 6 (Black-headed Grosbeak) to June 10 (American Goldfinch) (a difference of 35 days compared to 45 days for full breeding season beginning dates). Similarly, for end dates, the core breeding season

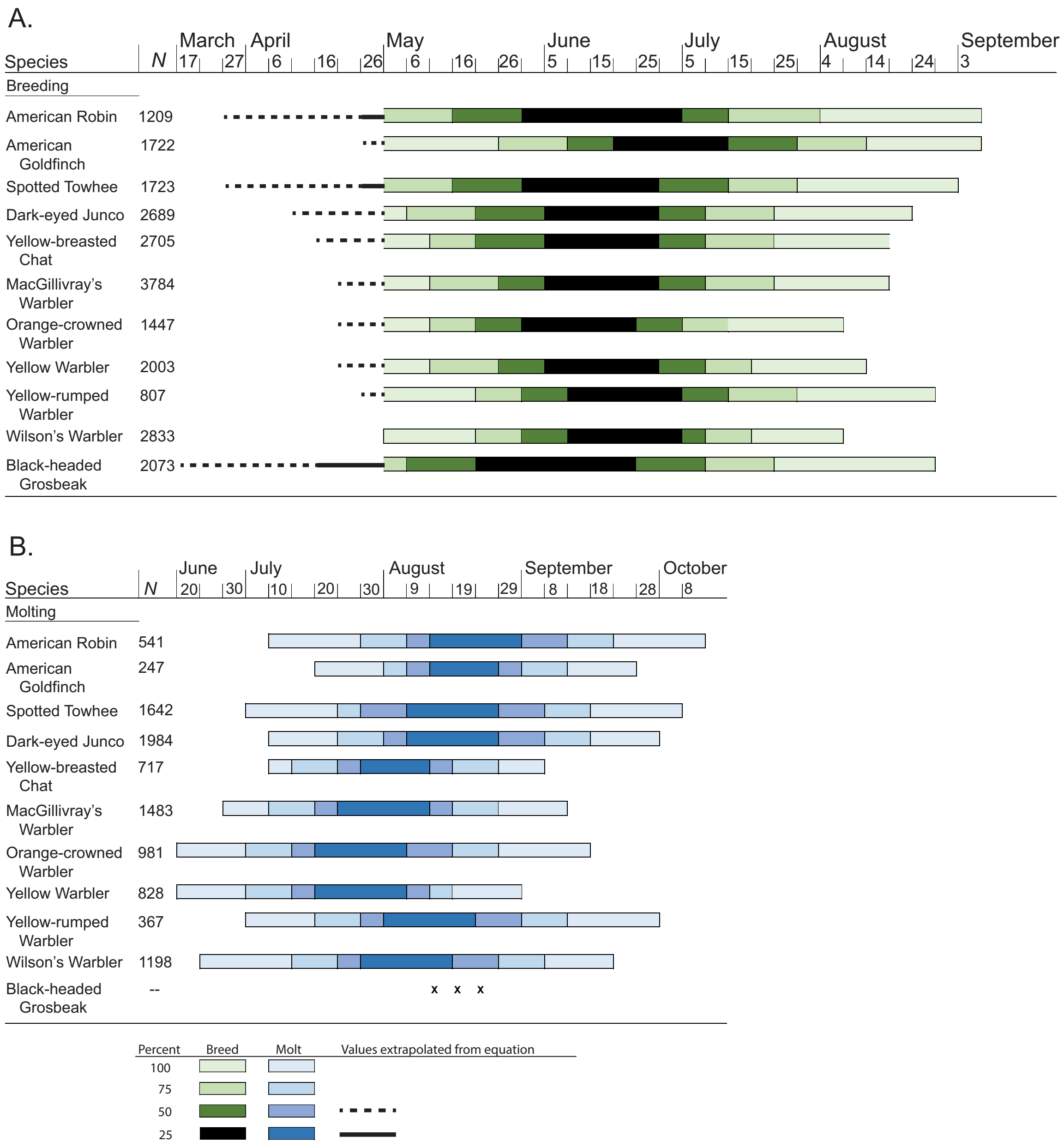

FIGURE 5 Breeding (A) and molting (B) season begin and end date estimates for the 11 most abundant culturally significant birds in the Klamath Siskiyou Bioregion by 5-day periods. Gradations of fill indicate the percentage of the calculated area under the curve. Dates are the first day of the 5-day period. *N* is the number of individuals captured and used to estimate polynomial equation. XXX indicates the species was not captured in high enough numbers during the season for this analysis.

end ranged from July 4 (Orange-crowned Warbler) to July 29 (American Goldfinch) (a difference of 25 days compared to 30 days for the full breeding season end dates).

Breeding start dates for species by regions ranged from the earliest date of March 7 for Dark-eyed Junco in MENDO and Black-headed Grosbeak at KLMTR to May 6 for Yellow-breasted Chat in SISKI (a difference of 60 days). End dates ranged from July 19 for Yellow-breasted Chat in SISKI to September 27 for American Robin in COAST (a difference of 70 days). Core breeding start dates ranged from May 1 for Black-headed Grosbeak in KLMTR to June 5 for Wilson's Warbler in KLMTR (a difference of 35 days).

Duration of breeding seasons for most species varied between regions (Figure 6). The most variable was Black-headed Grosbeak, with breeding seasons ranging from March 7–August 28 at KLMTR and from April 11 to August 18 at REDWD, with a difference of 35 days between start dates and durations of 175 and 125 days, respectively. Conversely, Yellow-rumped Warbler exhibited no variation in breeding

TABLE 3 Summary of breeding and molting season time spans in number of days for culturally significant bird species, listing the species, and/or region with the shortest and longest time spans for the division (species, region, or species–region) and season.

	Shortest time span		Longest time span	
Division and season	**Species and/or region**	**No. days**	**Species and/or region**	**No. days**
Species				
Breeding	Wilson's Warbler	100	American Robin, Black-headed Grosbeak	165
Molting	Yellow-breasted Chat	60	American Robin, Spotted Towhee	95
Region				
Breeding	KLMTR	120	REDWD	140
Molting	COAST	85	KLMTR, MENDO, MOUNT, SISKI	100
Species–Region				
Breeding	Yellow-breasted Chat-SISKI	75	American Robin-COAST	195
Molting	Yellow-breasted Chat-KLMTR	75	American Goldfinch-COAST	115

Note: Region abbreviations are: COAST, Coast; KLMTR, Klamath-Trinity; MENDO, Mendocino; MOUNT, Mountain; REDWD, Redwood; SISKI, Siskiyou.

season across region, running from April 21 to August 23 at both MENDO and MOUNT, a duration of 125 days. Yellow-breasted Chat had the shortest estimated breeding duration of 75 days in SISKI, while the American Robin had the longest of 195 days in COAST (Table 3).

On average, breeding season for residents began slightly earlier and lasted longer than migrants (Figure 5A). Breeding season start dates for residents averaged April 11 (March 27–April 22) and end dates averaged August 31 (August 22–September 7), for an average breeding duration of 143 days. Breeding start dates for migrants averaged April 16 (March 17–May 1) and end dates averaged August 15 (August 8–August 28) for a breeding duration of 121 days. Breeding season for residents had greater variability among species compared with migrants. Resident start dates differed by a month (March 27–April 26) while migrants differed by 15 days (April 16–May 1), if the Black-headed Grosbeak's early outlier is removed (March 17).

Molting season

We estimated that the molting season of the most abundant culturally significant bird species occurred from June 30 to October 7, with 75% of the season occurring from July 20 to September 17, 50% from July 30 to September 7, and 25% from August 14 to August 28 (Figure 3).

Regional estimates for the beginning of the full molting season ranged from June 24 in KLMTR, MOUNT, and SISKI to July 9 in COAST (a difference of 15 days; Figure 3). The end of the season for most regions occurred on October 2, ending in MENDO and COAST on October 7 (a difference of 5 days). The shortest molting time duration was 85 days in COAST, while the longest was 100 days in KLMTR, MENDO, MOUNT, and SISKI regions. The beginning of the core season ranged from July 25 (MOUNT and REDWD) to August 4 (COAST) (a difference of 10 days). The end of the core season ranged from September 2 (MOUNT and REDWD) to September 12 for the remaining regions (a difference of 5 days).

Beginning of the molting season for individual species ranged from June 20 for Orange-crowned and Yellow warblers to July 20 for American Goldfinch (a difference of 30 days; Figure 5B). The end of the season ranged from September 2 for Yellow-rumped Warbler to October 12 for American Robin (a difference of 40 days). Yellow-breasted Chat had the shortest molting season duration of 60 days, while American Robin and Spotted Towhee had the longest molting season duration of 95 days. We did not capture enough individuals of Black-headed Grosbeak in molt to estimate seasonality and duration.

Difference in dates for the core molting season was somewhat less than for the full season (Figure 5B). Core molting seasons for species ranged from July 15 for Orange-crowned and Yellow warblers to August 9 for American Robin and American Goldfinch (a difference of 25 days). Core molting season end dates ranged from August 13 for Yellow Warbler to September 12 for American Robin (a difference of 30 days).

We estimated molting start dates for individual species by region (Figure 7). The earliest molting start date was June 5 for Orange-crowned Warbler at MOUNT, while the latest was July 15 for American Goldfinch at COAST (a difference of 40 days). End dates ranged from September 2 for Orange-crowned Warbler at KLMTR to November 6 for American Goldfinch at COAST (a difference of 65 days). Start dates for core molting season ranged from July 5 for MacGillivray's Warbler at KLMTR and Orange-crowned Warbler at MOUNT to

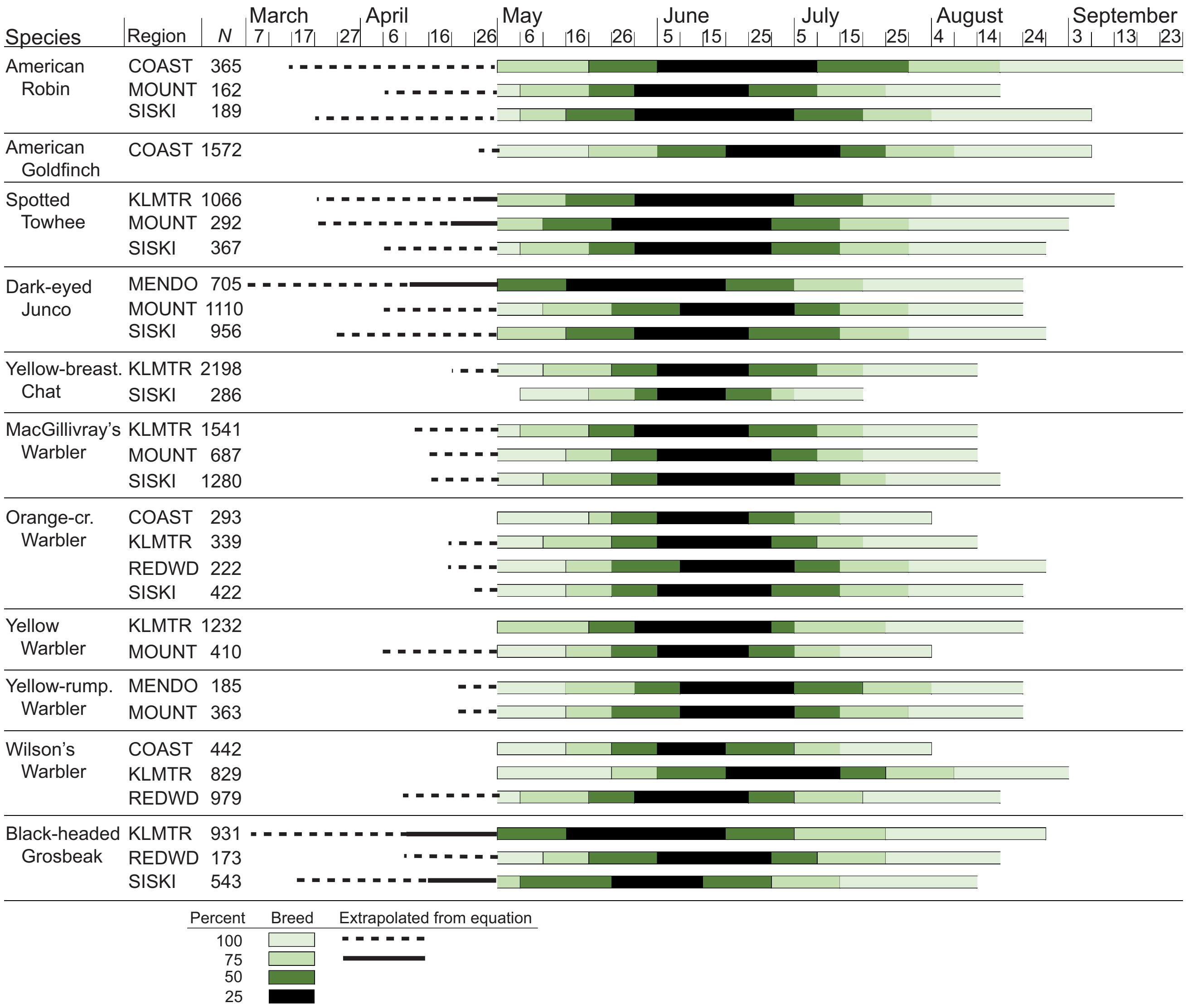

FIGURE 6 Breeding season begin and end date estimates for the 11 most abundant culturally significant birds in the Klamath Siskiyou Bioregion by region and 5-day periods. Gradations of fill indicate the percentage of the calculated area under the curve. Dates are the first day of the 5-day period. *N* is the number of individuals captured and used to estimate polynomial equation. Region abbreviations are: COAST, Coast; KLMTR, Klamath-Trinity; MENDO, Mendocino; MOUNT, Mountain; REDWD, Redwood; SISKI, Siskiyou.

August 19 for American Goldfinch at COAST (a difference of 45 days). End dates for core molting season ranged from August 8 for Orange-crowned Warbler at KLMTR to October 2 for American Goldfinch at COAST (a difference of 55 days).

Duration of molting seasons was less variable between regions when compared to breeding seasons for most species (Figure 7). The most variable species were Dark-eyed Junco and MacGillivray's Warbler; start dates for each had a 20-day difference between regions. Dark-eyed Junco start dates ranged from June 25 in MOUNT to July 15 in SISKI, with durations of 110 and 85 days, respectively. MacGillivray's Warbler start dates ranged from June 10 in KLMTR to June 30 in SISKI, with durations of 95 and 75 days, respectively. Spotted Towhee was the least variable, beginning on July 5 for all three regions in which it occurred and ending on either October 7 or October 17 (a difference of 10 days). The shortest molting season duration was 75 days for Yellow-breasted Chat at KLMTR; the longest duration was 115 days for American Goldfinch at COAST. We did not capture enough molting American Robin or Yellow-rumped Warbler in any one region for this analysis.

On average, residents started and ended molting later than migrants, while molting duration was similar (Figure 5B). Start of molt season for residents averaged July 10 (July 5–July 20) and end averaged October 2 (September 27–October 12) for an average molting

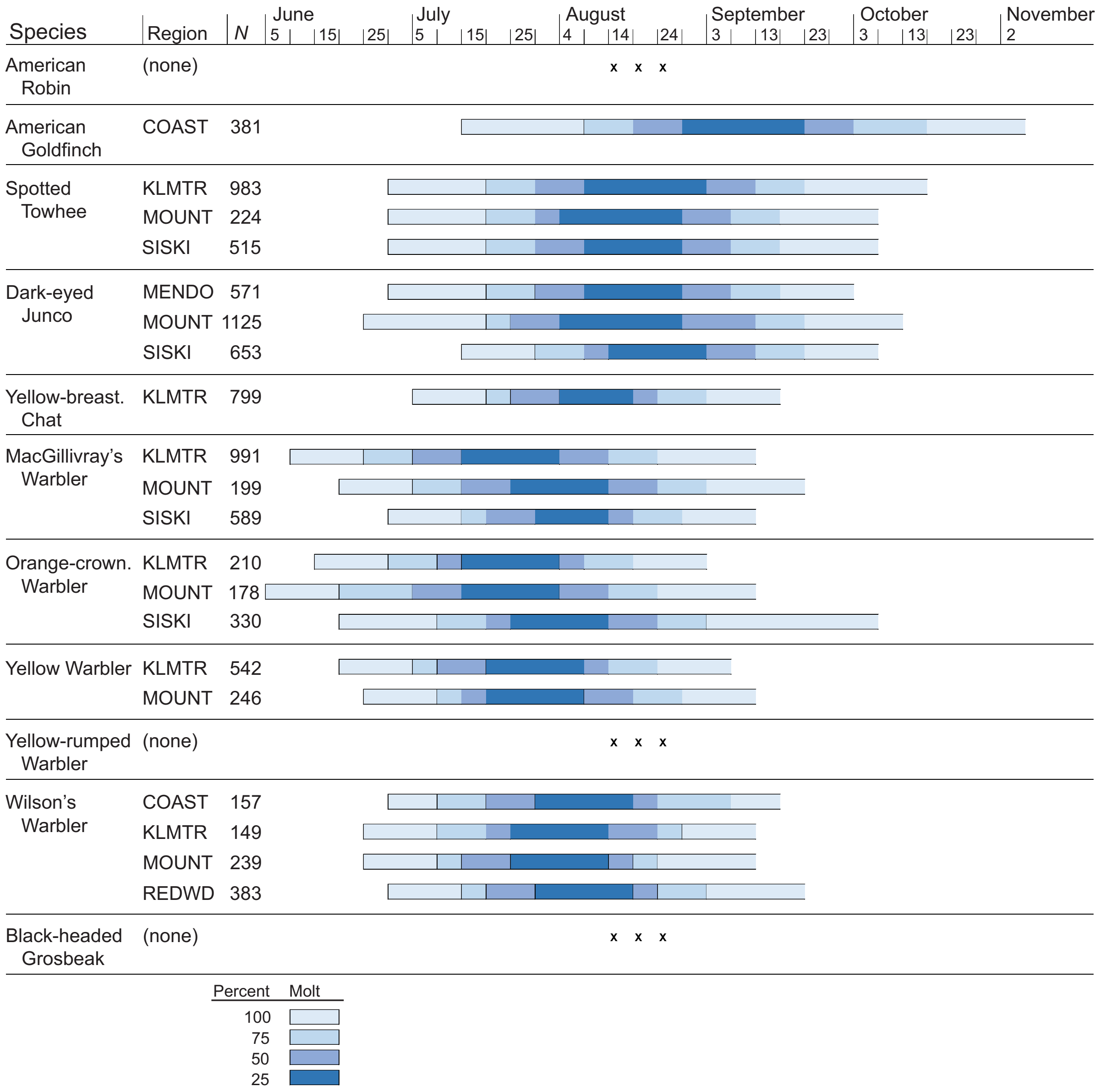

FIGURE 7 Molting season begin and end date estimates for the 11 most abundant culturally significant birds in the Klamath Siskiyou Bioregion by region and 5-day periods. Gradations of fill indicate the percentage of the calculated area under the curve. Dates are the first day of the 5-day period. *N* is the number of individuals captured and used to estimate polynomial equation. XXX indicates a species was not captured in high enough numbers during the season for this analysis. Region abbreviations are: ALL, all regions combined; COAST, Coast; KLMTR, Klamath-Trinity; MENDO, Mendocino; MOUNT, Mountain; REDWD, Redwood; SISKI, Siskiyou.

duration of 84 days, while migrants averaged June 27 (June 20–July 10) and end of season averaged September 12 (September 2–September 22), an average molting duration of 77 days.

Seasonal differences in use of regions by species

We found that many species used different regions for breeding and molting. One of the most distinct was the Black-headed Grosbeak, which is characterized by molt migration: it breeds in several regions of our study area but leaves the area to molt in the monsoonal regions of the Sonoran Desert (Figures 5B and 7; Pyle et al., 2009; Siegel et al., 2016). We did not capture enough molting American Robin and Yellow-rumped Warbler for analysis by region, though we did capture enough to analyze the molting season for the entire study area (Figures 5B and 7).

Regions KLMTR and SISKI were used by the most species for breeding, with seven species for each region

(Figure 6). By comparison, MENDO was used by only two species for breeding: Dark-eyed Junco and Yellow-rumped Warbler.

KLMTR and MOUNT were each used by six species for molting, the most for the season by a region (Figure 7). By comparison, COAST, MENDO, and REDWD were the least used regions for molting, with 1–2 species each.

Five species used the same regions for both breeding and molting, at least in part: Yellow Warbler used KLMTR and MOUNT; Dark-eyed Junco, MacGillivray's Warbler, and Spotted Towhee used KLMTR, MOUNT, and SISKI; and American Goldfinch used COAST (Figures 6 and 7). Other species added or subtracted one or more regions where they underwent molt. Two migrants were found upslope for molting: Wilson's Warbler used COAST, KLMTR, and REDWD for breeding and molting, and added MOUNT for the molting season; Orange-crowned Warbler used COAST, KLMTR, REDWD, and SISKI for breeding, which included two coastal regions, but were found more exclusively inland and higher in elevation for molting to KLMTR, MOUNT, and SISKI. One migrant was found downslope during molting: Yellow-breasted Chat used KLMTR and SISKI for breeding but was found only in KLMTR for molting.

DISCUSSION

Precipitous declines in bird populations across North America have renewed interest in the effects of management actions, such as prescribed fires and cultural burns, on avian communities and how the timing of such actions may influence survival and reproductive success. Overall, US bird populations have declined by an estimated 30% over the last 50 years, with forest birds decreasing by 22% (NABCI, 2019). Rosenberg et al. (2019) estimated that over 50% of western forest birds are suffering population declines. Across the Northern Pacific Rainforest Conservation Region (NABCI, 2020), which includes the Klamath Siskiyou Bioregion, over 60% of culturally significant species have shown a decline from 2005 to 2015, including 9 of the 11 species in our analysis, with the steepest declines for American Goldfinch and MacGillivray's Warbler (Table 1; Sauer et al., 2017). Only Yellow-breasted Chat and Black-headed Grosbeak showed increasing population trends. A regional study showed similar trends within the Klamath Siskiyou Bioregion, including Yellow-rumpled Warbler population declines and Yellow-breasted Chat and Black-headed Grosbeak population increases (Rockwell et al., 2017).

Our study demonstrated that the energetically taxing breeding and molting seasons of 11 culturally significant resident and migratory adult land bird species varied temporally and spatially in the Klamath Siskiyou Bioregion as supported by the wide variation in timing of lifecycle events. Nuanced differences in the timing of these avian lifecycle phases can present challenges for tribes and forest and wildland fire managers aiming to balance potential negative and positive effects of cultural burning and prescribed fires on bird communities (Huff et al., 2005, see also Karuk Tribe, 2019:73, fig. 3.8). Specifically, our results indicate that tribes and land managers could consider scheduling burns to avoid periods of physiological stress (breeding and molting), which varied by region and species across a variety of vegetation types.

Globally, paleoecological research has identified close relationships between fire ignitions and Indigenous peoples, as shown in Australia (Trauernicht et al., 2015), whereby the local avifauna is dependent on the resulting fire regime to such an extent that changes associated with the arrival of European settlers have endangered several fire-dependent endemic species (Olsen & Weston, 2005). Similarly, local tribal knowledge among the different tribes of northern California and southern Oregon have historically guided the application of fire use at specific times of year, with seasonal variation for different habitats in response to culturally determined cues, which naturally encompass and protect stressful phenological periods of the local fauna (Anderson, 1996, 2007; Anderson & Moratto, 1996; Knight et al., 2022). For example, guidance from ITEK among some tribal community members of the Karuk traditional belief systems, and current Karuk Tribal policy, leads practitioners to refrain from using fire for cultural burning when the Pleiades star cluster is absent from the sky, or beginning mid-April by the western calendar (Karuk Tribe, 2019). Reintroducing fire long absent from many of the habitats has ethical as well as sociocultural considerations that have not necessarily been considered by western-minded academically trained fire managers and ecologists.

Our research was conducted in response to the Karuk and other local tribes initially expressing concerns about federal and state agencies and organizations (e.g., USDA Forest Service, local Fire Safe Councils) conducting prescribed fires during the spring and early summer (when some tribal traditions generally end cultural burning as noted above) as well as other times of the year under conditions considered permissible to burn by local tribal traditions (Fry & Stephens, 2006; Karuk Tribe, 2019) for fire risk reduction, hazardous fuels abatement, and public safety in the Wildland Urban Interface and other areas of the landscape. As described above, agencies often schedule these burns when fire personnel and resources (such as engines and tankers) are more available to implement such management burns; that is, when they are not assigned to wildfires which typically occur during the summer and fall in this region. Adding to the complications of scheduling prescribed fires, available burn windows can be short (2–3 days) and few in number (as few as two windows per month), as seen in California's Lake Tahoe Basin (Striplin et al., 2020). Additionally, with expected temperature increases from climate change, the number, length, and timing of potential burn windows may change as observed in climate modeling for the southeastern United States (Kupfer et al., 2020) and Australia (Di Virgilio et al., 2020), resulting in reduced opportunities for prescribed fire use.

Breeding seasonality

Based on previous research, our expectation was that breeding would occur earliest at the lowest elevations (Bears et al., 2009; LaBarbera & Lacey, 2018; Perfito et al., 2004). In our study, we estimated on average REDWD (mean elevation 62 m) had the earliest breeding season start for all species combined (April 6), and SISKI, MOUNT, and MENDO (mean elevations 750–1249 m) had slightly later season starts (April 11) as expected. Unexpectedly, we found that the other two low-elevation regions, COAST (11 m) and KLMTR (347 m), had the latest starts to the breeding season (April 26). LaBarbera and Lacey (2018) reported the earliest hatching dates for Dark-eyed Juncos were at low elevations while they were later at high- and mid-elevation stations. Bears et al. (2009) reported that with increasing elevation (stations at 1000 and 2000 m), Dark-eyed Juncos delayed the development of reproductive structures (such as cloacal protuberances) and reduced the duration of their reproductive period to less than half of the time used by low-elevation birds. Similarly, Perfito et al. (2004) reported that the testicular development of Song Sparrows (*Melospiza melodia*) began earliest at coastal sites compared to higher elevation sites in the mountain foothills in Washington State. Perfito et al. (2004) also reported that testis development was more strongly associated with maximum temperature and emergence of new green shoots rather than elevation and that plant phenology tended to be more advanced on the coast than in the mountains early in the breeding season. This suggests that some habitat component other than elevation may have a greater effect on timing of breeding in COAST and KLMTR as compared to REDWD, contributing to later breeding season starts. Relative to elevation, the Karuk Tribe (2019:96) states "The [Yellow-breasted] chat is tied to the responsibility of humans to realize that something has to be done about fire. The chat is a migratory bird that nests in the spring. When we are burning [at] low [elevations], the return of the chat and other birds who have come back to nest, signals that we are to stop burning. Other avian elevational migrants and birds who nest at different elevations and times should be developed as cultural indicators for fire applications. Humans have burned as they moved up and down [seasonally] with birds for thousands of years."

In our study, we were able to compare breeding seasonality between multiple species in one region. We found the start of breeding seasonality differed by almost a month between five warbler species in one of the most used regions for breeding, KLMTR. By contrast, Flockhart (2010) reported that hatch dates were not significantly different between five species of warblers in their study area in Alberta, Canada, with mean hatch dates spanning only 7 days.

On average, we found breeding seasons for residents started slightly earlier (5 days) than migrants. If the early outlier Black-headed Grosbeak is removed from the migrants estimate, the difference increases to 10 days. By contrast, in England, Goodenough et al. (2010) reported a difference of almost a month in mean lay dates between residents and migrants. They reported that the mean lay date for four resident species, Blue Tit (*Cyanistes caeruleus*), Great Tit (*Parus major*), Coal Tit (*Periparus ater*), and Nuthatch (*Sitta europaea*), ranged from April 30 to May 7; conversely, they reported the mean lay dates for two migrant species, European Pied Flycatcher (*Ficedula hypoleuca*) and Redstart (*Phoenicurus phoenicurus*), were on June 5 and June 6, respectively.

Some of the greatest variation in breeding seasonality was within individual species between regions. Thus, minimizing the impact of burning on a single species can be influenced by localized seasonality as exhibited by the Black-headed Grosbeak, with a difference of over a month between breeding start dates by region, or by a more general seasonality—irrespective of location—as exhibited by the MacGillivray's Warbler, with a 5-day difference between regional start dates. Given variability in breeding seasonality exhibited by individual species, spring burns prior to April 21 in any region would avoid the majority of study species breeding throughout our study area, or prior to May 26 to avoid the average estimated core breeding season (Figure 3). By contrast, a spring burn that is regionally specific could be scheduled with more precision, such as burning prior to April 6 in REDWD to avoid most breeding birds in the region, or prior to May 16 to avoid the estimated core breeding season in that area. Among other indicators, some Karuk cultural fire practitioners understand the nesting of certain bird species to indicate when to stop burning in the late winter/early spring months (such as the Yellow-breasted Chat discussed earlier), while other indicators will present themselves to signify that certain types of cultural burning can resume again in mid-to-late June (William Tripp citing Karuk ITEK, personal communication). Thus, the breeding and molting timeframes outlined here are not fully aligned with the indicators that some Indigenous practitioners may use to indicate burn timing.

Molting seasonality

In our study, migrant species generally began and ended molt earlier than resident species. De La Hera et al. (2009) compared flight feather growth in migratory and sedentary populations of Blackcaps (*Sylvia atricapilla*) in southern Spain and reported that individuals that migrated grew their feathers faster, which produced lighter feathers than those in sedentary individuals, thus demonstrating a trade-off between molt speed and plumage quality in migratory birds. By comparison, Rimmer (1988) reported that migrant Yellow Warblers in James Bay, Ontario, regularly overlapped care of fledglings with the beginning of prebasic molt, then after a rapid, intense molt of 35–45 days, they began migration during the final stages of remigial molt in early September.

Over half of the species (6 of 11) in our study did not remain solely on their breeding grounds to molt; they may have dispersed within our study area or completely left the area to molt. Pyle et al. (2018) reported the probability of a breeding bird being recorded molting at the same station was about 0.47 (95% credibility interval = 0.38–0.57) in the western United States. Gilbert et al. (2020) reported that Orange-crowned Warblers in the Sierra Nevada foothills migrated to moister, higher elevation habitats to molt and that breeding Orange-crowned Warblers in central inner-coastal California were rarely observed molting on their breeding grounds, suggesting they may molt elsewhere. Cassin's Vireo in Washington State moved from lower elevation dry pine or Douglas-fir forests upslope at least 300 m, to molt in wetter, high-elevation Douglas-fir forests (Rohwer et al., 2008). Similarly, two species in our study (Wilson's and Orange-crowned warblers) were more abundant at higher elevations during molt or added higher elevation regions to molt. Two previous studies in our study region found support for this as well (Wiegardt, Barton, et al., 2017; Wiegardt, Wolfe, et al., 2017). Wiegardt, Barton, et al. (2017) showed that Wilson's Warblers were more likely to breed at lower elevations and molt at higher elevations. Wiegardt, Wolfe, et al. (2017) reported that long-distance migrants such as Orange-crowned Warblers were found at higher elevations during molt and Audubon's Warbler moved farther inland for molting compared to their breeding habitats. Both studies suggest that some individuals move altitudinally after breeding to complete the definitive prebasic molt.

In our study, all species completed molt in all regions by October 17 and after September 12 for the core molt season (Figure 6). Beginning prescribed fires after these dates would avoid the majority of molting birds across all regions.

Fire effects and planning

Researchers have investigated the indirect effects of fire on bird populations and communities, especially as related to changes in forest structure or food resources after wildfires and prescribed fires (e.g., Bagne & Purcell, 2009, 2011; Fontaine et al., 2009; Huff et al., 2005; Murphy et al., 2017; Russell et al., 2009; Seavy & Alexander, 2006, 2014; Stephens & Alexander, 2011; Stephens et al., 2015) and have documented that some species benefit from fire (e.g., Bagne & Purcell, 2011; Russell et al., 2009; Stephens et al., 2015). Thus, the absence of fire, including effects of fire exclusion on bird habitat quality and populations, is an additional and important concern when considering recovering declining bird populations. However, fewer studies have examined the direct effects of fire, which can include injury and mortality to nests, eggs, nestlings, fledglings, and adults (Bagne & Purcell, 2009; Erwin & Stasiak, 1979; Kruse & Piehl, 1986; Lyon et al., 2000). Wildland fire managers may need to consider the balance between the importance of a burn's scale, purpose, and objective (including its process and function) with the susceptibility of birds to such a fire for successful breeding and/or molting. While not directly documenting these effects, our study provides information that can be used to improve an understanding of potential fire effects on birds or avoid potentially deleterious direct effects of prescribed fire, cultural burns, and wildfires on culturally significant species by detailing intricacies of breeding and molting seasonality when adults and their young are most vulnerable.

Throughout our study area, lightning-caused fires historically occurred from June through October (Knapp et al., 2009), with some earlier season (late spring–early summer) burning attributed to Native Americans during the non-lightning ignition time of year. For example, Metlen et al. (2018) reported that burn seasonality was broadly distributed in the Rogue River Basin, OR, based on dendrochronological analysis of fire scars formed between 1650 and 1900. They found fire frequency peaked in mid-to-late summer, with 23% of fire scars in the earlywood (scars formed in late spring and early summer), 47% in the latewood (mid-to-late summer), and

30% at the ring boundary (late summer or fall). We estimated that the breeding season is nearing the end across all regions during late summer (Figure 3), so most young should be mobile and capable of moving away from low-intensity fires during this time. However, this is also the peak of the molting season for adults in all regions (Figure 3); thus, burns later in the fall (October through November) may reduce the direct negative impacts of fire on culturally significant birds during this physiologically demanding time.

Additionally, land managers responsible for scheduling prescribed fires or tribal practitioners conducting cultural burns may focus on other physical, climatic, ecological, and social factors rather than the potential impacts on birds for specific burns. However, consideration of the effects of fire on wildlife is mandated in certain cases—specifically, seasonal restrictions (limited operation periods) are in place for Northern Spotted Owls (*Strix occidentalis caurina*) and Pacific Fishers (*Pekania pennanti*) for burns where there is a federal or state nexus for action, and more general advisories are in place to limit adverse effects on migratory birds during burn planning in our study area (Knapp et al., 2009). Seasons and other time-of-year decisions are broad-scale considerations, while localized factors such as time of day, scale, location, fuel or vegetation type, and fire behavior may play a greater role for individual burns and may increase or decrease the direct effects of fire on different bird species. We suggest that if physical and climatic factors are optimal during breeding or molting periods, land managers could use our guidelines to consider options for lessening the impact of prescribed fires on culturally significant birds by noting the dates when 25%, 50%, or 75% of the breeding or molting season occurs and adjusting the burn date as possible within acceptable parameters, or consult local tribes to ensure that burning could be conducted to more locally relevant indicators. Further research on the timeframes when culturally significant birds first return to the study area and begin to work on their nests may bring additional nuance to these considerations as those timeframes may more closely align with cultural guidelines than the broader breeding and molting considerations. Considerations may be given to specific migrant or resident bird species associated with particular forest types scheduled to be burned. For example, land managers or tribal practitioners planning prescribed fires or conducting cultural burns in oak-dominated forests may consider the relationship between a particular bird species and the more specific habitat types along the prairie-oak habitat continuum in their planning (e.g., see fig. 2 in Altman & Stephens, 2012; fig. 3.1 in Karuk Tribe, 2019:60). Restoration strategies (including burning) in oak woodlands, a tribally important habitat type, can reduce densities of fire-intolerant conifers and hardwoods in encroached oak-pine dominated and riparian forests where fire as an eco-cultural process has long been absent (Long et al., 2018; Messier et al., 2012).

Several of our study species exhibited varied timing across multiple regions, suggesting that birds may respond to environmental cues such as vegetative structure or food availability to shift breeding seasonality across space and time (Hurlbert & Liang, 2012; Inouye et al., 2000), which may buffer some species from phenological mismatch or asynchronous timing in the availability of food and corresponding breeding activity (Reed et al., 2013). To help mitigate the effects of environmental change, forest and wildland fire management practices might consider integrating our recommendations to benefit culturally significant breeding and molting bird communities (Manuwal & Manuwal, 2002; Marzluff et al., 2000; McGarigal & McComb, 1995), at the same time as taking into consideration from our study that (1) several species (i.e., American Robin, Black-headed Grosbeak, and Spotted Towhee) suffered from serious uncertainty stemming from a breeding season that began much earlier than the start of our sampling period and (2) estimated models for several species-region combinations were found to have low adjusted R^2 values (including breeding Yellow Warbler at SISKI [$R^2 = 0.39$] and molting Wilson's Warbler at MOUNT [$R^2 = 0.39$]). Integration of ITEK, tribes, and cultural practitioners into management planning processes may bring additional accuracy and flexibility that could benefit these species, given annual variability and climate change that may shift breeding, nesting, and molting timeframes (Halupka et al., 2008; Hurlbert & Liang, 2012; Karuk Tribe, 2019).

Local tribal beliefs among tribes and their community members reflect a complex cultural process of values and practices to balance the effects of fire on breeding birds and may guide the timing of activities, particularly when considering the timing of conducting prescribed fires and cultural burning. For example, according to the beliefs of some tribal community members of the Karuk Tribe, in the springtime when the Pleiades cannot be seen from April to June, fire should not be used for broadcast burning but only for heating and cooking (Karuk Tribe, 2019; Long et al., 2020). It is unknown whether this belief system is reflective of other tribes in the study region. Such tribal burning practices may be reflected in fire history studies, such as that of Taylor and Skinner (1998), who conducted research in Karuk ancestral territory in mid to higher elevation mixed-conifer forests and found that the majority of fires (85%) burned during the dormant season of late summer and fall from 1626 to 1992, as based on the evidence of fire scars (ring position of a fire event).

Only 15% of documented fires occurred during the spring to midsummer when breeding birds are at increased vulnerability (Taylor & Skinner, 1998). Similarly, a study on neighboring Yurok and Karuk ancestral territories determined that about 9% of fires (from 107 events out of 172) with detectable seasonality occurred in the spring and early summer for the years 1393–1943 (earliest to last recorded fire scars) among 35 samples in the low-to-mid elevation Fish Lake basin, near Weitchpec, CA (Knight et al., 2022). Pullen (1996) summarized how 13 tribes in the greater Klamath Siskiyou Bioregion used fire. Across tribes, three traditions specifically involving spring burning were noted: burning hillsides in the late spring to improve hunting and reduce brush by the Tolowa Dee-Ni Nation; burning the base of sugar pine trees to obtain sap by the Takelma Tribe; and burning off the hillsides to ceremonially call the salmon to the rivers by the Tututni Tribe. All other fires were conducted in the summer or fall with up to 62% of fire uses occurring in the summer months, with the purposes of promoting growth of basketry materials, growing tobacco, and improving vegetation for wildlife. Additionally, Heizer (1967:233–234) reported that the Konomeho [Konomihu] Shasta Tribe on the Salmon River (bordering the Karuk Tribe) burned brush and logs near villages every spring before planting wild tobacco. An important difference in western ecology versus ITEK is western ecology's preoccupation with the negative effects of management action on species of concern (i.e., Federal- or State-listed Threatened-Endangered-Sensitive species) versus ITEK, which fosters a larger reverence for organisms and the natural world on which we depend (Karuk Tribe, 2019, see McKemey et al., 2019 for Australian aboriginal burning).

In the absence of natural fire regimes (including Indigenous burning), many culturally important values and forest values may be lost to forest degradation or subsequent unnaturally severe wildfires (Lake, 2011; Long et al., 2020). Returning application of fire as a management tool for ecological restoration will have mixed effects on avian populations (Bagne & Purcell, 2011; Seavy & Alexander, 2014). Changes in bird abundance following both prescribed fire (e.g., Bagne & Purcell, 2011; Dickson et al., 2009; Russell et al., 2009) and wildfire (e.g., Hutto et al., 2020; Seavy & Alexander, 2014) have been well studied, including response to intensity or severity and time since the burn (e.g., Smucker et al., 2005; Stephens et al., 2015). Yet, nuances of species' response to prescribed fire seasonality (Greenberg et al., 2019) and interactions with coarse-scale landscapes metrics (Morin et al., 2021) are only recently being examined and more research is warranted.

Consideration of breeding and molting seasonality of culturally significant birds may elucidate other ecological mismatches in burn timing, such as effects of fires at different times of year on vegetation vigor and regrowth, including culturally significant plant species (Kantor et al., 2020). In addition to avian lifecycle phenology as measured by the Western Julian calendar, identifying additional phenological indicators as understood in context of tribal cultures (e.g., flowering of abundant plant species) to inform prescribed fire and cultural burning timing may be important, particularly in the context of climate change.

Researchers have noted that some bird species have advanced their breeding season with earlier spring warming as a consequence of climate change. For example, Halupka et al. (2008) reported egg-laying dates of Reed Warblers (*Acrocephalus scirpaceus*) advanced 3 weeks between 1970 and 2006, but the end of the season did not correspondingly advance, resulting in a longer breeding season. They also reported that the median first egg date correlated significantly with increasing mean May to July temperatures. Vega et al. (2021) similarly described an advancement of 8.3 days in start of breeding, as measured by hatching time, in the northernmost populations of European Pied Flycatchers compared to 3.6 days advancement in the southernmost flycatchers over a 36-year span. As in the previous study, increasing temperature as well as vegetation greenness were important factors in advancing breeding season.

Little is known about the effect of climate change on molt (Seavy et al., 2018), though advancement in departure from breeding to wintering grounds may suggest a delayed or prolonged molt. For example, Møller et al. (2011) reported Barn Swallow (*Hirundo rustica*) arrival dates to their wintering grounds in South Africa advanced by 24 days between 1993 and 2010. With the implication that local bird populations may also experience changes to breeding or molting seasons with climate change, a tribal perspective relates that this is a further justification for a better understanding of migratory bird breeding phenology as an additional indicator for halting spring burn timing rather than waiting for the Pleiades to set below the horizon (David et al., 2018; Karuk Tribe, 2019; William Tripp citing Karuk ITEK, personal communication).

Our breeding data suggest that some species may begin breeding in our area prior to May 1, which aligns with the belief of some Karuk community members when burning should cease in the spring relative to when Pleiades falls under the nighttime horizon in mid-April (William Tripp citing Karuk ITEK, personal communication). Thus, for additional precision when planning spring burns, our results could be combined with local data on arrival dates for target species.

Our molting data suggest fall burns scheduled for late fall would reduce stress on molting individuals, as some species' core molt dates continue into mid-September, depending on region (Figure 7). Use of the quartiles estimated for each species by region and season can inform wildland fire planning with flexibility to schedule prescribed fires to reduce impact on culturally significant species. Additional input from tribal members and their understanding of ITEK may further refine these plans as to season, size, and location of burns (e.g., habitat type).

Returning cultural burning that reflects tribal values and aims to benefit bird communities is supported by cooperative partnerships between tribal members, scientists, land managers, agencies, and other entities. Partnership examples include tribes and agencies working together for the purposes of protecting culturally important sites during fire suppression operations (Lake, 2011), planning for habitat restoration and harvesting of local resources (Lake et al., 2017; Senos et al., 2006), and local agencies working with scientists to understand the effects of fire management on birds (Alexander et al., 2004, 2017; Stephens & Alexander, 2011; this study). Within this context, results from this research represent a unique coupling of long-term scientific bird monitoring and ITEK to inform an adaptive approach to prescribed fire and cultural burning (Clark et al., 2022). A prescribed fire may have cultural objectives, but cultural burning should be viewed separately as an ancient, independent, and unique system of stewardship relative to more recently derived western prescribed fire practices.

While bird species and individual birds may benefit from the effects of prescribed fires or cultural burning to vegetation and habitat, individual birds may also face direct harm from prescribed fires, cultural burns, and wildfires during their breeding season in the spring and summer (e.g., nests and presumably nestlings; Bagne & Purcell, 2009; Kruse & Piehl, 1986) and from increased physiological stress during their molting season in the late summer through fall. Thus, there are important management implications and risk assessments regarding the use of prescribed fire and cultural burning practices, or managed wildfire for various ecological and sociocultural resource objectives (including reducing the risk of large-scale, high-severity wildfires). We encourage the use of our robust dataset and results to conduct further studies and employ adaptive management guidance to reduce or mitigate the potential impacts of prescribed fire, cultural burning, managed wildfire, and other forest management practices on bird communities throughout northern California and southern Oregon. Results from our study can lead to a greater understanding of the local bird population's biology and support further studies to examine and articulate biologically and culturally meaningful guidelines to help balance the positive and negative impacts of prescribed fire on culturally significant bird species throughout the Klamath Siskiyou Bioregion.

CONCLUSIONS

1. Our results can be used to add greater precision to prescribed fire timing based on real-world data of breeding and molting seasonality of 11 culturally significant bird species throughout the Klamath Siskiyou Bioregion of northern California and southern Oregon. We suggest that, with similar research, this methodology can be adapted to other regions to inform wildland fire (including managed wildfire and prescribed fire) planning approaches and strategies. Those planning burns or managing fires may additionally consider using observations of other aspects of bird phenology such as migrant arrivals, nesting, and/or reproduction as indicators for limiting or ending burning in particular vegetation types as a local scale mitigation effort.
2. We recommend additional research on the effects of fire on birds, especially on species affiliated with habitats most in need of prescribed fires which may not be well-covered in these analyses (e.g., oak habitats), to determine nesting, breeding, and molting seasons for culturally significant birds, including the effects of fire severity, timing, and spatial scales and impacts of environmental change. Detailed analysis from such areas of research will better inform planning efforts to reduce the deleterious effects and enhance the benefits of prescribed fires on bird communities associated with at-risk habitats.
3. We recommend further study to quantify direct impacts (e.g., mortality, nest failure), potential benefits, and potential carry-over effects (e.g., reduced fitness) of different types and timing of fire on culturally significant bird species across their full annual lifecycle.
4. Our analysis can begin to inform trade-offs and synergies between tribal values regarding cultural burning and ethical considerations with prescribed fire management objectives. Similar analyses for additional avian species (such as Northern Spotted Owl), mammals (Pacific Fisher), and others would help integrate traditional, sociocultural considerations and wildlife conservation with western-style fire management planning and adaptive management. However, such analyses would not serve as a surrogate for direct tribal engagement.

Disclaimer statements

Culturally meaningful indicators and guidelines for cultural burning and other forms of Indigenous stewardship exist within Indigenous communities. Among tribes, birds are known to be indicators for certain aspects of the human–fire relationship. According to many tribes, including the Karuk, there is a need for this knowledge to be further understood and revitalized. This study is not intended to limit or otherwise inform the regulation of cultural burning or other forms of Indigenous stewardship, but to provide a dataset of avian lifecycle information to use when working to respect life as we restore balanced human–fire relationships from a tribal perspective. Tribal culture and ITEK inform tribal members on when, where, and how to burn. The development of the best available scientific information, such as this study and those integrating Indigenous knowledge, practice, and belief systems and Western science, can be instructive for the implications of fire use on birds and other species. This study is not a surrogate for Indigenous knowledge, which is contextualized in time and space by peoples of place. Indigenous knowledge holders and stewards should be the ones to contextualize how their knowledge systems apply.

The findings and conclusions in this publication are those of the authors and should not be construed to represent any official USDA, U.S. Government, or Tribal determination or policy.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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