The Journal of Wildlife Management 82(4):682–697; 2018; DOI: 10.1002/jwmg.21423

Review

Managing Emerging Threats to Spotted Owls

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ABSTRACT The 3 spotted owl (*Strix occidentalis*) subspecies in North America (i.e., northern spotted owl [*S. o. caurina*], California spotted owl [*S. o. occidentalis*], Mexican spotted owl [*S. o. lucida*]) have all experienced population declines over the past century due to habitat loss and fragmentation from logging. Now, the emerging influences of climate change, high-severity fire, and barred owl (*Strix varia*) invasion also appear to be synergistically and differentially affecting population trends of each subspecies. Our objective was to review the existing literature on the spotted owl to describe historical and emerging threats and whether those threats have been adequately examined for each subspecies. Using 527 publications from a Web of Science search of the literature from 1900–2015, we statistically evaluated the emphasis placed on each subspecies regarding 4 influences: mechanical tree removal, fire, climate change, and barred owl invasion. There were 98 papers that explicitly examined the effects of $\geq$1 of these influences. Most of these papers were focused on the northern spotted owl, and for all 3 subspecies, most papers examined short-term effects only. We used our results to identify significant information gaps relative to historical and emerging threats. Commercial timber harvesting remains a potential threat for all 3 spotted owl subspecies, but effects from forest thinning may be increasing because of the heightened emphasis on fuels reduction and forest restoration treatments on public lands. Owl response to mechanical tree removal, especially forest thinning, remains understudied. Climate change also may threaten all 3 subspecies. Changes in climate likely affect survival and reproduction of spotted owls and their prey, and alter habitat availability by affecting disturbance regimes and vegetation composition and succession, but little empirical information is available describing specific responses to climate change. The literature on response to high-severity fire is sparse for some subspecies, primarily short-term in nature, and not consistent. Barred owl invasion is a major threat to the northern spotted owl and the California spotted owl but does not currently threaten the Mexican spotted owl. Rigorous research on the response of spotted owls to all factors influencing population change, particularly for the Mexican spotted owl, is needed. The most useful information for predicting owl response to these threats stems primarily from long-term studies of owl demography. The lack of such studies within the range of the Mexican spotted owl greatly limits our understanding of its population dynamics and our ability to predict the effects of various threats on Mexican spotted owl populations. For all 3 subspecies, we encourage long-term studies of their responses to threats, using uniquely marked owls across large spatial extents to account for spatiotemporal variability in ecological conditions within and among subspecies.

KEY WORDS barred owl, climate change, conservation, demography, endangered species, fire, fragmentation, habitat loss, spotted owl, thinning.

The spotted owl (*Strix occidentalis*), one of the best-known icons of species conservation in North America, has 3 recognized subspecies: the northern spotted owl (*Strix occidentalis caurina*), the California spotted owl (*S. o. occidentalis*), and the Mexican spotted owl (*S. o. lucida*; American Ornithologists' Union 1957). These subspecies are geographically separated, except for some range overlap between the northern spotted owl and the California spotted owl in the southern Cascade Range (Fig. 1; Barrowclough et al. 2005, Gutiérrez and Barrowclough 2005). Over the past century, populations of all 3 spotted owl subspecies have declined (Seamans et al. 1999, Blakesley et al. 2010, Forsman et al. 2011, Conner et al. 2013, Dugger et al. 2016).

The northern spotted owl and the Mexican spotted owl have been listed as Threatened under the Endangered Species Act (ESA) since 1990 and 1993, respectively (U.S. Department of the Interior [USDI] 1990, 1993), but the California spotted owl remains unlisted. The 1994 Northwest Forest Plan (NWFP) was designed to protect critical

Received: 13 July 2017; Accepted: 24 November 2017

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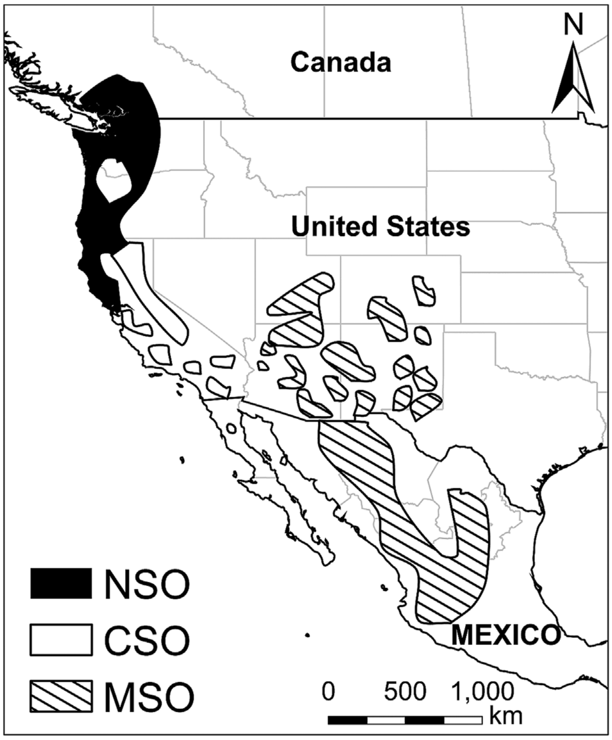

Figure 1. Ranges of the 3 spotted owl subspecies in North America (NSO = northern spotted owl, CSO = California spotted owl, MSO = Mexican spotted owl). The total range of the species was based on the spotted owl distribution dataset from BirdLife International and NatureServe (2015).

habitat for the northern spotted owl while maintaining a sustainable timber industry in the Pacific Northwest (U.S. Department of Agriculture [USDA], USDI 1994). The Mexican spotted owl does not have an equivalent, broad-scale planning document but is covered by an ESA Recovery Plan (USDI 2012). The California spotted owl has no formal protection under the ESA (Gutiérrez et al. 2017), but the Sierra Nevada Forest Plan Amendment provides some degree of old-growth habitat protection (USDA 2004). Regardless of the level of these conservation and planning efforts, the future of all 3 spotted owl subspecies remains uncertain.

Commercial timber harvesting, with associated loss and fragmentation of owl habitat, was historically considered the primary cause of population declines in all 3 subspecies (USDI 1990, 1993; Verner et al. 1992). More recently, emerging threats such as climate change (Glenn et al. 2010, Peery et al. 2012), high-severity wildfire (Clark et al. 2011, 2013; Keane 2017), barred owl (*Strix varia*) invasion (Sovern et al. 2014, Keane 2017), and forest thinning (Stephens et al. 2014) have been linked to the decline of the spotted owl (but barred owls have not affected the Mexican spotted owl). Although spotted owls evolved in ecosystems where fire is a natural process, we consider large, high-severity fires a potential emerging threat due to the apparent increase in these fire events in recent decades (Westerling et al. 2006, Miller et al. 2009, Miller and Safford 2012, Keane 2017). Spotted owl subspecies may differ in exposure, response, and vulnerability to these historical and emerging threats because of differences in their ecological characteristics, the environments in which they live, and management policies in those areas. For example, the barred owl has invaded the range of the northern spotted owl and the California spotted owl but has not invaded the range of the Mexican spotted owl (Peterson and Robins 2003), whereas the Mexican spotted owl is predicted to respond more negatively to climate change than the California spotted owl (Peery et al. 2012).

Understanding the differences in exposure and response to these known and potential threats among the 3 spotted owl subspecies is important for effective conservation planning and actions. Ideally, conservation plans for each spotted owl subspecies should be based on empirical data specific to that subspecies. The extent of research conducted on each subspecies, however, has been influenced by factors such as the economic effects of the timber industry in the region and the length of time that concern has been raised about a subspecies' status. As a result, the amount of spotted owl literature (and related knowledge) varies greatly among the 3 subspecies, with more information available for the northern spotted owl than for the other subspecies (Gutiérrez 2008). Because of this uneven distribution of knowledge, research results from 1 subspecies are repeatedly applied to other subspecies (USDI 2012). Knowledge also is unevenly distributed among potential causes of population change, and empirical data on owl response to some of these causes are sparse, especially for emerging threats.

Gutiérrez (2008) reported the number and proportion of spotted owl papers in the peer-reviewed literature for each subspecies from 1983–2007, and categorized them based on 5 different topics: natural history, population dynamics, management, policy or law, and other. Here, we extend the temporal coverage of that review by evaluating spotted owl literature published between 1900–2016, with a focus on exploring trends in the number of papers that addressed the historical and emerging threats (i.e., mechanical tree removal, climate change, wildfire, barred owl invasion) for each of the 3 subspecies. Our primary objectives were to quantitatively evaluate trends in the existing literature with respect to coverage of major research topics and historical and emerging threats by spotted owl subspecies; identify topics that appeared to be relatively understudied by subspecies, with an emphasis on historical and emerging threats; and discuss the current state of knowledge regarding the responses of each spotted owl subspecies to these threats. Our goal was to identify critical gaps in existing knowledge and highlight important research needs for each spotted owl subspecies for conservation and management.

METHODS

Literature Search

To objectively sample the spotted owl literature, we conducted a literature search on the Web of Science database on 25 December 2015 using the following criteria: topic = spotted owl, timespan = all years, and document types = article. We eliminated duplicate search results and articles that were not about spotted owls, using information from the abstracts. If a paper had no abstract, or if the abstract did not provide sufficient information, we reviewed the full text to determine whether it was a spotted owl article.

We read each paper and classified them into 1 of 4 subspecies groups: northern spotted owl, California spotted owl, Mexican spotted owl, or papers that addressed ≥ 2 subspecies. We also determined whether the paper addressed 1) barred owls, 2) climate (e.g., temperature, precipitation, monsoon season), 3) wildfire, 4) mechanical tree removal (e.g., thinning, clear-cut, salvage logging), 5) basic descriptive biology (e.g., appearance, vocal behavior), 6) distribution and abundance, 7) habitat selection, 8) connectivity, 9) economics and industry, 10) dispersal and movement, 11) population dynamics, 12) diet and prey relationships, 13) genetics, 14) parasites and diseases, or 15) policy and management. If the paper did not address any of these topics, we classified it as 16) other. We recorded whether each paper had an attribute listed above using a binary system (0 = no, 1 = yes), resulting in 16 binary variables for describing each paper in addition to the subspecies classification. We used these binary data in statistical analyses. Multiple authors independently scored the papers, and the initial scoring agreed >99% of the time. We re-evaluated papers scored differently among authors until we reached a consensus.

To qualify as a yes, we required the paper to provide new data or analysis on the topic. In addition, particularly with the topic of mechanical tree removal, we required a paper to specifically evaluate the effects in terms of owl response following the removal. Thus, papers that addressed habitat selection by owls, which allowed indirect inference about the effects of past timber harvest, received a 1 for habitat selection, and only papers that monitored owl response to specific treatments received a 1 for mechanical tree removal.

Statistical Analyses

We summarized the frequency of papers in each subspecies group by publication year, and determined the proportional representation of each subspecies in the papers analyzed. We summarized the frequency of papers that examined historical threat (i.e., mechanical tree removal) or emerging threats (i.e., barred owls, climate, wildfire) by subspecies group and by publication year separately.

To identify major groups of papers that addressed similar topics in the spotted owl literature and to evaluate how well these topics were represented in the literature for each subspecies, we conducted a polythetic agglomerative hierarchical clustering (PAHC) analysis using the 16 binary descriptor variables described above. Polythetic agglomerative hierarchical clustering is a quantitative approach that systematically combines descriptors into a single association analysis, and has been used in other literature reviews to identify meaningful groups among papers (McGarigal et al. 2016). Polythetic agglomerative hierarchical clustering organizes observations into clusters hierarchically by assigning each observation into its own cluster, and then joining clusters based on their multivariate similarity (McGarigal et al. 2000). Similarity is expressed in terms of distance, where greater distance between 2 observations indicates stronger dissimilarity, and vice versa. Because PAHC operates on a distance matrix (i.e., pairwise distance among observations), we used the DISTANCE function from ECODIST R package (distance [ecodist]; Goslee and Urban 2007) to transform our binaries into a Jaccard distance metric, which is appropriate for binary data because it weights only positive matches (i.e., the 1s in the binary dataset; Legendre and Legendre 1998). We performed the PAHC analysis using the HCLUST function (hclust [stats]) with Ward's minimum variance method (i.e., method = ward.D2) in R (R Development Core Team 2016).

After the PAHC analysis, we computed the agglomerative coefficient using the cluster package in R to measure the strength of the clustering structure. The agglomerative coefficient has a dimensionless range between 0 and 1, with small values indicating no clustering pattern and large values indicating a distinct clustering structure (Kaufman and Rousseeuw 1990). We used discriminant analysis to identify the multivariate combination of variables that best discriminated among the clusters identified by the PAHC analysis (McGarigal et al. 2000). We used the Kappa statistic to evaluate the strength of discrimination (Cohen 1960) and used variable loadings to identify variables that best discriminated among the clusters (McGarigal et al. 2000). We color-labeled each paper in the resulting PAHC dendrogram by subspecies to visually portray how papers of each subspecies were distributed among clusters.

To further examine subspecies representation among clusters, we performed 2 series of randomization tests. In the first series, we randomly assigned each paper to a subspecies group using the subspecies frequency from the sample of papers. In the second series, we assigned papers to subspecies if all subspecies were represented equally. We conducted 1,000,000 permutations for each series, calculated the respective kernel density distributions (i.e., theoretical distributions) for each cluster-subspecies combination group, and calculated the percentile of the resulting distributions that corresponded to the observed number of papers in each group. We followed the same procedures to examine the representation by subspecies in papers dealing with historical and emerging threats.

RESULTS

Subspecies Representation in the Literature

Our literature search identified 842 papers (Supplementary A, available online in Supporting Information). After screening for non-spotted-owl papers and duplicate search results, we retained a final set of 527 papers for quantitative analysis. Of the 527 spotted owl papers, 62.4% ($n = 328$) reported on the northern spotted owl, 16.0% ($n = 84$) on the California spotted owl, and 14.6% ($n = 77$) on the Mexican spotted owl. An additional 2.3% ($n = 12$) reported on the northern spotted owl and the California spotted owl, 0.4% ($n = 2$) on the northern spotted owl and the Mexican spotted owl, 0.4% ($n = 2$) on the California spotted owl and the

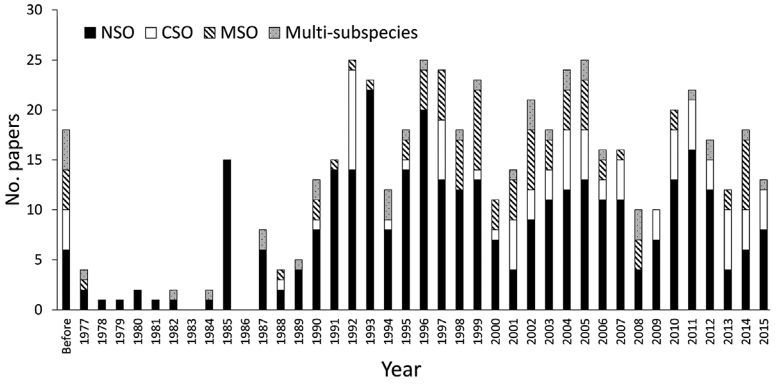

Figure 2. Number of publications for each spotted owl subspecies (NSO = northern spotted owl, CSO = California spotted owl, MSO = Mexican spotted owl) for 1900–2015, by year. Publications that reported on ≥2 subspecies were grouped into multi-subspecies. Publications prior to 1977 were grouped together in the before column.

Mexican spotted owl, and 4.0% ($n = 21$) on all 3 subspecies. One paper did not provide sufficient information for identifying the study subspecies.

After the literature review by Gutiérrez (2008), most papers published since 2007 continued to be on the northern spotted owl (Fig. 2). Annually, publications across the 3 subspecies became more evenly distributed beginning in 2001, with an increasing proportion of California spotted owl papers compared to pre-2001 (Fig. 2). However, the number of spotted owl publications declined by 24.5% between 1996–2005 and 2006–2015 (from 204 papers to 154 papers), despite an increase of 20% in California spotted owl papers (from 30 papers to 36 papers) between decades. Northern spotted owl papers declined by 19.3% between these decades (from 114 papers to 92 papers), and Mexican spotted owl papers declined by 63.8% (from 47 papers to 17 papers).

Attention Given to Historical and Emerging Threats in the Literature

Ninety-eight papers (18.6%) explicitly examined historical or emerging threats. Nineteen papers evaluated the effects of mechanical tree removal on the spotted owl, with the majority being northern spotted owl papers (12 of 19; Fig. 3). Twenty-six papers evaluated effects of climatic variables or climate projections on the spotted owl (Fig. 3). Thirty-two papers examined wildfire effects on the spotted owl or habitats (Fig. 3) and 40 papers studied relationships between barred and spotted owls (Fig. 3). The sum of these categories exceeded 98 because some papers examined multiple threats.

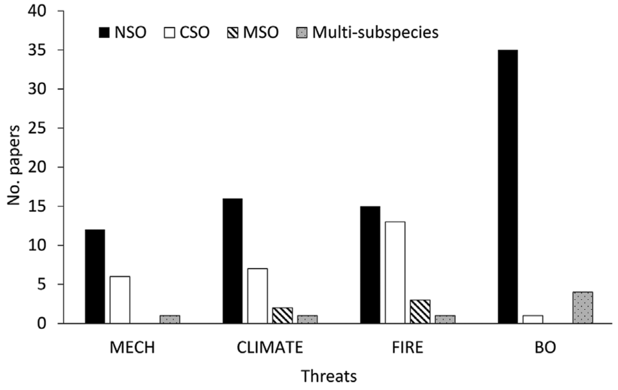

Figure 3. Number of publications on major historical and emerging threats to each spotted owl subspecies for 1900–2015 (NSO = northern spotted owl, CSO = California spotted owl, MSO = Mexican spotted owl, MECH = mechanical tree removal, CLIMATE = climate, FIRE = fire, BO = barred owl). Publications that reported on ≥2 subspecies were grouped into multi-subspecies.

Interest in the effects of various threats appeared to be increasing. Most papers addressing historical or emerging threats (93 total or 94.9%) were published since 2000 (Fig. 4), and 43.9% were published since 2010. Before 2000, only 5 papers were published on the historical and emerging threats we reviewed. Since then, there were 6 papers published on historical or emerging threats per year.

PAHC and Discriminant Analysis

The PAHC analysis produced 6 distinct clusters (agglomerative coefficient = 0.99; Fig. 5). All papers recorded as other (i.e., papers that did not include any of the specific topics we examined) were included in 1 cluster (no class in Fig. 5), which we excluded from further analyses because the category was non-informative.

The discriminant function analysis indicated strong discrimination among clusters (Kappa = 0.95, $P < 0.001$). The variable loadings from this analysis (Table 1) identified 4 major research topics that separated the clusters: habitat selection, population dynamics, management and policy, and economics. A *post hoc* examination indicated that cluster A was dominated by papers that examined habitat selection. Cluster B covered a broad range of miscellaneous topics. Cluster C consisted mostly of papers that examined population dynamics. Cluster D was dominated by papers pertaining to management and policy. All papers that examined economics of the timber industry were grouped in cluster E.

Papers were not evenly distributed among subspecies across clusters (Fig 5). For example, cluster E (i.e., economics of the timber industry group) contained 95% northern spotted owl papers and 5% Mexican spotted owl papers, whereas cluster A (i.e., habitat selection group) contained 56% northern spotted owl, 24% Mexican spotted owl, and 20% California spotted owl papers.

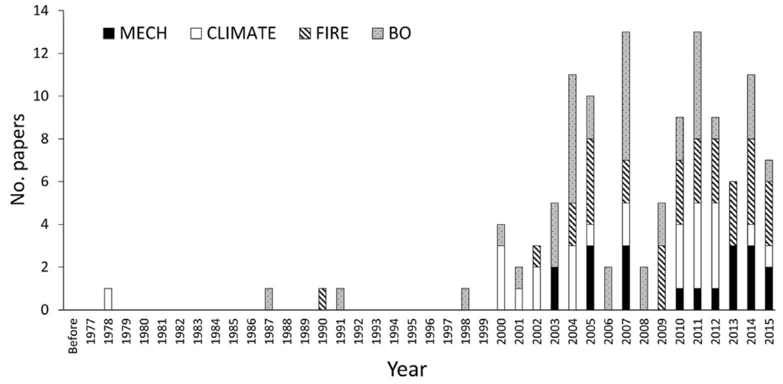

Figure 4. Number of publications related to historical and emerging threats by year for the period 1900–2015 (MECH = mechanical tree removal, CLIMATE = climate, FIRE = fire, BO = barred owl). Publications prior to 1977 were grouped together in the before column.

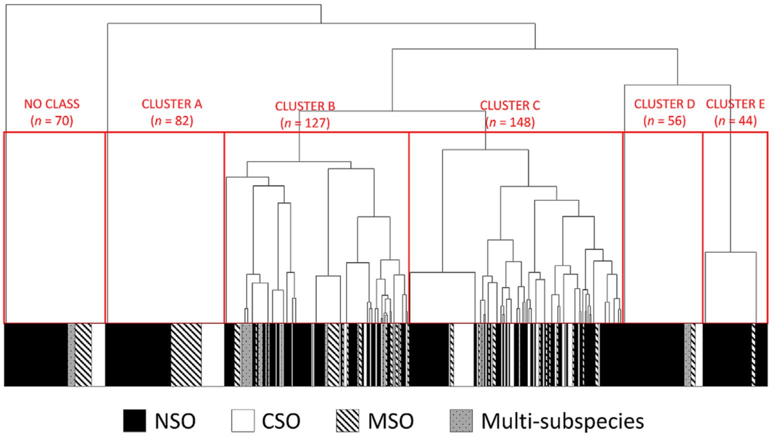

Figure 5. Polythetic agglomerative hierarchical clustering of 527 spotted owl papers published 1900–2015 based on variables using Jaccard distance and Ward's minimum variance fusion criterion. Red boxes indicate 6 distinctive clusters (no class = no classification, cluster A = habitat selection, cluster B = miscellaneous, cluster C = population dynamics, cluster D = management and policy, cluster E = economics). The height of the tree (i.e., black branching lines) along the *y*-axis represents the fusion distance. The *x*-axis represents all spotted owl papers analyzed. The bar along the *x*-axis represents the subspecies group of each paper (NSO = northern spotted owl, CSO = California spotted owl, MSO = Mexican spotted owl). Publications that reported on ≥2 subspecies were grouped into multi-subspecies.

Table 1. Variable loadings of 15 variables used in discriminant function analysis describing multivariate differences among polythetic agglomerative hierarchical clusters of spotted owl papers published 1900–2015. Function 1 is best at identifying cluster A (habitat selection) from other clusters. Function 2 is best at identifying cluster C (population dynamics) from other clusters. Function 3 is best at identifying cluster D (management and policy) from other clusters. Function 4 is best at identifying cluster E (economics) from other clusters. Loadings ≥|0.50| are denoted with an asterisk.

	Loadings			
Variable	**Function 1**	**Function 2**	**Function 3**	**Function 4**
Barred owl	0.17	−0.12	0.23	−0.11
Climate and climate change	0.27	0.30	0.02	−0.07
Fire disturbance	0.29	0.29	0.05	−0.08
Mechanical tree removal	0.23	0.25	0.02	−0.06
Basic biology description (e.g., appearance, vocal behavior)	0.05	−0.29	0.25	−0.08
Distribution and abundance	0.08	−0.42	0.38	−0.13
Habitat selection	−0.73*	0.38	0.12	−0.23
Connectivity	0.14	0.15	0.01	−0.04
Economics and timber industry	−0.01	−0.02	0.01	1.00*
Dispersal and movement	0.20	0.15	0.07	−0.07
Population dynamics	0.57*	0.52*	0.13	−0.17
Diet and prey relationship	0.06	−0.38	0.32	−0.10
Genetics	0.04	−0.27	0.23	−0.07
Parasites and diseases	0.03	−0.20	0.17	−0.06
Policy and management	0.16	−0.36	−0.87*	0.03

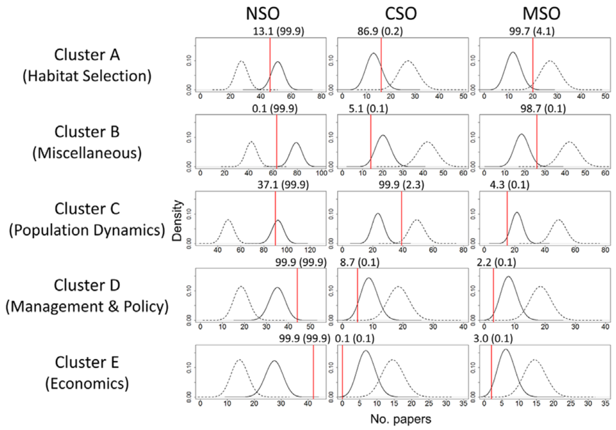

Figure 6. Theoretical distribution of spotted owl papers for each subspecies (NSO = northern spotted owl, CSO = California spotted owl, MSO = Mexican spotted owl) among clusters based on the frequency of subspecies papers published 1900–2015 in the original data (solid black curve) and an evenly distributed frequency of subspecies papers (dotted black curve), estimated with 1,000,000 random permutations. The *x*-axis represents the number of papers and the *y*-axis represents the kernel density estimates. Clusters and subspecies are sorted by rows and columns respectively. Red solid lines represent the observed number of papers. Numbers above the red lines represent the percentile rank of the observed number of papers in the 2 distributions (left for solid curve and right in parentheses for dotted curve). A high percentile rank indicates the observed number of papers is greater than expected in a theoretical distribution, and vice versa.

Randomization Tests

Randomization tests demonstrated uneven distribution of papers among subspecies. Relative to the actual frequency of papers by subspecies, research on the northern spotted owl focused more on economics (cluster E) and management and policy (cluster D) and less on habitat selection and population dynamics (clusters A and C, respectively) than expected by chance (Fig. 6). Conversely, research on the California spotted owl focused more on habitat selection and population dynamics and less on management, policy, and economics than expected by chance (Fig. 6). Research on the Mexican spotted owl focused more on habitat selection and less on population dynamics, management, policy, or economics than expected by chance (Fig. 6).

Relative to the number of papers randomized across subspecies, the northern spotted owl had more papers and the California spotted owl and the Mexican spotted owl had fewer papers in each cluster than expected by chance, reflecting the larger number of papers on the northern spotted owl (Fig. 6). Randomization results suggested that relatively understudied topics included population dynamics for the Mexican spotted owl and management and policy and economics for the California spotted owl and the Mexican spotted owl (Fig. 6). All topics were better studied for northern spotted owl than for the other subspecies.

In terms of historical and emerging threats, randomization tests again indicated uneven distribution of papers among subspecies and threats (Fig. 7). Relatively understudied emerging threats included wildfire for the northern spotted owl, barred owl invasion for the California spotted owl, and all threats for the Mexican spotted owl (Fig. 7).

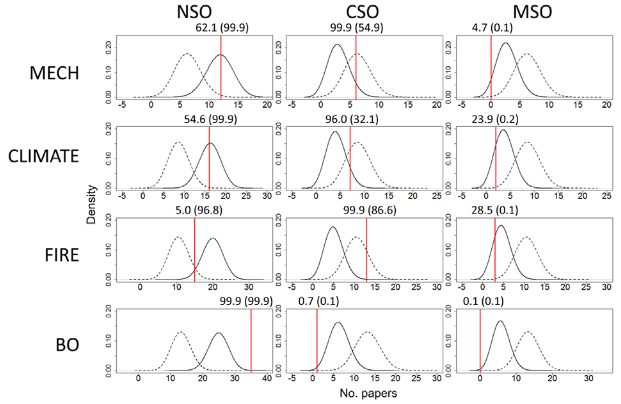

Figure 7. Theoretical distribution of historical and emerging threats (MECH = mechanical tree removal, CLIMATE = climate, FIRE = fire, BO = barred owl) papers among spotted owl subspecies (NSO = northern spotted owl, CSO = California spotted owl, MSO = Mexican spotted owl) based on the frequency of subspecies papers published 1900–2015 in the original data (solid black curve) and an evenly distributed frequency of subspecies papers (dotted black curve), estimated with 1,000,000 random permutations. The *x*-axis represents the number of papers and the *y*-axis represents the kernel density estimates. Threats and subspecies are sorted by rows and columns respectively. Red solid lines represent the observed number of papers. Numbers above the red lines represent the percentile rank of the observed number of papers in the 2 distributions (left for black curve and right in parentheses for dotted curve). A high percentile rank indicates the observed number of papers is greater than expected in a theoretical and vice versa.

DISCUSSION

Trends in the Literature

Subspecies emphasis.—Our quantitative analysis of 527 spotted owl papers revealed an uneven distribution of papers among subspecies, consistent with Gutiérrez (2008). Most papers across all research topics identified by PAHC analysis (Fig. 5) were on the northern spotted owl, likely reflecting the length of time that researchers have studied this subspecies and the economic and political climate around its conservation. Active research began with studies of the northern spotted owl in the late 1970s (Forsman et al. 1984), whereas work on the California spotted owl and the Mexican spotted owl largely began more than a decade later (Fig. 2). Reported expenditures on the northern spotted owl from 1996–2014 (the only years for which data were readily available) totaled $207.6 million, versus $66.5 million for the Mexican spotted owl (USDI 2016; note that the amount of these expenditures supporting research activities was not reported). Presumably at least part of this large discrepancy in expenditures reflects the greater economic value of timber resources within the range of the northern spotted owl relative to the Mexican spotted owl, and the consequently greater interest in addressing conflicts between conservation of owl habitat and extraction of timber. Studies on the northern spotted owl span a longer period than for the other subspecies, and expenditures on research and management are greater for the northern spotted owl than for the other subspecies. Comparative data were not available for the California spotted owl, however, because it is not listed under the ESA and so expenditures were not formally reported.

Mexican spotted owl papers represented a small fraction of manuscripts among major research topics, except for habitat selection (cluster A; Fig. 5). Because the Mexican spotted owl was listed as Threatened primarily because of concerns over habitat loss (USDI 1993), it is understandable that a relatively high proportion of Mexican spotted owl studies have focused on characterizing habitat. The general lack of population dynamics studies for the Mexican spotted owl, however, is notable (cluster C; Fig. 5), and severely limits our understanding of factors causing population fluctuations in this owl and how it might respond to emerging threats.

For the California spotted owl, few studies focused on the economics of the timber industry (cluster E; Fig. 5). This may indicate that forest economists had a greater interest in understanding how habitat protection for the listed northern spotted owl and Mexican spotted owl could affect the timber industry compared to the unlisted California spotted owl.

Our analysis documented a decrease in the number of spotted owl publications in recent years. The number of papers on the northern spotted owl and the Mexican spotted owl declined between 1996–2005 and 2006–2015, especially for the Mexican spotted owl (>63% decline in papers for the more recent decade). Despite the overall decline, the number of papers published on the California spotted owl have substantially increased, indicating a shift in research attention from the federally listed northern spotted owl and Mexican spotted owl to the unlisted California spotted owl. One possible explanation for this shift is the rising concern over observed increases in wildfire activity within the range of California spotted owl (Westerling et al. 2006, Miller et al. 2009, Miller and Safford 2012, Keane 2017). The amount and timing of wildfire-related California spotted owl papers support this hypothesis, with 11 of 14 such papers published since 2006. The increase in California spotted owl publications also could indicate increasing social and political pressure to advance knowledge of this subspecies before potential ESA listing.

Emphasis on historical and emerging threats.—Despite the substantial body of spotted owl literature, relatively few studies have focused on the effects of emerging threats (Fig. 4), and even fewer papers focused on the possible synergistic interaction of new and historical threats (Dugger et al. 2016). The relatively few papers that addressed those issues did not cover all subspecies, and generally left major gaps in understanding even for the subspecies addressed.

Direct empirical data on the effects of timber harvesting, thinning, and other mechanical treatments on spotted owls, and especially on the Mexican spotted owl, remain sparse (Figs. 3 and 7) even though timber harvesting was originally identified as the cause of the spotted owls' decline. The lack of information on the effects of forest thinning on owls is particularly concerning, given the recent management emphasis on landscape-scale restoration projects that likely will reduce canopy cover and create more open forest conditions across millions of hectares within the range of the spotted owl (Sisk et al. 2005, North et al. 2009, Roccaforte et al. 2010, USDA 2010).

Unsurprisingly, most of the papers that studied barred owl effects on spotted owls were northern spotted owl papers (Figs. 3 and 7), because this threat is greatest for the northern spotted owl. Barred owls have invaded much of the northern range of the California spotted owl, however, and are viewed as a significant threat (Keane 2017). Ecological niche models predict that barred owls will continue to expand to the south within the range of the California spotted owl but are unlikely to expand into the range of the Mexican spotted owl (Peterson and Robins 2003).

In terms of climate and wildfire effects, papers were especially lacking for the Mexican spotted owl (Fig. 3). The lack of such papers contrasts with the large body of literature on historical and changing fire regimes and climate within the range of Mexican spotted owl (Fulé et al. 2004, Westerling et al. 2006, Littell et al. 2009, O'Connor et al. 2014), the predicted large changes in climate in this region (Seager et al. 2007, Garfin et al. 2014), and the perception that many forests in the region have become increasingly fire-prone (Covington and Moore 1994, Fulé et al. 2004, Dillon et al. 2011). The few studies of Mexican spotted owl responses to wildfire evaluated only short-term effects and did not address the critically important issue of potential time lags between wildfire events and population responses (Bond et al. 2002, Jenness et al. 2004).

Extrapolating information among subspecies.—In evaluating the literature on spotted owls, we also observed a frequent, primarily uni-directional flow of information from better-studied to lesser-studied subspecies. We did not quantify this trend, but it appeared that papers on the ecology or management of California spotted owls were more likely to use information from papers on the northern spotted owl than vice versa, and papers on the least-studied Mexican spotted owl frequently cited papers on the northern spotted owl and the California spotted owl, whereas use of information derived for the Mexican spotted owl was relatively rare in papers on the northern spotted owl or California spotted owl.

The use of information from well-studied subspecies to guide management of lesser-studies subspecies was most pronounced in comprehensive planning documents, where scientists attempted to marshal the best available information. Two examples help illustrate this process. First, 2 recent reports on managing the California spotted owl in the Sierra Nevada Forests (Roberts and North 2012, Gutiérrez et al. 2017) cited multiple northern spotted owl papers to describe the potential negative effects of barred owls on spotted owls (Kroll et al. 2010; Dugger et al. 2011; Yackulic et al. 2012, 2014; Wiens et al. 2014). Second, the recovery plan for the Mexican spotted owl (USDI 2012) cited northern spotted owl and California spotted owl papers on fire effects extensively (Franklin et al. 2000, Lee and Irwin 2005, Ager et al. 2007, Bond et al. 2009, Clark et al. 2011), and extrapolated information on response to forest treatments from studies on the northern spotted owl and the California spotted owl (Meiman et al. 2003, Seamans and Gutiérrez 2007*a*, Gallagher 2010, Dugger et al. 2011, Stephens et al. 2014). In all cases this extrapolation of information among subspecies was caused by a lack of information specific to the focal subspecies.

Information Gaps and Research Needs

Results from our analysis, especially the randomization tests, suggested that all topics were better studied for the northern spotted owl than for the other subspecies, and that understudied topics included population dynamics for the Mexican spotted owl, and management, policy, and economics for the California spotted owl and the Mexican spotted owl (Fig. 6). Randomization tests based on historical and emerging threats also indicated uneven distribution of papers among subspecies and topics (Fig. 7), with understudied topics related to emerging threats including fire for the northern spotted owl, barred owl invasion for the California spotted owl, and all threats for the Mexican spotted owl (Fig. 7). Given that the Mexican spotted owl is the least studied subspecies in terms of response to threats (Fig. 3) and lives in a highly divergent ecosystem compared to the northern spotted owl and the California spotted owl, future research should focus on its ecology and vulnerability. Below, we discuss these information gaps as they relate to the historical and especially emerging threats discussed earlier.

Mechanical tree removal.—All 3 spotted owl subspecies typically nest and roost in mature or old-growth forests (Forsman et al. 1984, LaHaye et al. 1997, Hershey et al. 1998, May et al. 2004, Ganey et al. 2013), although Mexican spotted owls also nest and roost in rocky canyonlands (Rinkevich and Gutiérrez 1996, Willey and van Riper III 2007, Bowden et al. 2015). Because of the strong association between spotted owls and old forests containing large trees and high canopy cover (Forsman et al. 1984, Hershey et al. 1998, May et al. 2004, Ganey et al. 2016, North et al. 2017), commercial timber harvest historically was considered the most important threat to spotted owls throughout their range (USDI 1990, 1993; Verner et al. 1992). Old-growth forests that support spotted owls have high timber value and experienced intensive harvest over the past century, with approximately 61% loss of old-growth forest within the range of the northern spotted owl at the time of listing (USDI 1990) and approximately 76% loss within the range of the California spotted owl through 1993 (Beardsley et al. 1999). In the Southwest, old forests dominated by relatively large trees have been replaced by young stands with large numbers of smaller trees because of post-settlement large-scale timber extraction, overgrazing, and fire suppression (Fulé et al. 1997).

Commercial timber harvest remains a threat to existing habitat in many areas across the range of the spotted owl as it retains the potential to rapidly remove nesting habitat and increase landscape fragmentation, but the spatial extent of commercial harvest has declined in spotted owl habitat as forest management paradigms have changed (Davis et al. 2015). Management emphasis in many areas has recently shifted to forest restoration and thinning to reduce fuel loads and fire risk (USDA 2009, Society of American Foresters 2011, Schultz et al. 2012). Thus, the threat from the types of overstory removal common in the past is reduced today, but forest restoration and thinning activities also may threaten owls and their existing habitat, and thus may qualify as an emerging threat.

Information on the effects of forest thinning and restoration is unevenly distributed across subspecies. No empirical studies have evaluated these management activities on the Mexican spotted owl, and few studies are available for other subspecies. For the northern spotted owl and the California spotted owl, most existing studies indicate negative responses by owls to fuels reduction treatments (Meiman et al. 2003; Seamans and Gutiérrez 2007*a*; Stephens et al. 2014; Tempel et al. 2014, 2015), but the mechanisms driving the apparent negative responses are unclear and the range of treatments evaluated is relatively small.

Studies suggest that forest thinning could have positive and negative effects. For example, mechanical alteration of forests affects prey species, with effects ranging from positive to negative among species and studies (Amacher et al. 2008, Holloway and Smith 2011, Manning et al. 2012, Kelt et al. 2013, Stephens et al. 2014). Irwin et al. (2013, 2015) suggested that thinned stands might improve foraging habitat quality for the northern spotted owl and the California spotted owl by increasing prey availability. Moreover, Andrews et al. (2005) suggested that thinning could accelerate stand development and reduce the time needed to develop structure for nesting for the northern spotted owl. Several studies suggested that thinning could benefit the spotted owl by removing woody fuel and thus reducing risk of habitat loss to high-severity fire (Calkin et al. 2005, Lee and Irwin 2005, Ager et al. 2007, Roloff et al. 2012, Chiono et al. 2017). In contrast, Tempel et al. (2014, 2015) suggested that medium-intensity fuel treatments reduced habitat quality and reproductive success of the California spotted owl in the short term despite providing potential long-term benefits by reducing fire risks. Odion et al. (2014*b*) calculated that cumulative habitat loss to harvest and fire over a 40-year period in the Klamath and dry Cascades region in California, Oregon, and Washington would be greater with thinning than without thinning. In addition, some studies suggested that high-severity fires might have been characteristic of historical fire regimes within the range of the spotted owl, and therefore, suppressing high-severity fires through thinning could potentially reduce spotted owl habitat (Baker 2015*a*, Hanson and Odion 2016). Ultimately, owl responses to thinning depend on pre-treatment stand conditions and treatment intensity (Tempel et al. 2016). Despite the increasing emphasis on fuels reduction treatments and the potential for such treatments to affect large areas throughout the range of the spotted owl (Sisk et al. 2005, North et al. 2009, Roccaforte et al. 2010, USDA 2010), uncertainty remains regarding the response to mechanical treatments for all 3 subspecies.

Climate change.—Global climate has been changing rapidly since the beginning of the industrial era because of human activities such as deforestation, fossil fuel combustion, and land use change, and such change is projected to accelerate over the twenty-first century and beyond (Stocker et al. 2013). Climate models generally predict that climate will become warmer throughout the range of the spotted owl (Hoerling et al. 2013, Garfin et al. 2014, Mote et al. 2014), whereas predicted change in the amount and timing of precipitation are more variable throughout the range (Peterson et al. 2013, Walsh et al. 2014).

Changing climates can influence the survival, reproduction, and occurrence of spotted owls (Franklin et al. 2000, Seamans et al. 2002, Dugger et al. 2005, Glenn et al. 2011*a*, Stoelting et al. 2015), affect habitat availability by changing vegetation composition and succession, and indirectly affect spotted owls through impacts on their chief prey species, predators, competitors, pests, and diseases. Climate also influences fire regimes (Dale et al. 2001, Littell et al. 2009) by controlling the type and abundance of vegetation and fuels on the landscape, the flammability of fuel, the probability of fire ignition and spread, and the length of the fire season (Westerling et al. 2006). Therefore, changes in climate also indirectly influence the amount and rate of habitat loss or alteration by wildfire.

Information is generally lacking on how changing climates will affect all 3 subspecies of spotted owls. Climate change effects unfurl over long time periods, making them impossible to study directly with short-term studies. Our best information on how changing climates might affect spotted owls currently comes from empirical studies relating vital rates of marked spotted owls to weather and climate patterns (Seamans et al. 2002; Glenn et al. 2011*a*, *b*; Stoelting et al. 2015; Jones et al. 2016*b*). Demographic studies like these also provide the best option for monitoring longer-term response to changing climates.

For the northern spotted owl, many long-term demography studies exist that collectively cover a large and reasonably representative portion of their range (Anthony et al. 2006, Forsman et al. 2011). Studies modeling climate effects based on vital rates from these demography areas suggest that wet winters and hot, dry summers reduce survival, reproduction, recruitment, and population growth rates (Glenn et al. 2010, 2011*a*, *b*; Dugger et al. 2016). Winters within the range of northern spotted owl are predicted to be wetter but warmer (Mote et al. 2014, Walsh et al. 2014). Based on current information, the trend toward wetter winters could have negative effects. No empirical data, however, are available on how wetter but warmer winters will influence survival and reproduction.

For the California spotted owl, a few long-term demography studies exist in the Sierra Nevada and southern Cascades (Franklin et al. 2004; Blakesley et al. 2010; Jones et al. 2016*b*; Tempel et al. 2016, 2017). In modeling studies based on demographic rates, the California spotted owl generally responded similarly to the northern spotted owl with respect to climate, with reproductive output, survival, and population growth rate decreasing with increasing winter precipitation (Seamans and Gutiérrez 2007*b*). Local site extinction rates for the California spotted owl increased following multi-year heat waves (Jones et al. 2016*b*). Extreme dry periods may also reduce probability of breeding in this subspecies (Stoelting et al. 2015). Precipitation is projected to increase in most of California except the southernmost part (Peterson et al. 2013, Walsh et al. 2014), suggesting that California spotted owls inhabiting the northern to central parts of California might respond more negatively to climate change than do their southern counterparts. But, as with the northern spotted owl, winters are expected to warm within the range of California spotted owl (Garfin et al. 2014), which might cause California spotted owls to respond differently to increasing precipitation than predicted by current models.

There are no ongoing demography studies within the range of Mexican spotted owl, and past studies were few and relatively short in duration (Seamans et al. 1999, Stacey and Peery 2002, Ganey et al. 2014*c*). In contrast to the negative relationship between vital rates and precipitation for the northern spotted owl and the California spotted owl, survival and reproduction of the Mexican spotted owl in Arizona and New Mexico was positively related to precipitation from the previous year, previous winter, and previous monsoon season (Seamans et al. 2002). The projected drier climate and intensified droughts in the Southwest (Seager et al. 2007, Garfin et al. 2014) thus may have a stronger negative effect on the Mexican spotted owl than on the California spotted owl. Peery et al. (2012) modeled future populations of California spotted owls and Mexican spotted owls under 3 Intergovernmental Panel on Climate Change emissions scenarios, using the empirical relationships between weather and vital rates derived from the demography studies, and predicted that Mexican spotted owl populations would decline more rapidly and face greater extinction risk under climate change projections than the California spotted owl.

The information provided by long-term demography studies will be useful in modeling the effects of predicted changes in climate on population viability of spotted owls throughout their range (Peery et al. 2012, Jones et al. 2016*b*). Relationships between climate and demography are complex, however, and owls and their primary prey species and habitats may respond to changing climates in unexpected ways. This further highlights the ongoing need for monitoring owl demography to provide empirical data to iteratively improve models of climate and demography relationships over time. In this context, the lack of existing demography studies within the range of the Mexican spotted owl is problematic. Long-term studies of demographic rates throughout the range of this subspecies are needed, particularly as climate change within North America is predicted to be most pronounced within the Southwest (Seager et al. 2007, Garfin et al. 2014).

No empirical studies have formally evaluated relationships between climate change and populations of important spotted owl prey species, competitors, or predators, between climate change and habitat availability, or between climate change and potential parasites and diseases. Modeling studies generally suggest pronounced changes in geographic ranges of many tree species (Rehfeldt et al. 2012, Iverson and McKenzie 2013), re-assembly of species communities in novel ways in response to changing climates (Williams and

Jackson 2007), and range expansions by some potentially relevant disease organisms (e.g., West Nile virus; Fitzgerald et al. 2003, Komar 2003, Marra et al. 2004). The effects of such changes on spotted owls generally are unknown. Climate change will undoubtedly lead to loss of owl habitat when cool-adapted forests become constrained by the upper limits of elevational migration. Spotted owl populations may respond to rising temperature by shifting to suitable habitats at higher elevation or higher latitude, but uncertainty remains as to whether they can adapt to the rate of climate change because of limited dispersal options. Habitats of the 3 spotted owl subspecies are already located at some of the highest available elevations in their respective region, and past habitat loss and fragmentation due to timber harvest limits connectivity of populations and ability of migrants to colonize new areas beyond the current range. In this context, information regarding spotted owls' dispersal capacity and trends in habitat connectivity under plausible climate change scenarios is needed.

Barred owl invasion.—Most existing information on relationships between spotted and barred owls comes from studies of northern spotted owls. These studies indicate significant effects to northern spotted owls (Jennings et al. 2011, Sovern et al. 2014, Wiens et al. 2014, Dugger et al. 2016, Holm et al. 2016), and have led to experimental efforts to control barred owl numbers within the range of the northern spotted owl through lethal means (Diller et al. 2016, Dugger et al. 2016). Although lethal removal of barred owls appears to alleviate effects, the continued use of lethal control of barred owls in perpetuity may prove unacceptable to the public for economic and ethical reasons. Therefore, for the northern spotted owl, research attention should focus on other ways to mitigate the effects of barred owls on northern spotted owls. For example, does providing greater amounts or larger core areas of late seral forest habitat foster coexistence between these owls (Yackulic et al. 2014)? Are there particular geographic areas, forest types, or structural conditions that serve as refugia for northern spotted owls from barred owls (Kroll et al. 2016)? And if so, can protection of late seral habitats be shifted to such areas to favor northern spotted owl persistence?

Studies designed to understand competitive relationships between the California spotted owl and the barred owl also are needed. Although there are anecdotal reports of barred owls observed within the range of Mexican spotted owl (eBird 2017), it does not appear to be established as a breeding species within that range. Consequently, there is no apparent need for studies on interactions between barred owls and Mexican spotted owls. Managers, however, should remain vigilant for evidence of barred owl invasion within the range of the Mexican spotted owl.

Wildfire.—Wildfires are one of the most important disturbances that alter or modify spotted owl habitat, and have been for thousands of years. These fires can affect spotted owls through removal or alteration of the forests used for nesting, roosting, and foraging and may affect prey populations and communities. Additionally, there may be important interactions between changing climates, wildfire extent and severity, and forest treatments (Ganey et al. 2017).

Although spotted owls have evolved in fire-moderated ecosystems, considerable evidence suggests that recent, high-severity wildfires contributed to loss or significant alteration and fragmentation of spotted owl nesting habitat (USDA 2004, USDI 2013, Davis et al. 2015). Between 1994 and 2013, Davis et al. (2015) estimated that 191,900 ha of northern spotted owl habitat on NWFP federal lands were burned, representing 4 times the area of habitat loss due to timber harvest (47,000 ha) and 5.2% of the total protected habitat originally designated in 1994 (3,678,500 ha). Ager et al. (2012) simulated fire behavior in the Deschutes National Forest, Oregon, USA and predicted that 60% to 71% of burnable area in northern spotted owl habitats will experience active crown fire activity. In the Sierra Nevada, 85,046 ha of California spotted owl potential nesting habitat was burned by fire that resulted in $\geq$50% tree basal area mortality and reduced average canopy cover to <25% from 2000–2014 (Stephens et al. 2016). They estimated that at predicted rates of burning, the cumulative amount of nesting habitat burned at $\geq$50% tree basal area mortality would exceed the total existing potential California spotted owl nesting habitat within 75 years. No similar analyses exist for the Mexican spotted owl, but wildfires also have burned large areas with high severity within its range (Ganey et al. 2017).

Thus, the potential for rapid conversion of nesting habitat to nonforest or more open forest not suitable for nesting appears high in many parts of the range of the spotted owl (Ganey et al. 2017). Despite this potential, relatively few studies have examined the response of spotted owls to wildfire, especially for the northern spotted owl and the Mexican spotted owl.

Existing studies report that many wildfires, especially of low- to moderate- severity, have little or no significant adverse effects on short-term spotted owl occupancy and reproduction (Bond et al. 2002; Jenness et al. 2004; Roberts et al. 2011; Lee and Bond 2015*a*, *b*) and may have potential foraging benefits (Bond et al. 2009, 2016; Ganey et al. 2014*b*; Eyes et al. 2017), but that high proportions of severe fire in an owl's territory can result in negative effects on survival (Rockweit et al. 2017), occupancy (Lee et al. 2013, Lee and Bond 2015*b*, Jones et al. 2016*a*), and foraging (Jones et al. 2016*a*). These studies focused primarily on the California spotted owl, however, with few such studies conducted for the northern spotted owl and the Mexican spotted owl. Given differences in subspecies ecology and forest types inhabited, it may not be wise to generalize from the response of the California spotted owl to these other subspecies.

Moreover, although information on the California spotted owl and fire is more extensive than the other 2 subspecies, there is no consensus regarding whether the California spotted owl responds negatively to high-severity fires (Ganey et al. 2017). The hotly debated topic has been further fueled by contrasting results from 2 recent studies that examined post-fire occupancy rates of California spotted owls in the Sierra Nevada (Lee and Bond 2015*a*, Jones et al. 2016*b*). Lee and Bond (2015*a*) concluded that high-severity wildfire posed little threat to the California spotted owl because of higher observed occupancy rates in high-severity burned areas than in previously published reports, whereas Jones et al. (2016*b*) concluded that high-severity fire threatened the California spotted owl because post-fire occupancy probability declined by 22% and declined by almost 9-fold in areas that burned at >50% high severity. One important distinction between the 2 studies was that Lee and Bond (2015*a*) used nocturnal detections of unmarked owls, whereas Jones et al. (2016*b*) used marked owls, which likely contributed to differences in results. Another explanation for the difference in results between the 2 studies is the spatial variations and interactions of fire size and high-severity burned patches (Ganey et al. 2017). In Jones et al. (2016*a*), high-severity burned patches were large and contiguous and covered a greater portion of the study area. In contrast, the fire in Lee and Bond (2015*a*) had smaller high-severity burned patches that covered a smaller portion of the study area. These studies suggest that the effect of high-severity wildfires remains highly nuanced but can be negative under some circumstances, particularly when high-severity burned patches are large or extensive.

Fire studies on spotted owls generally focused on short-term results (Ganey et al. 2017). Spotted owls exhibit high site fidelity (Blakesley et al. 2006, Gutiérrez et al. 2011, Ganey et al. 2014*a*), and pre-fire residents may remain in or near their territories even after the habitat is burned. In addition, these burned areas will undergo gradual loss of perches as burned trees fall (Ganey et al. 2017). Salvage logging within burned areas hastens this process (Bond 2016), and in many existing studies fire effects were confounded with effects of salvage logging (Lee et al. 2012, Clark et al. 2013). Finally, although populations of some important prey species such as white-footed mice (*Peromyscus* spp.) and woodrats (*Neotoma* spp.) may increase following fires (Converse et al. 2006, Amacher et al. 2008, Roberts et al. 2015), we do not know how long such increases persist (Fontaine and Kennedy 2012). Consequently, it remains unclear whether the observed, short-term occupancy and reproductive rates will persist over longer time periods (Ganey et al. 2017).

Better information is needed for all 3 subspecies on the influence of fire severity and extent, and spatial pattern of post-fire landscapes, on owl demography at different spatial scales and across longer temporal scales. Where long-term, demographic study areas are affected by wildfires (Jones et al. 2016*a*, Rockweit et al. 2017), the resulting *de facto* before-after-control-impact (BACI) studies can provide such empirical data, which in turn can be used to improve simulation models assessing tradeoffs in amounts of habitat in landscapes with and without fuels treatments (Tempel et al. 2015). As noted above, the utility of these models currently is handicapped by a lack of knowledge on habitat suitability and owl demography in post-fire and post-treatment landscapes.

Another critical research gap concerns the historical extent of high-severity wildfire within the range of the spotted owl. Evidence suggests that the incidence of fires has been increasing within this range since the 1980s, but whether amounts of high-severity fire are unprecedented is unclear. There remains a fundamental disagreement in the literature over the nature of historical fire regimes in some of the drier forest types occupied by spotted owls throughout their range, and on whether current fire regimes differ significantly from those historical regimes. Some authors argue that human activities since European settlement have altered the distribution and types of vegetation and fuels on the landscape, leading to substantial changes in forest structures and fire regimes in drier forest types, with many forests throughout the range of the spotted owl now dominated by dense stands with shade-tolerant understories and small trees that are prone to high-severity wildfires (Skinner 1995; Fulé et al. 1997, 2004; Hessburg and Agee 2003; Hessburg et al. 2005). Other studies noted that warmer or drier climates increase the probability, intensity, and severity of fire in some regions, and the length of the fire season (McKenzie et al. 2004, Lutz et al. 2009, Hurteau et al. 2014), or that wildfires have become larger and more severe in the western United States as a result of these changes (Westerling et al. 2006, Littell et al. 2009, Miller et al. 2009, Dillon et al. 2011). In contrast, others argue that high-severity fire has not increased or deviated from historical conditions (Hanson et al. 2009, Williams and Baker 2012, Odion et al. 2014*a*, Baker 2015*b*, Hanson and Odion 2016). This debate is of fundamental importance to understanding potential effects of wildfire on spotted owls.

Better information also is required for all 3 subspecies on potential tradeoffs between the risks of high-severity wildfire and potential effects of forest treatments that reduce fuel amounts and continuity. Many modeling studies have evaluated such tradeoffs within the ranges of the northern spotted owl and California spotted owl, often with contradictory results (Lee and Irwin 2005, Ager et al. 2012, Baker 2015*a*, Hanson and Odion 2016, Chiono et al. 2017). These studies were hampered by the limited information available on owl response to the treatments modeled or the simulated wildfires. Empirical data is needed to inform and improve these models (Ganey et al. 2017). Future studies of this type also should include simulated changes in climate under a range of plausible emissions scenarios. Changing climate could strongly influence both length of fire seasons and fire severity, and those changes in turn could strongly influence the tradeoffs between treated and untreated landscapes (Littell et al. 2009).

Other emerging threats.—Two other threats deserve attention: novel diseases and the use of anticoagulant rodenticides. In terms of novel diseases, West Nile virus (WNV) recently spread rapidly in North America and caused significant mortality in many avian species, including some owls (Fitzgerald et al. 2003, Komar 2003, Marra et al. 2004). Although Hull et al. (2010) conducted an antibody analysis and reported no WNV infection in the spotted owl, we recommend continued monitoring of the distribution of the virus and its presence in the owl population. Early detection can reduce the chance of an outbreak of the virus, and might mitigate the effect if an outbreak happens. Climate change is exacerbating the spread of this and other novel disease organisms (e.g., Zika virus) and their vectors into areas where resident organisms have no history of exposure to those diseases, and therefore likely have no resistance.

A second potential threat relates to the use of anticoagulant rodenticides, particularly as used in illegal marijuana farms on public lands (Gabriel et al. 2012, 2013; Learn 2015). These rodenticides have been implicated in the deaths of numerous fishers (*Martes pennanti*) and barred owls within the range of the northern spotted owl. Researchers worry that the northern spotted owl may be more vulnerable to this poison than the barred owl, because the northern spotted owl preys more heavily on small mammals than do barred owls, and these small mammals are more likely to be exposed to rodenticides than other potential prey species (Learn 2015). Disease and rodenticide use are even less understood than the major threats discussed in this review, could exacerbate those threats, and should be another active area of investigation.

Synergistic interactions between threats.—Historical and emerging threats also may interact to synergistically affect spotted owls. For example, the extensive reduction and fragmentation of quality spotted owl habitat by historical commercial logging synergistically increases the risks posed by climate change, mechanical tree removal, and wildfire. The rapidity of barred owl invasion of northern spotted owl range, for example, has likely been facilitated by the highly fragmented mosaic of mixed seral forest created by historical commercial timber harvest. Furthermore, the threats potentially posed by high severity wildfire are greatly increased in the context of a landscape where spotted owl populations have already been depressed and quality owl nesting habitat already greatly reduced and fragmented by past timber harvest.

There is also an obvious synergy between the emerging threats of climate change and high severity wildfire. Recent and projected future climate change will increase the extent and severity of wildfire, which, given the potential vulnerability of spotted owls to the amount of severely burned area in a landscape (Jones et al. 2016*a*), will increase the negative effects of fire on spotted owl nesting habitat. Climate change may also affect relationships between barred owls and spotted owls, and the extent and type of mechanical harvest could also affect both processes. For all 3 subspecies, better information is needed on the interactions between historical patterns of habitat loss and emerging threats, and the efficacy of different management options (e.g., barred owl removal, fuels reduction) to facilitate species' recovery or improve habitat. Dugger et al. (2016) presented an example of such research where they investigated the effects of climate, barred owls, and the removal of barred owls on the northern spotted owl. Other examples include simulation models evaluating tradeoffs in amount of habitat in landscapes with and without fuels treatments (Ager et al. 2007, Odion et al. 2014*a*, Tempel et al. 2015, Chiono et al. 2017).

MANAGEMENT IMPLICATIONS

The identified threats for spotted owls pose broad, long-term risks for persistence. Further, these threats vary by both environmental context and subspecies. Most existing studies on spotted owls, however, report on short-term relationships between owl subspecies and their environments, are studied at small scales, and primarily target northern spotted owls. Long-term population-level studies and multi-scale analyses across broad spatial extents are needed, especially for the Mexican spotted owl, to provide information for conservation planning (Cushman 2006). To expand the spatiotemporal scope of studies, we see an opportunity in experimental BACI studies (Popescu et al. 2012) that combine fuels reduction, forest restoration, and maintenance of spotted owl habitat. These studies would evaluate the responses of spotted owls and small-mammal populations, and should be distributed across the ranges of all 3 subspecies. Information gained from these studies would be valuable in improving spatially explicit models of tradeoffs between forest treatments, landscape-scale fire risk, and amounts of spotted owl habitat (e.g., Calkin et al. 2005, Ager et al. 2007, Odion et al. 2014*b*, Hanson and Odion 2016, Chiono et al. 2017), which in turn should lead to more efficient and effective forest management. Lastly, when planners and managers use information from a surrogate subspecies because information on the focal subspecies is lacking, they should interpret such information cautiously and acknowledge uncertainty inherent in its use.

ACKNOWLEDGMENTS

We thank S. J. Hedwall for expertise and advice. We thank the many scientists and field crews whose hard work resulted in the body of literature evaluated here, for their many contributions to conservation of the spotted owl. We also thank C. E. Aslan and P. Z. Fulé for their reviews and comments on earlier drafts of this paper. We thank P. R. Krausman, K. S. McKelvey, G. M. Jones, and an anonymous reviewer for their insightful comments that helped improve this paper. Support for this work was provided by USDA Forest Service Rocky Mountain Research Station through a cooperative agreement with Northern Arizona University, Flagstaff, Arizona, USA.

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Associate Editor: Kevin McKelvey.

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