



Qualitative synthesis of temperate bat responses to silvicultural treatments—where do we go from here?

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Most bat species depend on forests for roosting, foraging, and drinking during part or all of their life cycles. Many of the world's forests are managed using a variety of silvicultural treatments and, over the past 40 years, researchers have studied the responses of bats to these treatments. I carried out a qualitative synthesis of the literature on roosting and foraging responses of temperate insectivorous bats to silvicultural treatments at the stand level to determine what treatments may be most compatible with conservation and to guide future research. Eighty-eight studies from Canada, the United States, Europe, Australia, and New Zealand, met review criteria. Based on my results, foraging and commuting habitat use was less affected by changes in forest structure and composition than roost habitat use. Mid-rotation treatments that reduce clutter while retaining overstory structure (e.g., thinning and fire) had more neutral and positive effects than treatments that removed all or most of the overstory. Based on an examination of the methods and assumptions of the 88 studies included in this review, I conclude that future studies should: 1) strive to account for treatment effects on detection probability of bats when using acoustic detectors; 2) examine responses of bats to silvicultural treatments outside the maternity season; 3) examine demographic and physiological responses to silvicultural treatments in addition to habitat use to fully understand the effects of these treatments on bat populations; and 4) use stand-level data to model forest management effects across large landscapes and over long time periods.

Key words: clearcut, fire, foraging, forest management, harvest, insectivorous bats, roosting, silviculture, thinning

Forests cover approximately 30% of the world's land base and provide important habitat for numerous plants and animals (Food and Agriculture Organization 2018). Although not all bats depend on forests, most bats use forests to some extent for roosting, foraging, and drinking water (Law et al. 2016). Unfortunately, bat population sizes around the world are decreasing, with 21.9% of the world's bat species considered to be vulnerable (8.5%), near threatened (6.6%), endangered (4.5%), critically endangered (1.9%), or extinct (0.4%—IUCN 2018). Loss of forests through conversion to agriculture or urban development is one of the most important causes of decreases of many of these species (Voight and Kingston 2016; Frick et al. 2020). In addition to forest loss, many of the remaining forests have been altered or currently are under some type of active management. For example, only 32.2% of the forested area in the United States falls under IUCN Protected Categories 1a and 1b (managed for science or wilderness—U.S. Department of Agriculture 2012) and in Europe almost no pristine forest remains, a result of human activity over the past

4,000–5,000 years (Bengtsson et al. 2000). Because changes in the amount, structure, and composition of forests can greatly affect bat populations, understanding the effects of past and current forest management is critical for long-term conservation.

Forests are managed through a variety of silvicultural practices that allow managers to manipulate stands of trees toward a desired future condition, whether that be for maintenance of old growth forest, for restoration of particular forest communities, for pulpwood or saw wood, for wildlife habitat, or for other uses (Guldin et al. 2007). Common silvicultural treatments include harvesting (ranging from single-tree selection to clearcutting), using prescribed fire, and using herbicides. These treatments change the composition and structure of forests, causing reduction in forest clutter and structural complexity, the loss or creation of snags, loss of particular tree species, and changes in other aspects of ecosystems, such as insect abundance and community composition. Changes in the structure and composition of a forest ecosystem through silvicultural practices can have significant impacts on the bats that use

the forest. For example, home range size and colony size of New Zealand long-tailed bats (*Chalinolobus tuberculatus*) decrease after clearcutting of plantation forest in New Zealand, indicating that clearcutting has negative effects on these bats (Borkin et al. 2011). In contrast, foraging activity of bats of some species is higher in areas that have been clearcut compared to more mature stands (Krusic et al. 1996; Grindal and Brigham 1998; Ellis et al. 2002).

Variation in responses to silvicultural treatments among bats of different species is often attributed to ecomorphology (Law et al. 2016). Large bats usually have high aspect ratios (long, narrow wings), high wing loading (high body weight relative to wing area), pointed wing tips, and narrow-band, low-frequency echolocation calls that make them highly adapted for foraging in open habitats and poorly suited for foraging in closed, cluttered habitats (Aldridge and Rautenbach 1987; Fenton 1990). In contrast, small bats usually have low aspect ratios (short, broad wings), low wing loading, and broadband, high-frequency echolocation calls that allow them to forage in closed, cluttered habitats. Further, bats of many species are edge-foragers with characteristics intermediate between closed- and open-space foragers. Because large bats are clutter-intolerant, they often respond positively to treatments that open up forests, such as thinning or harvesting (Law et al. 2016). The responses of small bats, however, vary considerably, possibly due to the type of silvicultural treatment and its intensity. Responses also vary with habitat function (e.g., foraging versus roosting).

Prior to the 1980's, research on forest bats was limited and only in the late 1980's and early 1990's did researchers begin to examine the relationships between forest management and bats (Brigham and Barclay 1996). Since that time, however, researchers around the world have addressed many questions regarding the effects of forest management and silviculture on bats from the stand to landscape scales, and much of this literature has been reviewed over the past decade (Hayes and Loeb 2007; Law et al. 2016; Meyer et al. 2016). Although Meyer et al. (2016) carried out a qualitative synthesis of the effects of logging, deforestation, and habitat fragmentation, on tropical bats, and Law et al. (2016) undertook an extensive review of responses of temperate-zone insectivorous bats to silvicultural treatments, no systematic reviews or quantitative assessments of the effects of forest management or silvicultural treatments on temperate bats have been conducted to date. Syntheses and meta-analyses based on systematic reviews are crucial for informing decision-makers, who ultimately set conservation and management policy (Pullin and Stewart 2006). Such analyses also serve to highlight knowledge gaps. Thus, the objectives of this paper were to undertake a qualitative synthesis of the literature on the responses of temperate insectivorous bats to silvicultural treatments at the stand level, to outline the pitfalls and problems with previous approaches, and to propose avenues for future research. I focused on stand-level responses because most studies were conducted at this level and landscape-level responses were more difficult to categorize due to greater variation in study designs and approaches. I hypothesized that bat responses to silvicultural treatments would differ

based on treatment, foraging guild (closed-, edge-, or open-space foragers), and behavior (i.e., foraging or roosting). For foraging behavior I predicted that edge- and open-space foragers would respond positively to treatments that created more open foraging spaces such as regeneration harvests (clearcuts and shelterwood cuts), prescribed fire, and thinning, and would respond negatively to second-growth forests. I further predicted that closed-space foragers would respond negatively to regeneration harvests and would have neutral or positive responses to mid-rotation treatments such as prescribed fire and thinning. For roosting behavior I predicted that bats would respond negatively to harvesting treatments due to the loss of roost structures, and respond positively to treatments such as prescribed fire that open up intact forests and have the potential to create roost structures.

METHODS

Following the guidelines for a systematic review (Pullin and Stewart 2006), I searched the ISI Web of Science and included the Web of Science Core Collection, BIOSIS Citation Index, BIOSIS Previews, Current Contents Connect, and Zoological Record. Topic searches were ["bat OR chirop*" AND "forest" AND "management"], ["bat OR chirop*" AND "silviculture"], ["bat OR chirop*" AND "fire"], ["bat OR chirop*" AND "clearcut"], ["bat OR chirop*" AND "clearfell"], and ["bat OR chirop*" AND "harvest"] for the years 1970 through March 2019. This resulted in 1,935 hits for forest management, 483 hits for fire, 366 hits for harvest, 182 hits for silviculture, 14 hits for clearcut, and 1 hit for clearfell. I discarded references based on titles if they did not deal with temperate-zone bats, the topic was not relevant, or they were conference proceeding abstracts. I also examined the literature cited sections of selected papers and those of two review papers (Hayes and Loeb 2007; Law et al. 2016) to find relevant papers. If a paper's relevance was not clear, I reviewed the abstract and, if necessary, the entire paper. I included only studies in which silvicultural treatments were compared to an untreated control. For example, I did not include studies that compared bat responses across a treatment such as the size of gaps (e.g., Fukui et al. 2011) or studies in which specific treatments within managed forests were not sampled but inferences were made about forest management nonetheless (e.g., Murphy et al. 2012; Pereira et al. 2016). I also did not include studies if the authors combined treatments because responses could not be attributed to a particular treatment (e.g., Betts 2009) or if they reanalyzed data from a previous study and the results were similar, because this would artificially inflate the results of that particular study (e.g., Ford et al. 2016). Because I was interested in the effects of ecomorphology on bat responses to treatments, I excluded studies in which the responses of all bat species were combined (e.g., Grindal and Brigham 1998; Malison and Baxter 2010).

I examined each paper that met the above criteria and determined the treatment or treatments applied, the behavior or parameters examined (i.e., roosting, foraging, demographic, or physiological), and the response of each species or group

of species to the treatment relative to the control. Search phase calls, which are used in both commuting and foraging, are used for identifying echolocation passes to species (e.g., [Preatoni et al. 2005](#); [Britzke et al. 2011](#)). Therefore, it usually is not possible to determine whether a bat is foraging or commuting based on its echolocation calls. Thus, use of the term “foraging response” also connotes commuting behavior for acoustic studies. The seven treatments examined among the studies were clearcut or shelterwood harvest (all or most of the overstory canopy was removed during harvest), fire (primarily prescribed fire although three studies examined wildfires), gap formation (small openings or gaps in the forest ranging from approximately 0.02 to 0.50 ha), history of plantation forestry, regrowth forest (dense, regenerating young forest consisting of saplings), thinning (removal of some trees within a forest stand at an intermediate stage of growth including selective cuts), and thinning followed by prescribed fire ([Table 1](#)). Only two studies examined thinning followed by prescribed fire, so these studies were included in the fire category.

Response variables varied greatly across studies. For example, response variables for foraging studies included number of acoustic files, probability of occupancy, and selection of foraging habitat based on radiotelemetry data. Thus, I categorized responses as positive, negative, or neutral instead of attempting to estimate effect sizes ([Pullin and Stewart 2006](#)). Foraging responses were based on significant differences (positive or negative) between treated and control sites in acoustic activity or occupancy, or foraging habitat or home range selection from radiotracking studies (i.e., preference or avoidance of treated areas). Roosting responses were based on selection or avoidance of particular areas based on availability. Responses were categorized for closed-space, edge-space, and open-space foragers ([Fenton 1990](#)). Most authors defined species as closed-, edge-, or open-space foragers, but if they did not, I searched other papers for the correct categorization. In the few cases where either the author did not categorize a species or I could not find a description for the species in the literature, I assumed that because both ecomorphology and echolocation frequency are related to body size ([Aldridge and Rautenbach 1987](#)), small bats (i.e., those < 9 g) were closed-space foragers and large bats (those ≥ 9 g) were edge- or open-space foragers.

I used a chi-square test of independence to test the effects of silvicultural treatment on each guild (closed-, edge-,

or open-space forager). I conducted post hoc tests with a Bonferonni correction to determine significant differences among treatments using the `chisq.posthoc.test` package in R (R Development Core Team 2019). I combined roost responses of edge- and open-space foragers for analysis because too few roost studies of edge- and open-space foragers existed to test effects for each group, the responses to treatments by both groups were similar, and because no study included both edge- and open-space foragers (i.e., there were no conflicts in responses).

RESULTS

Eighty-eight studies met the criteria for inclusion in the synthesis ([Supplementary Data SD1](#)). Most studies were carried out in the United States ($n = 47$) or Australia ($n = 21$), with the remaining studies from Europe ($n = 10$), Canada ($n = 8$), and New Zealand ($n = 2$). Within the United States, most studies were carried out in the Southeast ($n = 27$) followed by the Midwest ($n = 9$), and within Australia, most studies were carried out in New South Wales ($n = 13$). The number of studies that examined the effects of silvicultural treatments on bats increased steadily since the mid-1980s ([Fig. 1A](#)). Most studies (90%) took place over only one season and the majority of studies were carried out solely in summer or included summer ([Fig. 1B](#)). Several studies examined more than one treatment and some used more than one method (e.g., acoustics and telemetry; [Supplementary Data SD1](#)). The majority of studies that examined foraging responses to treatments used acoustic detectors although a few used radiotelemetry; all studies that examined roosting responses used radiotelemetry ([Table 1](#)). In addition to foraging and roosting studies, one study examined physiological responses of bats to wildfire and another study examined demographic responses of bats to regrowth forest.

Among closed-space foragers, neutral or positive foraging responses were more frequent for fire and thinning while negative responses were more frequent than neutral or positive responses for clearcut and shelterwood harvests, a history of plantation forestry, and regrowth forest ([Fig. 2A](#)). Nevertheless, the responses of closed-space foragers did not differ among treatments ($\chi^2 = 13.30$, $d.f. = 10$, $P = 0.21$). In contrast, the responses of edge- and open-space foragers did vary among silvicultural treatments ($\chi^2 = 25.58$, $d.f. = 10$, $P = 0.004$ and $\chi^2 = 28.60$, $d.f. = 10$, $P = 0.001$). Responses to regrowth forest were primarily negative for both groups and differed ($P < 0.0001$) from responses to fire, gap formation, history of plantation forestry, and thinning treatments, which were primarily neutral or positive ([Figs. 2B and 2C](#)).

No studies examined the effects of gap formation on roosting behavior. Closed-space foragers exhibited more positive and neutral responses than negative responses to fire and more negative responses than positive or neutral responses to clearcut and shelterwood harvests, a history of plantation forestry, regrowth forest, and thinning ([Fig. 3A](#)). However, the responses of closed-space foragers did not differ among the five silvicultural treatments ($\chi^2 = 11.47$, $d.f. = 8$, $P = 0.18$; [Fig. 3A](#)). Roosting responses of edge- and open-space foragers did vary

Table 1.—Summary of responses examined and methods used in studies included in a qualitative synthesis of studies conducted on effects of silvicultural treatments on temperate insectivorous bats.

Treatment	Foraging studies		Roosting studies	Other
	Acoustic	Telemetry		
Clearcut or shelterwood	22	3	7	0
Fire	12	2	9	1
Gap creation	5	0	0	0
History of plantation forestry	4	1	4	0
Regrowth forest	9	0	9	1
Thin	16	2	10	0
Thin + fire	2	0	0	0

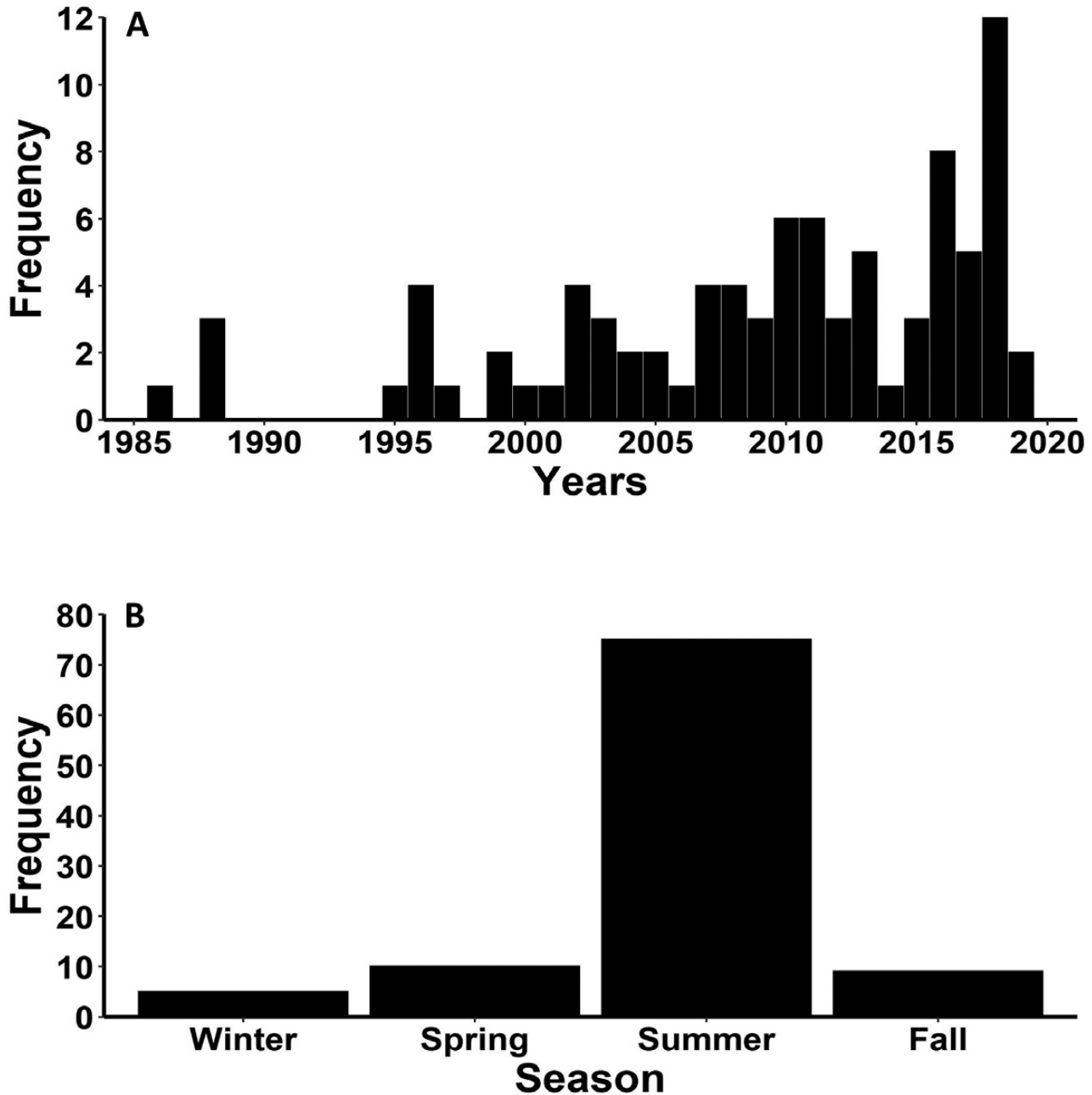


Fig. 1.—(A) Number of papers published between 1970 and March 2019 that tested the effects of silvicultural treatments on temperate insectivorous bats and met review criteria. (B) The number of reviewed studies that collected data in each season.

among silvicultural treatments ($\chi^2 = 16.01$, $df = 8$, $P = 0.05$). This group showed primarily negative responses to clearcut and shelterwood harvests, a history of plantation forestry, and re-growth forestry, primarily positive responses to fire, and primarily neutral responses to thinning (Fig. 3B) but, only responses to regrowth forest differed from other treatments ($P < 0.01$).

DISCUSSION

General responses.—My analysis of the literature included results of studies of bat responses to silvicultural treatments conducted on over 70 species across three continents. By

grouping all studies within treatments, using broad response categories (positive, negative, neutral), and grouping species into guilds, some of the subtleties of species-specific responses to variations in treatments (e.g., fire severity) and variations in study design (e.g., detector placement, time since treatment) were lost. Nonetheless, some general patterns regarding the effects of silvicultural treatments on temperate insectivorous bat foraging and roosting behavior emerged and generally were consistent with the conclusions of Hayes and Loeb (2007) and Law et al. (2016), who conducted more traditional literature reviews. Negative responses to silvicultural treatments were more common in studies examining roosting behavior than

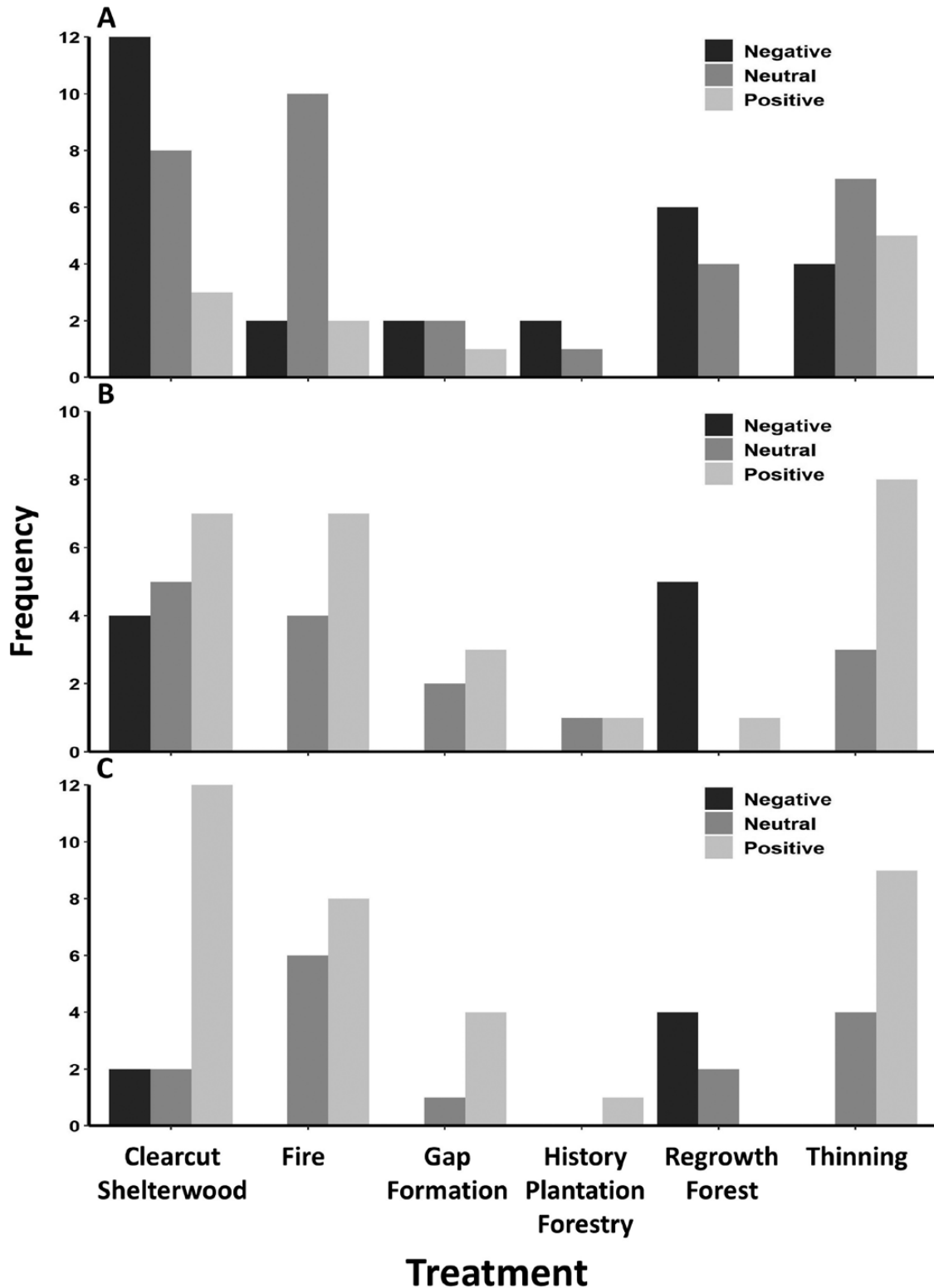


Fig. 2.—Number of studies in which the foraging responses of temperate insectivorous bats to silvicultural treatments were negative, neutral, or positive: (A) closed-space bats, (B) edge-space bats, (C) open-space bats.

foraging behavior, suggesting that bat foraging and commuting habitat use may be less affected by changes in forest structure and composition than roost habitat use (Figs. 2 and 3). In addition, among both roosting and foraging studies, bats were more likely to show positive or neutral responses to mid-rotation

treatments that reduced clutter while retaining overstory structure such as thinning and prescribed fire compared to treatments that removed all or most of the overstory.

As predicted, edge- and open-space foragers showed negative responses to regrowth forest both for foraging and roosting

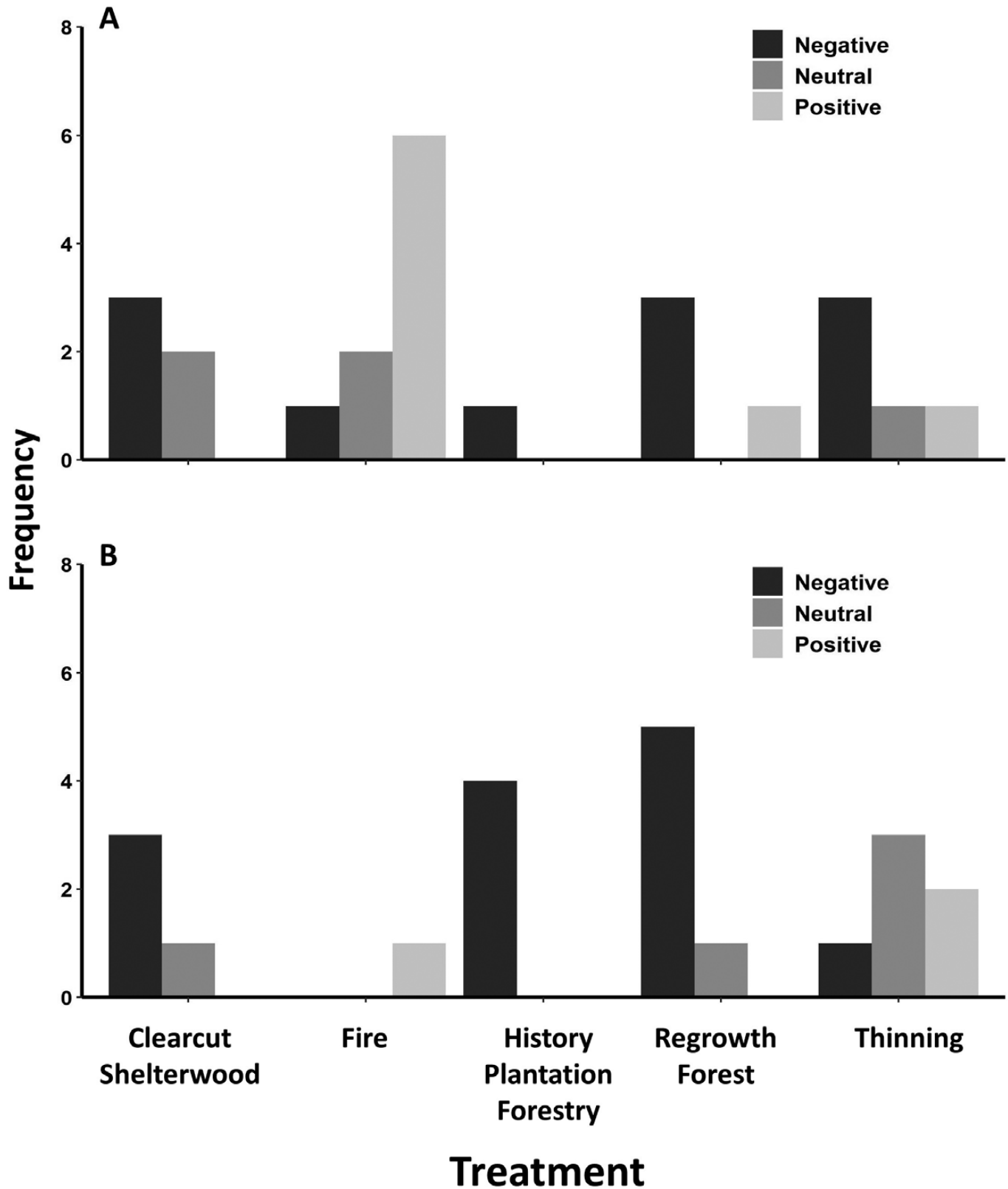


Fig. 3.—Number of studies in which the roosting responses of temperate insectivorous bats to silvicultural treatments were negative, neutral, or positive: (A) closed-space bats, (B) edge- and open-space bats.

habitat. Prior to self-thinning or mechanical thinning, regrowth forests usually have a dense canopy and subcanopy resulting in a high degree of clutter (Guldin et al. 2007). Most studies that

documented negative responses to regrowth forests attributed low activity or use to the dense vegetation found in these forests (Erickson and West 1996; Parker et al. 1996; Humes et al. 1999;

Law and Chidel 2001, 2002; Adams et al. 2009; Law et al. 2019). Thinning regrowth stands often increases foraging activity (Humes et al. 1999; Blakey et al. 2016; Gonsalves et al. 2018a, 2018b) leading to the hypothesis that regrowth forests are avoided because of dense clutter. A further hypothesis is that regrowth forests provide poor roosting habitat because of the scarcity of large snags for roosting (Erickson and West 1996; Parker et al. 1996; Humes et al. 1999), and dense vegetation that reduces solar radiation necessary for passive rewarming and prevents easy access to and egress from roosts (Kunz and Lumsden 2003; Barclay and Kurta 2007).

Although not statistically significant, foraging activity of closed-space foragers tended to decrease in response to clearcut and shelterwood harvests in most studies and did not recover in young regrowth forests, although neutral responses were observed in some studies. In contrast, open-space foragers showed a strong positive foraging response to clearcut or shelterwood harvest treatments and edge-space foragers also tended to respond in a positive or neutral fashion to harvesting. Because many species, particularly edge-space foragers, are more likely to forage near edges of cuts than in the center, some of the variation in responses by closed- and edge-space foragers to clearcut and shelterwood harvests may have been due to detector placement in acoustic studies (Grindal and Brigham 1999; Hogberg et al. 2002; Law and Law 2011; Webala et al. 2011); harvest tract size also may have been a factor (Grindal and Brigham 1998). Open-space foragers avoid highly cluttered habitats (Aldridge and Rautenbach 1987; Fenton 1990); therefore, it is not surprising that many studies documented increases in foraging and commuting activity or occupancy in response to the creation of open areas through harvesting for this group. In addition to creating open habitats with reduced clutter, harvesting results in hard edges between forest and open areas, thus generating habitat for both edge- and open-space foragers. Edges between forest and open areas provide important foraging and commuting areas for many species of bats because they aid in navigation, provide protection from predators, and have greater amounts of insect prey (Verboom et al. 1999; Law and Law 2011; Kalcounis-Rueppell et al. 2013).

Due to minimal tree overstory in areas that have undergone clearcut or shelterwood harvests, it is not surprising that both closed-space and edge- and open-space foragers showed predominantly negative roosting responses to these harvesting treatments. Nevertheless, western long-eared bats (*Myotis evotis*) in British Columbia sometimes use remnant stumps after clearcutting, possibly because of the thermal advantages associated with full solar exposure in an open habitat (Vonhof and Barclay 1997). Thus, even though regeneration harvests such as clearcutting and shelterwood harvests result in the loss of roosting habitat for bats of most species, a few bats are able to take advantage of the remaining structures.

Plantation forests often lack structures commonly used by forest bats for roosting, such as snags, hollow trees, and hardwood trees with large canopies (Ruczyński et al. 2010; Burgar et al. 2015). While bats use these forests for foraging, particularly edge- and open-space foragers (Fig. 2), studies to date

indicate that they avoid roosting in these forests (Fig. 3). Nonetheless, these forests represent important habitat for some species such as the endangered New Zealand long-tailed bat and lesser short-tailed bat (*Mystacina tuberculata rhyacobia*). Both species were assumed to rely on native forest but have since been recorded roosting and foraging in plantation forests (Borkin and Parsons 2010a, 2010b). Thus, highly managed forests such as plantations should not be dismissed as bat habitat (Russo et al. 2010).

The creation of gaps within intact forests often resulted in positive foraging responses by edge- and open-space foragers. Similar to clearcuts, gaps provide uncluttered foraging space as well as a hard edge (Crome and Richards 1988; Menzel et al. 2002; Loeb and O'Keefe 2011; Ketzler et al. 2018). It also has been hypothesized that higher insect abundance in gaps compared to closed-canopy forests contributes to greater use by foraging bats (Tibbels and Kurta 2003). Although I found no studies that explicitly tested the effects of forest gaps on roost use or selection, many studies have found that bats of some species commonly select roosts on the edges of, or near, gaps (Campbell et al. 1996; Callahan et al. 1997; Carter and Feldhamer 2005; Fabianek et al. 2015). Many studies have hypothesized that roosting on the edge of canopy gaps may allow bats to decrease energetic costs because of high solar radiation in these sites as well as close access to foraging sites (Loeb and O'Keefe 2011).

Responses of foraging bats to thinning and fire were similar (Fig. 2). In general, the response to thinning and fire by foraging bats was neutral or positive, especially for edge- and open-space foragers. Positive responses may be due to changes in forest structure, insect prey availability, or a combination of the two. Both thinning and fire reduce clutter (Peterson and Reich 2001; Fulé et al. 2004; Phillips et al. 2004), and observed positive foraging responses have often been attributed to a reduction of clutter (Smith and Gehrt 2010; Armitage and Ober 2012; Inkster-Draper et al. 2013; Gonsalves et al. 2018a). Studies that simultaneously examined insect availability and bat activity in relation to thinning found no significant effects of thinning on insect biomass, community composition, or abundance leading to the conclusion that changes in bat activity post-thinning were in response to structural changes in the habitat (Tibbels and Kurta 2003; Morris et al. 2010; Blakey et al. 2016; Gonsalves et al. 2018a, 2018b).

Although bats' responses to thinning appear to be due to structural changes, whether bats respond to changes in forest structure or insect abundance postfire is not clear. For example, Armitage and Ober (2012) and Cox et al. (2016) reported no increase in insect abundance in burned stands compared to unburned stands even though they found an increase in bat use of burned stands. In contrast, Lacki et al. (2009) and Malison and Baxter (2010) reported that use of foraging areas or bat activity was related to increases in insect abundance after prescribed or wildland fire and *Nyctophilus geoffroyi* in Australia were 1.1 g heavier and had shorter torpor bouts and longer normothermic bouts immediately following a wildfire compared to 2 years postfire (Doty et al. 2016). Doty et al. (2016) hypothesized that

the physiological responses of *N. geoffroyi* were due to greater prey abundance immediately after the fire as well as easier detection of prey due to reduced ground cover. Understanding responses of insect communities to fire and subsequent responses of bat communities may be confounded by differences among studies in burn severity (Malison and Baxter 2010; Burns et al. 2019), fire extent (Law et al. 2018b), time since last burn (Doty et al. 2016), fire frequency (Law et al. 2019), and the insect communities (Perry 2012). Thus, it is not possible at present to isolate which factor or factors bats are responding to postfire.

The number of studies examining the effects of thinning and fire on roost habitat use ($n = 19$) was far lower than the number of studies examining these treatments on foraging habitat use ($n = 34$), most likely leading to the nonsignificant results for close-space foragers. Nonetheless, some patterns still were evident. As predicted, closed-space foragers in several studies increased their use of, or selected, burned areas for roosting, but they tended to avoid thinned areas for roosting (Fig. 3). Thinning may provide some of the structural characteristics of good roost habitat (e.g., reduced clutter resulting in increased solar radiation and easier access and egress to roosts) but thinned stands may be too young in some cases to contain appropriate roost structures such as large snags, large trees with cracks and crevices, or large-canopy hardwoods or conifers for foliage roosters (Kalcounis-Rueppell et al. 2005; Barclay and Kurta 2007; Carter and Menzel 2007). Thinning also may reduce the number of snags in the stand (Law et al. 2016, 2018c). In contrast, prescribed fires as well as wildfires often occur in mature or old-age stands which contain larger roost structures than younger stands. Fire also may create suitable roost structures such as snags and cracks and crevices in live trees (Burns 1955; Paulsell 1957; Boyles and Aubrey 2006) although the net gain of snags is primarily in the small-size classes (Horton and Mannan 1988). However, in some cases, fires destroy snags or hollow-bearing trees (Parnaby et al. 2010; Lindenmayer et al. 2012). Thus, while mechanical thinning likely will increase foraging habitat for some bat species, fire appears to be more effective at creating both roosting and foraging habitat.

Caveats.—Several caveats regarding the studies included in this review should be considered when evaluating the preceding results and when designing studies in the future. These include: 1) the categorization of bats into foraging guilds; 2) reliance on acoustic detectors to study treatment effects on foraging habitat use and the assumptions inherent in these types of studies; 3) the strong bias toward conducting studies primarily during summer; and 4) the assumption that greater use of a particular treatment results in higher population levels or viability.

Many ways exist to categorize bats into foraging guilds based on wing morphology, body size, and echolocation call structures (e.g., Aldridge and Rautenbach 1987; Fenton 1990; Schnitzler and Kalko 2001) and these categories vary based on particular bat communities and on the researchers who define them. For example, some studies included in this review categorized species both by morphology and echolocation call structure (e.g., Adams et al. 2009), requiring me to combine categories used in their studies. The same species also may

be placed in different guilds by different researchers. Menzel et al. (2005), for instance, classified big brown bats (*Eptesicus fuscus*) as open-space foragers, whereas Jantzen and Fenton (2013) categorized them as edge-space foragers. While I was consistent in classifying species across studies based on the majority of authors' categorizations when data were presented for individual species, this was not always possible when data were grouped into guilds. Thus, some species may have been included in more than one foraging guild in some analyses in this review. As with any categorization of biological entities, it is likely that many species lie somewhere on a continuum among categories and thus, use of different categories or characterizations of species than those used here may result in slightly different conclusions.

While use of acoustic detectors has greatly increased researchers' abilities to study bat habitat use and bat responses to silvicultural treatments and other natural and anthropogenic disturbances, several things must be considered when designing acoustic studies and interpreting data (Britzke et al. 2013). In addition to issues related to species identification (e.g., Broders et al. 2004; Lemen et al. 2015; Russo and Voight 2016), using acoustic detectors to understand habitat use has many assumptions (Gannon et al. 2003). Hayes (2000) outlined practical solutions for dealing with some of these assumptions such as calibrating detectors to correct for variation among detectors and appropriate study designs to deal with temporal variation. These solutions eliminate or decrease differences in detectability across time and among similar habitats but, they ignore differences in detectability related to treatment effects, particularly if those treatments result in variation in clutter (Patriquin et al. 2003). For example, Burns et al. (2019) found that detection probabilities of *Eptesicus fuscus*–*Lasionycteris noctivagans* and *Lasiurus borealis*–*Nycticeius humeralis* were significantly higher in areas that had been burned compared to unburned sites. If treatment effects on detection probability are not included in the analyses of use or activity, then conclusions about the effects of silvicultural treatments on bat activity or occupancy may be biased (MacKenzie 2005). Of the 55 studies that used acoustic detectors to examine treatment effects on bat activity or occupancy, only Burns et al. (2019) and Starbuck et al. (2015) accounted for detection probability in their analyses of treatment effects. Thus, results of studies that use acoustic detectors and do not consider treatment effects on detection probability in their analyses may be biased. Inclusion of detection probabilities in future studies will result in more robust results.

Only 19 of the 88 studies (22%) considered in this review included data from outside the summer maternity season. While understanding how silvicultural treatments affect bats during the maternity season is very important, many critical life history stages occur during other seasons, including breeding, migration, preparation for hibernation, and hibernation itself (Weller et al. 2009). Migration is energetically expensive and although long-distance migrants such as *L. noctivagans* use heterothermy to reduce the need to stop and feed along the migratory route (McGuire et al.

2014), they require appropriate roost structures for use of torpor during the day. In addition, bats that enter hibernation with greater fat stores are more likely to survive white-nose syndrome (Cheng et al. 2019) suggesting that providing high-quality foraging habitat during fall is critical for species affected by this disease. Treatments such as prescribed fire often occur during fall, winter, and early spring and if studies are restricted to summer only, the direct or immediate effects of these treatments on bats are ignored (Braun de Torrez et al. 2018). In addition, clutter may be considerably reduced in deciduous forests during fall, winter, and early spring after leaf fall which may result in different patterns of use among silviculturally treated and untreated sites compared to summer. Other factors such as roost microclimates and insect abundances also differ among seasons (Kerth et al. 2001; Leksono et al. 2005; Ruegger 2019), which may affect relative use in treated and untreated sites.

Another assumption of most studies included in this review is that high activity levels or selection of a habitat for foraging or roosting equates to good habitat that ultimately will result in high abundance or viable populations (Barclay and Kurta 2007). High population density may not indicate better quality habitat but instead represent a habitat sink (Van Horne 1983; Pulliam 1988). Because bats have high mobility, changes in relative habitat use simply may reflect a shift in use from one treatment type to another but not reflect changes in populations. In addition, high prey abundance may mean that bats need less time to obtain required resources, resulting in lower activity levels. I only was able to find one study that examined demographic responses of temperate-zone bats to forest management (Law et al. 2018a). In contrast to most studies, which found negative effects of regrowth forest on bat foraging and roosting habitat use, Law et al. (2018a) found minimal effects of regrowth forest on abundance and survival of four species of bats over a 14-year period. As suggested by Law et al. (2016), long-term population studies are required to understand the full impact of silvicultural treatments on bats.

Examining physiological responses of bats to disturbance caused by silvicultural treatments is another way to determine their effects on bat demographics and viability (Geiser et al. 2018; Stawski and Doty 2019). The study by Doty et al. (2016), however, was the only study in this review to examine the physiological consequences of bats to any treatment. Physiological responses of *N. geoffroyi* (greater body mass, shorter torpor durations, and longer normothermic bout durations) immediately after a wildfire compared to 2 years postfire generally support studies based on foraging responses and suggest that bats tend to respond positively to fire. In contrast, in a tropical forest subject to logging, body weight and leukocyte numbers of some bat species were lower in areas recently disturbed by logging compared to unlogged areas (Selmann et al. 2017). Results of these few studies suggest that to understand fully the effects of silvicultural treatments on bat populations and fitness, researchers need to measure parameters such as survival, reproductive success, or the physiological consequences of using one treated area versus another, as well as relative use and selection.

Future research needs and directions.—Researchers have made considerable advances in understanding the effects of forest practices on bats over the past 40 years, but a great deal still needs to be learned. Several hypotheses need to be tested regarding forest management effects on bats at the population and landscape levels to allow managers to implement management strategies that provide healthy forests, needed goods and services, and roosting and foraging habitat for bats. For example, testing the hypothesis that the potential creation of roosts and decrease in clutter resulting from prescribed fire is a more favorable treatment for bats than thinning will help inform decisions regarding the best fuel reduction methods (e.g., Waldrop et al. 2016). Similarly, the hypothesis that plantation forests are avoided because they lack suitable roosts is important for industrial foresters and could be tested experimentally by providing artificial roosts. Several hypotheses that examine the effects of fire parameters on bats and their insect prey also need to be tested, including the hypothesis that bats respond differently to fires of different severities, time since last burn, frequencies, season, and extent. Testing the hypothesis that bats respond differently to prescribed fires and wildfires is important to understanding the importance of the use of prescribed fire as a tool for preventing destructive wildfires (Fernandes and Botelho 2003).

Hypotheses regarding study designs and their effects on the results of forest management research studies also need to be tested. For instance, researchers need to test the hypothesis that results gained from acoustic studies are similar to those gained from tracking studies when testing foraging responses to silvicultural treatments. Further, the lack of research on silvicultural treatments outside the reproductive period highlights the need to test the hypothesis that treatment effects will vary across seasons and species or guilds. Finally, studies are needed to test the hypothesis that bats will respond to silvicultural treatments at the population level (i.e., with increases or decreases in demographic parameters such as survival and reproductive success).

This review focused on studies undertaken at the stand scale and most studies were carried out over short time periods. But forest management occurs at the landscape scale (Guldin et al. 2007) and considering how treatments affect bat communities across large landscapes and over long time periods is important. For example, although edge- and open-space foraging bats often responded positively to clearcutting and shelterwood harvests, these areas eventually become regrowth forest, to which bats generally showed negative responses. Thus, many studies call for a mix of silvicultural treatments and forest age and composition classes across the forest (see Law et al. 2016). Effective forest management that aims to conserve or to recover bat populations will need to determine the level and timing of harvesting necessary to provide sufficient early, mid-, and late rotation forests to satisfy the roosting and foraging needs of all bats in the community over time. Spatially explicit landscape models such as LANDIS and LANDIS II, which simulate future forest conditions across a large landscape based on various forest management scenarios (e.g., amount, timing, and spatial distribution of harvests and other forest management practices),

have been used to simulate availability of habitat over time for wildlife, including bats (Shifley et al. 2006; Pauli et al. 2015). Spatial distribution models coupled with outputs of forest management or disturbance scenarios may also produce fruitful insights (e.g., Bosso et al. 2018). Factors such as connectivity among suitable habitats also need to be considered (Henderson and Broders 2008; Farrow and Broders 2011; Frey-Ehrenbold et al. 2013). Results of the studies reviewed here and of future studies can be used to develop long-term landscape models that can be used for effective bat conservation across large landscapes and long time scales.

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SUPPLEMENTARY DATA

Supplementary data are available at *Journal of Mammalogy* online.

Supplementary Data SD1.—Authors and years of publication of papers used in the qualitative synthesis of studies on responses of temperate-zone insectivorous bats to silvicultural treatments, reference number which corresponds to the full citation on the second worksheet, the general location of the study, the behavior or characteristic examined (roosting, foraging, demographic, or physiology), the method used to study the particular behavior and treatment, the season(s) in which the study was undertaken, the treatment number examined for studies where more than one treatment was examined, the method number for studies which used more than one method, the treatments examined for each method, and the responses of closed-space, edge-space, and open-space bats to each treatment. NA indicates no data were presented for a particular guild.

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