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Singing silver-haired bats (*Lasionycteris noctivagans*)

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Abstract

Characterizing sounds produced by animals can lead to better understanding of their behavioral ecology and conservation. While considerable focus has been on signals used by bats for echolocation, there has been less emphasis on nonecholocation sounds. We describe songs (i.e., acoustic vocalizations with distinctive syllable types in series or in complex motifs) produced by silver-haired bat (*Lasionycteris noctivagans*). Songs, characterized by a sequence (song phrase) of 3 distinct vocalization types, were confirmed by observing free-flying, silver-haired bats at mine hibernacula in British Columbia, Canada. The song patterns were relatively consistent with each song phrase consisting of a lead call, followed by a droplet call, and finishing with a series of multiple chirp calls. The function of the songs is unknown, however, as other bat species produce songs for mating, we propose silver-haired bat songs may similarly be associated with courtship or mating. Alternative functions cannot be ruled out, particularly because we recorded some songs outside of the accepted mating period. Other research has determined peak mating of silver-haired bats occurs in fall, and spring mating has been documented. Here we additionally provide evidence of winter mating in British Columbia. The proportion of silver-haired bat songs recorded relative to echolocation recordings varied across locations and seasons. While we recorded songs in

all months of the year, more than half of the songs were produced during winter, and 93.4% (of 1,857) were produced outside of summer months. Song production in summer could be associated with other behaviors such as learning or practice, establishing or maintaining social bonds, or male-male competition. To provide landscape and temporal context, we summarize acoustic datasets from numerous locations in western North America where recordings were made between 2005 and 2022.

Animal sounds are typically used for the purpose of communication. Discrete, often complex patterned vocalizations associated seasonally with courtship or territorial behaviors are typically referred to as songs (Catchpole and Slater 2008). Bats are well known for production of sound, though far more is known about the sounds they use for echolocation than for social communication. Research is increasingly identifying more about bat social communication, and in particular songs (Middleton et al. 2016, Smotherman et al. 2016, Bohn and Gillam 2018, Springall et al. 2019). Identifying and understanding bat sounds can be complicated by the fact that it is not always clear whether sounds are for echolocation, communication, or both. Social information may be encoded within echolocation calls (Jones and Siemers 2011), although many bat species produce sounds that are distinct from echolocation and produced exclusively for communication (Chaverri et al. 2018). Few species of bats have been reported to produce social calls with repetitive patterns, referred to as songs, but Smotherman et al. (2016) hypothesizes that singing-like behaviors are likely to be more widespread among bat species than currently documented.

Currently, only one species of bat in North America is known to produce songs (Brazilian free-tailed bat [*Tadarida brasiliensis*]; Bohn et al. 2008, 2009). Many species of North American bats, however, have been documented to produce social calls. In echolocating bats, nonecholocation sounds are typically referred to as social calls, deducing that sounds not used for echolocation must be used for some form of communication, such as conveying information about sex, social status, or territoriality (Chaverri et al. 2018). Differentiating songs from other forms of social communication for mammals depends on the repetitive and patterned nature of the sound. For example, echolocating toothed whales (Thomas et al. 2004) have been shown to communicate using simple whistle calls, not elaborate stereotyped patterns of sounds, and thus are classified as nonsinging mammals (Smotherman et al. 2016). However, humpback whales sing, producing elaborate vocalizations for courtship (Payne and McVay 1971). But complex repeatable patterns of sounds may not be enough to refer to a social call as a song; for example, some primates use complex combinations of repeated sounds to communicate to others about their environment, and because these are not associated with mating, have not been dubbed songs (Ouattara et al. 2009). Songs are typically produced in the context of courtship or mating (Smotherman et al. 2016), and thus to label a complex repeated sound pattern as a song also requires knowledge of context. For example, consideration of sounds produced in the presence of conspecifics or when the animal is alone may provide clues of song function.

It has been hypothesized that songs are associated with mating behavior (Behr and von Helversen 2004), although evidence has been slow to accumulate (Barlow and Jones 1997, Smotherman et al. 2016). Furthermore, some researchers have determined that in species that produce songs, mating is always associated with these signals (M. Knörnschild, Behavioral Ecology and Bioacoustics Lab, Museum of Natural History, Germany, personal communication). Songs may be produced outside of typical mating periods (Bohn and Gillam

2018, Runkel et al. 2021), and this may be associated with practice or learning of songs (Smotherman et al. 2016).

Here we describe a song pattern produced by a second species of North American bat—the silver-haired bat (*Lasionycteris noctivagans*). We based our findings on 2 categories of data: 1) source datasets comprised of both acoustic and capture data from sites where silver-haired bats could be identified as having produced the songs we describe here, and 2) non-source datasets comprised of other acoustic data that illustrate the geographic and temporal components of song production. Our source datasets consist of stationary bat detector recordings and bat captures from 2 known silver-haired bat hibernacula in British Columbia, and active acoustic monitoring in northwest Washington state. Non-source datasets are from stationary acoustic datasets from a variety of western North America locations over different time scales. Additionally, because automated classification of acoustic bat recordings is gaining in popularity, we summarize how popular software identifies recordings that contain silver-haired bat songs.

METHODS

Study species

In Canada, silver-haired bats are considered migratory, moving south for winter months (Naughton 2012) however, in British Columbia (BC) and parts of the northwestern U.S. (including Washington, Idaho and Montana), silver-haired bats are recorded year-round, flying in winter during hibernal arousals (Schowalter et al. 1978, Falxa 2007, Lausen et al. 2022). Banding records provide evidence that at least some silver-haired bats reside year-round at some mines in British Columbia (Lausen et al. 2022).

Study areas

Our recordings spanned several U.S. states and areas of BC. We recorded bats at 23 acoustic detector sites across western U.S. and Canada, each with varying degrees of forested/rocky terrain (Table S1, available in Supporting Information; Figure 1): California (4), Colorado (1), Idaho (3), Utah (2), Montana (2), Washington (one main active monitoring area), and British Columbia (BC; 10). At the Washington site, overwintering roosts of silver-haired bats were observed in bat boxes, under Douglas-fir and Western red cedar tree bark, and in small crevices on building exteriors. At 20 of the stationary recording sites, we had no knowledge of whether the sites were used by silver-haired bats for roosting. Two of the 10 monitored sites in BC were mine sites in forested areas where silver-haired bats hibernate and have been documented year-round (CA-9, CA-10; Figure 1, Table 1, S1). The CA-10 mine is an inaccessible and deep abandoned mine complex with many large (>16 m^2) openings and a central pit roughly 100 m in diameter. The CA-9 mine is an accessible (but gated) shallow (~50 m) mine with 2 large (>20 m^2) openings immediately adjacent to each other. Silver-haired bats use the CA-9 mine in both summer and winter and have been radiotracked to day roosts (summer and winter) in trees surrounding the mine (Lausen et al. 2022). Mist-net capture in winter of silver-haired bats flying in or out of each mine also facilitated examination of bats to determine sex, signs of breeding, etc. (Lausen et al. 2022).

Capture

Upon first recording these songs during the 2011 winter season, we were uncertain whether they were produced by big brown or silver-haired bats, because the echolocation calls that preceded or followed song phrases were ambiguous and could be attributed to either species (Betts 1998). We therefore conducted capture inventories at both mines, mist-netting and harp-trapping bats flying in and out of the entrances to identify species.
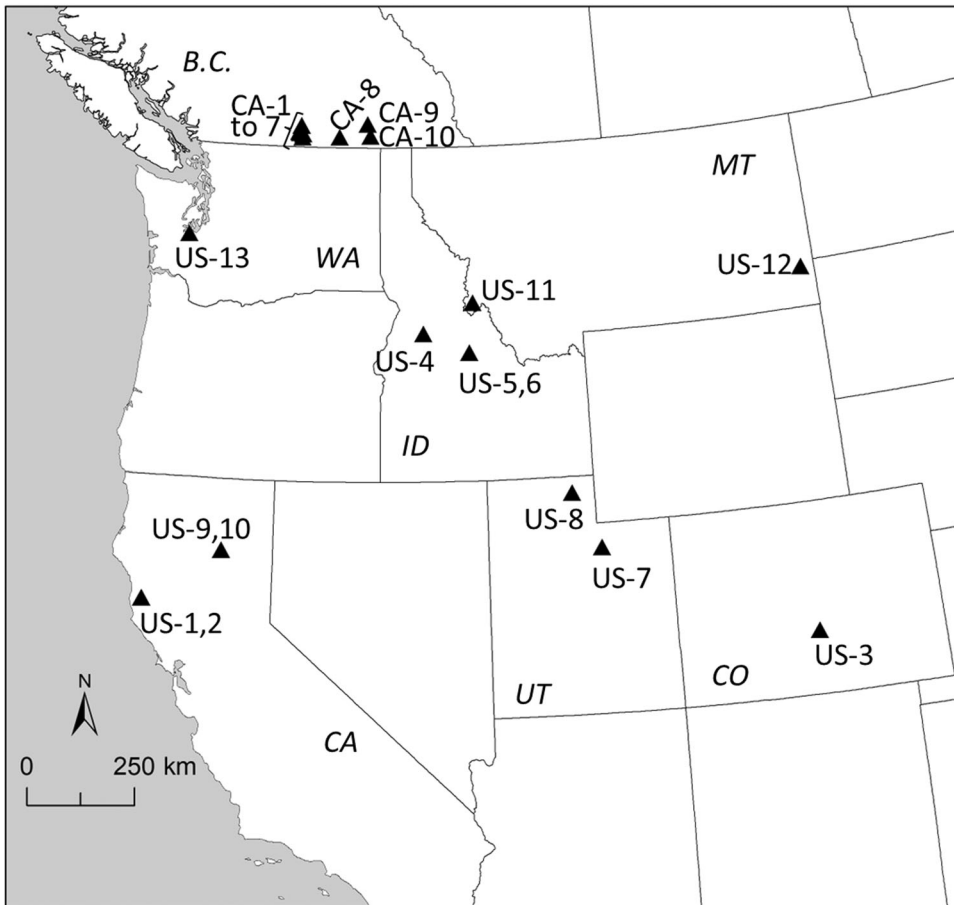
FIGURE 1 Map of all recording locations (Commission for Environmental Cooperation 2010): US-1 Jackson Demonstration State Forest (MT1); US-2 Jackson Demonstration State Forest (OT1); US-3 Royal Gorge BLM District, Fremont County; US-4 Payette National Forest Area 1; US-5 Payette National Forest Area 2; US-6 Payette National Forest Area 3; US-7 Uinta-Wasach-Cache National Forest Area 1; US-8 Uinta-Wasach-Cache National Forest Area 2; US-9 Lassen Volcanic National Park Area 1; US-10 Lassen Volcanic National Park Area 2; US-11 Painted Rocks Dam (Northern Rocky Mountains); US-12 Ekalaka Hills (Custer Gallatin Forest) Area 1; CA-1 Boar Skaha (Okanagan); CA-2 Darcus Vaseux Lake (Okanagan); CA-3 Skaha Cave Hill (Okanagan); CA-4 Skaha Fortress Bluffs (Okanagan); CA-5 Vaseux Lake Eagle Bluff (Okanagan); CA-6 Haynes Lease Ecological Reserve (Okanagan); CA-7 White Lake (Okanagan); CA-8 Gilpin Provincial Park; CA-9 Smallwood, Beasley; CA-10 REMAC Mine, Nelway.

To understand potential reasons for winter flight and song production, we also examined genitalia to assess any signs of mating activities.

Acoustic recording

We recorded bats passively using Anabat (models SD1 and SD2, Titley Scientific, Brendale, QLD, Australia), SM2Bat (model Plus, Wildlife Acoustics, Maynard, MA, USA), Anabat Swift (Titley Scientific, Brendale, QLD, Australia), SM4Bat (Wildlife Acoustics, Maynard, MA, USA), or D500X (Pettersson Elektronik, Uppsala, Sweden) bat detectors.

TABLE 1 Stationary bat detector locations and deployment effort summarizing: Locations of sites (map code; Figure 1), number of detectors (No. Dets), total number of monitored nights summed across all bat detectors (Nights), percentage of nights when there was bat activity when songs were recorded (Bat-Nights), and the percentage of low-frequency ($F_{minimum}$ <30 kHz) bat passes (LowF Passes) that contained songs produced by silver-haired bat (*Lasionycteris noctivagans*). Washington active monitoring site (US-13) not included in this table. Note high relative song production at US-2, CA-5, CA-9, CA-10 (the 3 Canadian sites are known bat hibernation areas).

Sites	Map Code	State/Prov	No. Dets	Start
Jackson Demonstration State Forest (MT1)[a]	US-1	California	1	23 May 2019
Jackson Demonstration State Forest (OT1)[a]	US-2	California	1	23 May 2019
Royal Gorge BLM District, Fremont County	US-3	Colorado	42	13 May 2021
Payette National Forest	US-4	Idaho	20	31 May 2019
Frank Church Wilderness (Stibnite #1)	US-5	Idaho	9	02 June 2020
Frank Church Wilderness (Stibnite #2)	US-6	Idaho	4	03 Aug 2020
Uinta-Wasach-Cache National Forest Area 1	US-7	Utah	8	13 Jul 2020
Uinta-Wasach-Cache National Forest Area 2	US-8	Utah	4	10 Aug 2020
Lassen Volcanic National Park Area 1	US-9	California	30	12 Aug 2019
Lassen Volcanic National Park Area 2	US-10	California	23	10 Aug 2020
Painted Rocks Dam (Northern Rocky Mountains)	US-11	Montana	1	19 Dec 2012
Ekalaka Hills (Custer Gallatin Forest)	US-12	Montana	1	Yr1: 25 Jun 2012, Yr2: 16 Apr 2013
Boar Skaha (Okanagan)	CA-1	British Columbia	1	05 Dec 2011
Darcus Vaseux Lake (Okanagan)	CA-2	British Columbia	1	04 Oct 2013
Skaha Cave Hill (Okanagan)	CA-3	British Columbia	1	19 Sept 2012
Skaha Fortress Bluffs (Okanagan)	CA-4	British Columbia	1	23 Mar 2013
Vaseux Lake Eagle Bluff (Okanagan)	CA-5	British Columbia	1	14 Oct 2014
Haynes Lease Reserve (Okanagan)	CA-6	British Columbia	1	05 Dec 2011, 05 Oct 2013
White Lake (Okanagan)	CA-7	British Columbia	1	07 Dec 2011
Gilpin Provincial Park	CA-8	British Columbia	1	27 Jun 2010, 20 Nov 2010
Smallwood, Beasley[b]	CA-9	British Columbia	6	05 Feb 2021
REMAC Mine, Nelway[c]	CA-10	British Columbia	1	16 Sep[c]

Sites	End	Nights	Bat-Nights (% w songs)	LowF Passes[d]
Jackson Demonstration State Forest (MT1)[a]	04 Nov 2019	165	148 (0.68%)	587 (0.17%)
Jackson Demonstration State Forest (OT1)[a]	12 Dec 2019	203	189 (25%)	1700 (13.4%)
Royal Gorge BLM District, Fremont County	06 Aug 2021	185	185 (4.3%)	9528 (0.29%)

(Continues)

TABLE 1 (Continued)

Sites	End	Nights	Bat-Nights (% w songs)	LowF Passes[d]
Payette National Forest	22 Jul 2019	92	92 (3.3%)	2282 (0.18%)
Frank Church Wilderness (Stibnite #1)	06 Jul 2020	122	122 (2.5%)	3249 (0.15%)
Frank Church Wilderness (Stibnite #2)	16 Aug 2020	52	52 (3.9%)	3173 (0.16%)
Uinta-Wasach-Cache National Forest Area 1	31 Jul 2020	36	36 (11%)	5280 (0.095%)
Uinta-Wasach-Cache National Forest Area 2	14 Aug 2020	16	16 (19%)	2,213 (0.32%)
Lassen Volcanic National Park Area 1	17 Aug 2019	81	81 (3.7%)	1,554 (0.26%)
Lassen Volcanic National Park Area 2	18 Aug 2020	65	65 (6.2%)	3,965 (0.13%)
Painted Rocks Dam (Northern Rocky Mountains)	15 Jan 2014	393	317 (21%)	5,474 (2.0%)
Ekalaka Hills (Custer Gallatin Forest)	Yr1: 18 Feb 2013 Yr2: 25 Jun 2013	243	203 (20%)	25,113 (0.16%)
Boar Skaha (Okanagan)	14 Apr 2012	131	46 (13%)	442 (1.6%)
Darcus Vaseux Lake (Okanagan)	15 Apr 2014	193	106 (19%)	1,279 (3.0%)
Skaha Cave Hill (Okanagan)	27 Apr 2013	206	77 (5.2%)	1,129 (0.53%)
Skaha Fortress Bluffs (Okanagan)	29 Apr 2013	37	29 (14%)	520 (0.77%)
Vaseux Lake Eagle Bluff (Okanagan)	16 Dec 2014	63	46 (15%)	190 (11.1%)
Haynes Lease Reserve (Okanagan)	19 May 2012, 28 Oct 2013	186	123 (9.7%)	1,513 (1.6%)
White Lake (Okanagan)	30 Apr 2012	145	54 (7.4%)	617 (1.3%)
Gilpin Provincial Park	15 Jul 2010, 14 Mar 2011	133	39 (7.7%)	1,225 (0.24%)
Smallwood, Beasley[b]	29 Apr 2021	498	160 (27%)	1,316 (14.1%)
REMAC Mine, Nelway[c]	28 Apr[c]	1146	887 (21%)	9,800 (11.1%)

[a]Six additional passive detectors recorded in this James Creek study area but did not record songs and were thus not included in our dataset.

[b]Known silver-haired bat hibernation site (trees, rock crevices, mine).

[c]Known silver-haired bat hibernaculum (mine) monitored for 9 winters (2011–2020), date range of monitoring varied yearly.

[d]Total includes passes identified as silver-haired bat (*Lasionycteris noctivagans*), big brown bat (*Eptesicus fuscus*), Brazilian free-tailed bat (*Tadarida brasiliensis*), and hoary bat (*Lasiurus cinereus*), through manual vetting for all Canadian sites and auto-identification for all US sites.

Data collected at the 2 mine hibernacula sites (CA-9 and CA-10) formed our source dataset as we could verify species and assess behaviors attributable to these recordings.

Our source dataset was supplemented with active recording data, whereby handheld full-spectrum bat detectors—either Petterson D240x (Pettersson Elektronik AB, Uppsala, Sweden) or EchoMeter Touch-Pro (Wildlife Acoustics Inc., Maynard, MA, USA)—were used to collect bat calls opportunistically. Silver-haired bat songs in Washington state were recorded by one of us (G. Falxa) opportunistically from November 2005 to October 2022, primarily in a lowland mixed-conifer wooded park (Squaxin Park) in Olympia, WA (Figure 1). Bats were recorded

primarily near forest edge adjacent to water features, roads, or other open nonforested landscapes in all seasons, and in particular active recordings were typically in November, when silver-haired bats were the only non-Myotis bats recorded (Falxa 2007). These active recordings were associated with silver-haired bats by observing a bat's flight pattern and foraging behaviors; during these recordings, bats producing low frequencies (low-frequency bats) were observed flying in slow, straight lines over open areas and along canopy edges while echolocation calls and songs of silver-haired bat were recorded. Some song-containing files were recorded in close proximity (1–50 m) to known silver-haired bat roosts.

All passive bat detectors were programmed to trigger on bat ultrasound and record up to a maximum duration of 15 s before beginning a new sound file. Adhering to standardized acoustic terminology (Loeb et al. 2015), we refer to single file (recording) as a bat pass, and we define a call as a single burst (pulse) of sound, whether it is echolocation or social in nature. A sequence of calls is any series of pulses, whether they are echolocation or social. To differentiate pulses produced in songs versus those typical of echolocation, we refer to pulses making up a song as syllables. Different types of syllables vary in frequency and duration parameters. A distinct sequence consisting of different types of syllables which is repeated to produce a song we refer to as a phrase. Generally, a song will consist of one or more phrases; however, if only part of a phrase was recorded, as long as the syllables present are clearly attributable to a phrase, then we refer to this as a partial song. In some cases, such as when a bat is only in the detection volume of a bat detector for a very short period of time, only partial songs (i.e., less than one complete phrase) were recorded.

We processed acoustic recordings using a variety of methods, with larger datasets first being processed with either Kaleidoscope Pro (Wildlife Acoustics, Maynard, MA, USA) or SonoBat (California State Polytechnic University, Humboldt, CA, USA) for auto-identification prior to manually vetting; some smaller datasets were examined without auto-identification as a first step. We manually vetted files using either Kaleidoscope Pro, SonoBat, AnalookW (C. Corben, hoarybat.com, MO) or Anabat Insight (Titley Scientific, Brendale, Australia). Recordings from BC were largely zero-crossing format, and all other datasets were recorded in full spectrum format. British Columbia datasets were manually vetted using a combination of AnalookW and Anabat Insight. Washington and Mendocino County, California datasets were manually reviewed using Kaleidoscope Pro. Recordings collected in Montana, Idaho, Utah, Colorado, and Lassen Volcanic National Park (California) were manually reviewed using SonoBat. Active recordings from Washington were reviewed by one of us (G. Falxa) manually to identify songs using both Sonobat3 and Kaleidoscope Pro. Files were manually analyzed in real-time (uncompressed) mode in order to ensure visualization of a song pattern; compressed mode can obscure the diagnostic song pattern if some song pulses are of low intensity.

For larger datasets that underwent automated classification, we determined that silver-haired bat songs were often misclassified as big brown bat, Brazilian free-tailed bat, pallid bat (*Antrozous pallidus*), Townsend's big-eared bat (*Corynorhinus townsendii*), western red bat (*Lasiurus blossevillii*), hoary bat, or long-eared myotis (*Myotis evotis*). Thus, files automatically classified as any of the above species were manually vetted to search for silver-haired bat songs. To avoid reporting extraneous results, we present silver-haired bat activity only in the context of low-frequency bat passes (minimum frequency <30 kilohertz [kHz], where one recorded file = pass), as silver-haired bat songs are most likely to be confused with echolocation calls of low-frequency bat species.

We refer to call parameters (measured in AnalookW, Anabat Insight and/or Kaleidoscope Pro) as follows: call body is the flattest part of the call (Figure 2A), with Sc being the slope of that call body in octaves per second (OPS); time between calls (TBC) is the amount of time between pulses; and minimum (F_{min})/maximum (F_{max}) frequencies refer to the lowest/highest frequency produced in one call. Generally, echolocation pulses of North American bats (low duty cycle) are frequency modulated (FM) and thus start high in frequency and end lower, having bandwidth greater than zero (Russo et al. 2018). If the call body is flat or nearly flat, bandwidth approaches zero and this is referred to as a quasi-constant frequency (QCF) component of a call. The rate of change of frequencies can vary as the call is produced (i.e., the slope changes over time) and may be gradual or sudden. In the latter, this change of slope creates a bend in the call, often called a knee (Figure 2A). The slope of the call from its start at F_{max} to the knee is measured as S1 (OPS), and the slope from the knee to the F_{min} is generally the call body and is the Sc as discussed above. We measured call duration (time from start to end of a pulse, measured in milliseconds [ms]).
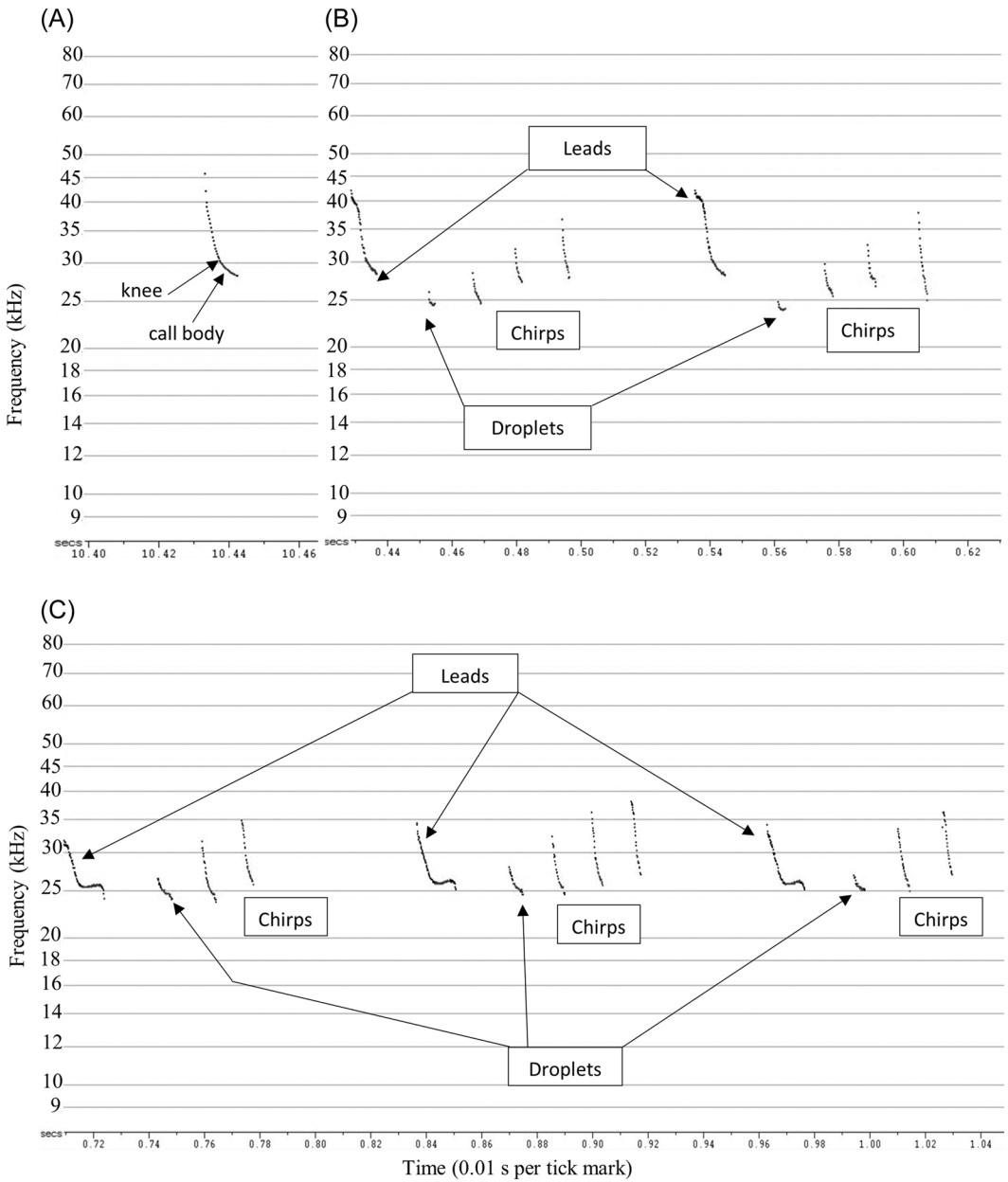
FIGURE 2 Typical phrases of the silver-haired bat (*Lasionycteris noctivagans*) songs, each containing 3 syllable types (lead, droplet, chirps). Typical short duration echolocation pulses of silver-haired bat for context (A). Lead resembling echolocation pulse except for an upsweep into the pulse (B). Lead with accentuated knee just prior to a flat call body (C).

All parameters were measured in zero-crossing format using AnalookW. Spectrograms in the figures are shown in True Time (x-axis shows the real time elapsed) unless specified (x-axis in Compressed Time shows only the time within each pulse in real time, with the time between the pulses largely removed, for display purposes). All spectrograms display a logarithmic frequency (y axis).

To assess the auto-identification treatment of songs, we processed all full spectrum song files using both Kaleidoscope Pro (classifier version North America 5.4.0) and SonoBat (versions 4.4.0 and 4.4.5 Great Basin classifier) including the following species (Kaleidoscope Pro): big brown bat; Brazilian free-tailed bat; California myotis (*Myotis californicus*); canyon bat (*Parastrellus hesperus*); fringed myotis (*M. thysanodes*); hoary bat; little brown myotis (*M. lucifugus*); long-eared myotis; long-legged myotis (*M. volans*); pallid bat; silver-haired bat; spotted bat (*Euderma maculatum*); Townsend's big-eared bat; western red bat; western small-footed myotis (*M. ciliolabrum*); and Yuma myotis (*Myotis yumanensis*). The Montana classifier set included eastern red bat (*Lasiurus borealis*) instead of western red bat, and additionally included northern myotis (*M. septentrionalis*). We used default settings for each software package (Kaleidoscope Pro Balanced; SonoBat 0.7 call quality, 0.9 sequence decision threshold). We examined each recording to ensure the software was triggering on the song pulses, and thus considering them in the auto-identification process. We calculated the percentage of misclassifications.

RESULTS

Captures

At the CA-10 mine we captured bats over 5 winters (here we define winter as 1 November–31 March) during 2012–2017 (22 nights), capturing a total of 400 free-flying bats: 48 (18 female, 30 male) Townsend's big-eared bats, 4 (2 f, 2 m) big brown bats, 134 (46 f, 88 m) silver-haired bats, 212 (85 f, 127 m) California myotis, and 2 (1 f, 1 m) Yuma myotis. At the CA-9 mine, over 10 winters (2011–2021; 52 capture nights), we captured 174 bats: silver-haired bat (42 f, 77 m), Townsend's big-eared bat (3 f, 1 m), long-legged myotis (1 m) and California myotis (24 f, 26 m). We never captured big brown bats at the CA-9 site; because of this, and the small number of big brown bats captured at the CA-10 mine site (4; 1%), we concluded that the songs recorded each winter at these sites could be attributed to silver-haired bat.

By examining genitalia, we observed evidence of mating in 15 bats during winter: Townsend's big-eared bat (1 f), California myotis (5 f, 4 m), and silver-haired bat (1 f, 4 m). Females exuded sperm from the vagina and/or their vagina was red and swollen, and males showed signs of erect penises.

Acoustic recordings

Our source acoustics dataset was compiled from data collected at the 2 BC mine sites used by silver-haired bats year-round. At CA-10, we recorded songs on 182 nights (1,088 song files) over 9 years (recording 1,146 detector-nights during September to April starting in 2011 through to spring 2020). At CA-9, we acoustically recorded from February through April 2021 deploying multiple detectors at known roost trees and the mine (498 detector-nights). Here we recorded songs on 44 nights (186 song files), each showing a relatively consistent pattern (Figure 2). We recorded numerous acoustic files that had search phase echolocation calls immediately preceding a song sequence (Figure 3). Flat ~25 kHz search phase echolocation pulses immediately before or after songs were also observed.

We identified nonecholocation sounds produced by silver-haired bats at the 2 mine sites, and 6 adjacent tree hibernacula. We define these as songs as they have a repetitive pattern and they have a short time interval between pulses, unlike that of search phase echolocation calls. We describe the songs as generally consisting of 3 syllables that we have named to provide descriptions and refer to their metrics (Table 2): lead, droplet, followed by chirps (Figure 2). The presence of all 3 types of syllables in this order produces a phrase that is repeated to produce the song. Samples of song recordings can be accessed online (https://doi.org/10.5061/dryad.j0zpc86m8).

Each phrase of a song consists of 4–8 syllables ($\overline{x}$ ± SE =5.1 ± 0.2; n = 47 phrases), although there may be exceptions as songs and the pulses that are produced can vary and are not always a standard pattern. The lead pulse
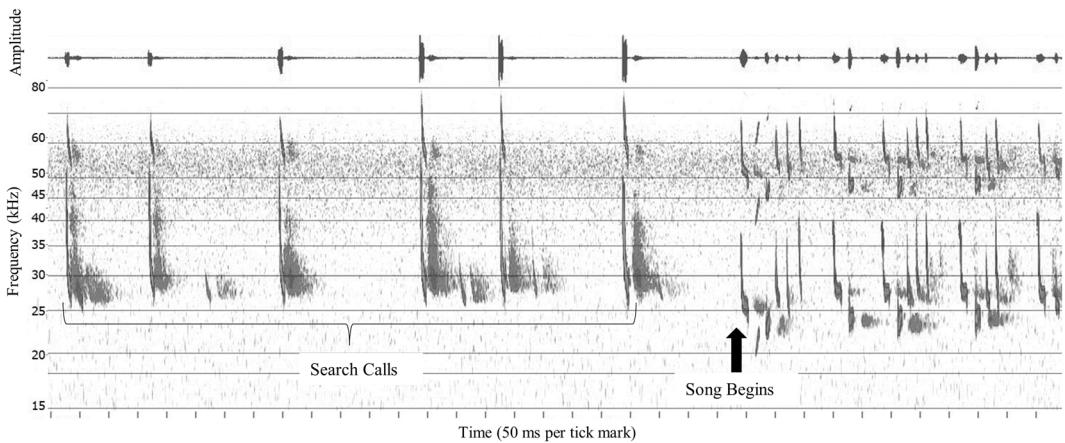
FIGURE 3   Silver-haired bat (*Lasionycteris noctivagans*) recording from site US-12, Ekalaka Hills, Montana, USA. Search phase calls are being produced at the start of the recording as the closest bat (greatest bandwidth search phase pulses) flies into detection range of the bat detector. The sequence shifts from search phase echolocation into song at the arrow. This spectrogram is displayed in full spectrum using Anabat Insight with F5 zoom. An oscillogram appears at top, representing relative loudness (amplitude).

TABLE 2   Mean zero-cross call parameters for the 3 pulse shapes (syllables) making up phrases (45) of songs produced by silver-haired bats (*Lasionycteris noctivagans*), ranging from 4–8 syllables each (*n* = 16 representative high-quality recordings subsampled from Nelway, British Columbia (CA-10), from 2014-2020). Bandwidth is Fmax − Fmin. Dur is duration of time from the start to the end of the pulse. Slopes in octaves per second (OPS) are the slope of the call body (Sc) and the slope of the initial part of the call prior to the call body (S1).

| | Mean Pulse Measurements (±SE) and [Range] | | | | | |
	Dur (ms)	Fmin (kHz)	Fmax (kHz)	Sc (OPS)	S1 (OPS)	Bandwidth (kHz)
Leads	9.4 (0.4)	25.0 (0.2)	32.8 (0.9)	10 (3)	129 (17)	7.8 (0.8)
	[4.5–14.2]	[23.3–28.8]	[26.2–48.5]	[−21–62]	[−209–351]	[2.5–23]
Droplets	3.65 (0.15)	23.6 (0.2)	26.4 (0.3)	18 (2)	214 (17)	3.3 (0.5)
	[1.5–5.9]	[21.8–29.4]	[23.0–34.6]	[−7–40]	[−53–560]	[0.5–24]
Chirps	2.79 (0.07)	25.5 (0.2)	35.2 (0.3)	114 (6)	326 (23)	9.9 (0.3)
	[1.2–7.1]	[22.5–33.9]	[24.8–46.0]	[−27–375]	[36.5–637]	[1.8–33]

(Figure 2) generally resembles an echolocation pulse, being broadband with an initial FM sweep followed by a QCF component. The lead pulse, which typically begins each song's phrase, often starts as either an upsweep (Figures 4A and 5B first lead), a flat component that progresses into a backwards S-shape (Figure 5C pulses 4, 8, 12), or a changing slope of dropping frequencies giving the initial part of the lead a wavy appearance (Figure 2B leads). The lead pulse can have lower minimum frequency than the droplet and chirps that follow it (Figure 5A), but more often has a higher minimum frequency (e.g., Figures 2B, 4B and 5B). Leads can have a more pronounced knee (Figure 2C, Figure 5A) than a typical echolocation pulse (Figure 2A), with a steep S1 and a nearly flat call body after the knee (Figure 2C). Droplets (usually the 2nd pulse in a phrase) are typically lower in minimum frequency and bandwidth from the lead syllable in their phrase (mean differences 5.7 ± 0.4 kHz and 3.8 ± 1.0 kHz, respectively). Chirps typically increase in frequency, and while minimum frequency can be highly variable, the maximum frequency more consistently increases an average of 4.2 ± 0.2 kHz (*n* = 129) with each subsequent chirp in the phrase. The time between the syllables is typically longest between the lead and droplet (18.0 ± 0.5 ms; *n* = 45), and shortest between the droplet-chirp and chirp-chirp syllables (8.56 ± 0.3 ms; *n* = 134). This is similar to the time between pulses during a feeding buzz (<10 ms between pulses;
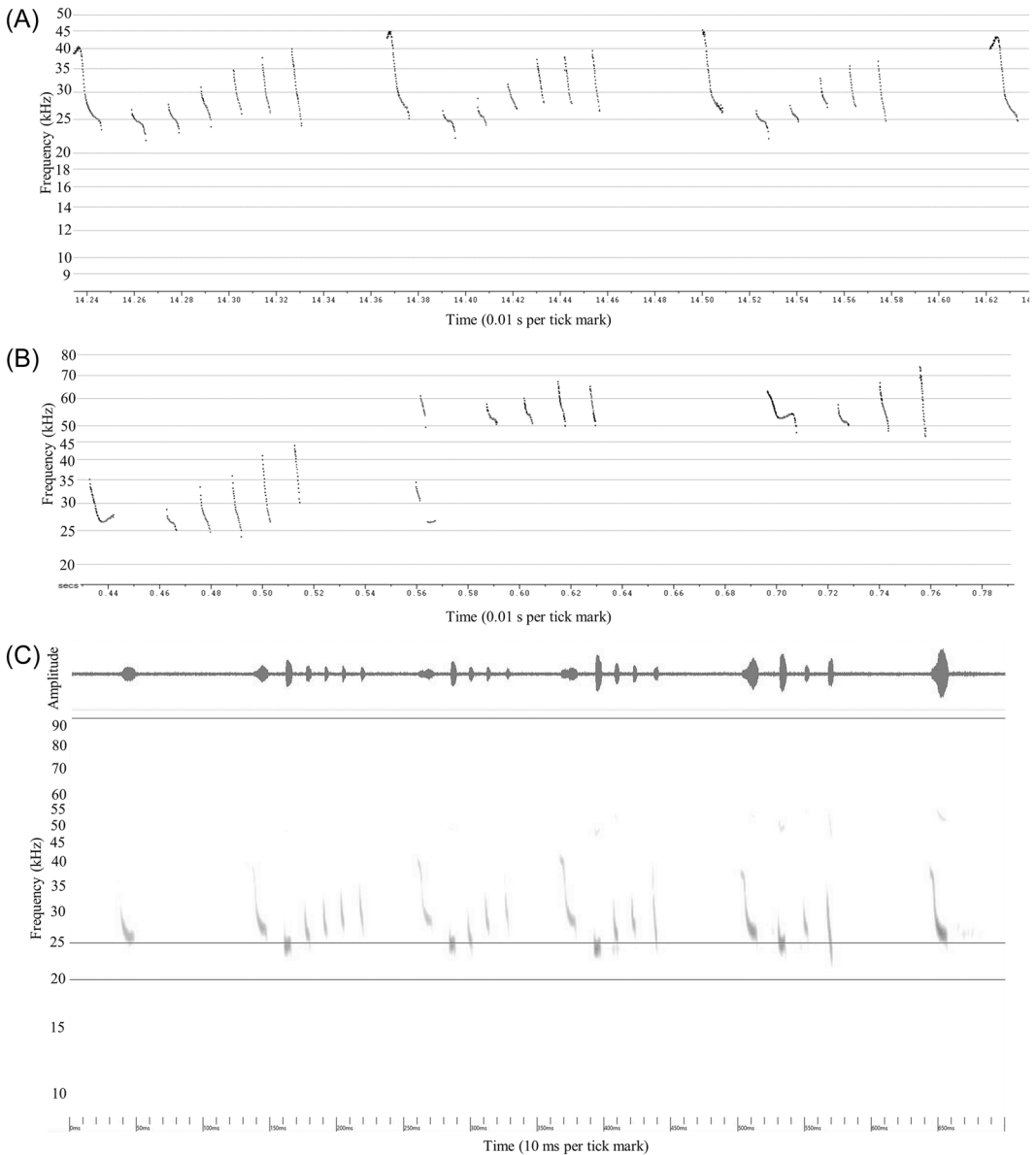
FIGURE 4 Zero-crossing (A, B; AnalookW) and full spectrum spectrograms (C, D; KaleidoscopePro). The 2 frequency lines in C and D spectrograms are 20 and 25 kHz, provided for context, and the top oscillogram in each spectrogram represents relative amplitude. A social upsweep into the lead pulses is seen in all song phrases (A). The second harmonic is prominent in B, and D. Some of the third harmonic is visible in D.

Griffin et al. 1960), which is a relatively short time period, especially in comparison to the search phase echolocation calls which are typically several hundred milliseconds apart.

Variation of song phrases is largely in the number of syllables. There can be more than one lead or droplet, and the number of chirps we observed varied from 2 to 6 but is likely to be higher when counted in full spectrum where quieter pulses would be recorded. The shapes of the leads and droplets could vary depending on the presence of upsweeps and accentuated knees with call bodies that range from flat to negative in slope, which could, with low
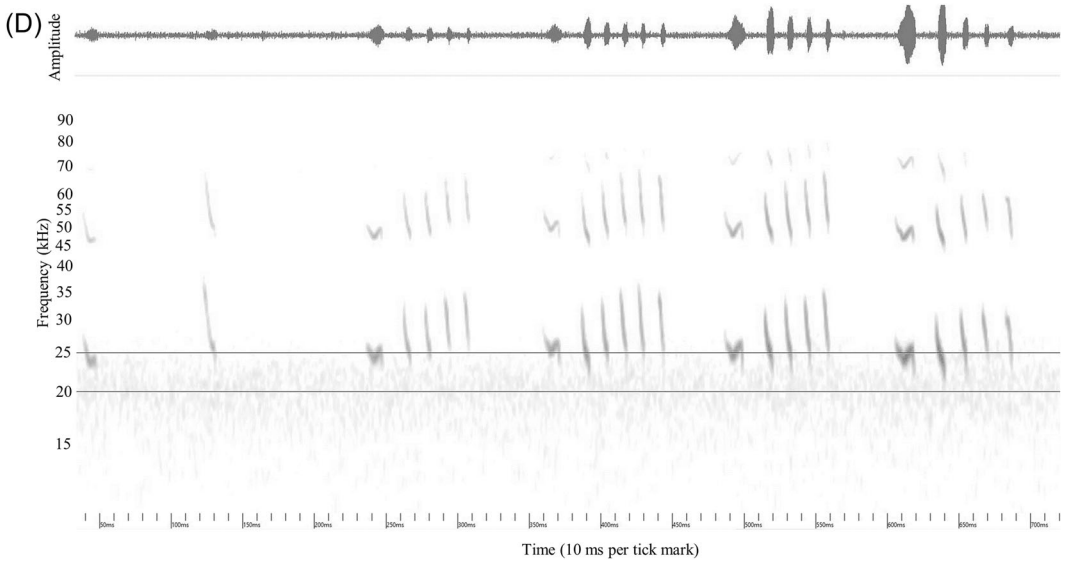
FIGURE 4 (Continued)

bandwidth, produce calls that are U-shaped (Figure 5D). We observed that the total duration of a typical song phrase with all 3 pulse types ranges approximately 85–150 ms, with the time between phrases typically very short (often ~30–50 ms; Figure 6). Most recordings of songs were of low amplitude (which can be visualized in the oscillogram of full spectrum recordings; Figure 3), suggesting songs are not produced as loudly as the echolocation pulses that immediately proceed or follow.

An individual bat detector recorded from 3 to 1,146 nights (22 locations, total detector-nights of recording across all detectors and all sites = 4,391; Table 1), with a mean number of recording nights (all detectors combined) per location of 204 ± 51 SE (median 139). We recorded bats on 3,073 nights (bat-nights), for a total of 82,149 passes of low-frequency bats, including silver-haired, big brown, pallid, Townsend's big-eared, fringed myotis, Brazilian free-tailed, and hoary bats. We recorded songs at all sites to varying degrees (Table 1, Table S1, available in Supporting Information), with a total of 1,875 files found to contain at least a partial song. At the 2 mine hibernacula (CA-9 and CA-10), and a rocky area known to have hibernating bats (CA-5), we monitored largely during winter, finding that a relatively high proportion of low-frequency bat passes at these sites contained songs (11-14%; Table 1). A site for which roost information is unknown (US-2), a high percentage (13%) of low-frequency bat passes contained bat songs. We documented production of songs in every month of the year, though this varied by season; 93.4% occurred outside of summer months (July and August), with 53.4% produced during winter (Figure 7). When the number of song files per season is adjusted for the number of bat-nights, 1.5, 0.8, 0.3, and 0.2 songs/bat-night were recorded in fall, winter, spring, and summer, respectively.

We processed 536 full spectrum song files using both auto-identification software packages. Using Kaleidoscope Pro, we observed that 68 of 235 (29%) files assigned an auto-identification label were correctly classified as silver-haired bats. Twenty-nine percent of song-containing files were misclassified as hoary bat, and 23% were misclassified as big brown bat (Table 3; Table S2, available in Supporting Information). Using SonoBat, 71 of 121 (59%) song-containing files that were assigned an auto-identification label were misclassified as hoary bat, 26% were misclassified as Brazilian free-tailed bat, and only 14% were correctly assigned to silver-haired bat (Table 3; Table S3, available in Supporting Information).
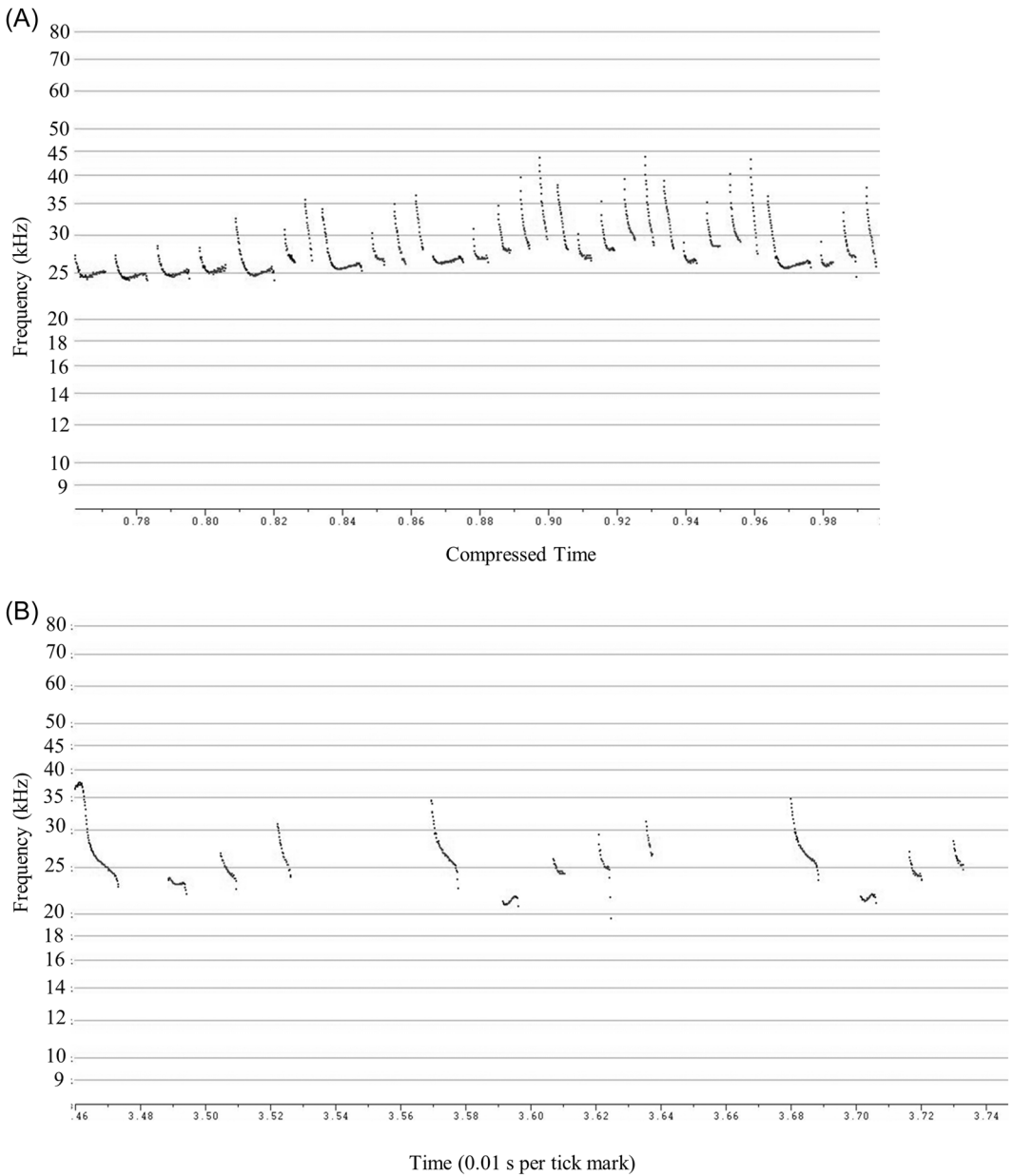
FIGURE 5 Some examples of variations observed in (*Lasionycteris noctivagans*) songs in AnalookW. A repetition of lead pulses occurs before any complete song phrases; the time axis shows compressed time, so the time axis which is 0.01 s per tick mark applies to within pulse measurements only (A). A combination of call features is seen including an upsweep into a lead, and the droplets have a squiggle shape (B). The lead calls can have the squiggle shape (C). The U-shaped calls that are associated with some song production (D) resemble partial but deeper squiggles, similar to those in C.
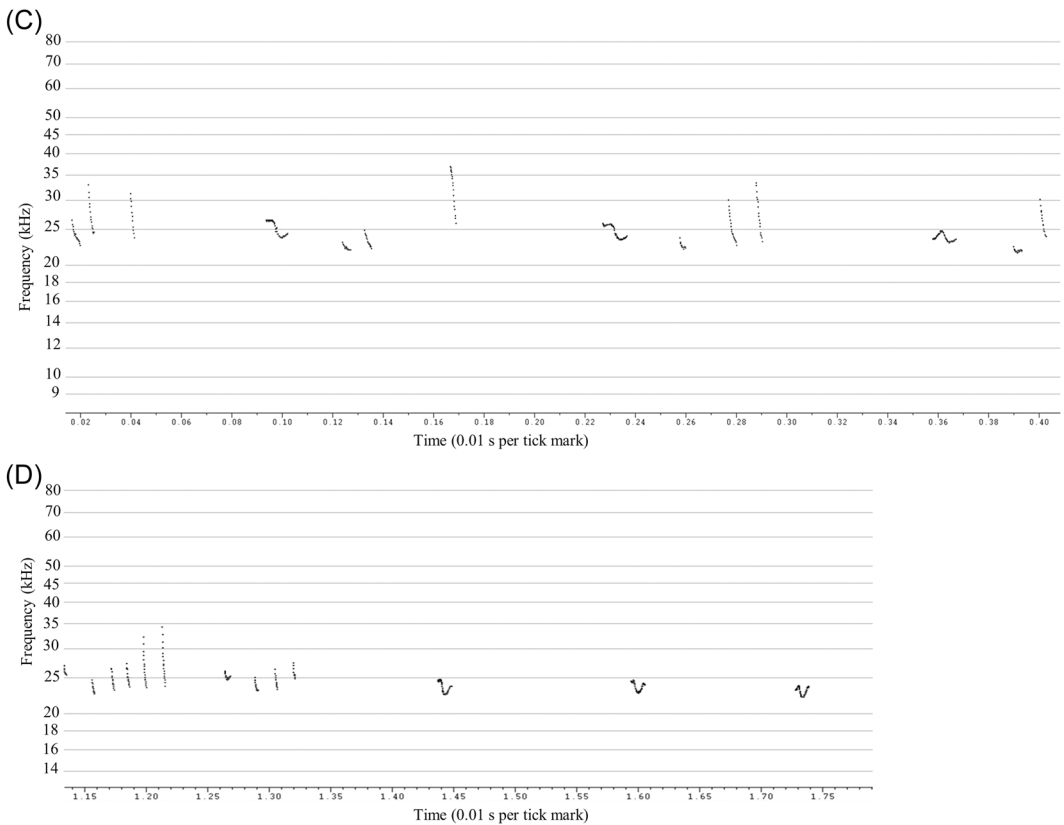
FIGURE 5 (Continued)

DISCUSSION

Through observation during active recording and capture at overwintering sites where silver-haired bats hibernate and fly outside their roost sites during mid-winter, we have identified a social ultrasonic pattern produced by silver-haired bats across their western range. This ultrasonic pattern consists of several predictable pulse types and shapes, with a series of recognizable calls repeated in a short time frame fitting the definition of a song (Smotherman et al. 2016). We observed variations (e.g., number of syllables) on the phrase pattern. Variations may sometimes have reflected different vocalization patterns of the individual, and/or the distance of the bat from the detector, resulting in lower intensity components not always being recorded. The beginning of the song consists of pulses that are highly reminiscent of echolocation pulses. Typical search phase echolocation calls can precede or follow these songs. We recorded numerous acoustic files that had a song sequence immediately preceded or followed by flat ~25 kHz search phase echolocation pulses, a call type known to be made by silver-haired or Brazilian free-tailed bats, but not big brown bats (Lausen et al. 2022). This provided further confirmation that the songs we recorded at the mine hibernacula were made by silver-haired bats.

Echolocation calls have evolved to optimize the ability to locate small insect prey and as such they are constrained in frequencies (wavelength) and timing (Bohn and Gillam 2018), but social calls aimed at communication should have fewer constraints. Songs have likely evolved with complex social interactions when greater information needs to be communicated (Smotherman et al. 2016). Use of lower frequencies are likely to be advantageous for communication calls because these longer wavelengths travel farther in air (Lawrence and Simmons 1982); thus, one could expect a song produced by a bat that was seeking a mate, or trying to communicate to a conspecific, to
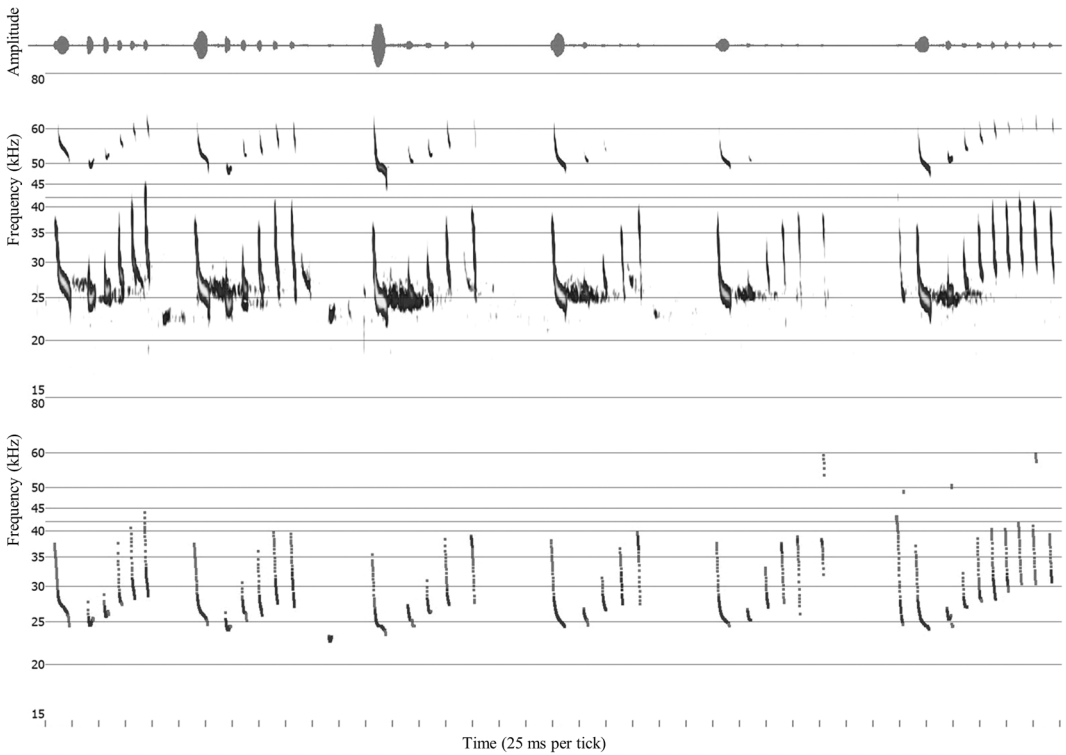
FIGURE 6 A spectrogram of silver-haired bat song (*Lasionycteris noctivagans*) displayed in real time in both full spectrum (top) and zero-cross (bottom) using Anabat Insight software (version 2.0.2), time axis view F6. Second harmonics are visible in the top full spectrum spectrogram; the oscillogram above the full spectrum spectrogram represents relative amplitude.

be lower in frequency than its typical echolocation calls (Barlow and Jones 1997). The songs that we observed were of frequencies not differing greatly from frequencies produced in echolocation calls, but some individuals were recorded producing pulses with lower frequencies, below the 23–25 kHz lowest minimum frequency typical of echolocation in silver-haired bats (Lausen et al. 2022).

The patterned nature of the songs and the variations among phrases that we observed were consistent across the western range of the silver-haired bat. However, more extensive recording across the range is warranted to investigate potential variation. Similar to our findings, Brazilian free-tailed bat, the only other species of bat in U.S. and Canada to date known to sing (Bohn et al. 2008, Bohn and Gillam 2018), also incorporates some echolocation-like pulses into their songs. Brazilian free-tailed bat songs also have a relatively standardized (stereotyped) pattern among conspecifics across the species' North American range and can differ in number of syllables within phrases (Bohn et al. 2009). Song pulse shapes produced by Brazilian free-tailed bats in flight have similarities to syllables that we present here for silver-haired bats (compare our Figure 2 [this study] to Figure 3 in Bohn and Gillam 2018 and Figure 1 in Bohn et al. 2013). Echolocation calls of Brazilian free-tailed bats and silver-haired bats are difficult to differentiate, with a great deal of overlap in echolocation pulse shapes and patterns (Ommundsen et al. 2017, Lausen et al. 2022). While there are some similarities in pulse shapes within the songs of each of these 2 species, the repetitive, predictable, and unique patterned phrases of silver-haired bats facilitate differentiation among these 2 species. In particular, we believe that the ascending frequency of chirps is diagnostic of silver-haired bat. The big brown bat is another species that is typically difficult to differentiate from silver-haired bat based on echolocation calls (Betts 1998), and is another species that has been recorded flying in winter (Lausen and Barclay 2006). Despite
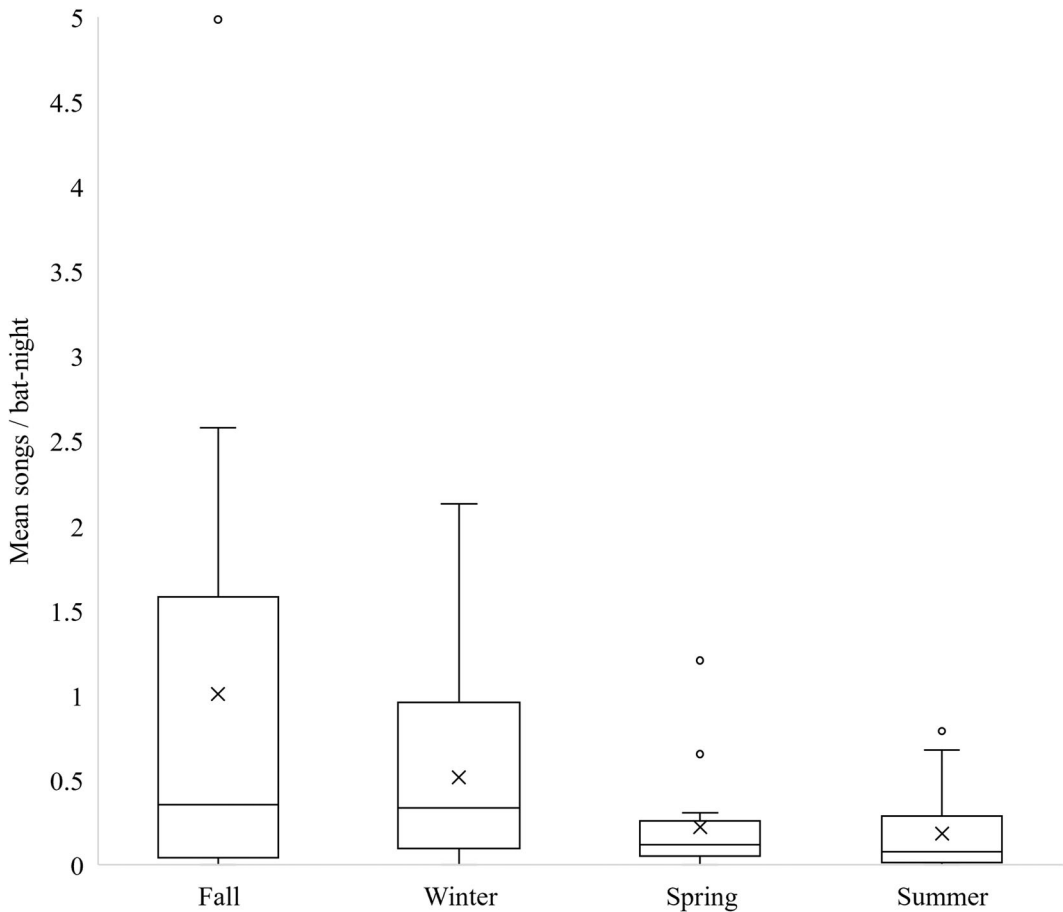
FIGURE 7 Box plot showing mean number of song recordings produced by silver-haired bats (*Lasionycteris noctivagans*) per bat-night across all sites by season. See Table 1 and S1B (in Supporting Information) for underpinning details of deployments and numbers of recordings at each site.

extensive acoustic study of big brown bats, no songs have been reported (Smotherman et al. 2016). Thus, the presence of the song we describe here will also aid in classifying silver-haired bat where big brown bat is also possible. This could become increasingly important for management and permitting now that silver-haired bat has been recommended as Endangered in Canada as a result of the threat of wind energy development (Committee on the Status of Endangered Wildlife in Canada 2023).

Like the songs of the Brazilian free-tailed bat, pulses making up the songs of silver-haired bats are most often frequency-modulated (FM), sweeping from high to low. This FM nature is especially true of the chirp syllables which typically ascend in frequency with each subsequent pulse. All of the pulses making up the song are produced in the typical frequency range of silver-haired bat echolocation (typically F_{min} 23 to ~30 kHz; Lausen et al. 2022), with the exception of some pulses at the beginning of phrases which can have minimum frequencies of 21.8 kHz. The time between the syllables is short (8–18 ms between pulses within a phrase), substantially shorter than the >100 ms typically between echolocation calls and are similar to the time between pulses of a feeding buzz (Griffin et al. 1960). This short time between pulses means that each pulse produced is not synchronized with wing beat rate and will thus result in higher energy expenditure to produce than echolocation calls (Jones 1999). Extremely rapid pulse repetition (short duration inter-pulse interval) in feeding buzzes is due to the need to receive reflected sound quickly for capturing a small moving prey item (Fenton and Bell 1979). If the rapid series of chirps that we

TABLE 3 Comparison of auto-identification of full spectrum recordings containing silver-haired bat (*Lasionycteris noctivagans*; Lano, LASNOC) songs (536 high quality files of 674 full spectrum song recordings from 2012–2021 from all US study sites and Beasley, British Columbia (CA-9); Figure 1 map). Kaleidoscope Pro (KSPro) was set to Balanced, and Sonobat was used with default settings (0.7 call quality, 0.9 sequence decision threshold). Other species labels are as follows: LASCIN/Laci, hoary bat (*Lasiurus cinereus*); EPTFUS/Epfu, big brown bat (*Eptesicus fuscus*); TADBRA/Tabr, Brazilian free-tailed bat (*Tadarida brasiliensis*); ANTPAL/Anpa, pallid bat (*Antrozous pallidus*); LASBLO/Labl, western red bat (*Lasiurus blossevilli*); CORTOW/Coto, Townsend's big-eared bat (*Corynorhinus townsendii*); MYOEVO/Myev, long-eared myotis (*Myotis evotis*).

Species Label (KSPro/Sonobat)	KSPro	Sonobat
LASCIN/Laci	68 (29%)	71 (59%)
LASNOC/Lano	68 (29%)	17 (14%)
EPTFUS/Epfu	55 (23%)	1 (0.83%)
TADBRA/Tabr	38 (16%)	32 (26%)
ANTPAL/Anpa	2 (0.85%)	0
LASBLO/Labl	2 (0.85%)	0
CORTOW/Coto	1 (0.43%)	0
MYOEVO/Myev	1 (0.43%)	0
Total files with species ID (% of dataset)	235 (44%)	121 (28%)

documented is not a form of echolocation, but is instead social communication as we hypothesize, then the purpose of such rapid repetition may be to quickly communicate information to a receiver that may or may not be in acoustic range for long, depending on whether one or both bats are in flight. This hypothesis that at least part of this signal is intended for a bat nearby is true of the higher frequency components of the songs which tend to be of low intensity and may not travel far. Similar to the progressively lowering intensity of the rapid pulses heard in a feeding buzz, the diminishing amplitude of the chirps suggests that either projecting the entire song sequence may not be important, or that the intended recipient is close by. While it seems intuitive that these songs are communicating directly to other bats, it is noteworthy that most of the winter recordings contained calls by a single individual. The presence of often just one bat in the recordings could suggest that the songs are not communicative in nature, or that there is often no receiver in close enough proximity to have a reply recorded. Alternatively, the bulk of the recordings may contain only one flying bat if the intended recipient is stationary (e.g., inside a roost) and either a reply is not expected (e.g., it is just a cue for the roosting bat to emerge), or not recorded on the detector; the 2 bats may need to be extremely close to one another for both the song from the sender and the song from the receiver to both be within range of the detector. Further research is needed to determine if these songs are more likely to be produced when in close proximity to conspecifics who are in flight or in roosts.

Our data and observations made by others confirm songs are produced by bats in flight. For example, the winter bat detector at CA-10 in BC was located outside a mine hibernaculum facing into a large open space above a pit with several openings into the mine. Therefore, all recordings at CA-10 were of bats in flight, not roosting. That silver-haired bats are in flight at the time of producing these songs is also supported by observations made by one of us (G. Falxa) when actively monitoring using a hand-held bat detector: silver-haired bats were observed flying in winter during active recording (songs observed in some recordings). Similarly, back-to-back recordings (30 seconds) of silver-haired bat songs made during driving transects where a bat detector is mounted on a vehicle and is thus in motion were shared with us (T. Ellis, Vancouver Island, BC, personal communication). That each song phrase typically starts with low frequency pulses resembling echolocation calls also supports our observations of bat song production while in flight. Singing silver-haired bats may capitalize on the lower frequencies (which travel further)

for some aspect of navigation, while inserting a series of rapidly produced high frequency syllables for social communication in between the lower frequency syllables. Brazilian free-tailed bats have been shown to produce songs while roosting (Bohn et al. 2008) and in flight (Bohn and Gillam 2018). Whether silver-haired bats produce songs while roosting has yet to be investigated.

Complex social calls that are best described as songs have been documented for less than 20 other species of bats in the world (Smotherman et al. 2016). Songs have been well described for the greater white-lined bat (*Saccopteryx bilineata*), in Central and South America (Behr and von Helversen 2004), and several European pipistrelles (e.g., Nathusius' pipistrelle [*Pipistrellus nathusii*; Russ and Racey 2007]; Hanák's dwarf bat [*P. hanaki*; Georgiakakis and Russo 2012]). From extensive studies of the small number of singing bat species, males produce complex social calls typically associated with courtship or territoriality (Smotherman et al. 2016). In the Nathusius' pipistrelle, advertisement calls are produced by males during the mating season (Russ and Racey 2007), and male greater white-lined bats produce either territorial or courtship songs (Behr and von Helversen 2004). Territorial songs differ substantially from those used to attract mates, with the former songs consisting of low frequency (audible to humans) and long duration calls which would travel great distances to deter other males nearby and possibly to dual-purpose attract distant females (Bradbury and Vehrencamp 1998). In contrast, the courtship songs are produced when 20–50 cm from a female, and are high in frequency (ultrasonic), with pulses that are on average shorter in duration (Behr and von Helversen 2004).

It is unlikely that the songs we describe here for silver-haired bat are for protecting food resources (e.g., insect prey) given that these calls are produced in winter when there are few, if any flying insect prey available. As we have observed individual silver-haired bats hibernating together in large mines sometimes in small clusters, territoriality seems unlikely. The songs we describe here are consistent with what might be expected of courtship songs. When we examined song production relative to the number of nights on which bats were detected, we determined that the highest per bat-night occurrences of singing were in fall, followed by winter, and then spring. In the US and Canada, the majority of mating by silver-haired bats is thought to occur in fall (Kunz 1982, Cryan et al. 2012), but spring mating has been observed in New Mexico (Clerc et al. 2022). Silver-haired bats have been captured with stored sperm remaining in their cauda epididymides as late as May in BC (Lausen et al. 2022), suggesting spring mating is also possible in the Pacific Northwest. Through examination of genitalia of free-flying silver-haired bats in winter, we determined that mating is also taking place in this season.

At previously known hibernation areas (CA-5, CA-9, CA-10) we monitored largely during winter, we found that a relatively high proportion of bat passes at these sites contained songs. We also recorded a high percentage of songs at a site for which bat roosting and migration information is not known (US-2). We propose that follow-up investigations at sites where song production is high may reveal important habitat for silver-haired bats.

We also documented song production at some of our recording sites in summer months. It is possible that there is already an uptick in songs by late summer (August) when migration, and thus mating, begins in some areas (Baerwald and Barclay 2011, Cryan et al. 2012). However, some songs were detected in July. While summer song production may reflect learning or practicing (Smotherman et al. 2016), it may be indicative of some low level of male-male competition which escalates during the mating seasons. Male-male competition is reason for song production in some bat species (Bohn and Gillam 2018) and thus we cannot rule this out as a potential reason for song production. At our study sites we have been unable to determine which sex is producing the songs that we recorded; therefore, we cannot know whether the songs recorded in our datasets were made by one or both sexes, and whether they are indeed associated with finding mates or courtship, or whether they have a broader behavioral function.

When examining acoustic datasets for songs, manual identification in True Time mode (versus Compressed) is required. True Time viewing is often needed to recognize songs, because some low intensity song components can be obscured when sonograms are compressed, sometimes rendering the pattern of syllables unrecognizable. Manual review of acoustic recordings is needed because the automated software analysis programs currently do not identify these types of social calls, and the presence of these songs in recordings can result in species misclassifications.

In addition to the datasets that we presented here, we confirmed unpublished silver-haired song recordings from the following locations: Alaska (K. Blejwas), Arizona (J. Szewczak), California (T. Weller), Colorado (D. Neubaum), Oregon (N. Schmidt), and Wisconsin (P. Wolff). While most of these locations are western U.S., the Wisconsin recording suggests that silver-haired bat songs may be identified throughout their range now that we have formally identified and described them.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

ETHICS STATEMENT

Bats were captured in accordance with the Canadian Council on Animal Care under permits CB09-59777, MRCB15-163558 and MRCB20-598305 (2011-2021) issued to C. Lausen by the British Columbia Ministry of Forest Lands and Natural Resource Operations.

DATA AVAILABILITY STATEMENT

Some data are available on request from the authors. A sub-sample of song recordings are publicly available on Dryad at this https://doi.org/10.5061/dryad.j0zpc86m8.

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SUPPORTING INFORMATION

Additional supporting material may be found in the online version of this article at the publisher's website.

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