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RESEARCH ARTICLE

An adaptation of dual-frame sampling for estimating bat population trends in multi-hibernacula systems

Theodore J. Weller[1] | **Katrina J. Smith**[2] | **Shawn C. Thomas**[3] | **James A. Baldwin**[4]

[1]USDA Forest Service, Pacific Southwest Research Station, 1700 Bayview Drive, Arcata, CA 95521, USA

[2]California Department of Fish and Wildlife, 1010 Riverside Drive, West Sacramento, CA 95605, USA

[3]Bat Conservation International, 500 North Capital of Texas Highway, Building 1, Austin, TX 78746, USA

[4]USDA Forest Service, Pacific Southwest Research Station, 800 Buchanan Street, Albany, CA 94710, USA

Correspondence

Theodore J. Weller, USDA Forest Service, Pacific Southwest Research Station, 1700 Bayview Drive, Arcata, CA 95521, USA.
Email: theodore.weller@usda.gov

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Abstract

Reliable estimates of population trends are important for prioritizing and implementing wildlife management actions. Abundance estimates are the most informative metric of population status but are difficult and costly to achieve for rare or elusive species. For bat species that are highly mobile and nocturnal, abundance estimates are usually only possible at their roosts. Although they are relatively easy to census in individual roosts, it is often unclear whether observed trends are representative of broader populations trends. Dual-frame sampling is useful for monitoring wildlife populations that exhibit site fidelity and are highly visible but where the proportion of the population in known sites is unknown. We adapted a dual-frame sampling approach to estimate abundance of Townsend's big-eared bats (*Corynorhinus townsendii*) hibernating in a system of >800 caves at Lava Beds National Monument (LBNM) in northern California, USA, in 2013–2022. Beginning with a list of opportunistically discovered hibernacula, we expanded inference to the entire system by randomly selecting sites and stratifying survey effort according to number of bats observed during previous counts. Following 4 years of surveys, we began substituting survey-informed estimates for some site types to improve efficiency of the monitoring effort. We estimated that a mean of 2,216 ± 112 (SE) bats hibernated at the study site annually and observed fluctuations of up to 22% around the mean population estimate and as much as 21% from the previous year. Despite annual fluctuations, we did not detect a trend in the number of hibernating bats at LBNM over the study period, underlining the challenges of detecting population trends in long-lived species not exposed to pronounced stressors. Because our analytical approach generates reliable estimates of trend while accommodating annual variability in survey effort among years, it should be attractive to wildlife managers faced with shifting priorities and resources.

KEYWORDS

cave, Chiroptera, *Corynorhinus townsendii*, dual-frame sampling, hibernation, monitoring, population estimate

Establishing trends in wildlife populations is fundamental for assessing their conservation status and setting benchmarks for appropriate management actions (Sauer and Knutson 2008, Fournier et al. 2019, Kiffner et al. 2020). Determination of population status or establishing population trends can be complicated for a variety of reasons including site selection, matching population metrics to information obtainable from the population, practical considerations, and resource limitations (Kraft et al. 1995, Calkins et al. 1999, Miller et al. 2012). Several metrics have been used to assess population trends including sign, activity indices, and site occupancy (Engeman and Allen 2000, Fattorini et al. 2011, MacKenzie et al. 2022), but the gold standard is quantifying changes in abundance for an individual species (Anderson 2001, Pollock et al. 2002, Noon et al. 2012). Nevertheless, reliable abundance estimates are difficult to achieve for many wildlife species, particularly if they are rare, elusive, or mobile (Duchamp et al. 2012, Miller et al. 2012, Conn et al. 2017).

A prominent exception exists for species that use the same sites repeatedly such as nesting, lekking, or rookery sites (Haines and Pollock 1998, Calkins et al. 1999, Yoccoz et al. 2001, Lowry et al. 2014, Shyvers et al. 2018). For bat species that are nocturnal and highly mobile, abundance estimates are generally only possible at their roosts, and are most accurate in circumstances where they roost conspicuously and in moderate numbers (Kunz 2003). Surveys of their winter roosts, or hibernacula, are particularly effective because roosts are often permanent, fidelity rates of individual bats are high, and bats are generally inactive, which simplifies counting (O'Shea et al. 2003, Hayes et al. 2009, Thogmartin et al. 2012, Kurta et al. 2020). The primary sample unit for such work is usually a single roost, either because it is the only one known or the only one to which surveyors have access (Ransome 1989, Clark et al. 1997, Dixon et al. 1998). In most cases, however, inference is desired about the broader population, usually including sites that have not been surveyed (Dixon et al. 1998, Russell et al. 2014, Humphrey and Oli 2015, Whiting et al. 2018). Inclusion of multiple sites increases complexities of site selection, field logistics, and data analyses (Prendergast et al. 2010, Humphrey and Oli 2015). Further, robust population estimates require that sites are selected from a probabilistic framework (Dixon et al. 1998, Anderson 2001, Yoccoz et al. 2001). In situations where bats roost conspicuously in sites that are relatively easy to access (e.g., caves, mines, buildings), biologists have used a variety of methods to identify potential roosts, survey a large proportion of them, and then make inference about local population trends (Humphrey and Kunz 1976, Whitaker and Gummer 2000, Prendergast et al. 2010, Uhrin et al. 2010).

Regional population assessments have been made by aggregating counts across many hibernacula (Thogmartin et al. 2012, Ingersoll et al. 2013, Barlow et al. 2015, Van der Meij et al. 2015, Whiting et al. 2018). An important assumption in such analyses is that a large proportion of the population is contained within the monitored hibernacula. Usually there is no effort to catalog the universe of potential hibernacula, which can lead to biased estimates (Ingersoll et al. 2013, Barlow et al. 2015, Fournier et al. 2019) and, in some cases, surprises. For example, the largest known hibernacula for Indiana bats (*Myotis sodalis*) was discovered in 2012, 3 decades after standardized surveys had begun (U.S. Fish and Wildlife Service 2019). Thus, the previous population estimates were not accurate and researchers did not know if declines in nearby caves in preceding years resulted from population declines or bats moving to the newly discovered hibernaculum (U.S. Fish and Wildlife Service 2019). Hence, comprehensive population monitoring requires an approach for estimating abundance when all sites are not surveyed and maintenance of the monitoring program requires regular surveys of existing known sites.

Dual-frame sampling approaches have been used to improve population estimates when the number of known sites is small relative to the number of potential sites on the landscape (Haines and Pollock 1998, Van Meter et al. 2008, D'Auria and Otto 2018, Shyvers et al. 2018). In dual-frame sampling, a list frame comprises all known sites and an area frame comprises sample units that are surveyed to locate new sites and recruit them into the list frame for future monitoring. The area frame is the geographic area of interest about which inference is desired and contains sites in the list frame and sites that have yet to be discovered or surveyed. Dual-frame sampling is particularly useful for monitoring wildlife populations that exhibit site fidelity and are highly visible (i.e., high detection probability; Haines and Pollock 1998). Roost monitoring for bats fits squarely into this paradigm because censuses are commonly repeated over time at known roosts and the number of roosts on the landscape is unknown or prohibitively large (Russell et al. 2014, Whiting et al. 2018).

Monitoring of Townsend's big-eared bats (*Corynorhinus townsendii*) at Lava Beds National Monument (LBNM) in northern California, USA, embodies several of these concepts. Biologists have censused known hibernacula in caves over several decades, but an unstructured program provided little consistency as to which caves were surveyed and when surveys occurred during each winter. Caves thought to contain the largest numbers of hibernating bats were counted more frequently, but there was no overarching monitoring strategy or systematic effort to locate additional hibernacula. These efforts were useful for assessing trends in abundance at individual caves (Weller et al. 2014) and, cumulatively, did not indicate long-term changes in the abundance of hibernating bats at those sites. It was unknown whether these patterns held for the full population of bats at LBNM because only about 12% of caves had been surveyed for bats during winter. The westward expansion of the fungal disease white-nose syndrome (Lorch et al. 2016) and the potential for associated decreases in population size (Frick et al. 2010, Cheng et al. 2021), increased frequency of movement between hibernacula (Clark et al 1997, Boyles et al. 2006, Bernard and McCracken 2017), and changes in hibernation behavior of bats (Langwig et al. 2012) necessitated improvement in monitoring methods to yield more sensitive and comprehensive annual population estimates.

Our objective was to create a monitoring program that resulted in annual estimates of the total population of hibernating bats at LBNM sufficient to determine population trends over time. A complete census of >800 named sites in LBNM was not feasible; as such, we needed a representative and efficient approach to site selection. Additionally, long-term success of the monitoring program required it to be resilient to variability in resources over time; thus, a rigid prescription for annual survey effort was not practical. We sought a monitoring strategy that surveyed the full spectrum of hibernacula sizes and structural types to reduce bias, accounted for the large number sites where few bats were expected, recruited additional hibernacula into our survey sample to improve comprehensiveness, and allowed survey effort to vary annually to increase flexibility.

STUDY AREA

Lava Beds National Monument is in northeastern California, approximately 250 km northeast of Redding, California, and 75 km southeast of Klamath Falls, Oregon, USA. The 18,896-ha monument contains the largest concentration of lava caves in the contiguous United States. Lava Beds National Monument lies at the convergence of the Sierra-Klamath, Cascade, and Great Basin geographic provinces and ranges in elevation from 1,236 m to 1,685 m. Accordingly, vegetation associations range from a low elevation sagebrush steppe community dominated by bluebunch wheatgrass (*Pseudoroegneria spicatum*) and basin or mountain big sagebrush (*Artemesia tridentata* ssp.), to an intermediate elevation, mixed woodland community dominated by western juniper (*Juniperus occidentalis*) and mountain mahogany (*Cercocarpus ledifolius*), with ponderosa pine (*Pinus ponderosa*) coniferous forest occurring at the highest elevations. In addition to bats, dusky-footed woodrats (*Neotoma fuscipes*) are commonly found in caves. Common ravens (*Corvus corax*), barn owls (*Tyto alba*), and great horned owls (*Bubo virginianus*) occasionally nest in caves. Prairie falcons (*Falco mexicanus*) and American kestrels (*Falco sparverius*) occur outside caves where bats are emerging during summer. The climate of LBNM is considered high elevation semi-arid desert with warm dry summers (June–August) and cool winters (December–March). From January 2013–March 2022, average annual high temperatures were 16.7°C and average annual low temperatures were 3.7°C. The monument received an average of 32 cm of precipitation annually during this period.

METHODS

Sample frame establishment

We implemented a modified dual-frame sampling framework (Haines and Pollock 1998) and used 10 years of survey data to adaptively introduce improvements into a population monitoring program for hibernating bats. We developed sample frames using a database maintained by LBNM that documents each of the unique geologic features in the monument, broadly referred to as caves. The database is updated regularly as new sites are encountered and documented. As of 2022, the database contained records of 812 sites. Most database records included information on surveyed length of cave, number of entrances, number of levels, and presence of sensitive biological, cultural, or geologic resources. We compiled additional site information from cave maps and reconnaissance records, including maximum ceiling height and slope of cave floors. We resolved missing information for a few sites with field visits.

We assigned sites to 1 of 4 site types, cave, bridge, surface tube, or non-cave, because we expected differences among them in terms of number of hibernating bats. Bridges were relatively short structures with multiple large (>1.5 m tall) entrances through which surveyors had a direct line of sight from one entrance to the other and hence there was no dark zone. Specifically, bridges had 2 entrances and a total length ≤30.5 m or >2 entrances and a total length ≤61 m. We did not consider multi-entrance structures >61 m in length as bridges and instead treated them as caves. Surface tubes had no maximum length but had maximum internal ceiling heights ≤1.5 m (entrance heights were ≤2.4 m). Generally, the entire length of a surface tube remained just below the ground surface and the downward slope of floors were ≤10°. We assigned any site that had a surveyed length of <15 m as a non-cave, regardless of its designated site type, as these sites do not contain deep zones with the stable thermal conditions necessary for bat hibernation. We categorized all other sites, including those with missing information, as caves. Although sites continue to be added to the LBNM database as they are identified and explored, most new additions are surface tubes.

We established 3 sample frames—a known frame, an unknown frame, and exclusion frame—that we updated annually based on number of bats and physical characteristics observed during surveys. We established our initial known frame using results of winter surveys conducted at 102 sites during 1991–2012 (Weller et al. 2014). Subsequent known frames included sites where ≥1 bat had been counted in previous years and sites where no bats were detected during a single previous survey. Our unknown frame is akin to an area frame conventionally used in dual-frame sampling, but because a list of discovered sites existed for our study area, it served as a second list frame composed of sites that had never been surveyed for bats in winter. The unknown frame contained sites that had not been surveyed previously and those in which no bats had been detected during the previous 2 consecutive surveys. The exclusion frame included sites where bats had not been detected during 3 previous surveys, were unsafe for entry by surveyors, or contained fragile or important cultural or natural resources that could be affected by surveys. In many cases, these sites were surveyed at least once prior to exclusion, with counts ranging from 0–4 bats.

In addition, we temporarily excluded sites from the known and unknown frames in a particular year if they could not be safely reached (e.g., snow or ice), if they had not yet been included in the database, or, rarely, to improve efficiency of annual survey effort (e.g., single site selected that was in an isolated area of LBNM).

We also stratified our known frame according to number of bats observed. Group 1 comprised caves in which the previous count was ≥30 bats. Group 2 comprised sites where 6–29 bats were counted during the previous survey. Group 3 included sites in which the previous count was 0–5 bats, excluding those where no bats were counted during 2 consecutive surveys. Prior to hibernacula surveys each year, we estimated the number of sites that could be surveyed based on expected personnel availability and weather conditions and selected sites as follows. We surveyed group 1 caves every year. We then apportioned the remaining number of surveys by randomly selecting an equal number of sites from group 2, group 3, and the unknown frame until we met our survey effort target. Following surveys each year, we updated our known, unknown, and exclusion frames and stratified our known frame based on the number of bats counted during previous surveys (Table 1).

During 2013-2016, we made no assumptions regarding the number of bats that may be present in sites as a function of site type, length, or other physical characteristics. In 2017, we began excluding surface tubes and bridges from known and unknown frames based on low numbers of bats observed in these site types and replaced surveys with count estimates for these site types (Table 1). In 2018, we stratified the unknown frame into 5 sub-groups based on cave length to evaluate predictions from a habitat selection model and surveyed 10 randomly selected caves per sub-group (Smith 2018). During 2018-2020, we temporarily excluded sites with 2 consecutive surveys without a bat observation. In 2019 and 2020, we temporarily excluded sites with lengths 15–35 m and ceiling heights ≥1.5 m based on habitat modeling results that indicated such sites were unlikely to contain large numbers of bats (Smith 2018).

We also allowed sites to be surveyed opportunistically. Personnel conducted opportunistic surveys when they had to enter sites during winter for purposes other than a bat survey. Consistent with area frame surveys in other dual-frame monitoring applications (Duchamp et al. 2012, D'Auria et al. 2018), we also allowed opportunistic surveys of additional nearby sites when a site in a remote region of the park had been randomly selected for survey.

TABLE 1 Number of sites surveyed for Townsend's big-eared bats annually at Lava Beds National Monument in California, USA, during 2013–2022. Presented are the number of sites in the known frame (groups 1–3) and unknown frame and sites that were excluded from selection permanently and temporarily for a given year. We stratified known frame groups based on number of bats counted during previous surveys: group 1 had ≥30 bats, group 2 had 6–29 bats, and group 3 had 0–5 bats.

	Known frame					
Year	Group 1	Group 2	Group 3	Unknown frame	Permanent exclusion	Temporary exclusion
2013	9	22	54	673	33	21
2014	10	23	62	659	37	21
2015	10	23	79	637	44	19
2016	10	17	96	623	46	20
2017	8	22	50	447	272	13
2018	11	23	51	316	280	131
2019	11	32	88	94	301	95
2020	11	30	77	51	559	84
2021	9	30	85	153	535	0
2022	8	30	90	149	535	0

We included surveys of opportunistically selected sites in our estimation process because their selection was unbiased (i.e., caves were not selected according to expectations about number of bats) and they facilitated efficient use of personnel.

Field surveys

During each annual survey effort, we conducted a single survey at each selected site and considered this a census of all bats hibernating at the site. Hibernation counts could be conducted any time between 15 November and 15 March, a period during which bats largely remain in hibernacula, but most counts (>95%) occurred during a single week in early January through mid-February. Personnel entered caves using appropriate personal protective equipment (e.g., helmets, gloves, knee pads) and survey equipment (e.g., headlamps, handheld spotlights, binoculars) and tallied all hibernating bats observed visually. Townsend's big-eared bats are the most prevalent species hibernating in LBNM caves and are generally easy to distinguish from other species of bats that occasionally hibernate in these caves (e.g., big brown bat [*Eptesicus fuscus*], *Myotis* spp.) because of their body shape, posture, conspicuously large ears (when unfurled), and propensity to hibernate on exposed ceilings and walls as opposed to within cracks and crevices. Townsend's big-eared bats at LBNM hibernate singly or in small groups of generally <20 individuals; we occasionally observed clusters of 30-65 individuals in the 2 largest hibernacula. Small aggregations of bats are ideal for using visual counts to estimate number of individuals (Kunz 2003). Alternatively, it is likely that bats roosting singly or in small groups could be missed, particularly in larger caves or those with high ceilings. We assumed that error associated with missing small numbers of bats in individual caves was consistent over the monitoring period.

Population estimates

We generated a monument-wide estimate of hibernating Townsend's big-eared bats by summing either an actual or estimated count for each site annually. If a site was surveyed in a given year, we included that count in the annual monument-wide estimate. If a site was not surveyed in a given year but had been surveyed in other years, we assigned it the mean (and variance) of all other counts at the site. For example, estimates for sites not surveyed in 2016 were based on any surveys conducted during 2013-2015 and 2017-2022. This includes sites that were added to the database during our study. For sites surveyed on 1 other occasion, we set the variance equal to the count, consistent with a Poisson distribution. We calculated annual estimates of mean and variance for each site type based on survey results from all other years and applied them to sites that had never been surveyed.

We assigned an inclusion probability to each site in each year. For sites in group 1 and those surveyed opportunistically, we assigned an inclusion probability of 1 because they were certain to be surveyed. For sites that we permanently or temporarily excluded, we assigned an inclusion probability of 0 because they were certain to not be surveyed in that particular year. For the monument-wide population estimate, we summed the actual counts of all sites with an inclusion probability of 1 and summed the estimated count for all sites with an inclusion probability of 0. Sites in exclusion frames were included in population estimates as either mean and variance of all other counts conducted at the site or by applying the annual estimate for number of bats at the appropriate site type.

For sites with an inclusion probability between 0 and 1 (groups 2, 3, and unknown frame) we used simple random sampling and ratio-estimation (Cochran 1977) within each group. Ratio estimation uses available information about each site to obtain a more precise estimate. Specifically, each site is assigned an auxiliary count that is roughly proportional to the actual count. When available, we used the mean of previous years' counts for a site. For sites that had not been surveyed, we used the mean count from sites of the same site type. Thus, we had an auxiliary count for each site whether it had been surveyed or not. For sites randomly selected for survey, we multiplied the count by the ratio of the mean of the actual counts to the mean of the associated auxiliary counts. Specifically, for N_i sites in group i, the auxiliary counts prior to any sampling for the jth site in that group was X_{ij} and the total of the auxiliary counts for group i was:

$$X_i = \sum_{j=1}^{N_i} X_{ij}.$$

A simple random sample of n_i sites was selected from each group and the observed numbers of bats in the jth selected site was y_{ij} and its corresponding auxiliary count for years when it was not selected was x_{ij}. The respective means were:

$$\overline{y}_i = \frac{1}{n_i}\sum_{j=1}^{n_i} y_{ij} \quad \text{and} \quad \overline{x}_i = \frac{1}{n_i}\sum_{j=1}^{n_i} x_{ij}.$$

The estimated number of bats in group i was:

$$\hat{B}_i = X_i \frac{\overline{y}_i}{\overline{x}_i}.$$

An estimate of the variance of $\hat{B}_i$ was

$$\hat{\sigma}^2_{\hat{B}_i} = \frac{N_i^2\left(1 - \frac{n_i}{N_i}\right)}{n_i(n_i - 1)} \sum_{j=1}^{n_i} \left(y_{ij} - x_{ij}\frac{\overline{y}_i}{\overline{x}_i}\right)^2.$$

We assumed the estimated number of bats in group i from the sites excluded from selection in a given year to be missing at random and we adjusted the estimate for that subset of sites with the same multiplicative factor that we used in the construction of $\hat{B}_i$ and labeled it $\hat{U}_i$. To account for the variability by using $\hat{U}_i$, we used the sum of the auxiliary counts as the associated variance $\hat{\sigma}^2_{\hat{U}_i}$. This is equivalent to assuming a Poisson distribution for those excluded sites.

The monument-wide estimate for number of hibernating bats was estimated to be:

$$\hat{b} = \sum_i (T_i + \hat{B}_i + \hat{U}_i),$$

where:

T_i = the number of bats in group i sites surveyed with probability 1,
$\hat{B}_i$ = the estimated number of bats in sites subject to a random sample (i.e., groups 2, 3, and unknown), where probability was proportional to number of sites in each group, and
$\hat{U}_i$ = the estimated number of bats in group i that were excluded from selection.

We considered the estimated variance for T_i to be zero. So, the monument-wide variance estimate was $\hat{\sigma}^2 = \sum_i \hat{\sigma}^2_{\hat{B}_i} + \hat{\sigma}^2_{\hat{U}_i}$. We calculated the approximate 95% confidence interval for the number of bats as $\hat{b} \pm 1.96\hat{\sigma}$. We performed all calculations using R (R Core Team 2021). We used a simple linear regression model to produce a parsimonious summary statistic of population trend using the lm function in R (R Core Team 2021) while acknowledging that the true trend may not be linear.

Simulation exercise

We conducted a simulation study to evaluate how the ratio estimation procedure compared to other possible sampling approaches in terms of population estimate precision and shape of the distribution (symmetrical about central estimate or skewed). To do so, we generated hypothetical annual populations of bats based on results of surveys from the 812 sites at LBNM. When a site had been surveyed in a particular year, we used the count from that survey. For sites that had been surveyed previously but not the given year, we generated a count from a Poisson or negative binomial distribution seeded by values of previous counts. For sites that had never been surveyed, we generated a count from a Poisson or negative binomial using the mean and variance from counts of other sites of the same type (e.g., cave, surface tube). We used a Poisson distribution when mean and variance were approximately equal and used a negative binomial when variance was much larger than the mean. Each site retained its actual group status for each year, including if it was moved to the exclusion frame. For each year, we selected 71 sites that approximated our mean annual survey effort of 73 surveys but resulted in an integer number of surveys. We used 3 sample selection schemes: A) simple random sample from all sites, B) original 8 group 1 sites were sampled and the 63 remaining surveys were allocated via a simple random sample without replacement from the remaining sites, and C) original 8 group 1 sites were sampled and the remaining surveys were allocated from 21 sites each from groups 2, 3, and the unknown frame, mimicking what was done in practice. For sampling scheme A, we estimated the population by multiplying the mean counts of selected sites by the 812 sites at LBNM. For sampling scheme B, we added counts from group 1 caves to the mean counts of selected sites multiplied by 804. We used 2 different estimation procedures for sample scheme C. We used a weighted sample means approach that added counts from group 1 sites to the sum of the number of sites in each group times the mean of the observed counts in the respective group. The second approach was the ratio estimation approach described above for our monument-wide population estimate. For each year and scenario, we used the constructed annual hypothetical populations and ran 10,000 sampling simulations to determine how each combination of sampling scheme and estimation method performed.

RESULTS

Survey results

During 2013-2022 we conducted 731 surveys of 331 sites, including 244 sites that had not been surveyed prior to 2012 (Table 2). Sites searched included 200 caves, 93 surface tubes, 10 bridges, and 28 non-caves. Of the 123 opportunistic surveys, 11 were at group 2 sites, 36 were at group 3 sites (20 of which had a previous count of zero), and 64 were sites from the unknown or exclusion frames. Prior to application of our adaptive sampling regimen in 2013, winter surveys had been conducted at 102 sites, of which 55 contained hibernating bats; 37 had ≥5 bats, 22 had ≥10 bats, and 8 had ≥30 bats. By the end of 2022, winter surveys had identified 122 sites that contained hibernating bats: 61 sites with ≥5 bats, 42 with ≥10 bats, and 13 with ≥30 bats (Figure 1). The number of hibernating bats counted during 2013–2022 ranged from 1,166 in 2021 when the fewest (n = 13) surveys were conducted to 1,792 bats in 2016 when the largest number sites were surveyed (n = 119). Counts at the original group 1 sites comprised 72–86% of the number of bats counted in 2013–2022.

We conducted 123 surveys at 93 of the 266 surface tubes at LBNM. No bats were observed in 73 surface tubes, a single bat was in 9, 2 bats were in 5, and 3-7 bats were in 6 of the surface tubes. We conducted 17 surveys at 10 of the 22 bridges at LBNM; we observed a single bat at 2 of the bridges and no bats during the other 15 surveys. We conducted 35 surveys at 28 of 208 non-caves; we observed a single bat during 1 survey and no bats during the other 34 surveys.

We calculated that, on average, 2.30 bats would be in each unsurveyed cave, but annual estimates ranged from 1.0–2.9 for 2013–2022 and standard deviations were high (Table 3). We estimated that each unsurveyed surface

TABLE 2 Number of sites surveyed for Townsend's big-eared bats annually at Lava Beds National Monument in California, USA, during 2013-2022. Presented are the number of sites surveyed for the first time and sites that had been surveyed in a previous year, whether sites were probabilistically or opportunistically selected, and number of each site type surveyed annually.

		Site status		Selection type		Site type			
Year	Surveys	Previous	New	Random	Opportunistic	Caves	Bridges	Surface tubes	Non-caves
2013	55	33	22	37	18	43	1	9	2
2014	88	56	32	60	28	61	4	17	6
2015	83	56	27	72	11	43	4	21	15
2016	119	77	42	96	23	68	5	34	12
2017	73	59	14	62	11	62	1	10	0
2018	86	32	54	80	6	64	0	22	0
2019	69	52	17	65	4	57	2	10	0
2020	72	53	19	71	1	72	0	0	0
2021	13	13	0	0	13	13	0	0	0
2022	73	56	17	70	3	73	0	0	0

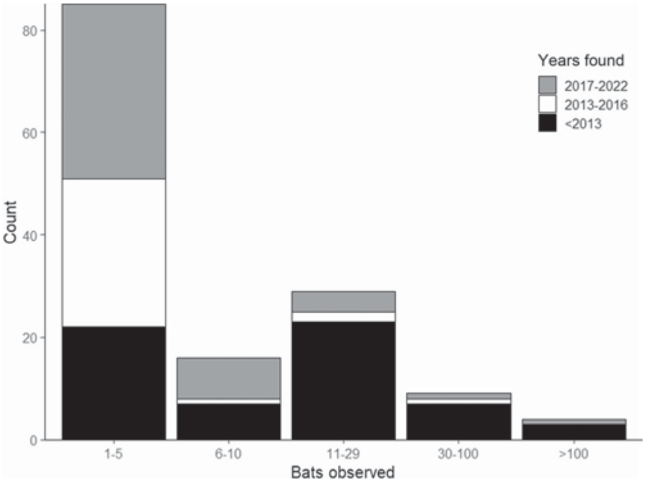

FIGURE 1 Number of hibernacula discovered in Lava Beds National Monument in California, USA, and the number of Townsend's big-eared bats using them during 3 survey periods: prior to our dual-frame approach (<2013), during 2013–2016 when all sites were surveyed regardless of site type, and 2017–2022 when sites were screened according to site type.

tube contained an average of 0.48 bats (annual range = 0.36–0.57), and that a single bat would be in 1 of 5 unsurveyed bridges and 1 of every 25 non-caves.

Population trends

Annual estimates for the number of hibernating Townsend's big-eared bats at LBNM ranged from 1,774 ± 93 (SE) bats in 2022 to 2,582 ± 68 bats in 2015 (Figure 2). We estimated that over the 10-year sampling period, an

TABLE 3 Annual estimated counts (SD) of Townsend's big-eared bats at Lava Beds National Monument in California, USA, during 2013–2022 at unsurveyed site types calculated using count results from surveyed site types. When site type was unknown, we applied the estimate for caves.

	Year										
Site type	2013	2014	2015	2016	2017	2018	2019	2020	2021	2022	Mean
Cave	2.66 (10.69)	2.82 (10.98)	2.57 (10.53)	2.79 (10.94)	2.37 (10.23)	2.32 (11.70)	2.71 (10.90)	1.77 (4.35)	2.54 (10.38)	2.84 (11.21)	2.30
Surface tube	0.46 (1.18)	0.36 (0.99)	0.52 (1.29)	0.57 (1.35)	0.51 (1.27)	0.45 (1.22)	0.52 (1.26)	0.48 (1.23)	0.48 (1.23)	0.48 (1.23)	0.48
Bridge	0.11 (0.33)	0.14 (0.38)	0.11 (0.33)	0.17 (0.41)	0 (0)	0.1 (0.32)	0.1 (0.32)	1.0 (1.0)	0.1 (0.32)	0.1 (0.32)	0.19
Not cave	0.04 (0.04)	0 (0)	0.07 (0.07)	0.06 (0.06)	0.04 (0.2)	0.04 (0.2)	0.04 (0.2)	0.04 (0.2)	0.04 (0.2)	0.04 (0.2)	0.04

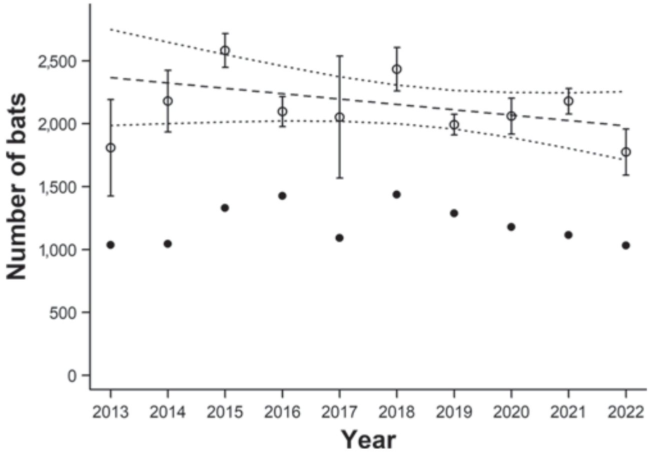

FIGURE 2 Annual estimates (open circles with standard error bars) of the number of Townsend's big-eared bats hibernating at Lava Beds National Monument in California, USA, during 2013–2022. The dashed line indicates the linear trend in estimates over this period and dotted lines show the 95% confidence interval on this trend. Filled circles represent the total of raw counts of hibernacula with ≥30 bats that were known in 2013 (group 1).

average of 2,116 (mean SE = 122) bats hibernated at LBNM. Annual sampling variance was 14,958 bats and total variance, which includes both sampling variability and annual natural variability in the population, was 62,201 bats, meaning that sampling variability represented 24.0% of the variability. Mean annual estimates fluctuated by up to 22% around the 10-year mean estimate, and annual population estimates ranged from 19% lower to 21% higher than the previous year (Figure 2). Over this same period, annual changes in the count from the original group 1 sites ranged from 31% lower to 24% higher than the previous year. The magnitude, and even direction, of percent change in group 1 totals and monument-wide population estimates were not always consistent (Figure 2). Slope estimates from the linear model of trend averaged −2.0%, but the 95% confidence interval overlapped zero (−5.0–1.0%), indicating no evidence of trend in the population during 2013–2022. We used the slope of the linear regression to summarize the overall trend during the study period while acknowledging that the trend in annual population estimates may not be linear. Further, the induced correlation among the annual estimates violates the assumptions of independence among residuals, but we assumed this would not have a large effect.

Sample scheme simulations

Applying the ratio estimation approach to the site selection scheme used at LBMN (sample scheme C) resulted in precise and accurate estimates of the constructed populations that improved over time (Figure 3). Using our site selection scheme but using weighted sample means rather than ratio estimation tended to provide somewhat less precise estimates particularly in later years. During 2013–2018, weighted sample means and ratio estimation estimates tended to be negatively skewed relative to the true population. This was because more non-cave site types were available to be selected in those years (Table 1) and most of these had few or no observed bats. Simple random sampling from all sites provided highly variable and negatively skewed population estimates. Simulations showed that though the accuracy of estimates that used simple random sampling from all but the group 1 sites was similar to weighted sample and ratio estimation approaches, estimates were more variable.

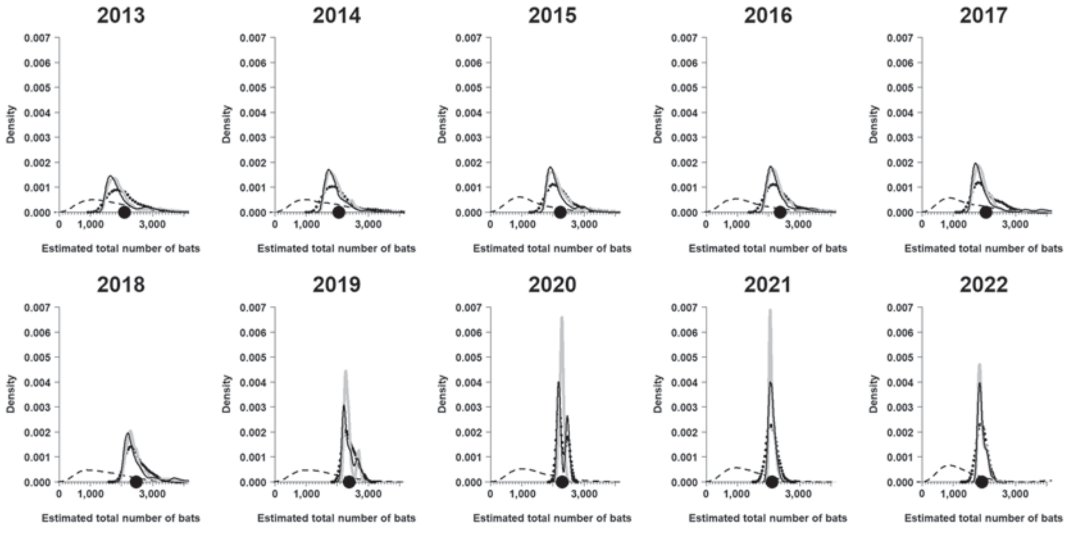

FIGURE 3 Results of 10,000 simulations per year for 4 approaches to estimating the number of Townsend's big-eared bats hibernating in 812 sites at Lava Beds National Monument in California, USA. Simulations assumed that 71 surveys were conducted each year. The large dot represents the true simulated population. The dashed line is simple random sampling of all sites (scheme A), the dotted line is surveys of the original 9 caves that contained ≥30 bats as of 2013 (group 1) and simple random sampling of the remaining sites (scheme B), the solid black line is surveys of group 1 sites with an equal sample from other groups using weighted sample means (scheme C—weighted sample means), and the solid gray line is surveys of group 1 sites with equal sampling from other samples using a ratio estimation approach (scheme C—ratio estimation).

DISCUSSION

Population trends

There was considerable variability among annual estimates but no evidence of a consistent trend in a population of bats hibernating in a large system of cave hibernacula at LBNM. Demonstrating linear trends in populations, especially from relatively short time-series datasets, can be challenging as these datasets are likely to be more reflective of fluctuations in response to annual stressors (Wauchope et al. 2019). Annual population fluctuations in other studies of hibernating bats have been attributed to annual changes in weather or prey availability without leading to persistent trends in population size (Ransome 1989, Humphrey and Olli 2015) and this appears to be the case at LBNM.

The relatively long lifespans of bats (Barclay and Harder 2003) make it likely that long-term data will be necessary to detect population trends unless they are influenced by acute stressors (Frick et al. 2010, Wauchope et al. 2019). This underscores the need for multiple years of baseline data, like those presented here, to better understand inherent variability in population estimates over time (Ingersoll et al. 2013, Fournier et al. 2019). Studies of shorter durations implemented to understand population changes in hibernating bats will be challenged to apportion stressor-related changes as opposed to normal population variability, except where changes are obvious (Thogmartin et al. 2012).

Small- and medium-sized hibernacula appeared to be influential to the overall population estimate and variability at LBNM (Figures 1 and 2), which supports the conclusion that assessments that focus only on large hibernacula can lead to biased population estimates (Fournier et al. 2019). Reliance on sentinel sites as an index to population trend is a common approach to monitoring, especially in the face of limited resources (Calkins et al. 1999, Weller et al. 2014, Whiting et al. 2018). Thus, a reasonable strategy for LBNM could have been to continue annual surveys of the original group 1 caves that comprised 57% of our annual population estimate, but only if interannual site fidelity to these sites was high (Thogmartin et al. 2012). While high site fidelity has often been assumed for hibernating bats, that assumption is far from perfect (Norquay et al. 2013, Humphrey and Oli 2015). Thogmartin et al. (2012) addressed this assumption by generating estimates for clusters of potential hibernacula within 16-km buffers around known hibernacula. At LBNM, which has hundreds of caves in close proximity, including in the nearby surrounding landscape outside the monument, we expected fidelity to individual caves would be lower than in other systems. In addition, subtle changes in population dynamics, such as a change in use of smaller hibernacula, may not be observable if the focus is only on larger hibernacula.

The dual-frame sampling approach also allowed us to increase the number of medium and large hibernacula discovered and surveyed at LBNM, which resulted in more accurate population estimates with less variance. For example, we were able to recruit 3 new hibernacula into group 1 (≥30 bats) and 10 new hibernacula into group 2 (6–29 bats) during our study, which improved the completeness and accuracy of our population estimate. Notably, we recruited a site from the unknown frame in 2020 that contained 112 bats, making it the fourth largest hibernaculum at LBNM. Group 1 sites are managed with year-round closure to the public to protect bats and hibernaculum conditions so identifying large hibernacula is an important management objective. Continuing to sample prospectively from the unknown frame, will improve the accuracy and, ultimately, the precision of population estimates as the range of variation in number of bats present in unsurveyed sites is quantified.

We were not able to formally estimate intra-annual variability in counts at individual caves. We considered 2 methods for doing so: multiple counts in a cave in a single year and independent counts by multiple observers during a single visit. Independent counts were not feasible because multiple surveyors would likely take cues from each other as they shone lights or lingered longer in certain areas indicating that bats may be present. We also rejected use of multiple counts per winter because of concerns about disturbing bats. Although previous research reported that 1–3 annual counts do not negatively influence bat population growth rates (Kilpatrick et al. 2020) and likely do not result in additional energy-depleting arousals for many individuals (Boyles 2017), we chose not to risk additional arousals that may lead to overwinter mass loss and lower survivorship, especially if populations face additional stressors (Boyles and Brack 2009). Although imperfect from a statistical perspective, use of a single, uncorrected, count at individual structures is a safe, defensible protocol for monitoring changes in abundance and factors affecting populations (Boyles 2017, Wauchope et al. 2019, Kilpatrick et al. 2020). Nevertheless, occasional repeated counts during the same winter at selected sites should be considered to help address this potentially important source of variability.

Development and maintenance of the sample frame

Typically, dual-frame sampling is used in a site occupancy framework to identify unknown occupied sites and combine them with information on known sites to estimate the number of occupied sites in a population (Shyvers et al. 2018). To generate a population estimate for Townsend's big-eared bats, we required information on whether individual sites were occupied by bats and how many bats were present at the site annually. Our unknown frame was a list frame of discrete sites that had not previously been surveyed for bats as opposed to standard-sized units of area that are searched to detect resources of interest as has been done in other systems (Van Meter et al. 2008, D'Auria and Otto 2018, Shyvers et al. 2018). A dual-frame sampling strategy was well-suited to our situation because we could stratify the known and the unknown frame of unsurveyed sites. This was important because LBNM sought to maintain the existing monitoring effort, based largely on surveys at sentinel sites, as we transitioned to an adaptive population monitoring program.

Originally, our unknown frame was unstratified; all sites, regardless of type, were randomly selected for survey. With >600 unsurveyed sites in the unknown frame, it was infeasible to survey all of them and we anticipated that not all site types would have equal probability of containing large numbers of hibernating bats. Survey effort costs were relatively high for infrequently used site types (surface tubes, bridges, non-caves) on a per bat basis, meaning fewer resources were available for surveys of sites with medium and large numbers of hibernating bats that had greater influence on population estimates. Hence, we refined our unknown frame adaptively as we quantified the range of expected bat abundance values by site type during the first 3 years of our study. For example, after 81 surveys of surface tubes, we began replacing field surveys with empirically generated estimates in 2017. In doing so, we excluded several hundred surface tubes from future surveys, thereby greatly reducing the number of sites in the unknown frame while at the same time accounting for the small number of bats that were occasionally observed in surface tubes. A similar strategy was employed in dual-frame sampling of greater sage-grouse (*Centrocercus urophasianus*) leks; randomly selected sample units were often unsuitable for sage-grouse, and these were excluded from surveys (Shyvers et al. 2018).

The development of an exclusion frame was important to our program for human safety and protection of fragile natural and cultural resources, and for improving survey efficiency by removing sites unlikely to contain large numbers of bats. Most excluded site types contained very few bats and count variability was low, so we assumed any change in bat abundance at these sites would have a limited effect on population trends. Systematic changes in roosting behavior that alter use of excluded site types over time could bias trend estimates (Miller et al. 2012), but we presumed that such changes would also be apparent during surveys of randomly selected group 3 sites (previous count 0–5 bats), which might trigger re-surveys of some excluded sites to determine whether similar phenomena were occurring in them.

Maintenance of sample frames is important to the success of dual-frame approaches (Watts and Duerr 2010, Sauer et al. 2011). We considered our sample frames dynamic and expected change based on results observed annually. At the conclusion of each winter sampling period, we used survey results to reassign each site to the appropriate sample frame and stratum for the following winter; thus, we simultaneously increased survey efficiency and reduced uncertainty around the population estimate by allowing allocation of more effort to surveys of hibernacula with higher abundance and variability and increasing probability of adding previously unknown hibernacula to our known frame. Apportioning approximately 30% of annual effort to sites that had not previously been surveyed was an efficient means of adding high abundance hibernacula to the pool of surveyed sites. More surveys of caves with larger numbers of bats should narrow confidence intervals in annual population estimates and, ultimately, reduce the costs of the monitoring program (Watts and Duerr 2010).

Our sampling approach also accommodated opportunistic surveys, which increased the number of sites surveyed annually and helped reduce the number of sites in the unknown frame. For example, when a randomly selected site required a long hike, we gained efficiencies in our field sampling by allowing opportunistic surveys of other caves in that area. Similarly, surveying sites visited for other management reasons enhanced our monitoring with negligible extra effort. The need to multi-task and creatively derive efficiencies is common in most natural resource management contexts. The addition of opportunistically identified sample units to list frames has been used to supplement population monitoring in other contexts (Raphael et al. 2007, Shyvers et al. 2018). The key to doing so rigorously is the ability to account for probability of selection. Following inclusion in the population estimate with selection probability of 1 during their initial survey year, we assigned sites to the appropriate stratum of the list frame thereafter. Because opportunistic sites were not selected based on expected bat abundance, they were an unbiased means of improving efficiency of annual monitoring efforts.

Monitoring can be more effective and efficient if site selection probabilities are weighted toward sample units with higher expected abundances (Miller et al. 2012, U.S. Fish and Wildlife Service 2020) or where resources have higher probabilities of detection. We stratified our known frame for this reason. Except for excluding certain site types, we had little ability to weight selection of unsurveyed sites. Modeling approaches have identified associations between hibernacula use, land cover types, and structural characteristics of caves and mines at broad spatial scales (Sherwin et al. 2003, Russell et al. 2014); however, these relationships remain poorly understood, particularly in western North America (Sherwin et al. 2003, Hayes et al. 2011). Attempts to use finer-scale features such as cave characteristics to prioritize winter survey effort based on expected abundance is an even larger challenge. For example, modeling approaches using a suite of site-specific cave characteristics was not effective for predicting abundance of hibernating bats at LBNM (Smith 2018).

Standardized survey timing

Intra-seasonal changes in bat abundance at individual sites introduces another challenge in estimating population trends based on a census of multiple sites (Ingersoll et al. 2013), which is of particular concern near the beginning or end of winter as bats are arriving or departing hibernacula (Calkins et al. 1999). In addition, inter-hibernacula movements during winter may reduce accuracy of population estimates if the survey period extends over many weeks because individuals may be counted more than once or not at all. This potential bias can be addressed by surveying many sites over a limited number of days (Boyles et al. 2006). The opportunity for inter-hibernacula movements at LBNM is high because of the density of available sites and the likelihood that individuals may be familiar with several of them. To address these issues, we scheduled a single hibernacula week in midwinter such that as many surveys as possible could be conducted during the period when we assumed bat abundance and site fidelity was highest and cave temperatures were lowest (Humphrey and Kunz 1976, Clark et al. 1997, Uhrin et al. 2010).

Establishing hibernacula week also generated regional enthusiasm, allowing us to recruit volunteer professional biologists keen to get underground and observe this charismatic bat species (Dambly et al. 2021). As a result, we were able to conduct more surveys than would have been possible using LBNM staff alone. Concerns about use of volunteers for such work include reliability of survey results and additional disturbance to hibernating bats (Stapelfeldt et al. 2020, Dambly et al. 2021). To address this concern, provide for surveyor safety, and produce reliable counts, we recruited trained biologists and paired them with surveyors experienced with counting bats in this system. Use of volunteers in such situations has been demonstrated to expand the number of sites that could be sampled and generate reliable counts without inordinate disturbance of bats (Barlow et al. 2015, Dambly et al. 2021).

Selecting a sampling approach

Our simulation exercise demonstrated that the ratio estimation approach we used provided accurate and precise population estimates, particularly in later years when our site elimination and selection schema were most fully realized. The weighted means and even simple random sampling of sites, once group 1 was accounted for, also produced reasonably precise estimates. Either of these would be reasonable alternatives if the goal was simply to maximize precision of estimates and trends; however, we had multiple objectives including monitoring hibernacula that contained both large and small groups of bats to observe changes in behavior that may occur and prospecting for additional large hibernacula by surveying sites that have never been surveyed. Hence, our sampling scheme resulted in improved population estimates over time and should become even better in the future as new information is obtained about un-surveyed caves.

A dual-frame approach at larger scales

We see potential for expanding our monitoring approach to other systems where bats hibernate conspicuously in accessible structures such as caves, mines, or buildings. A systematic approach to improving the comprehensiveness of the known set of hibernacula in the eastern United States has been recommended as a means of improving understanding of spatial distribution and population size estimates (Ingersoll et al. 2013, Russell et al. 2014). Across western North America, >1,000 Townsend's big-eared bat hibernacula have been identified and surveyed (Weller et al. 2018). In other words, a *de facto* list frame exists that could be used as a starting point for initiating a range-wide dual-frame monitoring program for this species. Owing to challenges of assembling a comprehensive database of all caves and mines over the distributional range of the species, a more conventional dual-frame approach may be more tractable. Under such a schema, the collection of sample units likely to contain caves or mines would comprise the area frame and individual sample units could be selected from a statistical framework, searched for caves or mines, and then surveyed for bats. The 100-km^2 grid cell framework of the North American Bat Monitoring Program (Reichert et al. 2021) could be adapted readily for such a purpose. Our sampling strategy is well-suited to such an approach and could prove effective as a range-wide population monitoring program for Townsend's big-eared bat. Nevertheless, for most bat species in western North America that do not hibernate in caves or mines (Weller et al. 2014), alternative strategies will be necessary for monitoring their population status.

MANAGEMENT IMPLICATIONS

We transformed a compilation of surveys at opportunistically discovered sites into a statistically robust yet flexible monitoring program that generates reliable annual population estimates for Townsend's big-eared bats. We demonstrated that trends based on surveys at known sentinel sites did not always reflect trend in the broader population. The primary program improvement was implementation of a statistical framework that assigned annual site selection based on stratification of the known, unknown, and exclusion sampling frames. Other program improvements included prioritizing surveys of hibernacula with higher bat abundance, incorporating survey-informed estimates of bat abundance at lesser-used site types in population estimates, planning survey logistics to maximize number of sites surveyed with available personnel, and standardizing a narrow temporal survey window. Cumulatively, these improved the accuracy and efficiency of trend estimates, which is vital for ensuring that management decisions, such as managing public use of cave resources and prioritizing restoration actions, are made using the most reliable information available. Our analytical approach intentionally accommodates variability in annual survey effort. If few sites are surveyed in some years, there will be a greater reliance on estimates for individual sites and an associated increase in variance of the monument-wide estimate in those years, but a credible annual estimate will result. For natural resource management entities where changes in priorities and staffing are common, flexibility in the type and quantity of survey effort necessary to meet monitoring goals is essential.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

ETHICS STATEMENT

Our study adhered to relevant regulations and guidelines regarding the ethics of animal welfare. We observed animals *in situ* but did not handle them for this study. We followed established protocols for internal surveys of hibernacula and took precautions to avoid undue disturbance of hibernating bats.

DATA AVAILABILITY STATEMENT

Data will be uploaded to North American Bat Monitoring Program database pending approval by National Park Service and with names and locations of sites obscured.

ORCID

Theodore J. Weller http://orcid.org/0000-0002-2914-5225

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