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# Estimating sample size for landscape-scale mark-recapture studies of North American migratory tree bats

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Concern for migratory tree-roosting bats in North America has grown because of possible population declines from wind energy development. This concern has driven interest in estimating population-level changes. Mark-recapture methodology is one possible analytical framework for assessing bat population changes, but sample size requirements to produce reliable estimates have not been estimated. To illustrate the sample sizes necessary for a mark-recapture-based monitoring program we conducted power analyses using a statistical model that allows reencounters of live and dead marked individuals. We ran 1,000 simulations for each of five broad sample size categories in a Burnham joint model, and then compared the proportion of simulations in which 95% confidence intervals overlapped between and among years for a 4-year study. Additionally, we conducted sensitivity analyses of sample size to various capture probabilities and recovery probabilities. More than 50,000 individuals per year would need to be captured and released to accurately determine 10% and 15% declines in annual survival. To detect more dramatic declines of 33% or 50% survival over four years, then sample sizes of 25,000 or 10,000 per year, respectively, would be sufficient. Sensitivity analyses reveal that increasing recovery of dead marked individuals may be more valuable than increasing capture probability of marked individuals. Because of the extraordinary effort that would be required, we advise caution should such a mark-recapture effort be initiated because of the difficulty in attaining reliable estimates. We make recommendations for what techniques show the most promise for mark-recapture studies of bats because some techniques violate the assumptions of mark-recapture methodology when used to mark bats.

*Key words*: capture probability, Burnham joint model, lasiurines, mark-recapture, migration, recovery probability, survival

## INTRODUCTION

To assess changes in the condition of bat populations, biologists can monitor various population parameters, including abundance, population change, and survival (Kunz *et al.*, 2009; O'Donnell, 2009). A common sampling and analysis framework used to estimate such population parameters is mark-recapture methodology (Schwarz and Seber, 1999). However, a challenge to conducting such studies is determining the level of sampling required to produce reliable estimates, especially when sample size depends on many factors, including the detectability of the species, desired precision, and scope of study (Williams *et al.*, 2001). Although population size (abundance) is a popular parameter of interest, satisfying the assumptions for models of abundance is more challenging than for models of other parameters, such as survival or population change ($\lambda$) (White *et al.*, 1982). Alternately, survival is a parameter that can be estimated directly from mark-recapture studies, and model extensions provide estimates of $\lambda$ (Pradel, 1996).

Recently, the status of bat populations has been of particular interest because landscape-level impacts, such as wind energy development and white-nose syndrome, are reducing or threatening bat populations in North America (Kunz *et al.*, 2007*b*; Frick *et al.*, 2010*b*). Accurately assessing bat population status is challenging, primarily because of the difficulty in observing and detecting bats (Kunz *et al.*, 2009). Compared to other wildlife species, bats are problematic because they are small, cryptic, nocturnal, inconspicuous when active, and live in sometimes inaccessible habitats. These challenges have not deterred bat marking studies dating back to 1916 in which unique bands were attached to the arm or leg of a bat (Allen, 1921).

Bat marking studies provided insights into bat ecology and life history, including longevity, development, migration patterns, homing ability, sex ratios, and, to some degree, survival and population size (Ellison, 2008). In the United States, such studies became popular from the 1950s through the 1970s, during which time there were 173 published studies involving bat banding (Ellison, 2008). Bat banding continues to be used to study bat population ecology (Dobony *et al.*, 2011), and some studies have addressed populations of migratory bats (Schorcht *et al.*, 2009). Mark-recapture studies of migratory tree-roosting bats in North America might provide an opportunity for assessing declines that would be caused by increased wind energy development. Such a study would attempt to capture large numbers of migratory tree bats, mark them, and then attempt to reencounter them as live recaptures or dead recoveries at mortality sites, such as at wind turbine facilities.

The primary challenge to a continent-wide bat-marking study is overcoming the low detectability of bats (Weller and Lee, 2007) and dead bats (Kunz *et al.*, 2007*b*). If the intent is to monitor populations of migratory bats, and identify factors that increase or decrease populations, then it is necessary to determine sample sizes that can produce reliable estimates. Conducting a study that produces estimates with large confidence intervals (CIs) would expend much time and money (Field *et al.*, 2005; Nichols and Williams, 2006).

Our objective was to estimate the sample sizes necessary for assessing a decline in North American migratory bat populations and understand how recapture and recovery rates impact sample size and reliability of estimates. We assessed sample sizes required to diagnose 10% and 15% annual declines in bat survival, mimicking a mark-recapture study that might be conducted to assess bat declines at a landscape-scale. To accomplish this, we simulated a mark-recapture study of a declining bat population over four time periods. We ran simulations using various sample size categories and compared confidence intervals (CIs) between time periods, among time periods, and among simulations. Additionally, we conducted sensitivity analyses of necessary sample sizes to varying recapture and recovery rates.

## Materials and Methods

The Burnham joint model (Burnham, 1993) uses information from recaptures of live individuals and discovery of dead individuals and has been used to model survival in fish (Keefer *et al.*, 2010), mammal (Hall *et al.*, 2001), and bird populations (Barker and White, 2001). This model allows encounters of live bats, such as at mist netting efforts, and allows incorporation of dead individuals found at known mortality sites, such as wind energy facilities (Kunz *et al.*, 2007*a*, 2007*b*). Melding information from recapture and recovery efforts can produce more reliable estimates of population parameters (Catchpole *et al.*, 1998). The Burnham joint model includes the following population parameters:

$S_i$ — the probability a bat alive at time $i$ is alive at time $i$+1 (survival);

$p_i$ — the probability a marked bat that is available for capture is encountered at occasion $i$ (recapture probability);

$r_i$ — the probability a marked bat that died between $i$ and $i$+1, is found, and its band is reported (recovery or reporting probability); and

$F_i$ — the probability that a bat at risk of capture at $i$ is available for capture at $i$+1 (fidelity).

We used the Simulation tool in Program MARK version 5.1 (White *et al.*, 2001) to estimate sample size needed to detect a decrease in population survival rate over four separate marking periods. We define the time between marking periods as years, but it can be years or decades.

For the parameter estimates, we reviewed the literature to find a range of values that were reasonable for North American bats. There are few annual estimates of bat $S$, but there are estimates of apparent survival ($\varphi$), which is the product of $S$ and $F$. We surveyed the literature and found several estimates of $\varphi$ for North American bat species, including Townsend's big-eared bat (*Corynorhinus townsendii*) (0.54–0.76 — Ellison, 2010), little brown bat (*Myotis lucifugus*) (0.81 — Keen and Hitchcock, 1980; 0.63–0.90 — Frick *et al.*, 2010*a*), eastern small-footed myotis (*M. leibii*) (0.42–0.76 — Hitchcock *et al.*, 1984), tricolored bat (*Perimyotis subflavus*) (0.41–0.46 — Davis, 1966), big brown bat (*Eptesicus fuscus*) (0.47–0.85 — Beer, 1955; Hitchcock *et al.*, 1984; O'Shea *et al.*, 2011), and Yuma myotis (*M. yumanensis*) (0.73–0.89 — Frick *et al.*, 2007). Because $\varphi$ includes the probability of emigration it is typically less than $S$ (Lebreton *et al.*, 1992), thus we chose $S_1$ that was at the top of the range of estimated $\varphi$ ($S_1$= 0.9). We ran two survival decline scenarios with the first being a more gradual decline of 0.10 per year ($S_2$ = 0.8, $S_3$ = 0.7, $S_4$ = 0.6). This decline approximates an 11%, 13%, and 14% decrease for the respective $S$ rates, and a 33% decrease in initial $S$ for the entire sample period. A similar annual decline of 10% annually for landscape-scale studies of bird populations is considered a rapid decline (Green, 1999). We ran a more dramatic survival decline in which there was a 0.15 decline in $S$ annually ($S_1$ = 0.9, $S_2$ = 0.75, $S_3$ = 0.6, $S_4$ = 0.45). This decline approximates a 17%, 20%, 25% decrease, respectively, with a 50% decline overall. The decline scenarios used in this study are arbitrary, but used as a starting point for estimating sample size requirements.

There are few published reports of recapture success for migratory tree bats. In north Georgia, USA, Baker (1965) recaptured 0 of 81 tagged *Lasiurus borealis*. As part of a review of bat banding, we solicited recapture and recovery data from bat biologists throughout USA. Four biologists reported recapture rates for migratory tree-roosting bats, with the highest recapture rate being 34% (10 of 29) for the use of plastic split-ring bands on *L. cinereus.* This high recapture rate was a result of actively searching known roosts for a resident colony of *L. cinereus*, and did not require typical capture devices, such as mistnets (R. Barclay, personal communication). Three other accounts documented much lower recapture rates: 2% (seven of 314

*L. borealis*; J. O'Keefe, personal communication), 3% (15 of 560 *Lasionycteris noctivagans*), and 7% (two of 30 *L. borealis*; L. Robbins, personal communication).

The recapture rates for long-distance migrants in North America are comparable to rates for European long-distance migratory bats. Recapture rates for European long-distance migrants, including *Pipistrellus pipistrellus*, *P. nathusii*, *Nyctalus leisleri*, *N. noctula*, and *Vespertilio murinus*, and the regional migrant, *Miniopterus schreibersii*, range from less than 1% to approximately 10% (Gaisler *et al*., 2003; Hutterer *et al*., 2005; Bisson *et al*., 2009). In Steffens *et al*.'s (2004) summary of 40 years of bat banding coordinated by Bat Marking Centre Dresden in Germany, live refind rates were the greatest recorded, ranging from 16.6–59.4% ($\bar{x}$ = 28.8%). These high recapture rates were facilitated by some species' frequent use of bat boxes. In our simulations, we used three estimates of *P* (0.01, 0.05, and 0.10) that are comparable to the majority of documented recapture rates.

There is limited information on the recovery rate for marked, recovered-dead North American migratory bats, so we utilized recovery rates for European migratory bats. Carcasses of previously-marked bats (recoveries) of five European long-distance migratory bats were recovered at rates ranging from 0.2–1% ($\bar{x}$ = 0.4%) (Steffens *et al*., 2004). Therefore, in our simulations we used recovery rates of 0.5% and 1%, as well as a conservative 2% to illustrate the impact of recovery rate on sample size.

Since *F* is fidelity to the banding site, or the probability of remaining in North America and being at risk of being detected, it is a complicated parameter for bats and there are no estimates of *F* for bats. Since bats must be in the study area, within range of a capture device, and then observed, *F* should be much lower. We used an optimistic estimate of 0.30, which suggests that a tagged bat has a 30% chance of being at risk of detection the following sampling event.

We ran simulations using sample sizes of 1,000, 10,000, 25,000, 50,000, and 100,000 individuals marked and released each year, and modeled simulations using 1,000 runs. We used a simple model structure in which *P*, *r*, and *F* were constant, while *S* was modeled as temporally variable. We considered the simulation a failure when estimates of parameters failed to converge and produce reasonable estimates of variability (variability = 0 or > 1). Variability (standard error) was estimated by Program MARK for each parameter in each simulation.

Our test of necessary sample size (power) was the proportion of simulations in which there was no overlap in the 95% CIs between each of the four years (annual differences) and between the first and fourth year (Nakagawa and Cuthill, 2007). We chose a 4-year period because in bird mark-resight data sets, at least 3 years of data is generally required to estimate detection probability (Anders and Marshall, 2005). Declines after four years are biologically extreme; therefore, we chose four years for the simulations.

## Results

Assuming $P = 0.05$, $r = 0.01$, $F = 0.30$, sample size of 1,000 individuals annually was insufficient to detect 0.10 or 0.15 decreases in survival (Figs. 1 and 2). However, many simulation runs were unsuccessful. For a 10% decline in annual survival, failure rate using 1,000 marked individuals each

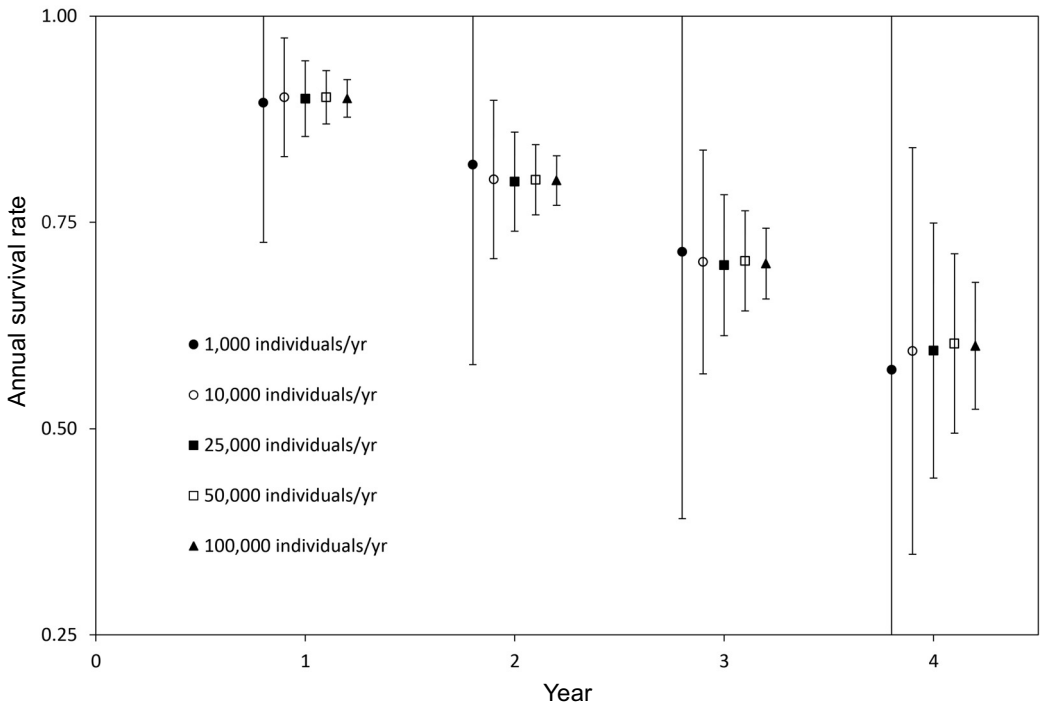


Fig. 1. Annual survival estimates (± 95% confidence intervals) from simulations of the Burnham joint model, assuming a decline in survival of 0.10 each of 4 years and sample sizes of 1,000, 10,000, 25,000, 50,000, and 100,000 individuals per year. The 95% confidence intervals for some estimates have been truncated at the *y*-axis maximum and minimum

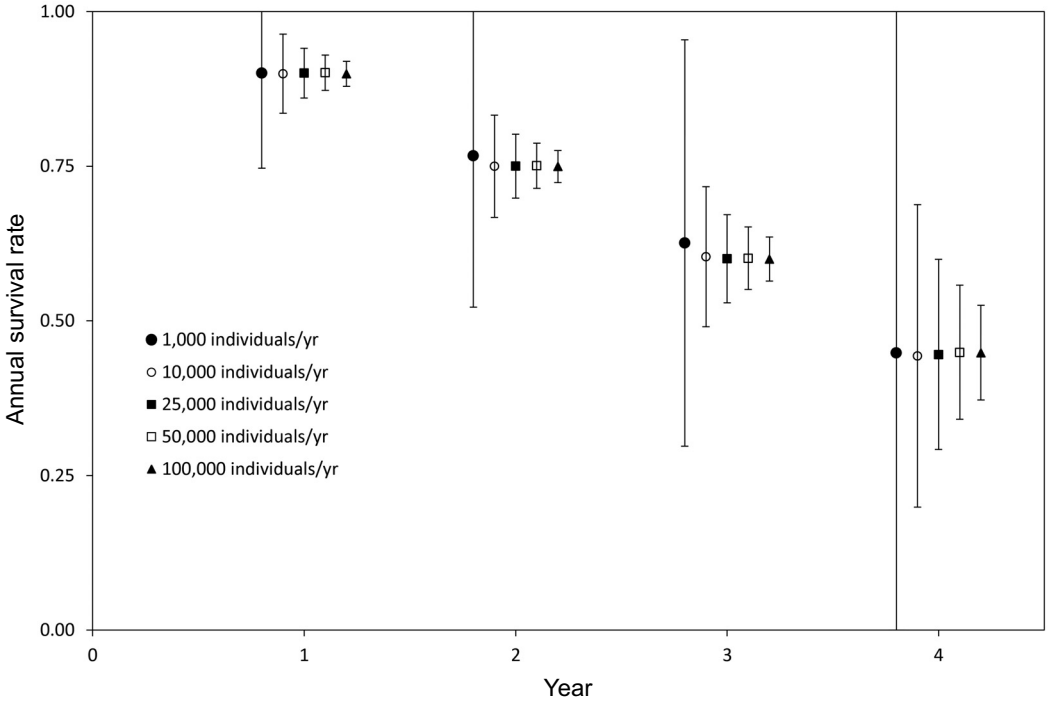


FIG. 2. Annual survival estimates (± 95% confidence intervals) from simulations of the Burnham joint model, assuming a decline in survival of 0.15 each of 4 years and sample sizes of 1,000, 10,000, 25,000, 50,000, and 100,000 individuals per year. The 95% confidence interval for one estimate has been truncated at the *y*-axis maximum

year was 42%. In other words, 42% of iterations lacked sufficient data to converge at parameter estimates. For a 15% decline annually, sample sizes of 1,000 individuals annually produce inaccurate and imprecise estimates (Fig. 2). Failure rate using 1,000 marked individuals per year was 36%.

At sample sizes of 10,000 individuals, the survival estimates for both the 10% and 15% annual declines are accurate, but do not allow detection of survival differences between years (95% CIs overlap) (Figs. 1 and 2). Failure rate using 10,000 individuals released each year was 1%. At 25,000 individuals annually and a 0.10 decline in survival annually, there is little power to detect differences between years (greatest power is 45%). For a 0.15 decline in survival, it is more likely (power > 75%) to detect annual survival differences, except between year 3 and 4 (power = 6%). Failure rate using sample sizes ≥ 25,000 individuals each year was 0%.

Using 50,000 individuals annually, the power to detect annual declines of 0.10 or 0.15 in survival is greater (>89% between years 1 and 2 and > 41% between years 2 and 3 — Table 1). However, power to detect survival declines of 0.10 and 0.15 between years 3 and 4 would be difficult (power = 1% and 40%, respectively). When sample sizes become as large as 100,000 individuals, power to detect differences between years is high except between years 3 and 4 (power = 14%) when annual survival decrease is 0.10. When the annual decrease in survival is 0.15, the power to detect differences using 100,000 individuals per year is high (power > 95%) for all time periods.

It is easier to detect long-term (four years) changes in survival. For example, if the intent is to detect a 33% decline in survival over four years, a sample size of 25,000 per year likely would be sufficient (Table 1; power = 97%). If the goal is to detect a decline of 50% in survival over four years, 10,000 individuals per year would provide 96% power.

Increasing *p* improved the ability to detect differences between and among years when survival decreased by 0.10 annually (Table 1). When *p* is increased to 0.10 and 100,000 individuals are marked annually, the power to detect differences between most years is high, except for between years 3 and 4 (power = 37%) (Table 1). Similarly, as *r* is increased to 0.02 and 100,000 bats are marked annually, the power to detect annual survival differences of 0.10 between all years is high (100%), except for between years 3 and 4 (67% — Table 2).

Using optimistic parameter values we explored the power required to detect annual differences when

TABLE 1. Power (%) to detect differences in survival between years given different capture probabilities (*P*) and sample sizes per year (*N*/yr). Survival probability was 0.9, 0.8, 0.7, and 0.6 for years 1, 2, 3, and 4, respectively. Recovery probability (*r*) and fidelity probability (*F*) are held constant ($r = 0.01$, $F = 0.3$)

| *N*/yr | Time periods (yr) | | | |
|---|---|---|---|---|
| | 1–2 | 2–3 | 3–4 | 1–4 |
| | | $P = 0.01$ | | |
| 1,000 | 3 | <1 | <1 | 16 |
| 10,000 | 7 | <1 | <1 | 25 |
| 25,000 | 28 | <1 | <1 | 87 |
| 50,000 | 78 | 17 | <1 | 98 |
| 100,000 | 100 | 74 | 20 | 100 |
| | | $P = 0.05$ | | |
| 1,000 | 7 | <1 | <1 | 17 |
| 10,000 | 10 | 1 | <1 | 43 |
| 25,000 | 16 | 11 | <1 | 97 |
| 50,000 | 89 | 41 | 1 | 100 |
| 100,000 | 100 | 96 | 14 | 100 |
| | | $P = 0.10$ | | |
| 1,000 | 3 | 1 | <1 | 13 |
| 10,000 | 9 | 2 | <1 | 57 |
| 25,000 | 49 | 16 | <1 | 99 |
| 50,000 | 95 | 67 | 4 | 100 |
| 100,000 | 100 | 99 | 37 | 100 |

*S* declined 0.10 annually. With a large *P* (0.10), an optimistically large *r* (0.05), and the same *F* (0.3), the sample size could be 50,000 individuals per year to detect annual differences in *S*. Except for between years 3 and 4 (87% power), there is 100% power of detecting differences in survival between and among all years.

## DISCUSSION

Our simulations suggest that to adequately detect even large annual declines in migratory bat populations an extraordinary effort is required to capture and recapture live bats, and recover dead marked bats. For example, sampling 100,000 bats annually may allow biologists to document declines when severe (10% or 15% annually). Assessing large declines over multiple years is more feasible, but still requires handling and marking 25,000 bats annually. The annual declines used in our simulations are relatively large (10%); thus, if true annual declines in bat populations are less, then our projected sample sizes would be insufficient. The effort required to capture and mark tens of thousands of bats may be better spent improving detectability of animals once they are marked.

Our results suggest that the key to successful mark-recapture investigations of bats is increasing detectability of live and dead individuals (Tables 1 and 2). For example, increasing *P* from 0.01 to 0.10 when *S* declines 10% annually means increasing the likelihood of detecting population decline over four years from 87% to 99% when sampling 25,000 bats annually. For migratory tree bats in North America, detection is complicated because individuals roost singly in trees and cannot be sampled at large roosting colonies, as has been done for many cavernicolous bats (Carter *et al.*, 2003). In our simulations, doubling *P* increased power, but not as dramatically as doubling our proposed *r* value (Table 2). This suggests that improvements to detection of dead bats at mortality sites can be valuable for reducing sample size and improving precision of estimates. Such improvements may be difficult because when searching for dead bats at wind turbine sites only about half of bat carcasses are found (Kunz *et al.*, 2007*a*; Arnett *et al.*, 2008). Ultimately, detectability drives the precision of the population parameter estimates and the necessary sample size (Burnham *et al.*, 1987). When recapture rates are high, not only are precise estimates of bat survival feasible, but comparisons of survival among bat species and among seasons can be accomplished with mark-recapture methods (Papadatou *et al.*, 2013; Giavi *et al.*, 2014). Although the required sample size seems dauntingly large, we believe the focus should be on

TABLE 2. Power (%) to detect differences in survival between years given different recovery probabilities (*r*) and sample sizes per year (*N*/yr). Survival probability was 0.9, 0.8, 0.7, and 0.6 for years 1, 2, 3, and 4, respectively. Capture probability (*P*) and fidelity probability (*F*) are held constant ($P = 0.05$, $F = 0.3$)

| *N*/yr | Time periods (yr) | | | |
|---|---|---|---|---|
| | 1–2 | 2–3 | 3–4 | 1–4 |
| | | $r = 0.005$ | | |
| 1,000 | 9 | <1 | <1 | 4 |
| 10,000 | 4 | 1 | <1 | 12 |
| 25,000 | 13 | 3 | <1 | 73 |
| 50,000 | 47 | 17 | <1 | 99 |
| 100,000 | 96 | 66 | 4 | 100 |
| | | $r = 0.01$ | | |
| 1,000 | 7 | <1 | <1 | 17 |
| 10,000 | 10 | 1 | <1 | 43 |
| 25,000 | 16 | 11 | <1 | 97 |
| 50,000 | 89 | 41 | 1 | 100 |
| 100,000 | 100 | 96 | 14 | 100 |
| | | $r = 0.02$ | | |
| 1,000 | 8 | 2 | <1 | 10 |
| 10,000 | 28 | 4 | <1 | 82 |
| 25,000 | 83 | 29 | <1 | 100 |
| 50,000 | 100 | 87 | 7 | 100 |
| 100,000 | 100 | 100 | 67 | 100 |

how to reduce the required sample size by increasing detectability and using modern analysis techniques to improve estimate of population parameters (Papadatou *et al*., 2013).

We advise caution when extrapolating these results to bat population monitoring programs. If the true parameter values for $P$ and $r$ are lower than those used in these modeling exercises, then necessary samples sizes to document declines are greater than projected in these simulations. Increasing $P$ and $r$ can improve power, but even when bats are present at some locations they can go undetected (Weller and Lee, 2007; Huso, 2011). Our simulations were designed to address the likely recovery and recapture opportunities for migratory species. Marking studies for communal roosting bats, in which individuals have high fidelity to an area that can be sampled effectively, should have higher $P$ and $r$. Thus, sample sizes may be smaller to produce more reliable estimates of survival and population change (O'Shea *et al.*, 2004; Schorcht *et al.*, 2009; Ellison 2010; Frick *et al.*, 2010*a*).

We elected to use a short time period (four years) to address the minimum time-increments we believe a landscape-scale population study should be conducted (Anders and Marshall, 2005). Because bats can live for multiple decades, population monitoring programs should span enough time to include the opportunity to encounter multiple generations at different ages. Increasing the number of sampling periods may increase the precision of survival estimates if detection and recovery probabilities are comparable to those used in our simulations. Long-term monitoring, in excess of the four years of our simulations, can identify time-specific impacts to populations and temporal trends in population abundance or survival (Ingersoll *et al*., 2013).

The choice of bat marking technique can impact sample size estimation. Passive integrated transponder (PIT) tags have been used extensively to study bat populations (Kerth and Reckardt, 2003; Neubaum *et al.*, 2005; Ellison *et al.*, 2007) with minimal tag loss, failure, or injury (Kerth and Konig, 1996; O'Shea *et al.*, 2004), but one study has shown high tag loss (Rigby *et al*., 2012). The use of bands is the most common marking method for bats, but may violate some of the assumptions for demography studies, including the assumption marked and unmarked individuals should have equal survival and capture probabilities and that the marking technique should not affect the individual's survival, capture probability, movement, or behavior (Thompson *et al.*, 1998; Kunz, 2003). Because injuries can be caused by metal and plastic bands (Lollar and Schmidt-French, 2002; Dietz *et al.*, 2006; Zambelli *et al.*, 2009), banding may violate both assumptions. Also, because bats may chew on the band, removing the unique markings (Trapido and Crowe, 1946; Bonaccorso *et al.*, 1976; Fleming, 1988) or removing the band entirely (Whitaker and Gummer, 2000; Frick *et al.*, 2010*a*), banding may violate the second assumption. Mark-recapture models can be robust to homogeneous (equally distributed among sampled individuals) PIT tag and band loss (Conn *et al*., 2004; Rotella and Hines, 2005), but when the recapture rates are low and when tag loss is heterogeneous, estimates of survival or abundance may be biased (McDonald *et al.*, 2003) and lose precision (Arnason and Mills, 1981; Rotella and Hines, 2005).

The feasibility of accurate estimates of bat population survival increases as the ability to detect marked individuals increases. Thus, as this study shows, increasing capture probability can decrease sample size. Improvements in the ability to recapture marked bats without handling via the use of PIT tags (Ellison *et al*., 2007; Adams and Hayes, 2008) may be ideal for monitoring populations because it can increase detections, reduce survey effort, and reduce handling stress for the animal. For example, if common roosts for North American migratory bats are detected, as has been done for various European species (Steffens *et al.*, 2004), then PIT tag readers can be installed to read tags as bats enter or exit such roosts. Additionally, if temporary roosts or activity centers are known (Cryan and Brown, 2007), then PIT tag readers may provide recapture data if installed near such roosts. One major problem with using PIT tags is cost, but this monetary hurdle may be outweighed by the benefits in quality of information if $P$ or $r$ can be substantially increased.

Recovering dead marked animals as small and cryptic as bats can be challenging. Most effort to recover dead bats has been focused at wind turbines that cause mass mortality (Hayes, 2013). However, even at these centers of bat mortality, discovery of dead bats is difficult because the unpredictability of how carcasses are distributed on the landscape, the ability of searchers to find carcasses, and the persistence of carcasses due to scavenging or decay (Kunz *et al*., 2007*a*). These challenges have led to novel search methods using canines (Arnett, 2006) and algorithms for estimating true mortality rate (Huso, 2011). As methods of detection ($r$) improve, the samples sizes for detecting population decline in migratory tree bats should decrease and, hopefully,

increase the precision of survival estimates. Our simulations indicate that increasing *r* can improve precision in survival estimation and reduce necessary sample size.

If the intent of a bat marking program is to estimate decline in a defined group of bats, and the only method of reencountering marked bats is via capture of live individuals or discovery of dead individuals, our simulations suggest the number of individuals marked and released each time period would need to be greater than 50,000. Although it may seem counterintuitive, we advocate for the use of mark-recapture techniques for understanding bat population ecology. The key to making mark-recapture studies of migratory bat populations economical and informative is improvements in the ability to detect marked bats. As illustrated in studies of some European migratory bats that show high philopatry to roosts (Papadatou *et al*., 2013; Giavi *et al*., 2014), there are methods of increasing estimates of detectability, and such improvements will reduce the required sample size for population studies.

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