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Performance of hierarchical abundance models on simulated bat capture data

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The ability to accurately estimate abundance is crucial to ecologists, conservationists, and managers to provide insight on species status, population trends, and viability. Acoustic detection and occupancy modeling can provide an understanding of resource use for bats, but these methods do not estimate how many bats are in an area, or how these numbers change over time. In North America, there is a heightened need to estimate bat abundance and trends in response to white-nose syndrome (WNS) and other threats to bat populations. We assessed the performance of the N-mixture model for repeated count data and the general multinomial-Poisson model for removal sampling to estimate bat abundance from simulated mist-net capture data. We evaluated performance under varying numbers of sites and visits, detection probabilities (*P*), and population sizes. We simulated four scenarios with a total of 85 combinations of parameter values each containing 1,000 replications. We used the UNMARKED package in R to fit the N-mixture and removal models. We calculated relative bias (RB), mean absolute error (MAE), and mean absolute percent error (MA%E) from model estimates to evaluate model performance. Relative bias, MAE, and MA%E decreased as p and bat abundance increased for all models. The removal model outperformed the N-mixture model in all scenarios except when $P = 0.05$. The N-mixture model had low RB, MAE, and MA%E when bat abundance was ≥ 70 and $P > 0.5$, but in other scenarios, errors were large. The mean of estimates from the removal model were unbiased and RB, MAE, and MA%E were very low for most scenarios. Use of the removal model with data from repeated mist-net surveys may allow resource managers and conservationists to better quantify how resource management and landscape composition affect bat species abundance and overall populations.

Key words: N-mixture models, multinomial Poisson models, removal sampling, abundance

Introduction

Wildlife management often requires estimates of animal abundance. Indices of abundance or estimates of site occupancy can be used to address ecological questions for wildlife. However, many conservation questions require knowledge of the actual number of animals such as those concerning species status. Species of conservation concern (SOCC), or those federally listed as threatened or endangered, are often the focus of studies to estimate abundance because of the need to understand factors driving their population numbers. Studies often seek to understand relationships between species abundance and specific habitat or landscape characteristics (Royle, 2004*a*), so they can inform conservation and management. Abundance estimates collected over time can be used to determine if species abundance is decreasing, increasing, or stable. Recent threats to bat populations in the eastern United States (e.g., white-nose syndrome, wind turbine fatalities, habitat destruction, etc.) provide heightened demand for methodologies that can estimate abundance at sites (Kunz *et al*., 2007; Puechmaille *et al*., 2011; Turner *et al*., 2011; Walters *et al*., 2013). Counts can be used as indices of abundance or used to estimate abundance by correcting for incomplete and variable detectability (Buckland *et al*., 2001; Rosenstock *et al*., 2002; Williams *et al*., 2002; Johnson, 2008). Analyses of relationships between abundance and environmental features can be confounded if detection probability (*P*) varies with the features being considered (Ruiz-Gutiérrez *et al*., 2010). Mark-recapture, removal, and distance-sampling methods are common approaches for estimating *P* and abundance (Buckland *et al*., 2001; Williams *et al*., 2002; Farnsworth *et al*., 2012). Accurately estimating abundance is challenging for rare species, species with low detectability, and species that are trap shy or avoid capture even if they are common on the

landscape and especially if *P* is variable or changes spatially and temporally.

Bats are difficult to count due to their cryptic behavior. Mark-recapture or distance sampling methods are largely not feasible for bats because of low recapture probabilities and it is difficult or impossible to measure distances to detections (Kunz and Kurta, 1988; Marques *et al*., 2013). For these reasons and others, bat studies usually have not attempted to measure abundance, and focus instead on site occupancy (MacKenzie *et al*., 2002; Amelon, 2007). Bat occupancy studies often use acoustic detectors to actively or passively record echolocation calls to determine the presence or non-detection of a species at a survey location (Yates and Muzika, 2006; Amelon, 2007; Marques *et al*., 2013; Walters *et al*., 2013; Starbuck *et al*., 2015). Even though abundance and occupancy are often related, bat occupancy studies only provide insight into resource use and cannot be utilized to estimate how many bats use an area, or how numbers change over time. Considering potential population impacts from WNS, wind energy, and anthropogenic changes to the landscape, we sought to provide guidance in examining the performance of new analytical tools for bat studies seeking to estimate species abundance.

Several methods exist for estimating abundance and detectability without individuals being marked or removed from the population, or measurements of distance (Kéry *et al*., 2005). These abundance models have been developed to account for rare species by allowing for low numbers of detections per site while incorporating meaningful site, habitat, and landscape covariates that influence *P* and abundance (Royle *et al*., 2004*a*, 2004*b*; Kéry *et al*., 2005). These models have potential utility in bat conservation and management because bat detection varies between sites based on habitat and landscape features, temporal factors, and abundance.

The N-mixture model for repeated counts and general multinomial Poisson model for removal sampling (hereafter N-mixture model and removal model, respectively) are potentially suitable for estimating abundance of bats from repeated mist-net surveys, and do not require distance measurements or mark-recapture to estimate abundance. The N-mixture model assumes a closed population between repeated visits at a site, and that species detectability across visits is independent. The removal model assumes that the population is closed, but that each repeated visit is dependent on previous visits. The removal model is a common survey method when estimating abundances in a closed population (Williams *et al*., 2002; Dorazio and Royle, 2003). Removal sampling requires that an individual must be removed from all subsequent visits at a site, either by physical removal from the population, marking captured individuals to remove from data, or by accounting for the reduction in trap-ability due to net avoidance behavior after initial capture (Williams *et al*., 2002; Royle, 2004*b*; Dorazio *et al*., 2005; Rigby, 2016). Removal can be achieved with bats by marking individuals with a unique wing band, hair clippings, or marking with a non-toxic marker that lasts the duration of the multiple visits to a site (Womack, 2017). The assumption that a population is closed between repeated visits should be met in summer bat studies (Veilleux and Veilleux, 2004; Menzel *et al*., 2005), especially if visits occur over consecutive nights during the maternity season. The assumption by the N-mixture model of independence between visits may be violated because bats exhibit net avoidance behavior after capture (Kunz and Anthony, 1977; Berry *et al*., 2004; Larsen *et al*., 2007). The removal model is not affected by net-avoidance behavior because only the first capture is used. Study design constraints (e.g., numbers of visits versus number of sites) and differences among species (e.g., rare versus common; high versus low *P*) could also affect the performance of N-mixture and removal models. The evaluation of models with simulated data is common in the literature as justification and validation of new analytical techniques for different taxa (Royle, 2004*a*; McCaffery *et al*., 2016; Rigby, 2016; Yamaura *et al*., 2016).

Models are available in the UNMARKED package in R that use count data to estimate *P* and abundance while incorporating meaningful site, habitat, and landscape covariates that could affect both *P* and abundance estimates (Royle *et al*., 2004*a*, 2004*b*). Several studies report success in predicting ecologically realistic abundance and density estimates for multiple bird species using models in UNMARKED (e.g., Reidy *et al*., 2014; Rigby, 2016; Roach, 2016). We sought to use several of these models to determine their utility in bat ecology.

We evaluated the application of N-mixture (Royle, 2004*b*) and removal models (Royle, 2004*a*) to estimate bat abundance from capture data. Our goal was to determine the utility of these two abundance models so that future studies might collect population demographic information beyond occupancy data to address the need for population demographic data over time to evaluate changes in population size. We simulated data to represent bat

captures from repeated mist-net surveys with known population sizes (Ń) and fit models to determine how accurately these models would estimate abundance. We evaluated the sensitivity of abundance estimates to the number of sites (Scenario 1), number of visits (Scenario 2), population size (Ń) and *P* (Scenario 3), and the effect of net avoidance behavior as represented by decreasing *P* at a site over time (Scenario 4). We designed scenarios to cover a range of parameter values that we considered possible based on a literature review and previous field studies of bat species and landscapes in the Eastern and Midwestern United States. We considered typical attributes of survey designs (number of sites and visits) as well as species' ecology (*P* and abundance) to help inform design and analyses in future studies.

Materials and Methods

Model Descriptions and Assumptions

We fit N-mixture models and removal models in R using the UNMARKED package with the pcount and multinomPois procedures, respectively (version 3.2 — Fiske and Chandler, 2011). We did not include any detection or abundance covariates but rather focused on the effects of study design constraints and model assumptions on abundance estimates. Both models require repeated visits at a site and assume a closed population for the time interval encompassing the visits. N-mixture models treat each visit as independent events and use a Poisson distribution. The removal model assumes that repeated visits at a site are dependent on previous counts because all individuals captured at a site during previous visit(s) are removed from counts for subsequent visits at a site (Fiske and Chandler, 2011). This can be done physically or by ignoring recaptures of marked animals. The removal model uses a Poisson distribution, which is often appropriate for count data with a high frequency of zeros (Fiske and Chandler, 2011).

Data Simulation

We created four scenarios by varying the number of sites, the number of visits, the number of bats and *P*, or *P* based on capture history to simulate net avoidance behavior. We manipulated these parameters across a realistic range of expected values for bat species. We generated 1,000 random data sets for each level of a parameter within a scenario, and fit models to the data. Baseline values of parameters were sites = 80, visits = 3, Ń = 70, and *P* = 0.5. We used these values for all parameters not being manipulated within a given scenario.

We selected baseline values and varied parameters to represent a range of likely conditions for surveys of bats and landscapes in the Eastern and Midwestern US. Studies here are often limited to three months (15 May–15 August — USFWS, 2018), which restricts number of sites and/or visits, or increases personnel, and labor expenditures. This restriction is based on the US Fish and Wildlife Service's Indiana bat (*Myotis sodalis*) survey guidelines; these dates are designed to detect female bats during the formation of maternity colonies through colony breakup throughout this species' range. We considered parameter values we thought representative for surveys of tree and cave roosting species during the maternity season in these landscapes such as eastern red bat (*Lasiurus borealis*), big brown bat (*Eptesicus fuscus*), northern long-eared bat (*M. septentrionalis*), gray bat (*M. grisescens*), Indiana bat, tri-colored bat (*Perimyotis subflavus*), hoary bat (*L. cinereus*), and evening bat (*Nycticeius humeralis*) based on our experience in the region (Womack, 2017). Males of these eastern US bat species are solitary or form small bachelor colonies, and we assumed that males were scattered throughout the landscape during summer. We simulated counts of captures for a given visit at a site using a binomial distribution (1 = captured or 0 = not captured) for each individual based on Ń and *P*. Captured individuals were totaled by visit for the N-mixture model, but only the first capture of an individual at a site was counted for the removal model. We repeated this process to generate count data for each visit at a site and for all sites. We used UNMARKED to fit the model and estimated abundance and standard error for the simulated data. We replicated this process 1,000 times for each parameter combination within all scenarios.

We evaluated both models' performance at 15, 30, 50, 60, 80, 90, and 120 sites, and held other parameters at baseline values in scenario 1. Our previous experience in the region suggests the potential for suitable mist-net weather on 60 nights from May 15th–August 15th, and we assumed a minimum of three visits, which would allow one team of field researchers to survey 20 sites per year. Another constraint is the number of federally permitted biologists available to conduct surveys; however, studies can occur over multiple years to offset this constraint. Given these constraints, we thought our range of 15 to 120 sites were reasonable values for a multiple year study. We used 80 sites in our baseline model. Womack (2017) surveyed 89 sites over a 3-year study in this region with a survey effort of approximately 1.5 federally permitted mist-net teams.

We simulated surveys based on 3, 4, and 5 visits to a site and held other parameters at baseline values in scenario 2. Since there is a tradeoff between the number of visits and the number of sites that can be visited for a given level of effort, we thought 3–5 visits was a realistic and relevant number of visits to consider.

We varied *P* (0.05, 0.1, 0.15, 0.2, 0.25, 0.4, 0.5, 0.75, and 0.9) and Ń (15, 35, 70, 110, and 150) in scenario 3. We chose values of *P* and Ń based on literature on *P* and maternity colony size estimates from emergence counts at roost locations within the Ozark region (Carers and Barclay, 2000; Schwartz and Schwartz, 2001; Amelon, 2007; Starbuck *et al*., 2015). In this region, mist-netting often occurs over water sources which are limited resources used by multiple maternity colonies and attract congregates of solitary roosting species and male bats, which potentially increases N and *P*. However, there are also likely survey conditions where N and *P* will be low, so we considered *P* = 0.05–0.9 and Ń = 15–150 and selected intermediate values for baseline values (0.50 and 70, respectively). We used *P* at 0.5 as our baseline for our other model scenarios because in our study region mist-netting occurs where both females and males congregate which would increase the *P* of individuals utilizing this limited resource. We chose Ń to represent rare (Ń = 15) to very abundant species (Ń = 150). Maternity roosts for northern long-eared bats generally have < 60 individuals (Carers and Barclay, 2000). Tri-colored bats maternity colonies range from 24–50 individuals (Schwartz and Schwartz, 2001).

Males for all species are either solitary or form small bachelor colonies during summer (Carers and Barclay, 2000; Schwartz and Schwartz, 2001); however, they do congregate at water sources (i.e., mist-net locations) along with female conspecifics in our study region. We chose 150 as our largest $\acute{N}$ because several maternity colonies could utilize the same mist net site for foraging or as a water source.

We simulated learned net avoidance behavior in scenario 4 by using $P = 0.5$ for an individual until it was captured, and then $P = 0.1$ for all subsequent visits at a site. We only evaluated the N-mixture model for this scenario because the removal model does not allow for recaptures of individuals on subsequent visits. We used parameters which violated the assumption for the N-mixture model that repeated counts were independent at a site in this scenario to understand how net avoidance affected the N-mixture model's performance.

Model Performance

We evaluated model performance by calculating mean relative bias (RB), mean absolute error (MAE), and mean absolute percent error (MA%E) across the 1,000 simulated data sets for each parameter level within a scenario as:

$$RB = (\hat{Y}/\acute{N}) - 1 \qquad \text{(Formula 1)}$$

$$MAE = (\sum|\acute{N}-\hat{y}_i|)/n \qquad \text{(Formula 2)}$$

$$MA\%E = 100[\sum|\acute{N}-\hat{y}_i|/y_i)/n] \qquad \text{(Formula 3)}$$

where $\acute{N}$ was the true abundance, $\hat{Y}$ the mean predicted abundance, $\hat{y}_i$ the predicted abundance for the ith simulation, and n the number of simulations (Mayer and Butler, 1993; Legates and McCabe, 1999; Efford and Dawson, 2009). Relative bias represents the ratio of the mean predicted abundance to known abundance, such that -0.25 and 0.25 would indicate predicted values were on average 25% greater (positive bias) and lesser (negative bias), respectively, than the known abundance. MAE and MA%E represent the mean absolute deviance in estimates from the known abundance in terms of the original units and as a percent, respectively, and therefore represent the variability of estimates from the true value. We summarized model predictions in box plots produced with default settings in program R that plotted the median, 25th and 75th percentiles with a box, whiskers representing ± 1.5 × the interquartile range (which approximates a 95% confidence interval), and data points falling outside the whiskers.

Results

We generated 85,000 simulated datasets to evaluate both models. In all cases the models at least partially corrected for individuals present but not detected because estimated mean abundance ($\bar{N}$) was greater than average number of captures, which can be estimated as $P \times \acute{N}$ (Tables 1–4). The removal model performed consistently better than the N-mixture model for all four scenarios except when $P = 0.05$. Relative bias averaged 0.59 and 0.03, and MA%E 70% and 6%, across all scenarios for the N-mixture model and removal model, respectively.

For scenario 1, the N-mixture model over estimated abundance with RB 0.29–0.51 and MA%E 39–51% for 15–120 sites and other parameters at baseline values, but surprisingly error was lowest for the lowest number of sites (Table 1). Relative bias was essentially 0 and MA%E was only 0.63–1.8% for the removal model and 15–120 sites and $\acute{N} = 70$ (Table 1). The distribution of estimates for the N-mixture model was much wider than for the removal model and mostly fell above the known abundance, while the distribution for the removal model was narrow and centered on the known abundance (Fig. 1).

In scenario 2, the performance of the N-mixture model improved as the number of visits increased 3–5 and other parameters were at baseline values,

Table 1. Mean abundances ($\bar{N}$), mean standard error of the estimates ($\overline{SE}$), relative bias (RB), mean absolute error (MAE), mean absolute percent error (MA%E) for the N-mixture and removal model based on 1,000 data simulations with a known population ($\acute{N}$) = 70, detection probability = 0.5, 3 visits to a site, and 15–120 sites

Model	$\acute{N}$	Sites	$\bar{N}$	$\overline{SE}$	RB	MAE	MA%E
N-mixture	70	15	90.35	26.67	0.29	27.95	39.93
		30	96.50	23.44	0.38	29.34	41.91
		50	100.12	20.46	0.43	31.26	44.65
		60	102.16	19.45	0.46	32.91	47.02
		80	104.22	17.85	0.49	34.57	49.39
		90	103.38	17.48	0.48	33.56	47.94
		120	105.59	16.17	0.51	35.69	50.99
Removal	70	15	70.09	2.69	0.00	1.26	1.80
		30	70.08	1.90	0.00	0.92	0.00
		50	69.97	1.47	0.00	0.70	1.00
		60	70.01	1.34	0.00	0.64	0.91
		80	70.03	1.16	0.00	0.54	0.78
		90	70.04	1.10	0.00	0.51	0.72
		120	70.03	0.95	0.00	0.44	0.63

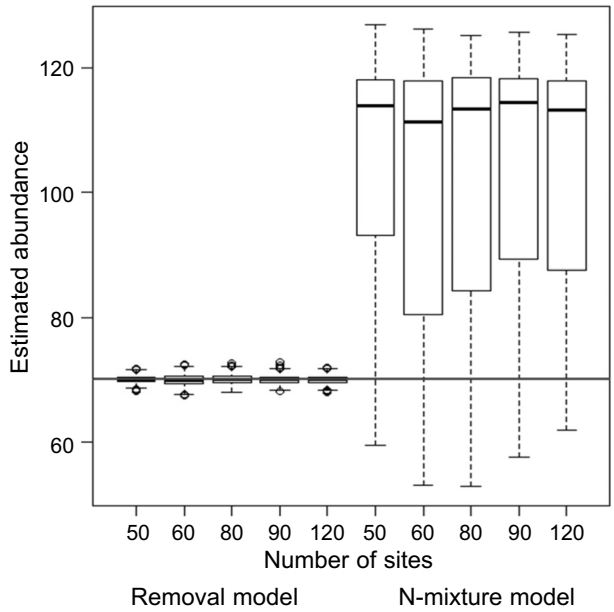

FIG. 1. Abundance estimates for the removal and the N-mixture models fit in the package UNMARKED based on simulated count data and different numbers of sites and a known population size = 70

but there was still substantial error and bias with RB 0.49–0.33 and MA%E 49–33% (Table 2). The distribution of estimates for the N-mixture model for 3–5 visits was much wider than for the removal model and mostly fell above the known abundance, while the distribution for the removal model was narrow and close to the known abundance (Fig. 2). The removal model generally had low bias and error with RB 0.0– -0.17 and MA%E 0.8–1.2% for 3–5 visits to a site (Table 2).

For scenario 3, the performance of the N-mixture model improved as P and $\acute{N}$ increased but bias and error were substantial for $P < 0.9$ when $\acute{N} = 15$ and $P < 0.75$ when $\acute{N} \geq 35$ with RB -0.45–2.99 and MA%E 1–237% (Table 3). Estimates for the removal model generally followed a similar pattern but bias and error were low except when p or $\acute{N}$ were very low with RB of 0.00–0.52 and MA%E 0–82% (Table 3). The removal model did not converge when $P = 0.05$ for all levels of $\acute{N}$ (Table 3). Estimates from both models had a broader distribution at low $\acute{N}$. In all cases the distribution of estimates was centered on $\acute{N}$ for the removal model while in most cases the N-mixture model had substantial bias, however at $P \leq 0.1$ for all values of $\acute{N}$ the removal model tended to produce more outlying-values than at greater values of P (Fig. 3).

The performance of the N-mixture model surprisingly improved in scenario 4 when we violated the model's assumption of independence; RB decreased from 0.49 to 0.06 while MA%E increased slightly from 49% to 53% (Table 4). The removal model, however, still had lower RB (0.0) and MA%E (0.78% — Table 4).

DISCUSSION

Our application of the N-mixture and removal models to simulated data highlighted the potential value of correcting abundance estimates for individuals present but not detected or captured. In all cases ($\bar{N}$) was greater the mean number of individuals captured (estimated as $P \times \acute{N}$). For example, when $\acute{N} = 150$, $P = 0.1$, ($\bar{N}$) was estimated as 96.66, and 157.46 by the N-mixture and removal models, respectively, even though the number of captures averaged 15 individuals.

The N-mixture model over-estimated abundance for most simulated scenarios. Our results were consistent with Rigby (2016), who examined the N-mixture model in the UNMARKED package for utility in estimating black throated blue warblers. Rigby (2016) found N-mixture model results were inflated for most years and were not correlated to true densities. However, one difference between our study and Rigby (2016) is that we did not use any

TABLE 2. Mean abundances ($\bar{N}$), mean standard errors of the estimates ($\overline{SE}$), relative bias (RB), mean absolute error (MAE), mean absolute percent error (MA%E) for the N-mixture and removal model based on 1,000 data simulations with a known population ($\acute{N}$) = 70, detection probability of 0.5, 80 sites, and 3–5 visits to a site

Model	$\acute{N}$	Visits	$\bar{N}$	$\overline{SE}$	RB	MAE	MA%E
N-mixture	70	3	104.22	17.85	0.49	34.57	49.39
		4	99.98	17.04	0.43	30.25	43.21
		5	93.15	14.64	0.33	23.37	33.38
Removal	70	3	70.03	1.16	0.00	0.54	0.78
		4	68.17	0.87	-0.17	0.22	1.99
		5	69.99	0.96	0.00	0.17	1.24

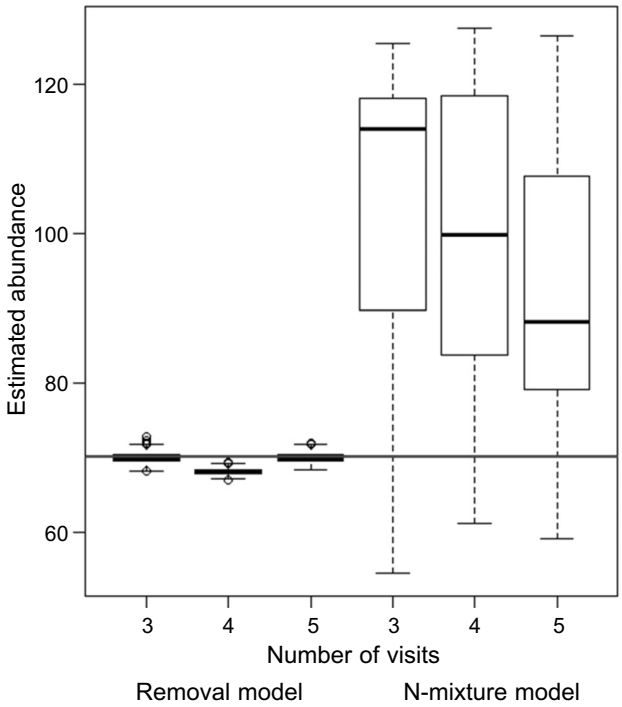

FIG. 2. Abundance estimates for the removal and N-mixture models fit in the package UNMARKED with simulated data for 3, 4, or 5 visits to a site and known population size = 70

covariates in our simulations nor used biologically collected data in this paper. We were purely interested in how each model performed without covariates to understand the potential utility in bat ecology studies. Womack (2017) did used the removal model to determine how abundance was related to habitat and landscape covariates in our study region with a sample size of 89 sites.

The N-mixture model only had a MA%E < 10% for Ń 15–110 and $P = 0.75$–0.9 or when Ń = 150 and $P > 0.40$. This is consistent with other studies indicating when P is high the N-mixture model can accurately estimate abundance (McIntyre *et al*., 2012; Yamaura, 2013; Rigby, 2016; Yamaura *et al*., 2016). Bats are cryptic species and are not likely to have counts close to the actual population abundance or $P = 0.9$ due to net avoidance behavior (Kunz and Kurta, 1988; Berry *et al*., 2004; Larsen *et al*., 2007). However, it is possible for some bat species when a mist-net location is over a water source and next to a maternity roost when young of the year are volant. Yamaura *et al*. (2016) suggests modifying the study design for species with low P by increasing sampling locations or otherwise increase the chance of detecting individuals (e.g., increase sampling time at a site) which should improve the N-mixture model performance (Drapeau *et al*., 1999). While we believe this suggestion is generally accurate, we had the lowest bias with the N-mixture model when the number of sites was the lowest. In addition, we found that the N-mixture model performed better when we violated the assumption of independence and P declined between repeated visits once an individual was captured, which is consistent with the idea that the model was underestimating P and overestimating Ń. We do not recommend use of the N-mixture model for field studies of bats in the Eastern United States given its low accuracy and high bias for most conditions simulated.

In contrast to the N-mixture model, the removal model generally performed well. The model only failed to converge in one instance when $P = 0.05$ and Ń = 15. With one exception, RB and MA%E only exceeded 0.05 and 10% for some combinations of Ń ≤ 70 and $P \leq 0.15$. Rigby (2016) similarly found that the removal model produced better estimates than the N-mixture model when applied to simulated bird point counts. Dorazio *et al*. (2005) found the removal model accurately estimated abundances of darter species by testing model performance on simulated data that fit the ecology of this species. The removal model accurately estimated mean abundances for all numbers of sites suggesting that unless the number of sites is extremely small, it does not affect abundance estimates for this model. The removal model estimated an unbiased mean abundance even with as few as three visits to a site in scenario 2. Fewer visits allow more sites to be sampled within the summer maternity season thus increasing sample size (number of sites). We found that the removal model estimated abundances accurately, on average, and with low relative bias for all P except for $P = 0.05$. The removal model failed to converge for any Ń when $P = 0.05$. Rigby (2016) similarly found the removal model had difficultly when P was low; otherwise, it outperformed the N-mixture model.

We suggest the use of the removal model in bat ecology as P for individuals is likely ≤ 0.25 and estimated population size for a site is greater than 15 individuals. We caution the use of this model for bat species with extremely low P because the model failed to converge when P was 0.05 estimated abundances ranged widely when P was 0.1. The model performed well with a moderate number of sites (50) and with only three repeated visits. The removal model's assumption of dependence between visits is consistent with bat behavior and known net avoidance by individuals that have been previously

TABLE 3. Mean abundances ($\bar{N}$), mean standard error of the estimates ($\overline{SE}$), relative bias (RB), mean absolute error (MAE), mean absolute percent error (MA%E) for the N-mixture and removal model based on 1,000 data simulations based on three visits to a site, 80 sites, and a known population of $\acute{N}$ = 15–150 and detection probability of P = 0.05–0.90. The removal model was unable to produce estimates of abundance when P = 0.05

$\acute{N}$	P	N-mixture					Removal				
		$\bar{N}$	$\overline{SE}$	RB	MAE	MA%E	$\bar{N}$	$\overline{SE}$	RB	MAE	MA%E
15	0.05	47.44	41.51	2.16	35.62	237.48	–	–	–	–	–
	0.10	57.45	38.43	2.83	43.09	287.29	22.78	56.10	0.52	12.31	82.04
	0.15	59.89	30.77	2.99	45.21	301.37	17.83	12.68	0.19	5.29	35.24
	0.20	62.20	29.39	3.15	47.32	315.44	15.65	3.13	0.04	2.28	15.20
	0.25	64.28	27.37	3.29	49.36	329.06	15.27	1.80	0.02	1.35	9.00
	0.40	62.87	25.61	3.19	47.93	319.54	15.07	0.73	0.00	0.48	3.18
	0.50	45.12	15.70	2.01	30.20	201.37	15.01	0.54	0.00	0.24	1.63
	0.75	34.24	13.61	1.28	19.38	129.20	15.01	0.44	0.00	0.05	0.34
	0.90	15.06	0.47	0.00	0.15	0.99	15.00	0.43	0.00	0.01	0.08
35	0.05	58.67	35.13	0.68	29.63	84.66	–	–	–	–	–
	0.10	67.61	26.82	0.93	34.35	98.13	42.94	22.56	0.23	6.99	12.02
	0.15	74.33	21.32	1.12	39.73	113.51	36.54	7.68	0.04	5.63	16.09
	0.20	77.87	20.46	1.22	43.05	122.99	35.89	4.20	0.03	3.25	9.27
	0.25	80.84	18.09	1.31	45.95	131.28	35.24	2.61	0.01	1.97	5.64
	0.40	80.64	20.59	1.30	45.77	130.78	35.03	1.11	0.00	0.72	2.04
	0.50	67.88	19.83	0.94	33.05	94.42	34.98	0.82	0.00	0.39	1.12
	0.75	36.42	1.92	0.04	1.80	5.13	35.00	0.67	0.00	0.08	0.23
	0.90	35.13	0.80	0.00	0.36	1.04	35.00	0.66	0.00	0.02	0.05
70	0.05	67.99	25.69	-0.03	12.52	17.88	–	–	–	–	–
	0.10	80.73	16.89	0.15	13.94	19.91	77.30	24.72	0.10	6.58	11.56
	0.15	88.31	13.31	0.26	18.95	27.08	71.24	9.67	0.02	6.19	10.13
	0.20	93.26	11.65	0.33	23.76	33.94	70.42	5.55	0.01	4.20	5.99
	0.25	98.36	10.92	0.41	28.57	40.82	70.34	3.66	0.00	2.77	3.96
	0.40	106.66	13.66	0.52	36.87	52.67	70.16	1.57	0.00	0.99	1.41
	0.50	104.14	18.31	0.49	34.44	49.20	70.03	1.16	0.00	0.54	0.78
	0.75	72.57	3.68	0.04	3.37	4.81	70.00	0.95	0.00	0.11	0.16
	0.90	70.19	1.31	0.00	0.74	1.05	70.00	0.94	0.00	0.02	0.03
110	0.05	76.91	19.48	-0.30	33.09	30.08	–	–	–	–	–
	0.10	89.92	11.71	-0.18	20.08	18.25	116.73	28.02	0.06	5.06	9.59
	0.15	98.58	9.40	-0.10	11.42	10.38	111.83	11.98	0.02	9.29	8.45
	0.20	106.04	8.53	-0.04	4.11	3.73	110.63	6.92	0.01	5.42	4.93
	0.25	112.77	8.19	0.03	3.55	3.23	110.51	4.57	0.00	1.52	1.57
	0.40	130.28	9.28	0.18	20.57	18.70	110.08	1.95	0.00	1.30	1.18
	0.50	136.51	12.78	0.24	27.15	24.68	110.02	1.45	0.00	0.71	0.65
	0.75	114.24	5.77	0.04	5.44	4.95	110.01	1.19	0.00	0.14	0.13
	0.90	110.30	1.86	0.00	1.16	1.05	110.00	1.17	0.00	0.03	0.03
150	0.05	82.77	15.55	-0.45	67.23	44.82	–	–	–	–	–
	0.10	96.66	9.59	-0.36	53.34	35.56	157.46	31.16	0.23	7.01	12.06
	0.15	107.60	7.62	-0.28	42.40	28.26	151.51	13.65	0.01	10.55	7.04
	0.20	117.19	6.93	-0.22	32.81	21.87	150.66	8.04	0.00	6.42	4.28
	0.25	126.10	6.63	-0.16	23.90	15.93	150.43	5.31	0.00	1.30	1.18
	0.40	150.87	6.88	0.01	2.55	1.70	150.08	2.28	0.00	1.42	0.95
	0.50	163.32	9.22	0.09	14.57	9.71	149.99	1.70	0.00	0.10	0.69
	0.75	155.67	7.79	0.04	7.21	4.81	150.00	1.39	0.00	0.17	0.11
	0.90	151.29	3.62	0.01	2.77	1.85	150.00	1.37	0.00	0.04	0.02

captured (Kunz and Anthony, 1977; Berry *et al*., 2004; Larsen *et al*., 2007). We suggest that researchers should be thoughtful in ensuring that the removal models assumption of a closed population is met between visits to a site. This can be accomplished by conducting surveys during the maternity season when site fidelity is high and keeping visits close together in time. While these methods can estimate and account for P, we agree with Rigby (2016) that it is still advisable

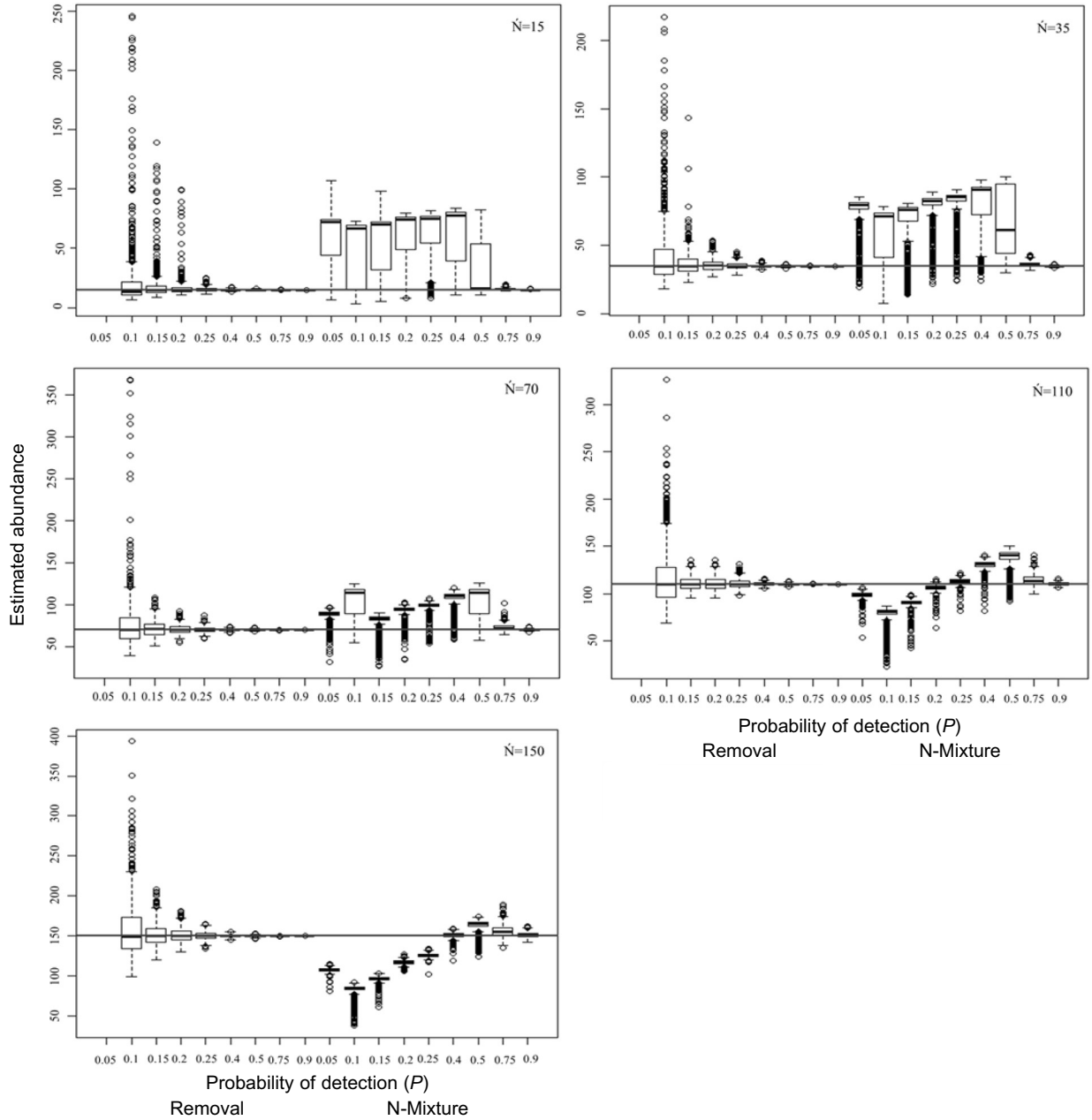

FIG. 3. Abundance estimates for the removal and N-mixture models fit in the package UNMARKED for various P and Ń. Models were fit to simulated count data for a population sizes indicated within each graph of Ń = 15, 35, 70, 110, and 150

to design studies that reduce potential biases in counts and ensure a reasonably high P and number of detections to result in the best possible abundance estimate.

TABLE 4. Mean abundances ($\bar{N}$), mean standard errors of the estimates ($\overline{SE}$), relative bias (RB), mean absolute error (MAE), and mean absolute percent error (MA%E) for the N-mixture and removal model based on 1000 data simulations with a known population of 70, 80 sites, three visits to a site, and probability of detection for first captures (P) and subsequent captures (P_1) of 0.5 and 0.1, respectively. The removal model only uses information on the first capture

Model	$\bar{N}$	$\overline{SE}$	P	P_1	RB	MAE	MA%E
N-mixture	104.14	17.85	0.5	0.5	0.49	34.57	49.39
	73.99	10.03	0.5	0.1	0.06	36.86	52.66
Removal	70.03	1.16	0.5		0.00	0.54	0.78

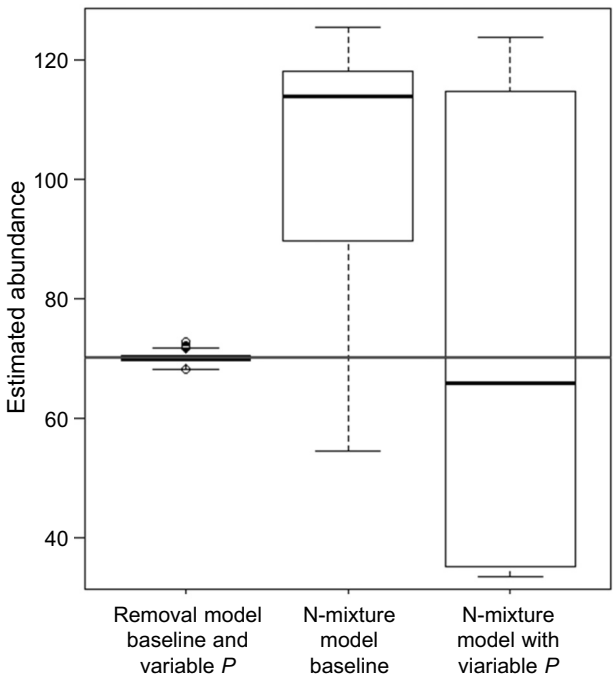

FIG. 4. Abundance estimates for the removal and N-mixture models fit in the package UNMARKED with constant detection probability (baseline) and with detection probability changing from 0.5 to 0.1 after an individual's first capture to simulate net avoidance behavior and known population size = 70. Results do not change for the removal model since it only uses an individual's first capture

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LITERATURE CITED

AMELON, S. K. 2007. Multi-scale factors influencing detection, site occupancy and resource use by foraging bats in the Ozark Highlands of Missouri. Ph.D. Thesis, University of Missouri, Columbia, MO, xiv + 223 pp.

BERRY, N., W. O'CONNOR, M. W. HOLDERIED, and G. JONES. 2004. Detection and avoidance of harp traps by echolocating bats. Acta Chiropterologica, 6: 335–346.

BUCKLAND, S. T., D. R. ANDERSON, K. P. BURNHAM, J. L. LAAKE, D. L. BORCHERS, and L. THOMAS. 2001. Introduction to distance sampling estimating abundance of biological populations. Oxford University Press, Oxford, 432 pp.

CARERS, M. C., and R. M. R. BARCLAY. 2000. Myotis septentrionalis. Mammalian Species, 634: 1–4.

DORAZIO, R. M., and J. A. ROYLE. 2003. Mixture models for estimating the size of a closed population when capture rates vary among individuals. Biometrics, 59: 351–364.

DORAZIO, R. M., H. L. JELKS, and F. JORDAN. 2005. Improving removal-based estimates of abundance by sampling a population of spatially distinct subpopulations. Biometrics, 61: 1093–1101.

DRAPEAU, P., A. LEDUC, and R. MCNEIL. 1999. Refining the use of point counts at the scale of individual points in studies of bird-habitat relationships. Journal of Avian Biology, 30: 367–382.

EFFORD, M. G., and D. K. DAWSON. 2009. Effect of distance-related heterogeneity on population size estimates from point counts. The Auk, 126: 100–111.

FARNSWORTH, K. D., O. LYASHEVSKA, and T. FUNG. 2012. Functional complexity: the source of value in biodiversity. Ecological Complexity, 11: 46–52.

FISKE, I. J., and R. B. CHANDLER. 2011. Unmarked: an R package for fitting hierarchical models of wildlife occurrence and abundance. Journal of Statistical Software, 43: 1–23.

JOHNSON, D. H. 2008. In defense of indices: the case of bird surveys. The Journal of Wildlife Management, 72: 857–868.

KÉRY, M., J. A. ROYLE, and H. SCHMIDT. 2005. Modeling avian abundance from replicated counts using binomial mixture models. Ecological Applications, 15: 1450–1461.

KUNZ, T. H., and E. L. ANTHONY. 1977. On the efficiency of the Tuttle bat trap. Journal of Mammalogy, 58: 309–315.

KUNZ, T. H., and A. KURTA. 1988. Capture methods and holding devices. Pp. 1–29, *in* Ecological and behavioral methods for the study of bats (T. H. KUNZ, ed.). Smithsonian Institution Press, Washington, D.C., 533 pp.

KUNZ, T. H., E. B. ARNETT, W. P. ERICKSON, A. R. HOAR, G. D. JOHNSON, R. P. LARKIN, M. D. STRICKLAND, R. W. THRESHER, and M. D. TUTTLE. 2007. Ecological impacts of wind energy development on bats: questions, research needs, and hypotheses. Frontiers in Ecology and the Environment, 5: 315–324.

LARSEN, R. J., K. A. BOEGLER, H. H. GENOWAYS, W. P. MASEFIELD, R. A. KIRSCH, and S. C. PEDERSEN. 2007. Mist netting bias, species accumulation curves, and the rediscovery of two bats on Montserrat (Lesser Antilles). Acta Chiropterologica, 9: 423–435.

LEGATES, D. R., and G. J. MCCABE, JR. 1999. Evaluating the use of 'goodness-of-fit' measures in hydrologic and hydroclimatic model validation. Water Resources Research, 35: 233–241.

MACKENZIE, D. I., J. D. NICHOLS, G. B. LACHMAN, S. DROEGE, A. J. ROYLE, and C. A. LANGTIMM. 2002. Estimating site occupancy rates when detection probabilities are less than one. Ecology, 83: 2248–2255.

MARQUES, J. T., M. J. RAMOS PEREIRA, T. A. MARQUES, C. D. SANTOS, J. SANTANA, P. BEJA, and J. M. PALMEIRIM. 2013. Optimizing sampling design to deal with mist-net avoidance in Amazonian birds and bats. PLoS ONE, 8: e74505.

MAYER, D. G., and D. G. BUTLER. 1993. Statistical validation. Ecological Modelling, 68: 21– 32.

MCCAFFERY, R., J. J. NOWAK, and P. M. LUKACS. 2016. Improved analysis of lek count data using N-mixture models. Journal of Wildlife Management, 80: 1011–1021.

MCINTYRE, A. P., J. E. JONES, E. M. LUND, F. T. WATERSTRAT, J. N. GIOVANINI, S. D. DUKE, M. P. HAYES, T. QUINN, and A. J. KROLL. 2012. Empirical and simulation evaluations of an abundance estimator using unmarked individuals of cryptic forest-dwelling taxa. Forest Ecology and Management, 286: 129–136.

MENZEL, J. M., W. M. FORD, M. A. MENZEL, T. C. CARTER, J. E. GARDNER, J. D. GARNER, and J. E. HOFMANN. 2005. Summer habitat use and home-range analysis of the endangered Indiana bat. Journal of Wildlife Management, 69: 430–436.

PUECHMAILLE, S. J., G. WIBBELT, V. KORN, H. FULLER, F. FORGET, K. MÜHLDORFER, A. KURTH, W. BOGDANOWICZ, C. BOREL, T. BOSCH, *et al.* 2011. Pan-European distribution of white-nose syndrome fungus (*Geomyces destructans*) not associated with mass mortality. PLoS ONE, 6: e19167.

REIDY, J. L., F. R. THOMPSON, and S. W. KENDRICK. 2014. Breeding bird response to habitat and landscape factors across a gradient of savanna, woodland, and forest in the Missouri Ozarks. Forest Ecology and Management, 313: 34–46.

RIGBY, E. A. 2016. Simulating effects of imperfect detectability in bird surveys. Ph.D. Thesis, University of Minnesota, Minneapolis, MN, x + 324 pp.

ROACH, M. C. 2016. Breeding bird response to pine-savanna and woodland restoration in the Ozark-Ouachita Interior Highlands. M.Sci. Thesis, University of Missouri, Columbia, MO, ix + 126 pp.

ROSENSTOCK, S. S., D. R. ANDERSON, K. M. GIESEN, T. LEUKERING, and M. F. CARTER. 2002. Landbird counting techniques: current practices and an alternative. The Auk, 119: 46–53.

ROYLE, J. A. 2004*a*. Generalized estimators of avian abundance from count survey data. Animal Biodiversity and Conservation, 27: 375–386.

ROYLE, J. A. 2004*b*. N-mixture models for estimating population size from spatially replicated counts. Biometrics, 60: 108–115.

ROYLE, J. A., D. K. DAWSON, and S. BATES. 2004. Modeling abundance effects in distance sampling. Ecology, 85: 1591–1597.

RUIZ-GUTIÉRREZ, V., E. F. ZIPKIN, and A. A. DHONDT. 2010. Occupancy dynamics in a tropical bird community: unexpectedly high forest use by birds classified as non-forest species. Journal of Applied Ecology, 47: 621–630.

SCHWARTZ, C. W., and E. R. SCHWARTZ. 2001. The wild mammals of Missouri. University of Missouri Press. Columbia, MO, 368 pp.

STARBUCK, C. A., S. K. AMELON, and F. R. THOMPSON. 2015. Relationships between bat occupancy and habitat and landscape structure along a savanna, woodland, forest gradient in the Missouri Ozarks. Wildlife Society Bulletin, 39: 20–30.

TURNER, G. G., D. M. REEDER, and J. T. H. COLEMAN. 2011. A five-year assessment of mortality and geographic spread of white-nose syndrome in North American bats and a look to the future. Bat Research News, 52: 13–27.

USFWS (UNITED STATES FISH AND WILDLIFE SERVICE). 2018. Range-wide Indiana bat summer survey guidelines. Endangered species, Midwest Region, US Fish and Wildlife Service. Last updated April 2018, 61 pp.

VEILLEUX, J. P., and S. L. VEILLEUX. 2004. Intra-annual and interannual fidelity to summer roost areas by female eastern pipistrelles, *Pipistrellus subflavus*. The American Midland Naturalist, 152: 196–200.

WALTERS, C., A. COLLEN, T. LUCAS, K. MROZ, C. SAYER, and K. E. JONES. 2013. Challenges of using bioacoustics to globally monitor bats. Pp. 479–500, *in* Bat evolution, ecology, and conservation (R. A. ADAMS and S. C. PEDERSEN, eds.). Springer, New York, 547 pp.

WILLIAMS, B. K., J. D. NICHOLS, and M. J. CONROY. 2002. Analysis and management of animal populations: modeling, estimation, and decision making. Academic Press, San Diego, CA, 817 pp.

WOMACK, K. W. 2017. Multi-scale factors related to abundance of bats and insect prey in savannas, woodlands, and forest in the Ozark Highlands, USA. Ph.D. Thesis, University of Missouri, Columbia, MO, 177 pp.

YAMAURA, Y. 2013. Confronting imperfect detection: behavior of binomial mixture models under varying circumstances of visits, sampling sites, detectability, and abundance, in small-sample situations. Ornithological Science, 12: 73–88.

YAMAURA, Y., M. KERY, and J. A. ROYLE. 2016. Study of biological communities' subject to imperfect detection: bias and precision of community N-mixture abundance models in small-sample situations. Ecological Research, 31: 289–305.

YATES, M. D. and R. M. MUZIKA. 2006. Effect of forest structure and fragmentation on site occupancy of bat species in Missouri Ozark forests. Journal of Wildlife Management, 70: 1238–1248.

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