
ESTIMATING SUMMER SURVIVAL, TEMPORARY EMIGRATION PROBABILITIES, AND CAPTURE RATES FOR A POPULATION OF THE COPE'S GRAY TREEFROG/EASTERN GRAY TREEFROG COMPLEX IN NORTHWEST MISSOURI, USA

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Abstract.—Accurate monitoring of population parameters is an essential element of conservation efforts. I used a popular sampling method (PVC pipes) in conjunction with Pollock's Robust Design to estimate a set of parameters (survival, temporary emigration, and capture rates) in habitats adjacent to six breeding sites of the Gray Treefrog complex (*Hyla versicolor*/*H. chrysoscelis*). I monitored treefrogs using 16 PVC pipe refugia per site. I checked pipes twice per week from May through August 2015–2019, and analyzed data in Program MARK, comparing 19 models by QAIC_c. Model selection favored models with time-constant weekly survival ranging from 0.86–0.96, Markovian movement in and out of the study area, and similar capture and recapture rates ranging from 0.62–0.82 annually. Compared to other studies my results suggest low summer survival, substantial fidelity to the sampled areas during the summer, and minimal trap response.

Key Words.—capture probability; *Hyla*; mark-recapture; survival; temporary emigration

INTRODUCTION

Biologists face a wide range of challenges in managing wildlife populations, regularly dealing with environmental and structural uncertainties, and often with only partial control of how effective their management actions are (Nichols et al. 1995). Included in these challenges is the problem of imprecise monitoring of populations, which necessarily limits the effectiveness of these management actions (Johnston et al. 2015). Monitoring wildlife, including amphibians, can provide practical information managers can use to focus conservation efforts. For example, Adams et al. (2013) used data from the U.S. Geological Survey Amphibian Research and Monitoring Initiative to detect a 3.7% decline in occupancy from various sites across the USA from 2002 to 2011. Similarly, Weir et al. (2014) and Villena et al. (2016) used call survey data from the North American Amphibian Monitoring Program to find multiple negative occupancy trends for anuran species in the northeastern and southeastern U.S. Well-designed monitoring programs can produce needed long-term data sets (Whiteman and Wissinger 2005; Greenberg et al. 2018), vital rate parameter estimates (Semlitsch et al. 1996), and a baseline for population models to calculate growth rates over time and even assess proposed management actions (De Minin and Griffiths 2011; Crawford et al. 2022).

Monitoring amphibians can be accomplished using a number of established techniques, including Visual Encounter Surveys, Call Surveys, drift fence arrays, cover boards, and even the collection of environmental DNA (Hutchens and DePerno 2009; Moss et al. 2022). These surveys are often used for occupancy detection, or estimating species richness, which can be less time and cost-intensive (Pollock et al. 2002) but may lose information provided by the more labor-intensive abundance estimates resulting from census or mark-recapture studies (Johnston et al. 2015). Such studies require researchers to trap individuals over extended periods, but which allows population analyses not possible with occupancy monitoring, such as the estimation of survival rates (Palomar et al. 2022) or detection rates (Bailey et al. 2004).

One widely employed method for terrestrial sampling of hylid treefrogs has been the use of polyvinyl chloride (PVC) pipes (Boughton et al. 2000; Zacharow et al. 2003; Cohen et al. 2016) placed in the ground or attached to trees, which the frogs use as refugia. This method has been used successfully to assess site fidelity, spatial distribution, and habitat selection in hylid populations (Johnson et al. 2007; Pittman et al. 2008; McDonald et al. 2018) and allows for repeated recaptures for mark-recapture studies. A complicating factor when monitoring a population of marked animals arises when those animals may temporarily move out of the sampled area

(temporary emigration). Such might occur as treefrogs move to upland sites farther from breeding ponds or to other bodies of water for feeding or overwintering (Johnson et al. 2007). Marked individuals may be erroneously considered dead when they are simply unavailable for capture, resulting in biased or unreliable survival estimates (Kendall et al. 1997).

Pollock's Robust Design (Pollock 1982) accounts for situations in which temporary emigration is an issue. The Robust Design is a mark-recapture procedure combining Cormack-Jolly-Seber (Seber 1965; Jolly 1965; Cormack 1973) open models with closed capture models. It takes the standard return rate of an animal in a mark-recapture study, which is a function of the survival rate (ϕ_i) and the capture probability, and decomposes the capture probability into four parameters, two estimating the probabilities of temporary emigration away from and back into the sampling site (γ'_i, γ''_i), and two dealing with the probability of initial capture (p_{ij}) and probability of subsequent recaptures (c_{ij}). Although capture rates are rarely estimated, recapture rates have been reported for a few species using PVC pipe refugia (Boughton et al. 2000; Pittman et al. 2008). These estimates, however, depend on the treefrogs being available for capture and may be overestimated if temporary emigration occurred. In addition, the potential for trap-shy or trap-happy frogs may occur, causing recapture rates to be lower or higher than initial capture rates (Kendall et al. 1997; Kendall 1999).

The Robust Design uses a unique sampling schedule where a series of primary sampling periods are spaced apart far enough in time that one can estimate survival and temporary emigration rates, while also allowing for losses (death, permanent emigration) and additions (births and immigration). Each primary sampling period is composed of multiple secondary sampling periods spaced close enough that one can assume no losses or additions allowing the estimation of initial capture and recapture probabilities (Kendall 2019). The Robust Design has been used successfully with amphibian populations in multiple studies (Price et al. 2012; Bendik 2017; Russell et al. 2019).

It was my goal with this study to investigate the suitability of using the Robust Design to monitor population parameters for a population of hylid treefrogs sampled using PVC pipe traps. If effective, this may provide an efficient technique for the long-term monitoring of hylid treefrog populations, and potentially be instrumental in developing an understanding of survival rate variation in the Gray Treefrog complex. This information would be useful for the purpose of developing a population model describing their population dynamics.

MATERIALS AND METHODS

Study species.—The diploid Cope's Gray Treefrog (*Hyla chrysoscelis*) and tetraploid Eastern Gray

Treefrog (*Hyla versicolor*) are a pair of morphologically indistinguishable species, and are treated as single group in this study. These species often occur in sympatry, although in northwest Missouri, where this study took place, Cope's Gray Treefrogs are thought to predominate (Briggler and Johnson 2021). Both species breed in shallow fishless wetland habitats during April through July (Briggler and Johnson 2021). Using PVC pipe traps, Johnson et al. (2007) found that after breeding, *H. versicolor* occupied terrestrial habitats 1–200 m from the breeding ponds where they had been marked.

Study area.—This study took place at Northwest Missouri State University and the Moberly Outdoor Education and Recreation Area (MOERA) in Nodaway County, Missouri, USA (40°26'26"N, 94°46'16"W), during the summers of 2015–2019. I sampled the habitat around four ponds beginning in 2015, and two inlets of neighboring Moberly Lake beginning in 2016 (Fig. 1). I removed one pond from the study in 2017 (this pond was on campus approximately 10 km from the other sites). Ponds and inlets at MOERA averaged a distance of $456.4 \pm$ (standard deviation) 214.66 m from each other. Ponds and inlets were relatively shallow (≤ 1.5 m deep). MOERA ponds averaged $1,075 \text{ m}^2 \pm 829 \text{ m}^2$ in size. The smallest pond (300 m^2) would typically dry in August, while the next smallest (1,950 m^2) dried once in August 2018. The total area of the inlets was not covered by my sampling protocol, but the area that was covered (as measured by the outermost PVC pipes) averaged $1,243 \text{ m}^2 \pm 416 \text{ m}^2$. Both inlets receded substantially in August 2018.

Field methods.—I placed PVC pipes in upland areas adjacent to each pond or inlet extending from the edge of the water out 50 m. Within this zone, I randomly selected four trees, each serving as a center point for an array of four PVC pipes ($n = 16$ pipes for a given pond or inlet). Each array of four pipes consisted of a 0.6-m pipe attached to the tree at about 1.5 m height (Boughton et al. 2000), a single 1-m tall pipe hammered upright into the soil 2 m away from the tree in the direction opposite the edge of the water, and two 1-m tall pipes placed upright in the soil at 2 m and 5 m away from the tree towards the edge of the water (Fig. 1). Pipes were allowed to stand in the water if the tree was close enough to the edge of the water. All PVC pipes had a 3.8-cm diameter (Boughton et al. 2000; Pittman et al. 2008).

I checked all pipes twice weekly, on two consecutive days, from May to August. I gently removed treefrogs found in pipes into a plastic bag, determined their sex by noting the throat coloration (dark for males), weighed them to the nearest 0.1 g, and measured snout-vent length (SVL) mm to the nearest 1 mm. Any treefrog < 32 mm SVL was considered a juvenile (Briggler and Johnson 2021). I used new bags for each treefrog

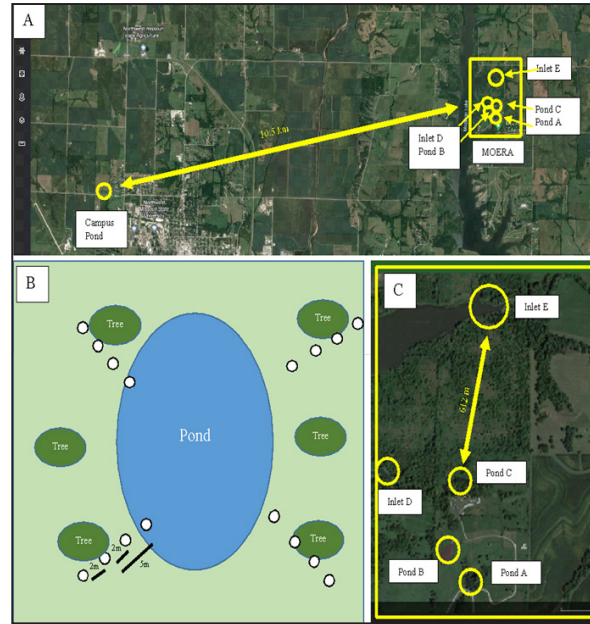


FIGURE 1. Visual representation of sampling locations for Gray Treefrog complex (*Hyla versicolor*/*H. chrysoscelis*). (A) Image of study area showing Campus Pond and Mozingo Outdoor Education and Recreation Area (MOERA) in Nodaway County, northwest Missouri, USA. (B) Schematic representation of the sampling array. White circles represent the 16 PVC pipes arranged around randomly selected trees within 50 m of the edge of the water. (C) Detail showing relative distances for ponds and inlets at MOERA. (Source for A and C: Google Earth 9.169.0.0. 2021 <https://earth.google.com>).

or group of treefrogs found in a single pipe. I marked new individuals with visible implant alphanumeric tags (VIA tags; Northwest Marine Technology, Inc., Shaw Island, Washington, USA) just under the skin in the right tibiofibular section of the leg. Clemas et al. (2009) reported VIA tags to be a reliable marking method for anurans. I sterilized the injection syringe by isopropyl alcohol before and after each use and treated the injection site with New Skin® (Moberg Pharma, Cedar Knolls, New Jersey, USA) before the treefrog was returned to its pipe.

Statistical analysis.—Following the Robust Design, each week was a primary sampling period with the 2

d considered secondary samples (Fig. 2). I developed 19 models with variations on five parameters to test a set of *a priori* hypotheses regarding the Gray Treefrog complex population in my study area (Table 1). I defined parameters estimated in this study as follows:

(1) ϕ_i : Survival probability from primary sampling period i to $i + 1$, functioning as a weekly survival rate for this study. In candidate models, survival rate was considered to be time-dependent (models 1–5, 10–13) or constant (models 6–9, 14–19).

(2) γ'_i : Probability that an individual remains unavailable for capture between primary sampling periods. In this study I interpret this to mean that a treefrog beyond

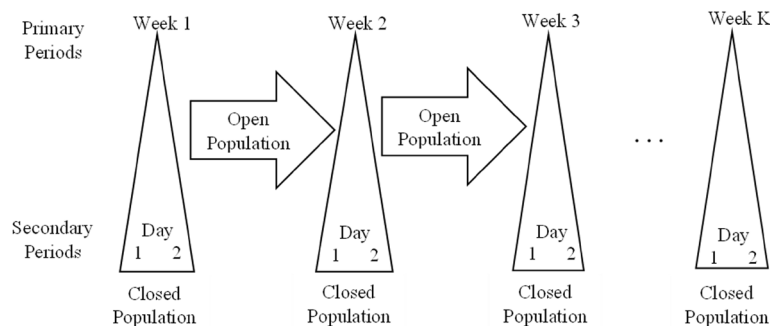


FIGURE 2. Sampling for this study was conducted to allow application of Pollock's Robust Design. Starting each year in mid-May and ending in mid-August to early September, I checked all pipes at each pond or inlet for Gray Treefrog complex (*Hyla versicolor*/*H. chrysoscelis*) individuals on two consecutive days each week. Each week (1 through K) represents a primary period and assumes an open population, while the two consecutive days represent two secondary sampling periods assuming a closed population. (Figure adapted from Pollock, 1982).

TABLE 1. Nineteen candidate models for summer population dynamics of Gray Treefrog complex (*Hyla versicolor*/*H. chrysoscelis*) in Nodaway County, Missouri, USA. Each model (#) estimates survival (ϕ), temporary emigration parameters (γ' , γ''), capture (p), and recapture probabilities (c). Parameters could vary between primary sampling periods (t) or be fixed across all primary sampling periods (.). Temporary emigration parameters could also be random ($\gamma'=\gamma''$), Markovian (γ' , γ'' estimated separately), or no movement could occur ($\gamma'=1$, $\gamma''=0$). Capture probability could vary between both primary and secondary sampling periods (t, t), (t, .), or (.,.). Recapture probability could vary between secondary sampling periods (t) or be held constant (.) or be constrained to be equal to p ($p=c$). Column k_{2019} represents the number of parameters in each model in year 2019 (years with different primary periods would have a slightly different number of parameters).

#	ϕ	γ'	γ''	p	c	k_{2019}
1	t	t, Markovian	t, Markovian	t, t	t	74
2	t	t, Markovian	t, Markovian	t, .	t	65
3	t	t, Markovian	t, Markovian	t, .; $p=c$	t; $p=c$	50
4	t	t, Random	t, Random	t, .	t	57
5	t	t, Random	t, Random	t, .; $p=c$	t; $p=c$	42
6	.	t, Markovian	t, Markovian	t, .	t	57
7	.	t, Markovian	t, Markovian	t, .; $p=c$	t; $p=c$	43
8	.	t, Random	t, Random	t, .	t	45
9	.	t, Random	t, Random	t, .; $p=c$	t; $p=c$	30
10	t	., Markovian	., Markovian	t, .	t	46
11	t	., Markovian	., Markovian	t, .; $p=c$	t; $p=c$	38
12	t	., Random	., Random	t, .	t	45
13	t	., Random	., Random	t, .; $p=c$	t; $p=c$	30
14	.	., Markovian	., Markovian	., .; $p=c$., $p=c$	4
15	.	., Markovian	., Markovian	., .	.	5
16	.	., Random	., Random	., .; $p=c$., $p=c$	3
17	.	., Random	., Random	., .	.	4
18	.	., No Movement	., No Movement	., .	.	3
19	.	., No Movement	., No Movement	., .; $p=c$., $p=c$	2

the 50-m buffer zone around the pond or inlet and cannot access a PVC pipe between primary sampling period i and $i+1$. The probability, $1-\gamma'_i$ is that of being away from the sampled area during primary sampling period i but entering the sampling area at $i+1$ (Kendall et al. 1997). In candidate models, the probability of remaining away from the sampled area was time-dependent (models 1–9) or constant (models 10–19).

(3) γ''_i : Probability of temporarily emigrating from the sampled area between primary periods i and $i+1$. For this study, the treefrog is available for capture at primary period i but not $i+1$. The probability, $1-\gamma''_i$ is that of being in the sampled area during primary sampling period i , and staying in that area, available for capture, at $i+1$ (Kendall et al. 1997). In candidate models, the probability of moving away from the sampled area was time-dependent (models 1–9) or constant (models 10–19). In addition, temporary emigration (γ' or γ'') could be either Markovian (models 1–3, 6, 7, 10, 11, 14, 15), random (models 4, 5, 8, 9, 12, 13, 16, 17), or there could be no movement (models 18, 19). Markovian temporary emigration means that the probability of an individual being outside the sampling area in primary period i depends on its location at primary

period $i-1$. This requires that $\gamma' \neq \gamma''$ (Kendall et al. 1997). For random emigration, however, the probability of an individual being outside the sampling area in primary period i is independent of its state at $i-1$. This can be characterized by a single parameter γ_p , which is the same as $\gamma'_i = \gamma''_i$ (Kendall et al. 1997). No temporary migration is also possible and acted as a null model against random and Markovian temporary migration. To model no temporary migration, I set $\gamma'_i = 1$ and $\gamma''_i = 0$, so that the probability of moving into the sampling area if an individual is not there already is $0 = (1 - \gamma')$ and the probability of leaving the sampling area if an individual is there is also 0 (Kendall 2019).

(4) p_{ij} : Probability that an individual is captured at secondary sample j within primary sampling period i , given that it is available for capture. For this study, this is the probability of detecting and capturing a treefrog in a PVC pipe, given that it is making use of the sampled area. In candidate models, capture probability was fully time-dependent (for both primary and secondary sampling periods, model 1) or time-dependent for primary sampling periods only (constant for secondary sampling periods, models 2–13) or constant (models 14–19).

(5) c_{ij} : Probability that an individual is recaptured at secondary sample j within primary sampling period i , given that it is available for capture, specifically, the probability of finding and capturing a previously marked treefrog in a PVC pipe, given that it is making use of the sampled area. In candidate models, recapture probability was time-dependent (models 1–13) or constant (models 14–19). In some models, capture probability and recapture probability were constrained to be the same ($p = c$, models 3, 5, 7, 9, 11, 13, 14, 16, 19).

I compared models using corrected quasi-Akaike's Information Criterion for low sample sizes (QAIC_c) in Program MARK (Anderson et al. 1994; White and Burnham 1999; Burnham and Anderson 2002). Because some ponds had low sample sizes, I pooled ponds and inlets together by year and tested models against the combined data for each year. Goodness-of-fit tests were not available for robust design models in Program MARK, so I collapsed data into an analysis of primary periods only for each year and used Program RELEASE Test 2 and Test 3 to estimate \hat{c} .

Post-hoc analysis.—Pooling data in this study required two major assumptions: that populations at all ponds and inlets had similar parameters, despite wide distances between these sites in some cases; and that males and females had similar parameters. To test these assumptions, I performed a *post-hoc* analysis using the top performing models from the pooled data analysis on two modified datasets. The first was to address the geographical assumption regarding the pooling of data across ponds and inlets. I tested this using a reduced dataset by removing all capture histories from the Campus Pond (10.5 km away from the nearest study site) and Inlet E (612 m away from the nearest study site; Fig. 1). All other ponds and inlets were no more than 200 m apart. Johnson et al. (2007) reported movements of Eastern Gray Treefrogs (*Hyla versicolor*) of 200 m or more from artificial refugia, so it seemed reasonable to pool data for these sites (Ponds A, B, C, and Inlet D) and treat them as single population. Subtracting Inlet E and the Campus Pond reduced the capture histories per year by an average proportion of 0.14 ± 0.03 (standard error). If the Campus Pond and Inlet E represented different populations, we would expect to see a change in selected top models or parameter estimates for those Closest Sites Models.

Similarly, I addressed the assumption that males and females had similar parameter values by fitting the top performing models to those treefrog capture histories to which I was able to assign a sex (96% of cases), using sex as a dummy variable. Model selection for this required doubling the number of parameters to estimate, one set for males and one set for females. If a sex effect was sufficient to warrant the added parameters, those Sex-specific Models should outperform the original models

(on this slightly smaller dataset) where the parameters were constrained to be the same for both sexes.

RESULTS

I analyzed five consecutive years of pooled pond and inlet data for the study site. Each year, I sampled 15–20 primary sampling periods composed of two secondary sampling periods each. By year, I sampled 64, 96, 80, 80, and 80 pipes, respectively, with individual frogs captured from 1–27 times (Table 2). I sampled 24 treefrogs in 2015, 63 in 2016, 33 in 2017, 59 in 2018, and 45 in 2019. Mean number of captures by pipe and sampling area varied from 0 to 8.6 (Table 3). The mean sex ratio across years (M:F) was 2.09 ± 0.73 (standard error; error given for all other means). I recaptured some treefrogs across multiple years. In 2016, I recaptured two (8%) treefrogs from the 2015 summer. In 2017, I recaptured five (8%) treefrogs from the 2016 summer. Even greater proportions were recaptured from the previous year in 2018 (6, 18%) and 2019 (11, 19%). Average between-year recapture rate was 0.13 ± 0.03 .

Goodness of fit tests provided low estimates of overdispersion (mean $\hat{c} = 1.06 \pm 0.06$), suggesting good model structure and unbiased estimates. Models 14 and 15 were selected as the best models most often (Table 4). These two models had a $\Delta\text{QAIC}_c < 2$ for all years except 2019 (in 2019 model 15 had $\Delta\text{QAIC}_c = 2.11$ relative to model 14). In 2017, model 16 was also a top model with a $\Delta\text{QAIC}_c < 2$ compared to the best model. Mean Akaike weight for model 14 was 0.45 ± 0.13 ; for model 15 it was 0.47 ± 0.15 , and for model 16 it was 0.05 ± 0.05 . Thus, models 14 and 15 were heavily favored and very similar to each other. In both models weekly survival was constant, and emigration was Markovian and constant. In model 14, I considered capture and recapture probabilities to be the same and constant. In model 15, I considered capture and recapture probabilities to be different, but constant. Averaging top models across years, weighted

TABLE 2. The mean number of captures of individuals of Gray Treefrog complex (*Hyla versicolor*/*H. chrysoscelis*) for years 2015–2019, including standard error (SE) and range, for Nodaway County, Missouri, USA. The number of treefrogs identified as male or female each year and the resultant sex ratio (M:F) are provided in the last three columns.

Year	Mean	SE	Range	Male	Female	Sex Ratio
2015	4.29	0.77	1–17	20	4	5.00
2016	6.33	0.74	1–27	35	26	1.35
2017	4.42	0.63	1–12	12	11	1.09
2018	4.52	0.56	1–19	34	25	1.36
2019	3.80	0.57	1–20	28	17	1.65

TABLE 3. Mean (\pm standard error) number of captures of individuals of Gray Treefrog complex (*Hyla versicolor*/*H. chrysoscelis*) across years (2015–2019) for sampling area and pipe location in Nodaway County, Missouri, USA. Pipe locations were centered on randomly selected trees, with one pipe 2 m away from the tree opposite the edge of the water (2 m away), one pipe attached to the tree (on tree), one pipe 2 m away from the tree towards the edge of the water (2 m towards), and one pipe 5 m away from the tree towards the edge of the water (5 m towards).

Pipe Location	Pond A	Pond B	Pond C	Campus Pond	Inlet D	Inlet E
2 m away	2.20 \pm 1.02	4.20 \pm 0.97	3.80 \pm 1.74	1.60 \pm 1.76	7.40 \pm 1.49	4.20 \pm 1.38
on tree	0.80 \pm 0.20	4.20 \pm 2.60	1.60 \pm 0.68	0.00	3.80 \pm 1.55	1.40 \pm 0.25
2 m towards	0.60 \pm 0.60	7.00 \pm 2.51	2.60 \pm 1.21	0.40 \pm 0.67	8.60 \pm 1.44	1.80 \pm 1.03
5 m towards	0.20 \pm 0.20	1.80 \pm 0.97	0.20 \pm 0.20	0.40 \pm 0.33	7.60 \pm 1.85	2.60 \pm 1.44

according to the number of treefrogs used to estimate parameters, weekly mean survival was 0.89 ± 0.02 , while the probability of staying away from the sampled area (γ') was 0.79 ± 0.06 , and the probability of migrating from the sampled area (γ'') between primary periods was 0.26 ± 0.04 . The mean probability of capture (p) was 0.77 ± 0.03 , and the probability of recapture (c) was 0.69 ± 0.04 (Table 5). Using these estimates, the probability of a treefrog being in the study area and captured in a pipe was ($p * [1 - \gamma'']$), or 0.57. Likewise, the probability of a treefrog entering the study area and then being captured was ($p * [1 - \gamma']$), or 0.16. Therefore, the probability of a treefrog being in the study area and being captured in a pipe was ($0.57 + 0.16$) or 0.73.

Post-hoc analysis.—For Closest Sites Models, model selection analysis largely chose the same models as the original analysis for this reduced dataset. Top performing models included Models 14, 15, and 16 as in the original analysis, and were usually selected in the same order. The exceptions to this were in years 2016, where model

14 slightly outperformed model 15 ($\Delta\text{QAIC}_c = 1.42$), a reversal from the original analysis, and in 2017, where model 16 slightly outperformed models 14 and 15 ($\Delta\text{QAIC}_c = 1.12, 3.13$ respectively). Model averaging across the top model for each year produced no significant changes in parameter estimates from the original analysis (Fig. 3).

Similarly, for Sex-specific Models, there were few changes in model selection results, and Sex-specific Models never outperformed the original models sufficiently to be selected as a best model. There was only one exception: for 2018 the two top models were model 15 (no sex-specific parameters) and model 15-sex (same as model 15 but each parameter was sex-specific, $\Delta\text{QAIC}_c = 3.13$). Model averaging across the top model for each year also produced no significant changes to parameter estimates from the original analysis (Fig. 3).

DISCUSSION

Survival.—While survival for this population of treefrogs appears to be high from week to week, there

TABLE 4. Best models ($\Delta\text{QAIC}_c \leq 2$) selected from a series of 19 candidate models for pooled water bodies in each of the years 2015 – 2019 for Gray Treefrog complex (*Hyla versicolor*/*H. chrysoscelis*) summer population dynamics in Nodaway County, Missouri, USA. Models are judged relative to the best performing model (lowest QAIC_c , $\Delta\text{QAIC}_c = 0$). QAIC_c Weight represents the relative likelihood for each model within a given year, and k is the number of parameters each model estimates.

Year	Model	QAIC_c	ΔQAIC_c	QAIC_c Weight	k
2015	14	206.84	0.00	0.71	4
2015	15	208.62	1.78	0.29	5
2016	15	945.56	0.00	0.64	5
2016	14	946.69	1.12	0.36	4
2017	14	314.91	0.00	0.45	4
2017	16	315.99	1.08	0.26	3
2017	15	316.89	1.98	0.17	5
2018	15	738.25	0.00	0.98	5
2019	14	487.87	0.00	0.74	4

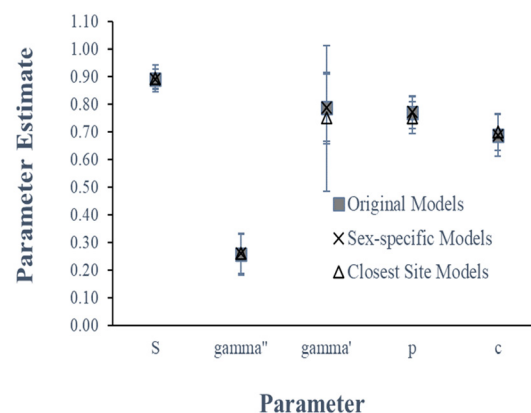


FIGURE 3. Model-averaged parameter estimates for top performing post-hoc models (Sex-specific Models, Closest Sites Models) compared to model-averaged parameter estimates for top performing models from the original analysis (Original Models). Gamma'' and Gamma' refer to γ'' and γ' . Error bars represent 95% confidence intervals, so overlapping confidence intervals represent no significant difference between estimates.

TABLE 5. Parameter estimates from the top performing models for Gray Treefrog complex (*Hyla versicolor*/*H. chrysoscelis*) study populations in Nodaway County, Missouri, USA. Model represents the top model (described in Table 1) chosen by QAIC_c for that year; Treefrogs represents the number of individual treefrogs captured in that year. ϕ is estimated weekly survival rate, γ'' & γ' are temporary emigration probabilities, p is the capture rate, and c is the recapture rate. Standard error (SE) is adjusted by the variance inflation factor ($\sqrt{\hat{c}} \times \text{SE}$). Weights for weighted means are based on the number of treefrogs sampled in a given year.

Year	Model	Treefrogs	$\phi \pm \text{SE}$	$\gamma'' \pm \text{SE}$	$\gamma' \pm \text{SE}$	$p \pm \text{SE}$	$c \pm \text{SE}$
2015	14	24	0.96 \pm 0.06	0.35 \pm 0.09	0.89 \pm 0.08	0.81 \pm 0.06	0.81 \pm 0.06
2016	15	63	0.91 \pm 0.03	0.14 \pm 0.04	0.83 \pm 0.11	0.77 \pm 0.05	0.67 \pm 0.04
2017	14	33	0.86 \pm 0.04	0.23 \pm 0.07	0.60 \pm 0.20	0.80 \pm 0.04	0.80 \pm 0.04
2018	15	59	0.88 \pm 0.02	0.32 \pm 0.05	0.70 \pm 0.08	0.82 \pm 0.04	0.62 \pm 0.04
2019	14	45	0.87 \pm 0.09	0.31 \pm 0.08	0.93 \pm 0.07	0.66 \pm 0.04	0.66 \pm 0.04
Weighted Mean			0.89 \pm 0.02	0.26 \pm 0.04	0.79 \pm 0.06	0.77 \pm 0.03	0.69 \pm 0.04

would be a cumulative toll on the population. The average length of the summer sampling period was 16.6 weeks. Survival over this time period is projected to be $0.8916.6 = 0.14$, assuming constant survival week to week. As such, the summer survival rate around these ponds and inlets can be expected to be quite low for this population. Suggestively, the percentage of treefrogs recaptured each summer from the previous summer was 13%, somewhat consistent with the estimated summer survival rate, and similar to the 2–9% annual recapture rate reported by Greenberg et al. (2018). The weekly survival rate estimate is lower than those made for related taxa (Table 6). Rice et al. (2011) reported a two-week survival rate for Green Treefrogs (*Hyla cinerea*) and Squirrel Treefrogs (*Hyla squirella*) post-removal of Cuban Treefrogs (*Osteopilus septentrionalis*) in pine rockland and mangrove habitat in Florida, where both averaged about 0.90 survival in both the wet and dry seasons. My 2-week survival rate would be 0.79. Similarly, Waddle et al. (2008), in a study evaluating the effects of toe-clipping on survival in Green Treefrogs and Squirrel Treefrogs, reported a monthly survival rate (depressed monotonically by the number of toes removed in Green Treefrogs) of 0.75–0.85 and 0.85–0.86, respectively. This would occur if the corresponding weekly rates of survival were 0.93–0.96 and 0.96, respectively. Finally, in a study of European Treefrogs (*Hyla arborea*), where recapture rates in an isolated pond (no immigration) were considered the same as survival

rates (conflating detection and survival rates), Friedl and Klump (1997) reported an annual survival rate of 37% for males and 20% for females, corresponding to a 0.98 (males) and 0.97 (females) weekly survival rate in this study system. In their discussion, they also suggest that the annual recapture rates reported by Ritke et al. (1991) represent a survival rate of 30% and 29% for males and females, respectively. These would equate to a weekly survival rate of 98% for each sex. These estimates may be imprecise because of the assumptions they are built on, but they are not dissimilar from my range of 0.86–0.96. It is likely, however, that in this widely distributed species, living in varied habitats, there would be a wide range of survival rates (Friedl and Klump 1997). In addition, survival rate is likely not constant from year to year, nor is it likely constant within a given year. My sampling period covered the breeding and summer post-breeding periods for the Gray Treefrog complex, which necessarily increases predation risk as male treefrogs call for females, advertising their location to predators, and survival over this time period may differ substantially from that of another period, such as overwintering survival.

Temporary migration.—The temporary migration parameters, γ' and γ'' , are interpreted to represent the probability of leaving the study area. For this study, treefrogs must simply be away from PVC pipes surrounding a pond or inlet, presumably moving back

TABLE 6. Weekly survival rates (WSR) for the Gray Treefrog complex (*Hyla versicolor*/*H. chrysoscelis*) population in Nodaway County, Missouri, USA, and other congeneric populations also sampled using PVC pipe traps.

Study	Common Name	Species	WSR
This Study	Gray Treefrog Complex	<i>Hyla versicolor/chrysoscelis</i>	0.89
Rice et al. 2011	Green Treefrogs	<i>Hyla cinerea</i>	0.95
Rice et al. 2011	Squirrel Treefrogs	<i>Hyla squirella</i>	0.95
Waddle et al. 2008	Green Treefrogs	<i>Hyla cinerea</i>	0.93–0.96
Waddle et al. 2008	Squirrel Treefrogs	<i>Hyla squirella</i>	0.96
Friedl and Klump 1997	European Treefrogs	<i>Hyla arborea</i>	0.98

into the water or farther away. This would not be unusual; Johnson et al. (2007) found that during the post-breeding season, Eastern Gray Treefrogs were recaptured an average distance of 30 m (males) and 80 m (females) away from ponds during the breeding season, increasing to 60 m and 90 m, respectively, during the non-breeding season. Similar movements in my study population might explain the strong male bias I found in captured Gray Treefrogs and demonstrates the necessity of accounting for temporary emigration when attempting to estimate survival rates. My models compared random migration, Markovian migration, and no migration at all, and found support for Markovian migration. The weekly survival rate ignoring temporary emigration parameters (no movement) would have been underestimated as 0.83 rather than 0.89, resulting in a summer sampling period survival estimate of 0.04, a 10% decrease from the current estimate.

The best models suggested that on average, a treefrog that was away from the study area had a 0.79 probability of staying away and a low 0.21 probability of entering, while conversely, those treefrogs in the study area available to be sampled would leave at the low probability of 0.26 and remain at a 0.74 probability. In other words, treefrogs within the study area were unlikely to leave, and those outside the study area were unlikely to enter. This (along with my relatively high recapture rates) supports the concept of high site fidelity to a particular body of water. Such high site fidelity has been reported for populations of Cope's Gray Treefrog (Ritke et al. 1991; Boughton et al. 2000; Pittman et al. 2008), but others have cautioned that site fidelity may not be as high as is commonly assumed given the documented mobility of these treefrogs (Johnson and Semlitsch 2003; Johnson et al. 2007). Regardless, the high fidelity to the PVC pipes in the sampling areas of this study implies that PVC pipe traps are effective for long-term monitoring studies.

Capture and recapture rates.—Differences in initial capture and recapture rates would imply a trap-happy ($p_{ij} < c_{ij}$) or trap shy ($p_{ij} > c_{ij}$) effect; however, estimated capture and recapture rates were sufficiently similar that for most years (2015, 2017, 2019) a model constraining these parameters to be equal (model 14) was selected as the top model. In 2016, models 14 and 15 were considered equally explanatory ($\Delta\text{QAIC}_c = 1.12$), implying little difference in capture and recapture rates. Only in 2018 did these two parameters differ and only model 15 was selected as best (next best model $\Delta\text{QAIC}_c = 8.41$). In this particular year, recapture rates were low implying an avoidance of pipes post-capture (mean $p_{ij} = 0.82 \pm 0.04$ (standard error), mean $c_{ij} = 0.62 \pm 0.04$). This year was also a drought year with significant drying of my sampled bodies of water, though it is unclear whether this caused the apparent change in model selection. Nevertheless, this

result suggests in some years, sampling may see changes in recapture response, and researchers cannot assume p and c will remain constant based on short-term datasets.

Capture and recapture rates were also high, suggesting that if a treefrog were in the study area, its probability of using of the pipe, being detected within the pipe, and finally, being secured from the pipe is high, regardless of whether it had been captured previously or not. Although the reporting of capture rates is uncommon in the literature, recapture rates have been reported. Boughton et al. (2000) reported a 70% recapture rate for four *Hyla* species combined: *Hyla squirella*, *H. cinerea*, the Barking Treefrog (*H. gratiosa*), and the Pine Woods Treefrog (*H. femoralis*), which is very similar to my estimated mean of 69%. Pittman et al. (2008), studying Cope's Gray Treefrog reported a recapture rate of 42%. These are naïve recapture rates, ignoring temporary emigration, but even when considering this, the probability of having treefrogs in this population available for capture and actually capturing them is high (0.73). The general lack of a trap-shy response in most years and the relatively high probability of capture using PVC pipes also speaks to their effectiveness as a monitoring tool (Boughton et al. 2000; Pittman et al. 2008).

Conclusion.—Monitoring anuran populations is an essential element of determining the needs and success of conservation efforts. For species that cannot be easily detected visually, such as the hylids of the Gray Treefrog complex, capture-mark-recapture monitoring is often required. Using a PVC pipe array, this study was able to successfully monitor and collect data on a population of the Gray Treefrog complex in northwest Missouri, sufficient to estimate important vital rates over a 5-y period using Pollock's Robust Design. Model selection implied a weekly survival rate comparable to, if slightly lower, than other studies, when taking temporary emigration into account. Model selection indicated Markovian movement in and out of sampling sites and constant and similar capture and recapture rates. These estimates provide important information about the population ecology of *Hyla chrysocelis* and *Hyla versicolor*. My results suggest the utility of using a Robust Design analysis coupled with a PVC pipe trap array for long-term summer monitoring of the Gray Treefrog complex. These results also contribute a survival rate parameter that may lead to the development of a working population model for the Gray Treefrog complex, which may help provide insight into the conservation of this group, or of other hylid species of conservation interest. My analysis, however, depended on assuming similar parameter estimates between species, males and females, adult age classes, and ponds. More and longer studies are needed to clarify the vital rates within these categories. Nevertheless, this study presents an effective methodology for estimating and tracking the

variation in hylid survival in the long-term. I recommend designing future monitoring studies for Gray Treefrogs to incorporate the Robust Design with PVC pipe trap arrays as part of their sampling protocol.

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