Population Estimates of *Hyla cinerea* (Schneider) (Green Tree Frog) in an Urban Environment

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Abstract - *Hyla cinerea* (Green Treefrog) is a common wetlands species in the southeastern US. To better understand its population dynamics, we followed a relatively isolated population of Green Treefrogs from June 2004 through October 2004 at a federal office complex in Lafayette, LA. Weekly, Green Treefrogs were caught, measured, marked with VIE tags, and released. The data were used to estimate population size. The time frame was split into two periods: before and after August 17, 2004. Before August 17, 2004, the average estimated population size was 143, and after August 24, 2005, this value jumped to 446, an increase possibly due to tadpoles metamorphosing into adults.

Introduction

Recently, declines in some amphibian populations around the world have been reported (Young et al. 2001). There has been much discussion in the literature about causes and general nature of the reported declines (Sala et al. 2000). There is now growing recognition of the need for long-term monitoring of amphibian populations. The University of Louisiana at Lafayette (UL Lafayette) and the United States Geological Survey National Wetlands Research Center (USGS NWRC) have initiated a project in partnership to monitor and model frog populations at the National Wetlands Research Center/Estuarine Habitat and Coastal Fisheries Center research complex, with an initial focus on *Hyla cinerea* (Schneider) (Green Treefrog).

With the increase in urbanization and the spread of suburbs, wildlife populations at the urban/suburban interface may become isolated. By monitoring a local, relatively isolated population of frogs, we hope to gain a greater understanding of the population dynamics of this species. We followed the population over a breeding season, and used the field data to develop a population dynamics model and make weekly estimates of population size.

The study site was located at the UL Lafayette campus on land leased to the NWRC and the National Marine Fisheries Service (NMFS) (henceforth the NWRC/EHCFC complex) in Lafayette, LA. The site was chosen because of previous observations showing an abundance of Green Treefrogs and suitable breeding habitat for these frogs. Over a five-year period preceding this study, several anuran species had been seen or

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heard at the NWRC/EHCFC complex. These include *Bufo fowleri* (Hinckley) (Fowler's Toad), *Bufo nebulifer* (Gulf Coast Toad), *Elutherodactylus planirostris* (Cope) Greenhouse Frog, *Gastrophryne carolinensis*(Holbrook) (Eastern Narrow-mouthed Toad), *Rana catesbeiana* (Shaw) (American Bullfrog), *Rana utricularia* (Cope) (Southern Leopard Frog), *Hyla squirella* (Bosc) (Squirrel Treefrog), *Rana clamitans clamitans* (Latreille) (Bronze Frog), and *Pseudacris crucifer* (Wied-Neuwied) (Spring Peepers) (J. Carter, pers. observ.).

The Green Treefrog is a common anuran in the southeastern United States, ranging from Delaware southward to southern Florida and the Florida Keys, and westward through Mississippi River Valley into southern Illinois, and extends further westward into eastern and southern Texas (Winston 1997). They are often found in floodplains, large lakes, smaller ponds, and swamps (Gunzburger and Travis 2004); marshy areas that have an abundance of emergent and floating vegetation, grasses, and cattails along the banks (Winston 1997); and in temporary aquatic habitats (Wright 1932). Adult Green Treefrogs feed on small arthropods and live on plant stems in trees and shrubs near water, while the tadpoles feed on algae and prefer shallow water in dense vegetation. Colors of the Green Treefrog range from green to reddish-brown, and its size ranges from 3.2 cm to 6.4 cm. Green Treefrogs have been documented to mate from April to the end of August (Dundee and Rossman 1989).

Methods

Field-site description

The NWRC/EHCFC complex contains a network of artificial ponds and reflecting pools (Fig. 1). The landscape fringing the ponds simulate different wetland types, including emergent marshland and swamp. Buildings limit access to the field surrounding the NWRC complex. The eastern border of the pond complex is made of sidewalks, four lane roads, and is across the street from a medium-density housing complex.

In the fields adjacent to the ponds are seasonal wetlands, with the closest being approximately 60 m away. The ponds in front of the NWRC were created in 1992 at the time the NWRC was built. The ponds and reflecting

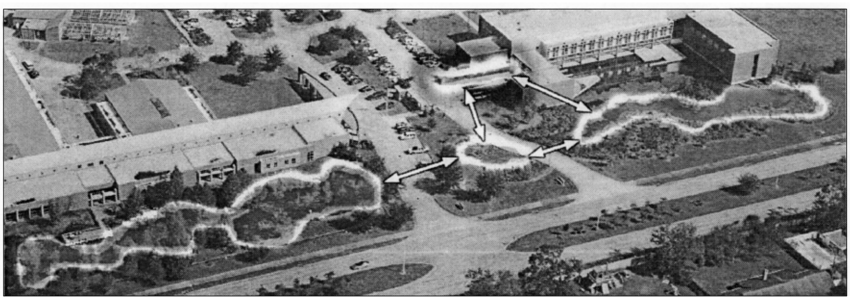

Figure 1. NWRC/EHCFC Pond complex. Pond outlines are highlighted in white. Arrows show likely migration routes between ponds.

pools adjacent to the EHCFC were created in 1999 when that complex was built. Before construction of the two building complexes, the area was an open field with some shallow seasonal wetlands. The region is at the eastern edge of a historical coastal prairie. More recently, the parcel of land was used as a pig farm and then later converted to open field. Land management in the adjacent fields has varied over the years, but at different times, different parts of the area have been leveled or contoured to prepare the land for construction, to remove wetlands, or to encourage meadow-nesting birds.

Mark-recapture technique

Capturing was conducted at least one hour after sunset, and lasted between 2100 and 2300 hours central daylight time. Each pond was divided into approximately four quadrants. For each quadrant, a group of three people searched the area for 15 minutes while listening for Green Treefrog calls. Individuals were visually sighted and caught by hand. Captured individuals were placed in plastic bags that were labeled to indicate capture site and the individual who captured it. Only one frog was placed in each bag, and bags were not reused. We measured the snout to tail length, and if not previously marked, the frogs were marked with Visible Implantable Fluorescent Elastomere (VIE) tags (Gillette 2003). A combination of colors and locations on the body were used to indicate week of first capture. A UV-light and specialized UV glasses were used during the examination to detect any fluorescent marks that may have been present. Placement locations on the body (Fig. 2) were chosen after we conducted a pilot study to determine which locations retained tags (J. Carter, unpubl. data). After marking, frogs were released in approximately the same locations where they were caught. For previously caught frogs, we noted their length and the week of initial capture. All Green Treefrogs that were captured were marked, and we made no distinction between adult, juvenile, and recent metamorphs, except to note the length of the animal and an incompletely absorbed tail, if present. We did not use a "termination" mark with recaptured frogs.

The survey was conducted once a week for 18 weeks, from June to October of 2004. For each night of surveying, we recorded weather conditions, time spent in the field, and catch efforts. In addition, these methods

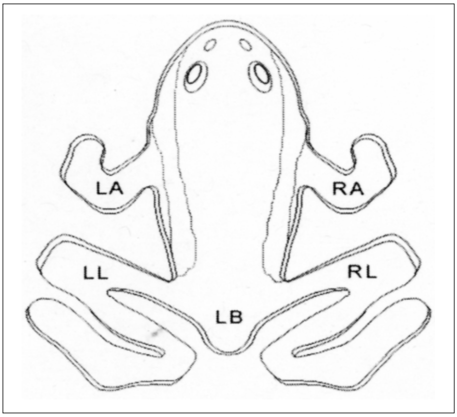

Figure 2. Letter codes indicate locations where elastomere markers were placed on the frog's body.

Table 1. Adult frog capture summary over 18-week period. Total captures (TC) = new captures + recaptures. NC = new captures. R = recaptures.

				Recaptures by week																	
Week	NC	TC	R	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
1	18	18	0	~																	
2	14	16	2	2	~																
3	24	26	2	2	0	~															
4	15	25	10	5	1	4	~														
5	18	30	12	3	2	2	5	~													
6	9	22	13	9	1	0	3	0	~												
7	2	9	7	4	1	1	1	0	0	~											
8	6	24	18	8	3	2	5	0	0	0	~										
9	3	10	7	2	0	1	2	1	1	0	0	~									
10	1	8	7	2	0	1	0	1	0	0	1	2	~								
11	12	13	1	0	0	0	0	0	0	0	1	0	0	~							
12	9	12	3	1	0	0	0	0	0	0	0	0	2	0	~						
13*	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	~					
14	6	8	2	0	0	1	0	0	1	0	0	0	0	0	0	0	~				
15	2	5	3	0	0	0	0	0	0	0	0	0	0	0	1	0	2	~			
16	4	6	2	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	~		
17	5	9	4	0	0	0	0	1	1	0	0	1	0	0	1	0	0	0	0	~	
18	7	10	3	0	0	1	0	0	1	0	0	0	0	0	0	0	0	1	0	0	~
Total	164			9	8	14	16	3	4	0	2	3	2	0	2	0	3	1	0	0	

*No captures during sampling on week 13.

were supplemented by calling surveys to evaluate which species were present, if they were breeding, and what their abundance was.

Frequent visits to the complex were made as early as March; however, no mating calls were heard until early April. Similar to Gerhardt (1987), we observed that most captured individuals resumed performing mating calls within a few minutes.

Statistical estimation of the weekly population size and further inferences

Our capture-recapture protocols followed the Unknown Capture History Protocol as outlined in Burnham et al. (1987). This sampling scheme involves drawing a random sample, marking the individuals, and releasing them. Data of previously marked individuals in the sample allows estimation of the population. A heuristic idea of this sampling process is outlined in Figure 3. Frog population in week-i was estimated using the sample information of marked frogs that had been captured in the previous weeks. The probability distribution of the number of marked frogs in a particular week appears to be a generalization of the well-known hypergeometric distribution.

The probability (conditional) distribution of the observed data (number of marked and unmarked frogs) is:

$P(X_{ki} = x_{ki},\ 1 \le i \le k - 1 \mid X_{lj} = x_{lj};\ l = 1, 2, \ldots, [k - 1], j = 1, 2, \ldots, [l - 1]) =$

$$\frac{\left[\prod_{l=1}^{k-1} \binom{M_l - \sum_{j=1}^{l} x_{lj}}{x_{kl}}\right] \binom{N_k - \sum_{l=1}^{k-1}\left(M_l - \sum_{j=1}^{l} x_{lj}\right)}{M_k - \sum_{i=1}^{k-1} x_{ki}}}{\binom{N_k}{M_k}}, \qquad (1)$$

where: N_k = population size in week-k, unknown; M_k = size of the sample drawn in week-k; and X_k = number of frogs in the sample (in week-k) of size M_k that were caught and marked earlier (Fig. 4).

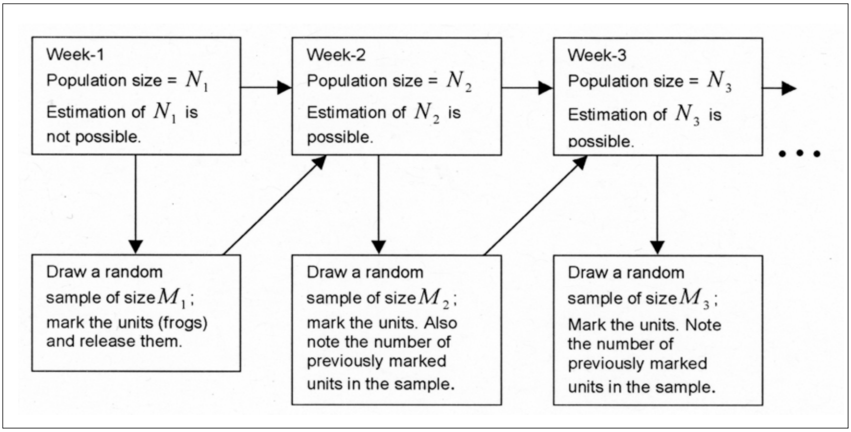

Figure 3. Statistical model used to make population estimates.

Note that $X_k = X_{k1} + X_{k2} + ... + X_{k(k-1)}$, where X_{ki} = number of frogs in week-*k* sample that were marked in week-*i*, $i = 1, 2, ... (k\text{-}1)$; for convenience, $X_{ij} = 0$ for $i = j$ (since a frog cannot be recaptured the same week it is originally marked). The model development is described in detail in Appendix 1. Maximizing (1) with respect to N_k gives $\tilde{N}_k$ = the estimated population size in week-*k*.

Results

Weekly captures and recapture numbers are summarized in Table 1. The last week we heard frogs during the monitoring run was week 10 (10 August 2004).

The lowest weekly population estimate (Table 2) was 125 frogs in week 6, and the highest weekly estimate was 1429 frogs in week 11 (17 August 2004). By using week 11 as a dividing line, the data can be separated into two periods. Before week 11, the average population estimate was 173 with a standard deviation of 92.19. After week 11, the average population estimate was 445.7 with a standard deviation of 114.42.

Average length data for Green Treefrogs caught are in Table 3. For the first 10 weeks, average frog length was greater than 30 mm. From weeks 11–18, the average length varied from week to week between 24 and 38 mm.

Discussion

An important premise of this study is that the population we are studying is in fact a year-round population, not simply a breeding population.

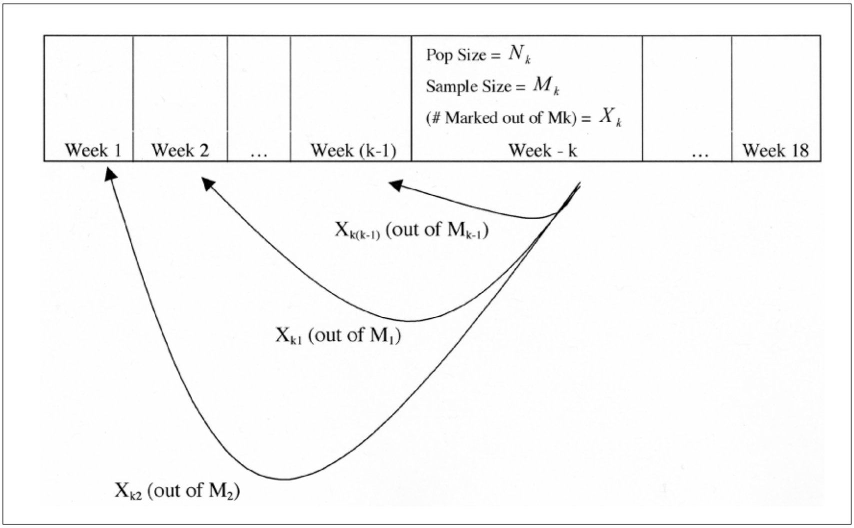

Figure 4. A visual respresentation of the sampling scheme that gives the probability (conditional) expression in week 1.

While it is probable that Green Treefrogs migrate to the pond complex from the surrounding areas, we feel this migration is limited and consider the area a habitat island within the large landscape. There are several lines of evidence to support this view. First, we regularly surveyed areas around the NWRC/EHCFC for frogs away from the ponds, but rarely found them. Frogs were only occasionally found away from the pond

Table 2. Population estimates per week.

Week	Lower 95% CI bound	Estimated population size	Upper 95% CI bound
2	57	143	519
3	143	415	1520
4	99	140	236
5	128	177	285
6	119	150	228
7	106	125	218
8	116	133	179
9	120	151	269
10	113	123	207
11	331	1429	8249
12	231	487	1395
13*			
14	222	523	1873
15	156	228	605
16	199	416	1469
17	196	341	769
18	246	523	1398

*No capture data for sampling week 13.

Table 3. Weekly summary data on green treefrog body lengths in millimeters.

Week #	N	Min	Max	Mean	Median	STD
2	14	20	50	37.5	40	10.0
3	24	16	50	32.5	35	10.9
4	15	30	40	34.2	35	4.2
5	18	20	45	32.1	30	6.7
6	9	20	50	37.0	40	7.6
7	2	20	50	32.7	30	9.0
8	6	15	50	30.2	30	8.7
9	3	25	50	34.5	30	7.6
10	1	20	50	35.0	35	11.6
11	12	15	55	27.6	20	13.7
12	9	15	55	27.5	20	11.9
13*	0					
14	6	20	40	27.5	25	5.9
15	2	20	25	24.0	25	2.2
16	4	30	55	38.3	37.5	9.3
17	5	15	40	25.1	22	9.5
18	7	20	55	31.5	27.5	12.9

*No captures during sampling on week 13.

complex. Second, we have set out PVC pipes to act as artificial habitat. While we have found Green Treefrogs in our pipes around areas immediately adjacent to the pond complex, we have rarely found them away from the area. One of the authors (J. Carter) has inspected the adjacent roadway after rains for evidence of frog movement from a housing complex across the street to the study site and has not found any dead frogs on the road. Finally, call monitoring was conducted in conjunction with the mark-recapture work. We have never heard Green Treefrogs calling from areas adjacent to our study site. So while it is likely that some frogs migrate from and to the study site, we feel that the site, because of geography, remains relatively isolated from other centers of population.

We caught frogs from 17 June 2004 to 22 October 2004. The data can be separated into two periods, before and after week 11 (August 17^{th}). Before this date, mating calls for Green Treefrogs were noted, but not afterwards. If we treat week 3 as an outlier, the first period's estimated population average is 142.75 ± 17.33. Week 11 appears to be an outlier with an estimated population of 1429. This value is a one-week ten-fold increase. There are two possible explanations for that increase.

One possibility is that our estimations were affected by differences in catchability. Only male frogs call, and when they stop calling, they are harder to catch. Before week 11, our sample sizes averaged about 25 frogs per night, and after week 11, the average sample size decreased to approximately 10 frogs each night. Because our catching methods relied, in part, on listening for frog calls, our method is biased towards males, and our estimate for this period will be based on mainly the male population. If we assume that there is an equal ratio of males to females in the population, we may have underestimated the population by a half during the first half of our study. After the breeding season, males no longer call. Thus, our catch efforts are a result of unbiased sampling of males and females. Under this scenario our estimate is more representative of the population in the second half of the capture period. In that case, the population didn't change, instead our estimates became better.

A second explanation may be that our estimates reflected an actual increase in population size during week 11 due to an influx of recent metamorphs into our frog population. This could be due to immigration, but is more likely due to the flush of recent metamorphs into the population that our simulation modeling efforts predicted. An increase due to immigration of breeding adults is unlikely because calling activity decreased after the increase in population. One would expect calling activity to increase under these circumstances. Furthermore, adult frogs are larger than juveniles and recent metamorphs. If the increase was due largely to a influx of adults, we would have expected a significant increase in the average size. Instead, the median size of frogs caught decreased.

In the above estimation procedure, it is assumed that in week-k (k = 1, 2, … 18) the population size N_k was constant at the time of sampling (in other words, population size should not vary significantly for any reason). The estimated population sizes for week 3 and week 11 had unexpected variance. Reexamining the original samples from week 3 and week 11 revealed that there were a small percentage of frogs captured with marks from previous weeks (7.7% and 8% respectively). Compared to the rest of the data set, these particular weeks' samples seem to be outliers. The time-series plot supports this hypothesis (Fig. 5). The time-series plot separates into two periods, before and after week 10. After week 10, the population size appears to have abruptly increased, which may have been due to metamorphs entering the frog population.

We also considered the measured length of frogs caught. Before week 11, the average length of the frogs caught was greater than 30 mm. In week 11, the average dropped to 27.7 mm and did not rise above the first 10-week average for 5 weeks. However, the variance associated with these lengths overlapped, and therefore, the significant difference in lengths cannot be justified. Nevertheless, the median length did decline

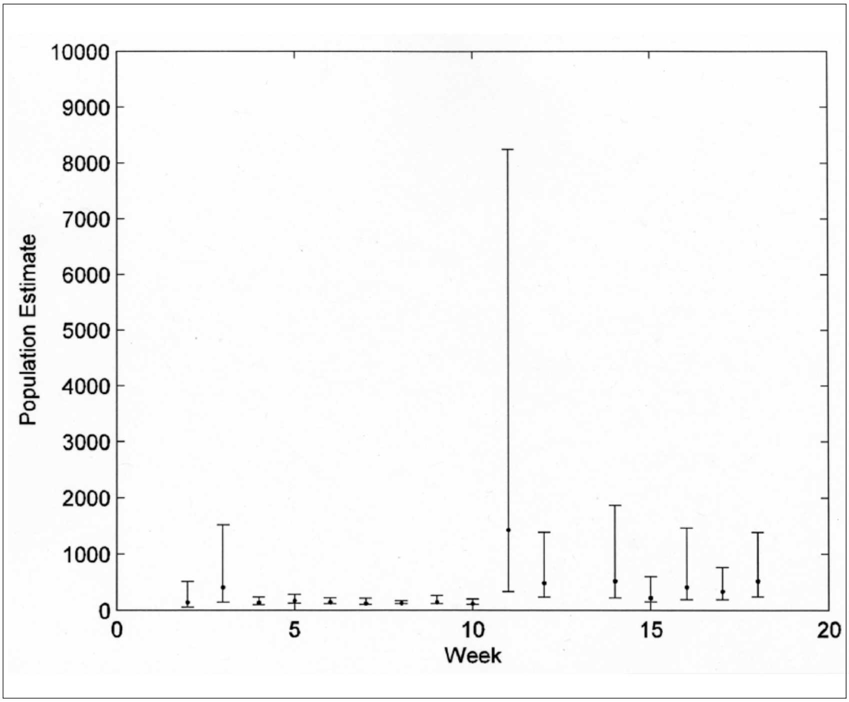

Figure 5. Time-series plot of the estimated population size by the maximum-likelihood estimator model (for each week, the vertical line provides an approximate 95% confidence interval of the population size, with the dot indicating the point estimate).

by 10 mm or 1/3 for the two weeks after Week 11 and did not rise to pre-Week 11 levels for 6 weeks. During this same period, our estimated population size increased significantly. Both of these observations could be explained by metamorphs entering the frog stage. We created an age structured metapopulation dynamics model for the ponds in the NWRC/EHCFC to help us better understand how our population may change over the season (J. Carter et al., unpubl. data). The results from this model also support the idea that a population increase might be expected midseason as a result of the influx of metamorphs.

Wright and Wright (1995) report that adult male and adult female Green Treefrogs range in size from 37–59 mm and 41–63 mm, respectively. The sizes of frogs caught in the second half of the study would lend support to the idea that more subadults were being caught, and not significantly more adult females.

It is also interesting to note that calling activity significantly declined after week 10. The Green Treefrog is noted for calling through the end of August if the weather is suitable (Dundee and Rossman 1989). In order to effectively attract females, male frogs expend large amounts of energy in producing calls (Bosch and de la Riva 2004). The surplus energy needed to make these calls is not available if the frog experiences stress due to a decrease in food supply. Therefore, we speculate that if a sudden increase in population size did occur, this might cause increased competition for food, and males would stop calling. If this is the case, we may be able to use this relationship as a method for estimating the local carrying capacity for adults in the system.

In addition to estimating the populations of adult Green Treefrogs, we attempted to estimate the tadpole populations for that species using the techniques outlined in Jung et al (2002). However, initial capture and recapture rates of tadpoles were too low to make reliable population estimates.

Conclusions

Our population estimates varied during the study; there were approximately 140 individuals during the first 10 weeks, then an increase in population size around week 10, and finally a comparative decline for the rest of the sampling period. These results are in agreement with population-dynamics modeling work (A.S. Ackleh, S. Boudreaux, S. Karhbet, L. Pham, and B. Price, unpubl. data) which predicts that the adult population in the pond complex should increase as tadpole cohorts that hatched out earlier in the summer metamorphose to adult frogs. The sudden decrease in Week 11 of median size of frog length supports this conclusion. After the abrupt population increase in week 10, the frog count steadily declines for the rest of the summer. This larger population estimation could either reflect (1) an actual decline (caused by recent metamorphs moving out of the ponds), (2) an artifact of our catch method (males calling less reduces our catch success rate), or (3) a combination of these two factors.

Although the use of VIE tags was helpful in identifying Green Treefrogs for weekly mark-recapture analysis, this technique did not allow for individual identification. This method limited our ability to look at capture history, develop accurate estimations of survival probability, or estimate growth rates. In the future, we are plan to mark frogs as individuals using alpha-numeric tags.

Acknowledgments

This project was funded through the National Science Foundation under grants #DMS-0311969 and #DUE-0531915. We would also like to thank the NWRC for providing training, equipment, and access to and use of their facilities. Jim Delahoussaye provided frogs for our pilot study. Kathleen Roberts provided technical assistance with VIE tagging. The order of authorship was randomly chosen and does not reflect relative contribution to this work.

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Appendix 1: Statistical model.

First we consider the case of week 2. Draw a sample of size M_2 (known) from the population of size N_2 (unknown). Let X_2 denote the number of marked frogs in this sample that were caught earlier (in week 1). Note that X_2 is a random variable and hence has a probability distribution. The probability that $X_2 = x_2$ (some observed value) is:

$$P(X_2 = x_2) = \frac{\binom{M_1}{x_2}\binom{N_2 - M_1}{M_2 - x_2}}{\binom{N_2}{M_2}}, \quad \text{(A1)}$$

where $N_2 - M_1 > 0$, $(N_2 - M_1) - (M_1 - x_2) > 0$, and $N_2 > M_2$. According to our notations in (1), $x_2 = x_{21}$. Note that N_1 = population size in week 1, and M_1 is the first week's sample size (caught, marked, and released).

The only unknown element in the probability expression (A1) is the population size N_2 which is the unknown parameter in the probability model, known as the hypergeometric probability model. The restrictions given after (A1) can be summarized as $N_2 > \max\{M_1, M_2, (M_1 + M_2 - x_2)\}$. When the probability expression (A1) is viewed as a function of x_2 (the observed value of the random variable associated with the experiment of mark-recapture sampling scheme for week-2), it is called a (discrete) probability distribution. The same expression (A1), when viewed as a function of the unknown parameter N_2, is called a likelihood function, and it is denoted by $L(N_2| x_2, M_1, M_2)$ (i.e. a function of N_2 given that x_2 is the observed value of X_2, and the sequential sample sizes up to week-2 are M_1 and M_2, respectively). We follow the method of Maximum Likelihood Estimation (MLE) to estimate N_2. The MLE of N_2, denoted by $\tilde{N}_2$ is obtained by maximizing $L_2(\tilde{N}_2| x_2, M_1, M_2) = P(X_2 = x_2)$ with respect to N_2; i.e.,

$$\max_{N_2} L_2(N_2| x_2, M_1, M_2) = L_2(\tilde{N}_2| x_2, M_1, M_2). \quad \text{(A2)}$$

The MLE is a preferred estimation technique because the estimate of the parameter is known to have nice theoretical asymptotic properties. The estimate $\tilde{N}_2$ is the value of the parameter N_2, which makes $X_2 = x_2$ most probable since we have already observed it.

Next we consider the case of week 3. Draw a sample of size M_3 (known) from the population of size N_3 (unknown). Let X_3 denote the number of marked frogs in this sample that were caught earlier. X_3 is a random variable and has two components X_{31} and X_{32} such that

$$X_3 = X_{31} + X_{32}, \quad \text{(A3)}$$

whereX_{31} = number of frogs in the week 3 sample marked in week 1, and X_{32} = number of frogs in the week 3 sample marked in week 2.

The probability distribution of observing $(X_{31} = x_{31}, X_{32} = x_{32})$ is (given that we had observed $X_2 = x_2$ in week 2):

$$P(X_{31} = x_{31}, X_{32} = x_{32} | X_2 = x_2) = \frac{\binom{M_1}{x_{31}}\binom{M_2 - x_2}{x_{32}}\binom{N_3 - \{M_1 + (M_2 - x_2)\}}{M_3 - x_{31} - x_{32}}}{\binom{N_3}{M_3}}, \quad \text{(A4)}$$

Again, note that the above expression has the only unknown element N_3.

Maximum Likelihood Estimation yields $\tilde{N}_3$ such that

$$\underset{N_3}{\mathrm{Max}}\, L_3(N_3 | \ x_2 \colon x_{31}, x_{32}; M_1, M_2, M_3) = L_3(\tilde{N}_3 | \ x_2 \colon x_{31}, x_{32}; M_1, M_2, M_3).$$

Notice that the estimate $\tilde{N}_3$ is dependent not only on (x_{31}, x_{32}) (i.e., what we observe in week 3), but also on x_2 (i.e., what we had observed in week 2). This is because the probability distribution (A4) is the conditional distribution of the data observed in week 3, given what has been observed in week 2. Continuing in this fashion, we obtain the probability model (1) for week *k*.

Interestingly, we have noted that if we use slightly less precise information, then still our population estimates remain the same with the observed frog data. The probability model (1) is a generalization of the standard hypergeometric distribution, which uses the precise, past weekly recapture data on a conditional basis. If we combine the past weekly data as a simple "past data" and use the standard hypergeometric distribution, then

$$P(X_k = x_k | X_l = x_l, 1 \le l \le k-1) =$$

$$\frac{\binom{M_1 + (M_2 - x_2) + (M_3 - x_3) + \ldots + (M_{k-1} - x_{k-1})}{x_k}\binom{N_k - [M_1 + (M_2 - x_2) + (M_3 - x_3) + \ldots + (M_{k-1} - x_{k-1})]}{M_k - x_k}}{\binom{N_k}{M_k}}, \text{(A5)}$$

where $M_{(k-1)} = M_1 + (M_2 - x_2) + \ldots + (M_{(k-1)} - x_{k-1})$ is the total number of marked frogs in the population in week-*k*. (It is assumed that all the frogs marked earlier but which didn't get caught in week *k* are still alive.)

One can maximize the above (A5) with respect to N_k to get another estimate, say, N^*_k, of N_k, the population size in week-*k*. Our numerical computations have shown that $N^*_k \approx \tilde{N}_k$.

The slightly less precise model (A5) (which combines all the week-wise recapture data into a single "recapture observation") has one advantage. The moment expressions for X_k are known for (A5), whereas no such expressions are available for the model (1). Therefore, we use (A5) to get approximate confidence bounds for the estimates of N_k.

Using the probability model (A5), mean of $X_k = \mu_k = M_k\left(\frac{M_{(k-1)}}{N_k}\right)$ and standard deviation of $X_k = \sigma_k = \sqrt{M_k\left(\frac{M_{(k-1)}}{N_k}\right)\left(1 - \frac{M_{(k-1)}}{N_k}\right)\left(1 - \frac{M_k - 1}{N_k - 1}\right)}$. It is expected that X_k should fall within $2\sigma_k$ of μ_k with probability 0.95 (roughly), i.e.,

$$0.95 \approx P(\mu_k - 2\sigma_k \le X_k \le \mu_k + 2\sigma_{kk}).$$

The two inequalities inside the last probability expression can be inverted to get upper and lower confidence bounds, which have been calculated in Table 2.

Weekly population estimates and the corresponding approximate 95% confidence bounds are plotted in Figure 5.

Notice that the upper confidence bound for the population size is further away from the population estimate compared to that of the lower confidence bound. This indicates that the population estimates are highly positively skewed, and this is expected considering the fact that each population size N_k ($2 \le k \le 18$) takes values over the space $\{1,2,3, \ldots \infty\}$, which has a finite lower bound, but infinite upper bound.