Size and Structure of Two Populations of Spotted Turtle (*Clemmys guttata*) at Its Western Range Limit

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Abstract.—Determining demographic properties for threatened and endangered species is paramount for crafting effective management strategies for at-risk populations. Collecting sufficient data to quantify population characteristics, however, is challenging for long-lived species such as chelonians. One such species in Illinois is the state-listed as Endangered Spotted Turtle (*Clemmys guttata*). While demographic data exist for populations from other extremes of the range of the species, no similar investigation has been published for Illinois, in which only two isolated populations remain extant. We used a long-term mark-recapture data set to analyze changes in sex and stage structure, abundance, and population growth between 1988 and 2016. Both populations exhibited a strong adult bias (76.5–90.6%) and an even adult sex ratio throughout the duration of the study. At one site the estimated population abundance increased, although there was a decreasing trend in the growth rate over time. Population size and growth rate remained relatively stable at the other site. Sex and stage distributions in the Illinois *C. guttata* populations were consistent with those of other populations, but the two populations are not experiencing the steep declines documented throughout the remainder of the range of the species despite threats from habitat limitations, subsidized mesopredator abundance, poaching, and traffic. We recommend increasing available habitat as the most effective strategy to reduce risks to *C. guttata* persistence in Illinois.

INTRODUCTION

Habitat loss and fragmentation are leading causes of declines in freshwater turtle populations, which may have limited ability to disperse away from reduced and degraded habitat patches to acceptable habitat patches (Ernst and Lovich 2009; Harden et al. 2009) due to the absence of other critical habitat on the landscape (Gibbs 1993), vagility (Whitney Anthonysamy, unpubl. data), or reliance on specific environmental signals. For example, Snake-necked Turtles (*Chelodina rugosa*) remain in the mud of dried ponds until the onset of the rainy season (Fordham et al. 2007), and hatchling Sonoran Mud Turtles (*Kinosternon sonoriense*) disperse when rains flood their nest (van Lobel Sels et al. 1997). Habitat specialists are particularly susceptible to habitat fragmentation and loss (Bender et al. 1998) due to the elimination of niche requirements and increasing hostile dispersal conditions (Shepard et al. 2008). Thus, this combination of factors can initiate demographic instability, which can cause loss of genetic diversity (Marsack and Swanson 2009; Willoughby

et al. 2013). Such threats are of increasing concern for rare or endangered species about which we lack basic information which can better direct conservation resources, such as population size and structure (Dunstan et al. 2011; Bartman et al. 2016). For instance, unbalanced sex and stage structure can impact population vital rates, reduce the effective population size, and lead to decreased genetic variability and reduced recruitment (Gibbs and Amato 2000; Skalski et al. 2005; Grayson et al. 2014). Determining population size and structure is therefore crucial to accurately assessing the status of a species (Chase et al. 1989). Additionally, estimates of long-term trends are important for updating listings (Troeng and Rankin 2005), justifying conservation attention (Chan and Liew 1996), and evaluating the effectiveness of management (Sai et al. 2016) or harvest (Brown et al. 2011) actions.

Acquiring long-term datasets on population dynamics requires extensive time and effort, particularly for long-lived chelonian species (Congdon et al. 1993; Brodman et al. 2002); however, extrapolation from limited contemporary datasets runs the risk of

underestimating the real extent of fluctuations in a population (McClenachan et al. 2006), especially given the extent of habitat alteration over the last century. One chelonian species that has been detrimentally affected by a changing landscape is the Spotted Turtle (*Clemmys guttata*). This small, semi-aquatic species inhabits a broad geographic range throughout the eastern USA (Ernst and Lovich 2009), though populations are patchily distributed and found only within complexes of wetland and upland habitats used for breeding, nesting, and brumation (Ernst 1970; Perillo 1997; Wilson 1997; Milam and Melvin 2001). Even relatively intact populations are often small and further threatened by roads, pollution, habitat loss, and poaching (Ernst 1995; Barnwell et al. 1997; Litzgus and Brooks 2004; Litzgus and Mousseau 2004a). Furthermore, individuals have limited home ranges (Ward et al. 1976; Semlitsch and Bodie 2003) and high site fidelity, which inhibit their ability to disperse from degraded habitat. The International Union for the Conservation of Nature (IUCN) estimates the species has likely undergone a 50% reduction from historical abundance levels principally due to irreversible habitat loss (IUCN 2011). Between 2003 and 2013, *C. guttata* gained some measure of protection, listing, or recognition of conservation in all states where it occurs (CITES 2013). Furthermore, the species has been petitioned for listing under the U.S. Endangered Species Act (Adkins Giese et al. 2012).

Since first being documented in Illinois in 1927, several populations of *C. guttata* have become extirpated in the state due to extensive habitat loss and poaching (Johnson 1983). The species is currently listed as endangered in Illinois, and only two *C. guttata* populations remain. Both these populations face the same set of threats plaguing previous populations. Poaching, for instance, is facilitated by the online availability of locality data. The species can also suffer from road mortality and predation from subsidized mesopredators (unpubl. data). Furthermore, genetic analysis indicated a historical bottleneck and subsequent genetic divergence between the two populations and predicted an imminent loss of genetic diversity (Anthonysamy et al. 2017), increasing the urgency of intervention to conserve the two remaining populations. Although biologists have studied both populations since the late 1980s, no analyses have yet examined long-term trends in population parameters.

The objective of our study was to complete the demographic profile of *C. guttata* at the western limits of its range. We characterized the population size and structure of the two remaining populations within Illinois and analyzed population growth over a 28-y period to inform management goals for long-term conservation. We then compared the study populations to infer regional risk to the species and contextualized the Illinois populations within the known demographic variation of the species across its range.

MATERIALS AND METHODS

Study site.—We conducted capture-mark-recapture on two populations (hereafter referred to as Site 1-R and Site 2-L) in Illinois, USA. We have not reported specific locations in consideration of poaching threats (Lindenmayer and Scheele 2017) and at the request of the land management agencies involved in conservation efforts. Both sites had extensive wet-mesic dolomite prairie habitat including sedge meadow, cattail marsh, wet-mesic prairie, and dolomite prairie. They were bounded by the Des Plaines River and were found within a matrix of urban and industrial development. We began surveys at both sites in 1988, completing 11 surveys through 2008 at Site 1-R and 19 surveys through 2016 at Site 2-L.

Data collection.—Between 1988 and 2016, we used a combination of capture techniques including visual encounter surveys and trapping with 30.5-cm minnow traps (Promar, Gardena, California, USA) and collapsible hoop nets during the spring active season spanning from approximately mid-April to late June. Captured individuals received a unique notch code on their marginal scutes (Cagle 1939) and were classified by sex and stage. We delineated sex and stage categories according to the development of secondary sexual characteristics (SSC) such as cloacal position in relation to the carapace edge, facial coloration, and the presence or absence of a plastral concavity. If SSC were emergent (7–10 y old; Ernst and Lovich 2009), we classified the turtle as an adult and then determined its sex. We considered individuals of unknown sex to be juveniles or hatchlings, the latter identified by the presence of a yolk sac scar or the absence of growth rings beyond the areolar. We also produced diagrams or photographs of shell patterns to confirm individual identities in case of damage to the notches or mortality, which necessitated reconstructing partial or disarticulated shell remains.

Population structure.—We expressed the adult sex ratio of *C. guttata* as the proportion of female captures among all female and male adult captures and the age class ratio as the proportion of adult captures among all hatchling, juvenile, and adult captures. We used an Exact Binomial Test for Goodness-of-fit (Pilgrim et al. 1997) within the statistical computing software R version 3.4.2 (R Core Team, Vienna, Austria) to test for sex ratio equality at $\alpha = 0.05$ for each survey season. We used a Bonferroni correction for repeated tests, producing $\alpha_{crit} = 0.0063$ for site 1-R and 0.0036 for site 1-L. We tested for trends in adult sex ratio and age

class ratio using a time series approach to account for possible autocorrelation between years. We restricted the population structure data to years in which the captured sample size was > 10 individuals, performed a logit transformation on the data, and used the auto. arima function from the forecast package version 8.2 (Hyndman and Khandakar 2008) in R version 3.5.3 (R Core Team, Vienna, Austria). We set differencing (d) to 0, included a linear time covariate to model trend, and determined the appropriate number of autoregressive (p) and moving-average (q) parameters using AICc. We calculated 95% confidence intervals using the confint function in R to determine if the slope was significantly different than zero.

Population size and growth rate.—We compiled individual capture histories consisting of live encounters during only the spring active season of each survey year and included sex as a group covariate. We then used Program MARK version 8.1 (White and Burnham 1999) and RMark version 2.2.0 (Laake 2013) in R to construct a biologically relevant set of candidate models. We used the POPAN formulation (Riedle 2014) of the Jolly-Seber model (Souza and Abe 1997) to increase the likelihood of model convergence (Arnason and Schwarz 1998). We then ranked models using AIC to determine meaningful covariates and to identify the top model, which had the lowest AIC and the most weight. Annual post-birth abundance (N-hat) was calculated iteratively for each site using the initial population size and real parameter estimates of *pent* (probability of entrance into the population). We then constructed 95% confidence intervals of derived estimates of population size and sex-specific survival rates (Phi) using the top model for each site.

We used our derived population size estimates to calculate the geometric mean of average between-year growth rates as an estimate for the finite rate of increase (lambda, λ) between years (Udevitz and Ballachey 1998). We used the Gmean function from the package DescTools version 0.99.28 (Signorell 2019) in R version 3.5.3 (R Core Team, Vienna, Austria) to calculate the 95% confidence intervals for geometric means. We then assessed trends in the population growth rates using the time series approach described previously but without data transformation. Each data point represented the growth rate based on two consecutive sampling years; we excluded all other intervals in the determination of average population growth rate. A value of λ = 1.0 indicates no growth (i.e. a stable population size), while λ > 1.0 indicates a growing population and λ < 1.0 indicates a declining population. A regression slope significantly different than zero thus suggests either a long-term decline (negative slope) or increase (positive slope) in population growth rate.

RESULTS

Population structure.—We had 289 captures of adults at Site 1-R, of which 150 (51.9%) were of females (Table 1). In years with a sample size > 10 individuals (Gibbs and Steen 2005), adult sex ratio varied from 38.5–77.8%. We totaled 682 captures of adults at Site 2-L, and the population exhibited a slightly lower adult sex ratio (46.8%) and a narrower range when n >10 (27.3–53.1%) over all captures than at Site 1-R (Table 2). The adult sex ratio did not differ significantly from equality at either site (Tables 1 and 2). The adult sex ratio was 0.45 for both sites when considering the number of unique individuals of each sex instead of the total number of capture events.

The auto.arima function indicated an ARIMA(1,0,0) model (first-order autoregressive) was needed to correct autocorrelation for the age class ratio model at Site 2-L. An ARIMA(0,0,0) model indicated no substantial autocorrelation was present and was appropriate for age class ratio at Site 1-R and adult sex ratio at both sites (Table 3). The 95% confidence intervals indicated no trend in adult sex ratio or age class ratio for either site (Table 3).

Population size and growth rate.—We calculated population sizes for Site 1-R and Site 2-L using capture histories for 84 and 168 individuals, respectively. The top model for each site as indicated by the lowest ΔAIC each indicated that apparent survival (Phi) was sex-dependent and capture probability (p) was time-dependent but differed in terms of *pent* which was constant for Site 1-R and time-dependent for Site 2-L (Table 4). Phi was comparable between sexes and populations. At Site 1-R, Phi_{female} = 0.94 (0.92, 0.96) and Phi_{male} = 0.92 (0.89, 0.95) while at Site 2-L, Phi_{female} = 0.94 (0.93, 0.96) and Phi_{male} = 0.92 (0.92, 0.95).

The top POPAN model parameters resulted in an estimated increase in abundance for the Site 1-R population from about 56 individuals to about 116 individuals from 1989–2010 (Table 5; Fig. 1A). Site 2-L also appears to have increased slightly since initial surveys were conducted but has remained stable after 2005 (Table 6); however, confidence intervals for Site 2-L indicate the overall difference could still be a result of sampling error. For both sites, the 95% confidence interval is largest for the first survey season in 1988 due to the inherent difficulty of estimating the first sampling occasion using maximum likelihood. Overall, the Site 1-R population has increased in size whereas the Site 2-L population size has not throughout the duration of the study (Fig. 1).

Both sites maintained an estimated λ > 1.0 (λ_{1-R} = 1.21, λ_{2-L} = 1.03). The growth rate deviated from stability at Site 1-R but not at Site 2-L (Fig. 2). The auto.arima function
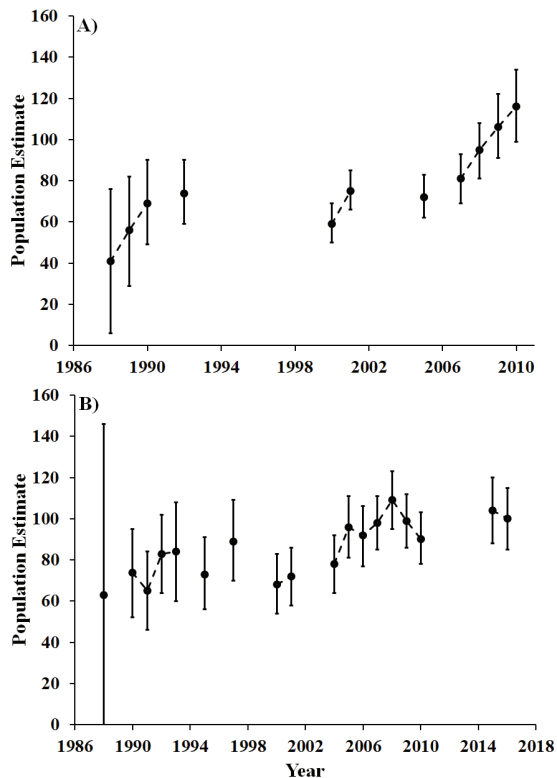
Figure 1. Changes in size of two Spotted Turtle (*Clemmys guttata*) populations in Illinois, USA, based on Jolly-Seber model calculations. Bars represent 95% confidence intervals. (A) Site 1-R: estimates span from 1988–2010. (B) Site 2-L: estimates span from 1988–2016.

indicated an ARIMA(0,0,0) model fit best for population growth rate at Site 1-R whereas an ARIMA(1,0,0) model fit best for Site 2-L (Table 3). The 95% confidence intervals indicated a decreasing trend at Site 1-R but no trend at Site 2-L (Table 3).

DISCUSSION

Both Illinois populations of *C. guttata* exhibited robust population structure. The population at Site 1-R had a slightly higher proportion of females than the population at Site 2-L (Tables 1 and 2); however, neither site differed significantly from equality in adult sex ratio over the length of the study. Equal adult sex ratio is consistent with other populations of *C. guttata*. For instance, Ernst (1976) in southeastern Pennsylvania and Litzgus and Mousseau (2004a) both recorded equal adult sex ratios. A major deviation from equality occurred in an island population in Ontario, Canada, where the adult sex ratio was 3.83F:1M, which the authors attributed to the unusual habitat type (Reeves and Litzgus 2008). Our finding also supports the trend observed for semi-aquatic turtle species in general, which typically adhere more closely to equal adult sex ratios than do fully aquatic chelonian species (Gibbs and Steen 2005).
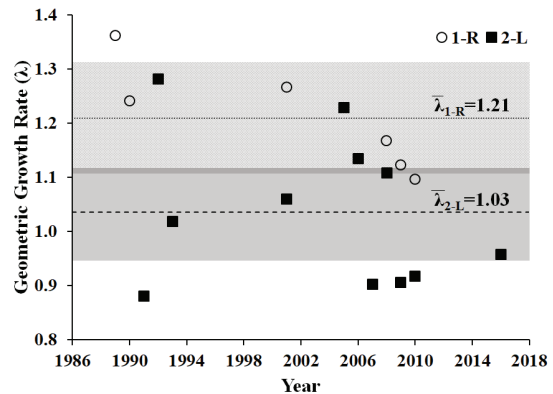

Figure 2. Geometric growth rate for two populations of Spotted Turtles (*Clemmys guttata*) in Illinois, USA, from 1988–2016. The dotted and dashed lines represent the average values for sampled years at Sites 1-R and 2-L, respectively. Shaded bands represent 95% confidence intervals, while the darkest band indicates the area of overlap.

Equality of sex ratios reduces the difference between the population size and the effective population size and is an important consideration for small populations because genetic resilience can be compromised by a skewed sex ratio (Guo et al. 2002; Traill et al. 2010). While there has not yet been a quantitative assessment of genetic heterozygosity within and between the Site 1-R and Site 2-L populations, future management should consider the genetics of these populations because of their limited size. For example, a genetic analysis of *C. guttata* populations in Canada discovered that, despite good retention of heterozygosity, low allelic richness when the effective population size was small (< 50 individuals) suggested the occurrence of genetic drift (Davy and Murphy 2014). Genetic drift was found to be both accelerated and masked in a small population of the Ornate Box Turtle (*Terrapene ornata*) with a history of persistent bottleneck (Kuo and Janzen 2004), further supporting the need for long-term genetic monitoring of *C. guttatta* in Illinois.

The bias toward adults in both Illinois populations is consistent with the life-history strategy of other long-lived organisms in which few individuals survive to maturity but high adult survival rates drive population persistence (Litzgus and Mousseau 2004b; Enneson and Litzgus 2009). For instance, Congdon et al. (1993, 1994) documented a similar pattern of adult-biased populations in which high adult survival is fundamental to stable population growth in two other aquatic turtle species, Blanding's Turtle (*Emydoidea blandingii*) and Common Snapping Turtle (*Chelydra serpentina*), and Cunnington and Brooks (1996) found the same bet-hedging pattern in *C. serpentina* and the marine Loggerhead Seaturtle (*Caretta caretta*). Known *C. guttata* populations from other locations also reflect such a bet-hedging strategy. For example, populations at the northern and southern range limits of the species favored adult over juvenile

TABLE 1. Sex and stage ratios by season for the Site 1-R population of Spotted Turtles (*Clemmys guttata*) in Illinois, USA, from 1988–2010 based on raw capture counts by season. Adult sex ratio (ASR) was calculated as the proportion of captured females to total adult captures. Age class ratio (ACR) was calculated as the proportion of adult captures to all captures. Overall ASR and ACR were calculated for the sum of all individual capture events (Sum). Only the overall ASR was calculated for the number of unique captured individuals (# Individuals) due to changes in the age class of an individual over time. We calculated average ASR and standard error for the Sum.

Year	Adult Sex Ratio				Age Class Ratio				
	Female	Male	Total	ASR	Adults	Juveniles	Hatchlings	Total	ACR
1988	2	0	2	1.00	2	0	0	2	1.00
1989	14	15	29	0.48	29	10	0	39	0.74
1990	0	1	1	0.00	1	0	0	1	1.00
1992	25	19	44	0.57	44	5	2	51	0.86
2000	21	14	35	0.60	35	13	0	48	0.73
2001	14	4	18	0.78	18	8	5	31	0.58
2005	24	17	41	0.59	41	16	0	57	0.72
2007	28	33	61	0.46	61	15	9	85	0.72
2008	15	24	39	0.38	39	4	0	43	0.91
2009	7	11	18	0.39	18	0	3	21	0.86
2010	0	1	1	0.00	1	0	0	1	1.00
Sum	150	139	289	0.52	289	71	19	379	0.76
# Individuals	55	66	121	0.45					
Ave. ASR (weighted across all years)				0.48					0.83
Standard Error				0.30					0.14
Ave. ASR (weighted across years, n > 10)				0.53					0.76
Standard Error				0.13					0.11

captures (Litzgus and Mousseau 2004a; Reeves and Litzgus 2008) with a calculated age class ratio of 93.3% adults (Litzgus 2006). At mid-latitude, Ernst (1976) found a heavy adult bias of roughly 70% in southeast Pennsylvania, USA, and Breisch (2006) reported an age class ratio of 57.1% in West Virginia, USA. It is unclear whether naturally high mortality, survey bias, different habitat use, or a combination of factors best explains the low capture rates of approximately 10–40% for juveniles and hatchlings. Low captures rates for these stages are typical for freshwater turtle species (Marchand and Litvaitis 2004; Pike et al. 2008) and can represent stable levels of adult survival (Hall et al. 1999). The stable population sizes we found suggest that recruitment into the adult population is occurring.

We determined that the Site 1-R and Site 2-L populations are similar in abundance and represent the lower end of known population sizes, which range from 30 to 1,205 individuals (CITES 2013), though the general trend for the species is decreasing abundance. In Ontario, Canada, Seburn (2003) speculated a possible decline of 20% over 18 y and Jacqueline Litzgus (per. comm.) recorded a 50% decline in annual spring survey captures at a long-term monitoring site over the past 20 y. Populations in the Midwest of the USA exhibited similarly precipitous declines over the past century (Lovich 1987; Brodman et al. 2002); however, our results indicated Illinois populations appear to be stable in size. The Site 2-L population growth rate showed no directional trend or significant change from stability. At Site 1-R the mean population growth rate is significantly higher than 1.0, though the time series analysis indicated a decreasing trend. The trend suggests the growth rate was high in early years but is more recently approaching stability ($\lambda = 1.0$). Thus, populations in Illinois do not appear to be experiencing rapid declines as documented in other areas. Nonetheless, numerous threats remain and may need to be addressed for populations to remain stable.

Overall, the amount of available habitat on the landscape limits the presence of *C. guttata* in Illinois, and the populations at the two sites with appropriate habitat features remain stable but small. Because small populations are more susceptible to genetic drift and demographic stochasticity, maintaining adequate population abundance is crucial to long-term genetic fitness and persistence (Traill et al. 2010). Genetic structure between isolated but nearby populations can be attributable to natural landscape heterogeneity and has been documented for Maximilian's Snake-headed Turtle (*Hydromedusa maximiliani*; Souza et al. 2002) and *E. blandingii* (Mockford et al. 2005). The differentiation between the Site 1-R and Site 2-L populations, however, include evidence of a past

TABLE 2. Sex and stage ratios by season for the Site 2-L population of Spotted Turtles (*Clemmys guttata*) in Illinois, USA, from 1988–2016 based on raw capture counts by season. Adult sex ratio (ASR) was calculated as the proportion of captured females to total adult captures. Age class ratio (ACR) was calculated as the proportion of adult captures to all captures. Overall ASR and ACR were calculated for the sum of all individual capture events (Sum). Only the overall ASR was calculated for the number of unique captured individuals (# Individuals) due to changes in an individual's age class over time. We calculated average ASR and standard error for the Sum.

Year	Adult Sex Ratio				Age Class Ratio				
	Female	Male	Total	ASR	Adults	Juvenile	Hatchlings	Total	ACR
1988	10	15	25	0.40	25	7	0	32	0.78
1990	17	15	32	0.53	32	13	3	48	0.67
1991	3	5	8	0.38	8	2	0	10	0.80
1992	25	29	54	0.46	54	11	1	66	0.82
1993	3	8	11	0.27	11	3	0	14	0.79
1995	9	14	23	0.39	23	4	0	27	0.85
1997	13	18	31	0.42	31	6	1	38	0.82
2000	19	21	40	0.48	40	5	1	46	0.87
2001	25	31	56	0.45	56	9	3	68	0.82
2004	31	28	59	0.53	59	16	5	80	0.74
2005	17	17	34	0.50	34	9	0	43	0.79
2006	35	40	75	0.47	75	32	2	109	0.69
2007	5	4	9	0.56	9	4	0	13	0.69
2008	33	43	76	0.43	76	25	4	105	0.72
2009	1	1	2	0.50	2	0	0	2	1.00
2010	4	3	7	0.57	7	2	0	9	0.78
2015	38	37	75	0.51	76	10	0	86	0.88
2016	31	34	65	0.48	64	5	0	69	0.93
Sum	319	363	682	0.47	682	163	20	865	0.79
# Individuals	94	113	207	0.45					
Ave. ASR (weighted across all years)				0.46					0.80
Standard Error				0.07					0.09
Ave. ASR (weighted across years, n > 10)				0.45					0.91
Standard Error				0.07					0.08

bottleneck event (Anthonysamy et al. 2017), which supports anthropogenically mediated reduced gene flow (Mockford et al. 2005). Species persistence may also be achievable through establishing new populations with sufficient suitable habitat to support survival and recruitment (Temple 1987; Berglind 2005).

The differences we detected in population structure between the two populations in Illinois were minor but may be precursors to significant future differentiation in demographic vital rates (Bobyn and Brooks 1994). Such variation may result from population-level adaptations to site-specific conditions (Ometto et al. 2015) and may require specific management efforts at the site level. Further, although Illinois *C. guttata* populations appear demographically healthy, being small isolated populations, they remain susceptible to stochasticity, anthropogenic disturbances, and genetic degradation. We thus recommend two primary conservation actions to improve the long-term prospects for *C. guttata* in Illinois. First, as the two distinct populations show genetic differentiation, reconnecting them is potentially damaging to their local genetic adaptations and logistically unfeasible given practically irreversible land use changes. Management efforts should focus on increasing abundance in areas of suitable habitat and on restoring additional habitat to support higher abundances than exist currently at either site. An increased population size will reduce the likelihood of regional and site-specific extirpation (Akçakaya 2001) by dampening small population threats. Habitat for *C. guttata* can be expanded and improved at both sites through control of native cattails (*Typha* spp.) and subsequent enlargement of native sedge meadows for feeding and reproduction. Secondly, continued monitoring of known populations coupled with updated assessments of population size using robust estimators should be used to evaluate any actual versus perceived successes of management actions geared toward *C. guttata* (Dodd and Seigel 1991).

TABLE 3. Top ARIMA models (df = degrees of freedom) for adult sex ratio (ASR), adult class ratio (ACR), and population growth rates (PGR) for two populations of Spotted Turtle (*Clemmys guttata*) in Illinois. We calculated estimated values (Estimate) as well as standard error (SE), 95% lower confidence levels (LCL), and 95% upper confidence levels (UCL). We considered values of $P \leq 0.05$ significant.

Site	Variable	Top.Model	df	Estimate	SE	LCL	UCL	*P*
1-R	ASR	ARIMA(0,0,0)	7	0.003	0.013	-0.022	0.028	0.803
1-R	ACR	ARIMA(0,0,0)	6	0.014	0.030	-0.044	0.073	0.652
1-R	PGR	ARIMA(0,0,0)	4	-0.009	0.002	-0.013	-0.005	0.011
2-L	ASR	ARIMA(0,0,0)	12	0.013	0.008	-0.003	0.029	0.126
2-L	ACR	ARIMA(1,0,0)	12	0.028	0.019	-0.010	0.065	0.178
2-L	PGR	ARIMA(1,0,0)	8	-0.006	0.003	-0.012	0.000	0.101

Efforts to conserve *C. guttata* have benefitted from multiple studies of populations throughout their range, and the populations examined through our study have abundance and structure estimates within the known variation from other range extremes. We interpret consistency in structure between Illinois and other populations of *C. guttata* to indicate relative demographic stability in the Illinois populations. In contrast, we maintain range-wide concerns for the continued persistence of *C. guttata* based on trends in abundance, although our study indicates *C. guttata* are not currently facing such declines in Illinois.

TABLE 4. Set of 10 POPAN candidate models for deriving population estimates for two populations of Spotted Turtle (*Clemmys guttata*) in Illinois, USA. Models are ranked by ΔAIC for each site such that the lowest ΔAIC indicates the best model and described by the number of parameters (npar), Akaike Information Criterion score (AIC), difference between a given model's AIC score and the top model's AIC score (ΔAIC), model weight (weight), cumulative weight of all higher-ranked models (weight), and measure of variance (-2lnL). The global model is bolded, and the null model is italicized.

Mode	npar	AIC	ΔAIC	weight	weight	-2lnL
Site 1-R						
Phi(~Sex)p(~time)pent(~1)N(~1)	16	806.77	0.00	0.86	0.86	774.77
Phi(~Sex)p(~time)pent(~time)N(~1)	25	810.47	3.71	0.13	0.99	760.47
Phi(~-1 + Sex + time)p(~-1 + Sex + time)pent(~time)N(~1)	36	816.99	10.22	0.01	1.00	744.99
Phi(~-1 + Sex * time)p(~time)pent(~time)N(~1)	52	835.90	29.13	0.00	1.00	731.90
Phi(~-1 + Sex * time)p(~-1 + Sex * time)pent(~-1 + Sex * time)N(~1)	94	873.32	66.55	0.00	1.00	685.32
Phi(~time)p(~time)pent(~time)N(~1)	32	878.03	71.27	0.00	1.00	814.03
Phi(~-1 + Sex + time)p(~Sex)pent(~time)N(~1)	26	927.37	120.60	0.00	1.00	875.37
Phi(~-1 + Sex * time)p(~Sex)pent(~time)N(~1)	44	947.71	140.94	0.00	1.00	859.71
Phi(~Sex)p(~Sex)pent(~1)N(~1)	8	1148.45	341.68	0.00	1.00	1132.45
Phi(~1)p(~1)pent(~1)N(~1)	4	1201.56	394.79	0.00	1.00	1193.56
Site 2-L						
Phi(~Sex)p(~time)pent(~time)N(~1)	39	1823.34	0.00	0.91	0.91	1745.34
Phi(~Sex)p(~time)pent(~1)N(~1)	23	1827.90	4.57	0.09	1.00	1781.90
Phi(~-1 + Sex + time)p(~-1 + Sex + time)pent(~time)N(~1)	57	1839.03	15.70	0.00	1.00	1725.03
Phi(~-1 + Sex * time)p(~time)pent(~time)N(~1)	87	1867.33	44.00	0.00	1.00	1693.33
Phi(~time)p(~time)pent(~time)N(~1)	53	1912.11	88.77	0.00	1.00	1806.11
Phi(~-1 + Sex * time)p(~-1 + Sex * time)pent(~-1 + Sex * time)N(~1)	157	1931.56	108.23	0.00	1.00	1617.56
Phi(~-1 + Sex + time)p(~Sex)pent(~time)N(~1)	40	2308.93	485.59	0.00	1.00	2228.93
Phi(~-1 + Sex * time)p(~Sex)pent(~time)N(~1)	72	2349.93	526.60	0.00	1.00	2205.93
Phi(~Sex)p(~Sex)pent(~1)N(~1)	8	2522.49	699.15	0.00	1.00	2506.49
Phi(~1)p(~1)pent(~1)N(~1)	4	2603.73	780.39	0.00	1.00	2595.73

TABLE 5. Population size estimates (N_c) and annual recapture rates (p) for the Site 1-R population of Spotted Turtles (*Clemmys guttata*) in Illinois, USA, from 1988–2010 based on results of POPAN Jolly-Seber model calculations. Schnabel Closed Population Model estimates were obtained from unpublished reports. Raw capture counts (RCC) by season and previously calculated closed model estimates are included for comparison. The asterisk (*) denotes population estimates derived using the Lincoln-Peterson Index, and 95% C.I. is the 95% confidence interval of the population estimate.

Year	RCC	POPAN Open Model			Schnabel Closed Population Model	
		N_c	95% C.I.	p	N_c	95% C.I.
1988	2	41	6, 76	0.05	–	–
1989	39	56	29, 82	0.69	51	40, 61
1990	1	69	49, 90	0.01	–	–
1992	51	74	59, 90	0.64	101*	76, 125
2000	48	59	50, 69	0.67	63	46, 91
2001	31	75	66, 85	0.37	–	–
2005	57	72	62, 83	0.74	–	–
2007	85	81	69, 93	1.00	–	–
2008	43	95	81, 108	0.50	–	–
2009	21	106	91, 122	0.21	–	–
2010	1	116	99, 134	0.01	–	–

TABLE 6. Population size estimates (N_c) and annual recapture rates (p) for the Site 2-L population of Spotted Turtles (*Clemmys guttata*) in Illinois, USA, from 1988–2016 based on results of POPAN Jolly-Seber model calculations. Raw capture counts (RCC) by season and previously calculated closed model estimates are included for comparison. Schnabel Closed Population Model estimates were obtained from unpublished reports. The asterisks (*) denote population estimates derived using the Lincoln-Peterson Index, and 95% C.I. is the 95% confidence interval of the population estimate. Abundances in 1988 and 1990 each have two closed population estimates.

Year	RCC	POPAN Open Model			Schnabel Closed Population Model	
		N_c	95% C.I.	p	N_c	95% C.I.
1988	32	63	-20, 146	0.47	41	32, 51
					58	–
1990	48	74	52, 95	0.65	58	–
					105*	–
1991	10	65	46, 84	0.15	137*	–
1992	66	83	64, 102	0.71	118*	–
1993	14	84	60, 108	0.15	115*	–
1995	27	73	56, 91	0.32	–	–
1997	38	89	70, 109	0.37	–	–
2000	46	68	54, 83	0.51	64	48, 95
2001	68	72	58, 86	0.70	91	71, 126
2004	80	78	64, 92	0.78	106	84, 144
2005	43	96	81, 111	0.43	–	–
2006	109	92	77, 106	0.98	–	–
2007	13	98	85, 111	0.13	–	–
2008	105	109	95, 123	0.96	95	88, 103
2009	2	99	86, 112	0.02	–	–
2010	9	90	78, 103	0.11	–	–
2015	85	104	88, 120	0.91	–	–
2016	70	100	85, 115	0.77	–	–

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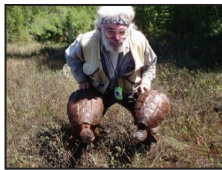
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