Experts correctly describe demography associated with historical decline of the endangered Indiana bat, but not recent period of stationarity

Wayne E. Thogmartin[a, *], Carol Sanders-Reed[b], Jennifer A. Szymanski[c], Lori Pruitt[d], Michael C. Runge

[a]*United States Geological Survey, Upper Midwest Environmental Sciences Center, La Crosse, WI 54603, United States*

[b] *IAP World Services, Upper Midwest Environmental Sciences Center, 2630 Fanta Reed Road, La Crosse, WI 54603, United States*

[c]*United States Fish and Wildlife Service, Division of Endangered Species, U.S. Fish and Wildlife Resource Center, 555 Lester Avenue, Onalaska, WI 54650, United States*

[d]*United States Fish and Wildlife Service, Division of Endangered Species, Bloomington Field Office, 620 S. Walker Street, Bloomington, IN 47403, United States*

[e]*United States Geological Survey, Patuxent Wildlife Research Center, Laurel, MD 20708, United States*

[*]*Corresponding author.* Phone: +1 608 781 6309; fax: +1 608 783 6066

E-mail addresses: wthogmartin@usgs.gov (W. E. Thogmartin), carolsr@swcp (C. Sanders-Reed), Jennifer_Szymanski@fws.gov, Lori_Pruitt@fws.gov, mrunge@usgs.gov (M. C. Runge)

PeerJ Preprints | https://doi.org/10.7287/peerj.preprints.2790v1 | CC BY 4.0 Open Access | rec: 8 Feb 2017, publ: 8 Feb 2017

ABSTRACT

Demographic characteristics of bats are often insufficiently described for modeling populations. In data poor situations, experts are often relied upon for characterizing ecological systems. In concert with the development of a matrix model describing Indiana bat (*Myotis sodalis*) demography, we elicited estimates for parameterizing this model from 12 experts. We conducted this elicitation in two stages, requesting expert values for 12 demographic rates. These rates were adult and juvenile seasonal (winter, summer, fall) survival rates, pup survival in fall, and propensity and success at breeding. Experts were most in agreement about adult fall survival (3% Coefficient of Variation) and least in agreement about propensity of juveniles to breed (37% CV). The experts showed greater concordance for adult ($\bar{x}_{CV-ad}$= 6.2%) than for juvenile parameters ($\bar{x}_{CV-juv}$= 16.4%), and slightly more agreement for survival ($\bar{x}_{CV-Surv}$= 9.8%) compared to reproductive rates ($\bar{x}_{CV-Repr}$= 15.1%). However, survival and reproduction were negatively and positively biased, respectively, relative to a stationary dynamic. Despite the species exhibiting near stationary dynamics for two decades prior to the onset of a potential extinction-causing agent, white-nose syndrome, expert estimates indicated a population decline of -11% per year (95% CI = -2%, -20%); quasi-extinction was predicted within a century ($\bar{x}$ = 61 years to QE, range = 32, 97) by 10 of the 12 experts. Were we to use these expert estimates in our modeling efforts, we would have errantly trained our models to a rapidly declining demography asymptomatic of recent demographic behavior. While experts are sometimes the only source of information, a clear understanding of the temporal and spatial context of the information being elicited is necessary to guard against wayward predictions.

Key words: Anchoring, Expert elicitation, *Myotis sodalis*, Population models

Introduction.

Parameters describing the demography of many bats species are poorly known. For the endangered Indiana bat (*Myotis sodalis*) in eastern North America, this is no different despite this species being the subject of much concern and study (e.g., Kurta and Kennedy 2002). Age-specific survival rates are known largely from one study conducted in the mid-1970s (Humphrey and Cope 1977), with the data recently re-analyzed (Boyles et al. 2007). Parameters describing reproduction are even less well described (e.g., Mumford and Calvert 1960, Humphrey et al. 1977). Much inference about the demography of Indiana bats is therefore drawn from related Myotids such as the little brown (*M. lucifugus*), northern long-eared (*M. septentrionalis*), and southeastern myotis (*M. austroriparius*) bats.

Recently, the fast-spreading disease white-nose syndrome has caused considerable concern for the Indiana bat and sympatric hibernating bat species of eastern North America because of its potential for acting as an agent of extinction (Buchen 2010) – the loss of 18,662 Indiana bats from white-nose syndrome in 2008 alone represented a loss of an estimated ~4% of the range-wide population. Thogmartin et al. (2012a) suggested as much as 1/3, or >100,000 individuals, of the Indiana bat population was at high risk to infection, and no populations were sufficiently isolated as to be without risk. This novel threat increases the urgency for understanding the population dynamics of this endangered species. Unfortunately, the paucity of demographic information for the Indiana bat hampers development of models capable of characterizing the risk posed by this novel disease.

In response, the U.S. Fish and Wildlife Service convened species experts and endangered species biologists to identify key demographic features determining the population dynamics of this species (Szymanski et al. 2009). The form of the resulting model was a stage-based matrix demographic population model (Lefkovitch 1965, Caswell 2001; Fig. 1), details of which are described in Thogmartin et al. (2013). Parameters for this model were envisioned to come from experts. Expert opinion is often used to characterize and parameterize ecological models when other data are scarce or unavailable (Johnson and Gillingham 2004, O'Neill et al. 2008). Our purpose here is to provide sufficient detail for understanding the scope of species demography expected to be parameterized by each expert, not to describe the demographic model per se, for which details will be provided elsewhere.

The demographic parameters determining the fate of individuals were represented as transition probabilities describing the likelihood of an individual passing from one class to another. The two basic vital rates were survival of individuals from one time step to another and reproduction events from which new individuals may be formed. The matrix model focused on adult and juvenile females in winter when long-term population surveys for this species are conducted (Clawson 2002, Tuttle 2003) and when white-nose syndrome is expected to impact the species most. Over the rest of the year, the population was divided into reproductive and non-reproductive segments. In the summer, another stage was added for the offspring, Pups (P), assumed to be born to a gender ratio of 0.50. Juvenile females were defined as females born in the previous summer. Transitions from winter to summer included overwinter survival (φ^{W}) and propensity to reproduce (p), and from summer to winter included summer survival (φ^{S}) and fall survival (φ^{F}). The reproductive transitions included summer survival of reproductive females (φ^{S}), reproductive rates (b), and fall pup survival ($\emptyset_{FP}^{F}$) (Table 1).

The objective of this model was to allow U.S. Fish and Wildlife Service biologists to predict potential consequences of white-nose syndrome. Because there was little direct information for parameterizing the model once it was built, the opinion of experts was elicited to characterize species demographic rates. Our objective is to describe results of this elicitation process, describing for the first time parameters necessary for a functioning 12-parameter model of Indiana bat demography. We compare these demographic rates to expectations derived from life history considerations as well as historical time series of counts.

Methods.

We conducted an iterative two-stage elicitation from experts (Hoffman et al. 1995, Kadane and Wolfson 1998, O'Hagan 1998, Ayyub 2001). The first stage involved eliciting parameter estimates in winter 2009–2010 from experts primarily affiliated with the initial structured decision-making workshop. These experts were people with a good knowledge of the species and general properties of population ecology and were able to express their opinions in a simple probabilistic manner. Experts were affiliated with the U.S. Fish and Wildlife Service (*n* = 4) and U.S. Army Corps of Engineers (*n* = 1). After obtaining their initial independent estimates, we facilitated a discussion among the experts discussing how their estimates translated into annual rates of survival and reproduction. The experts were then allowed to alter their estimates. Once estimates from the initial set of experts were in hand, parameters for the demographic model were elicited from an expanded set of experts in summer 2010 (Appendix A). This second set of experts were provided the initial set of estimates upon which to reflect. Parameter estimates were received from seven new experts from academia (*n* = 3), U.S. Geological Survey (*n* =2), U.S. Forest Service (*n* = 1), and the Indiana Department of Natural Resources (*n* = 1, the state where Indiana bats are most abundant). These estimates were combined with those from the previously gathered set (Appendix B). Two of the seven new experts simply agreed with the results from the previous group; for these two experts, we assigned the mean, maximum, and minimum of the initial set of estimates. One expert agreed with the previously defined estimates except for one parameter, juvenile winter survival, and was therefore similarly assigned estimates where none were explicitly given. The other four experts assigned, in some cases, new maximal or minimal values for parameters; to arrive at a reasonable value for the mean parameter, in such cases we assigned the midpoint between the former opposite bound and the new bound. For instance, if the expert assigned a new maximum, we found the midpoint between the new maximum and the old minimum to identify the 'mean'. In two cases, when the expert provided only annual demographic estimates rather than seasonal ones, we used an optimization algorithm (Microsoft Solver) to identify the approximate seasonal values that one could possess given only an annual estimate. Upon receiving the second set of estimates, we provided the experts an opportunity to reflect upon their estimates, facilitated dialogue among them, and then allowed them to modify their estimates.

To understand how well these expert estimates comported with our understanding of the life history of this species, we calculated annual survival rates (i.e., $\varphi_{\text{Winter}} \times \varphi_{\text{Summer}} \times \varphi_{\text{Fall}}$) and then calculated the proportion of individuals alive at different year intervals. This proportion alive was plotted against years, an exponential function fitted to the expert-derived estimated proportion alive, and then compared to literature-derived estimates of lifespan. Laval and Laval (1980) captured one Indiana bat 20 years after being banded as an adult. Paradiso and Greenhall (1967) reported a longevity record for Indiana bats of at least 13 years 10 months (based on time between banding and recovery of a male bat). Definitions of maximal life span indicate this is the age of the oldest 1% of a population, others identify this estimate as the age of the oldest 10% of a population, and still others indicate it is the maximum life span somatically possible (i.e., the Hayflick limit) for the species (Gavrilov and Gavrilova 1991). If these definitions were used with respect to the Laval and Laval (1980) life span, we should expect expert estimates to yield ≥1%

of individuals surviving to year 20. Alternatively, if the expert estimates comport with the 14-year life span, we should expect ≥1% of individuals to survive to this commonly cited age. We also calculated mean life span for each of the expert estimates according to Brownie et al. (1985), sensu Sendor and Simon (2003):

$$MLS = \left(1 - \emptyset_{Juv}\right)\frac{-1}{\ln\left(\emptyset_{Juv}\right)} + \emptyset_{Juv}\frac{-1}{\ln\left(\emptyset_{Ad}\right)}$$

Caswell (2001) provided a matrix approach to life span estimation that when applied to our matrices provided similar results as Brownie et al. (1985).

Results.

The experts provided insight into 12 demographic parameter estimates (Table 2, Fig. 2). They were most in agreement with adult fall survival (3% Coefficient of Variation) and least in agreement with the propensity of juveniles to breed (37% CV). The experts showed more concordance for adult parameters ($\bar{x}_{CV-ad}$= 6.2%) than for juvenile parameters ($\bar{x}_{CV-juv}$= 16.4%), and slightly more agreement for survival rates ($\bar{x}_{CV-Surv}$= 9.8%) compared to reproductive rates ($\bar{x}_{CV-Repr}$= 15.1%).

The experts typically suggested at least some values credibly below those necessary for stationary dynamics ($\bar{x}_{below}$ = 2.6 parameters, $\bar{x}_{above}$= 0.5 parameters) (Table 2). The expert estimates for adult summer and adult fall survival, with 8 and 9 experts, respectively, were negatively biased, credibly differing from the set of parameters yielding a stationary dynamic (Fig. 4). Assuming the form of our model was correct, experts were positively biased relative to stationary conditions for both adult and juvenile reproduction.

Expert survival estimates, when incorporated in the model, yielded a mean lifespan of ~2.9 years (range = 1.9–4.2 years) and maximal life spans of 13 years (the oldest 1% cohort) or ~5 years (the oldest 10% cohort) (Fig. 3). Fewer than 15 out of 10,000 individuals were predicted to remain alive at the maximal life span, 20 years, observed by Laval and Laval (1980). Comparatively, assuming stationary demographic conditions, we predicted considerably different maximal life spans, ~24 years for the oldest 1% cohort and ~12 years for the oldest10% cohort.

The expert estimates yielded finite rates of change ranging from 0.78 to 0.99 ($\bar{x}_{\lambda}$= 0.89 [95% CI = 0.80, 0.98]) which indicated the experts believed the species to be declining in abundance at a rate of -11% per year (95% CI = -2%, -20%). Given a starting population of 500,000 bats, 10 of 12 experts predicted species quasi-extinction (<250 remaining females) within a century (median = 61 years to QE, range = 32, 97) (Fig. 5). The average population size after a century was ~25,000 bats, a predicted decline of 95%. Population estimates from trend analyses (Thogmartin et al. 2012b) place the mean population size at no less than 250,000 and more likely ~400,000. Applying the expert estimates to the lowest expected population size, 250,000 bats, again 10 of 12 experts predicted quasi-extinction within a century (median = 56 years to QE, range = 29, 88).

We fitted expert trajectories by eye to the observed 1982–2009 time series of total hibernacula counts (as curated by A. King, U.S. Fish and Wildlife Service). Select expert estimates were able to describe the period of decline between 1982 and 2002, but not the apparent increase in bat numbers thereafter (Fig. 5, inset). The expert estimates describing the periods of decline were, sequentially, experts 8, 7, 3, 7 again, and then 8 again (Table 2); the rates from these experts (range φ_{Fall} = 0.91–0.93) were ≥0.02 units outside of the set of stationary rates for adult fall survival.

Discussion.

Despite the species exhibiting near stationary dynamics (1.4% mean annual increase; 95% CI = -2.8, +5.7%) for the 20 years prior to the onset of white-nose syndrome (Thogmartin et al. 2012b), the experts did not describe demographic characteristics capable of sustaining this species. Rather, their demographic estimates characterized a quickly declining population, perhaps the one leading to the listing of this species as Endangered under the Endangered Species Act. Indiana bat population size declined from millions in the 19th century to ca. 880,000 in the 1960/1970 era to 680,000 by 1980 (Clawson 2002, USFWS 2007). These historical rates of decline between the 1960s and the 1980s appear to vary between 1.2% and 3.0% per year. The experts generally well over-estimated this pattern in decline, however, providing parameter estimates suggesting a population decline of 11% per year.

Boyles et al. (2007, table 1) provided a re-analysis of annual survival data from work first published by Humphrey and Cope (1977). Based upon a Cormack-Jolly-Seber analysis, they estimated annual survival (proportion surviving through the season) to vary between 0.23 and 0.65 for Indiana bats in Wyandotte Cave, Indiana, between winters 1952/1953 to 1969/1970; our set of experts provided seasonal survival estimates, when integrated to annual survival estimates (Table 2), that generally exceeded these values – but which were still insufficient for maintaining stationary abundance. Indiana bats in Wyandotte Cave have been increasing since 1983 (Thogmartin et al. 2012b), an increase not possible given the survival estimates provided by Boyles et al. (2007) nor by the experts unless there was a dramatic and sustained influx of bats from surrounding hibernacula. The experts may have been trying to reconcile what they knew from the literature and survey data to explain this observed demography. These two sources of information likely helped the experts to bracket their estimates but absent robust estimation of recent patterns in demography from beyond that of Wyandotte Cave, this bracketing of estimates was insufficient for describing current species-wide patterns in Indiana bat demography.

These biases in the expert estimates also led to a biased understanding of Indiana bat life history. The expert-derived estimate of mean life span (~2.9 years) was similar to the age-0 life expectancy reported in a U.S. Fish and Wildlife Service biological assessment (2.993 years) (U.S. Fish and Wildlife Service 2000). However, this lifespan is nearly half of the model-based estimate we derived for a stationary population (5.7 years).

We believe there are at least a couple reasons for the experts' biased view of species demography. Most population-level information for hibernating Indiana bats is derived from counts at the hibernaculum (e.g., Clawson 2002, Crimmins et al. 2014). Our research indicates these hibernacula are typically only one patch in a population of interacting patches (Thogmartin et al. 2012b). But, because surveys at hibernacula are intermittently conducted and statistical methods for analyzing these data were heretofore naïve (they fail to accommodate inter-hibernacula movement, for instance), gaining a species-wide perspective in such a vacuum of coherent information is difficult (Thogmartin et al. 2012b). Further, fluctuations in abundance among hibernacula only serve to obfuscate regional patterns in demography. Lastly, the longer-term historical context of the Indiana bat, based upon the presumption that Indiana bats once numbered in the millions (e.g., Tuttle 1997, USFWS 2007), likely also biased experts against providing estimates relevant to the period immediately prior to onset of white-nose syndrome.

Spatially limited or historically distant population dynamics can lead to misleading estimates for recent species-wide conditions; coupled with a relatively sparse literature describing demography of Myotid bats, including Indiana bats, the few sources of information that do exist are likely over-emphasized by experts when forming their opinion about demographic estimates. Some of the most important research on characteristics of Indiana bat demography took place during the 1950s, 1960s, and 1970s (e.g., Easterla and Watkins 1969, Humphrey and Cope 1977, Humphrey et al. 1977, Clawson et al. 1980), during which the species was declining by as much as 3% per year. We suspect that the expert perspective of Indiana bat demography was strongly influenced by this literature published during the period of the species' decline rather than the experts' knowledge of recent population status and trends.

Conclusions.

Expert estimates are sometimes essential for understanding ecological systems, and many times are the only information available, but the dynamics of wildly fluctuating species such as bats demand an understanding of their status and context before they can be used successfully. Although previously understood, the importance of providing or discerning the context in which experts form their opinion cannot be overemphasized. Were we to use the expert estimates without understanding their underlying context, we would have trained our models to a rapidly declining demography that was not symptomatic of recent demographic behavior. Through iterative feedback among the modelers and the experts, we were able to reconcile and understand differences among the experts, past and present population trends, and the published literature.

Acknowledgments.

We thank S. Amelon, M. Armstrong, R. Barclay, E. Britzke, T. Carter, P. Cryan, W. Frick, S. Johnson, A. King, A. Kurta, R. Niver, and T. O'Shea for their valuable opinions on Indiana bat demography and life history. We appreciate the comments of R. E. Russell and C. P.

McGowan on an earlier version of this manuscript. Any use of trade, product, or firm names are for descriptive purposes only and do not imply endorsement by the U.S. Government.

References.

Ayyub, B. M. 2001. Elicitation of expert opinions for uncertainty and risks. CRC Press, Boca Raton, FL.

Boyles, J. G., Walters, B. L. Whitaker Jr., J. O., Cope, J. B. 2007. A reanalysis of apparent survival rates of Indiana myotis (*Myotis sodalis*). Acta Chiropterologica 9, 127–132.

Brownie, C., Anderson, D. R., Burnham, K. P., Robson, D. S. 1985. Statistical inference from band recovery data – A handbook. US Fish and Wildlife Service, Resource Publication 156, Washington, D.C.

Buchen, L. 2010. Disease epidemic killing only US bats. Nature 463, 144–145.

Caswell, H. 2001. Matrix population models: Construction, analysis, and interpretation. Sinauer, Sunderland, MA.

Clawson, R. L. 2002. Trends in population size and current status. Pages 2–8 in The Indiana bat: biology and management of an endangered species (Kurta, A., and J. Kennedy, editors). Bat Conservation International, Austin, Texas, USA.

Clawson, R. L., LaVal, R. K., LaVal, M. L., Caire, W. 1980. Clustering behavior of hibernating *Myotis sodalis* in Missouri. Journal of Mammalogy 61, 245–253.

Crimmins, S. M., McKann, P. C., Szymanski, J. A., Thogmartin, W. E. 2014. Effects of cave gating on local Indiana bat (*Myotis sodalis*) population trends. Acta Chiropterologica 16:129–137.

Easterla, D. A., Watkins, L. C. 1969. Pregnant *Myotis sodalis* in northwestern Missouri. Journal of Mammalogy 50, 372–373.

Gavrilov, L. A., Gavrilova, N. S. 1991. The biology of life span: A quantitative approach. Harwood Academic, New York, NY.

Hoffman, R. R., Shadbolt, N. R., Burton, A. M., Klein, G. 1995. Eliciting knowledge from experts: A methodological analysis. Organizational Behavior and Human Decision Processes 62, 129–158.

Humphrey, R. S., Cope, J. B. 1977. Survival rates of the endangered Indiana bat, *Myotis sodalis*. Journal of Mammalogy 58, 32–36.

Humphrey, S.R., Richter, A.R., Cope, J.B. 1977. Summer habitat and ecology of the endangered Indiana bat, *Myotis sodalis*. Journal of Mammalogy 58, 334–346.

Kadane, J. B., Wolfson, L. J. 1998. Experiences in elicitation. Journal of the Royal Statistical Society Series D: The Statistician 47, 3–19.

Kurta, A., Kennedy, J. (editors). 2002. The Indiana bat: biology and management of an endangered species. Bat Conservation International, Austin, TX.

Laval R. K., Laval, M. L. 1980. Ecological studies and management of Missouri bats, with emphasis on cave-dwelling species. Missouri Department of Conservation, Jefferson City, Missouri, USA.

Lefkovitch, L. P. 1965. The study of population growth in organisms grouped by stages. Biometrics 21, 1–18.

Mumford, R. E., Calvert, L. L. 1960. *Myotis sodalis* evidently breeding in Indiana. Journal of Mammalogy 41, 512.

O'Hagan, A. 1998. Eliciting expert beliefs in substantial practical applications. Journal of the Royal Statistical Society Series D: The Statistician 47, 21–35.

Paradiso, J. L., Greenhall, A. M. 1967. Longevity records for American bats. American Midland Naturalist 78, 251–252.

Sendor, T., Simon, M. 2003. Population dynamics of the pipistrelle bat: effects of sex, age and winter weather on seasonal survival. Journal of Animal Ecology 72, 308–320.

Szymanski, J. A., Pruitt, L., Runge, M. C., Armstrong, M., King, R. A., McGowan, C., Niver, R., Sparks, D., Brewer, D. C. 2009. Developing performance criteria for a population model for Indiana Bat conservation. A case study from the structured decision making workshop, December 8–12, 2008, National Conservation Training Center, Shepherdstown, West Virginia, USA.

Thogmartin, W. E., King, R. A., Szymanski, J. A., Pruitt, L. 2012a. Space-time models for a panzootic in bats, with a focus on the endangered Indiana bat. Journal of Wildlife Diseases 48, 876–887.

Thogmartin, W. E., King, R. A., McKann, P., Szymanski, J. A., Pruitt, L. 2012b. Population-level impact of white-nose syndrome on the endangered Indiana bat. Journal of Mammalogy 93, 1086–1098.

Thogmartin, W. E., Sanders-Reed, C., Szymanski, J. A., King, R. A., Pruitt, L., McKann, P. C., Runge, M. C., Russell, R. E. 2013. White-nose syndrome is likely to extirpate the endangered Indiana bat over large parts of its range. Biological Conservation 160, 162–172.

Tuttle, M. D. 1997. A Mammoth discovery. BATS 15, 3–5.

Tuttle, M. D. 2003. Estimating population sizes of hibernating bats in caves and mines. Pages 31–40 in Monitoring trends in bat populations of the United States and Territories: problems and prospects (T. J. O'Shea and M. A. Bogan, editors). U.S. Geological Survey, Biological Resources Division, Information and Technology Report, USGS/BRD/ITR-2003-0003, Reston, Virginia, USA.

United States Fish and Wildlife Service. 2007. Indiana bat (*Myotis sodalis*) draft recovery plan: first revision. U.S. Fish and Wildlife Service, Fort Snelling, Minnesota..

Table 1. Definition of parameters for demographic model of single hibernaculum Indiana bats.

Parameter	Definition	Pup	F_J	F_A	N_J	R_J	N_A	R_A
φ^W	Survival from hibernation to emergence from hibernaculum		$\varphi^W{}_{FJ}$	$\varphi^W{}_{FA}$				
φ^S	Survival from emergence to hibernation				$\varphi^S{}_N$		$\varphi^S{}_N$	
φ^S	Survival from emergence to parturition					$\varphi^S{}_{RJ}$		$\varphi^S{}_{RA}$
φ^F	Survival from parturition (or birth) to hibernation	$\varphi^F{}_P$				$\varphi^F{}_{RJ}$		$\varphi^F{}_{RA}$
b	Reproductive rate: proportion of pregnant females giving birth to one offspring					b_J		b_A
p	Propensity to reproduce: proportion of females becoming pregnant		p_J	p_A				
T^S	Spring Take: number of animal killed during late winter until parturition (includes late winter take, take during spring migration and pre-reproductive take)		$T^S{}_J$	$T^S{}_A$				
T^F	Fall Take: number of animals killed on fall migration until hibernation (includes fall migration, swarming, and early winter)				$T^F{}_N$	$T^F{}_R$	$T^F{}_N$	$T^F{}_R$
T^P	Pup Take includes take of pups without concurrent take of the mother.	T^P						

PeerJ Preprints | https://doi.org/10.7287/peerj.preprints.2790v1 | CC BY 4.0 Open Access | rec: 8 Feb 2017, publ: 8 Feb 2017

Table 2. Expert-estimated parameter values for demographic model of Indiana bat population dynamics, with maximum, minimum, and average of the expert set. Derived parameters (annual survival rate, proportion alive) follow the expert set. Characteristics of the parameter values at a stationary population dynamic are provided for reference (estimates outside of the range of stationarity are bold, blue for above and red for below).

Parameter	Expert	1	2	3	4	5	6	7	8	9	10	11	12	Stationarity (95% CI)
Adult φ_{Winter}		0.980	**0.850**	0.950	0.930	0.950	0.932	0.960	0.932	0.932	0.932	**0.875**	0.932	0.945 (0.89,0.98)
Juvenile φ_{Winter}		0.950	0.800	0.900	0.850	0.950	0.890	**0.960**	0.890	0.890	0.890	**0.500**	**0.663**	0.842 (0.67,0.95)
Non-reproductive $\varphi_{Summer\&Fall}$		0.850	0.900	**0.930**	0.800	**0.700**	0.850	0.920	0.825	0.836	0.836	0.875	0.836	0.852 (0.75,0.92)
Adult φ_{Summer}		**0.800**	0.950	0.900	**0.820**	**0.750**	**0.844**	0.915	0.925	**0.844**	**0.844**	**0.844**	**0.844**	0.915 (0.88,0.95)
Juvenile φ_{Summer}		0.780	0.800	0.800	0.750	**0.700**	**0.925**	0.820	0.900	0.766	0.766	0.875	0.766	0.817 (0.73,0.91)
Adult φ_{Fall}		0.950	**0.900**	**0.930**	0.950	**0.900**	**0.926**	**0.910**	**0.926**	**0.926**	**0.926**	0.998	**0.926**	0.98 (0.95,0.997)
Juvenile φ_{Fall}		**0.950**	0.900	0.830	**0.950**	0.800	0.886	0.845	0.886	0.886	0.886	**0.500**	0.886	0.825 (0.64,0.94)
Pup φ_{Fall}		**0.500**	**0.500**	**0.500**	0.600	0.600	0.650	0.558	0.540	0.540	0.540	0.875	0.540	0.657 (0.53,0.82)
Adult Breed Propensity (*p*)		0.850	0.950	**0.650**	0.940	0.850	0.848	**0.975**	0.875	0.848	0.848	0.848	0.848	0.877 (0.76,0.97)
Juvenile Breeding Propensity		0.400	0.800	**0.100**	0.750	0.500	0.750	0.806	0.510	0.510	0.510	0.510	0.510	0.487 (0.16,0.79)
Adult Breeding Success (*b*)		0.800	0.950	0.950	0.900	0.880	0.896	0.975	**0.731**	0.896	0.896	0.896	0.896	0.888 (0.79,0.97)

PeerJ Preprints | https://doi.org/10.7287/peerj.preprints.2790v1 | CC BY 4.0 Open Access | rec: 8 Feb 2017, publ: 8 Feb 2017

Juvenile Breeding Success	**0.700**	0.850	**0.900**	0.850	0.800	0.750	0.806	0.820	0.820	0.820	0.820	0.820	0.801 (0.71,0.88)
Reproductive Adult Annual φ ($\varphi_{\text{Winter}} \times \varphi_{\text{Summer}} \times \varphi_{\text{Fall}}$)	0.745	0.727	0.795	0.724	0.641	0.728	0.799	0.798	0.728	0.728	0.737	0.726	0.867
Non-repro. Adult Annual φ	0.791	0.689	0.822	0.707	0.599	0.734	0.804	0.712	0.721	0.721	0.764	0.721	0.834
Repro. Juvenile Annual φ	0.704	0.576	0.598	0.606	0.532	0.729	0.665	0.710	0.604	0.604	0.219	0.603	0.697
Non-repro. Juvenile Annu. φ	0.767	0.648	0.695	0.646	0.532	0.670	0.746	0.651	0.659	0.659	0.219	0.658	0.729
Adult Reproduction ($p \times b$)	0.680	0.903	0.618	0.846	0.748	0.760	0.950	0.640	0.760	0.760	0.760	0.759	0.586
Juvenile Reproduction	0.280	0.680	0.090	0.638	0.400	0.563	0.650	0.418	0.418	0.418	0.418	0.418	0.150
Proportion alive at 14 years	0.008	0.005	0.018	0.006	0.001	0.007	0.023	0.019	0.006	0.006	0.004	0.006	0.072
Proportion alive at 4 years	0.159	0.124	0.175	0.147	0.084	0.168	0.213	0.179	0.138	0.138	0.077	0.136	0.259

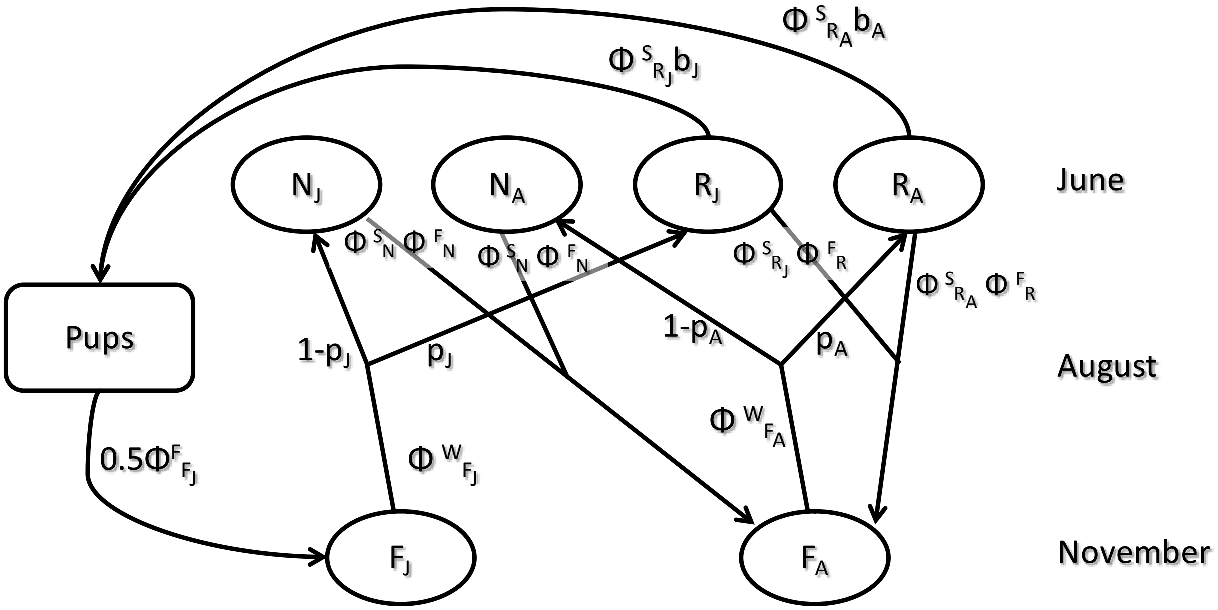

Figure 1. Schematic life-cycle diagram for the Indiana bat population model, female segment only and without spatial structure.

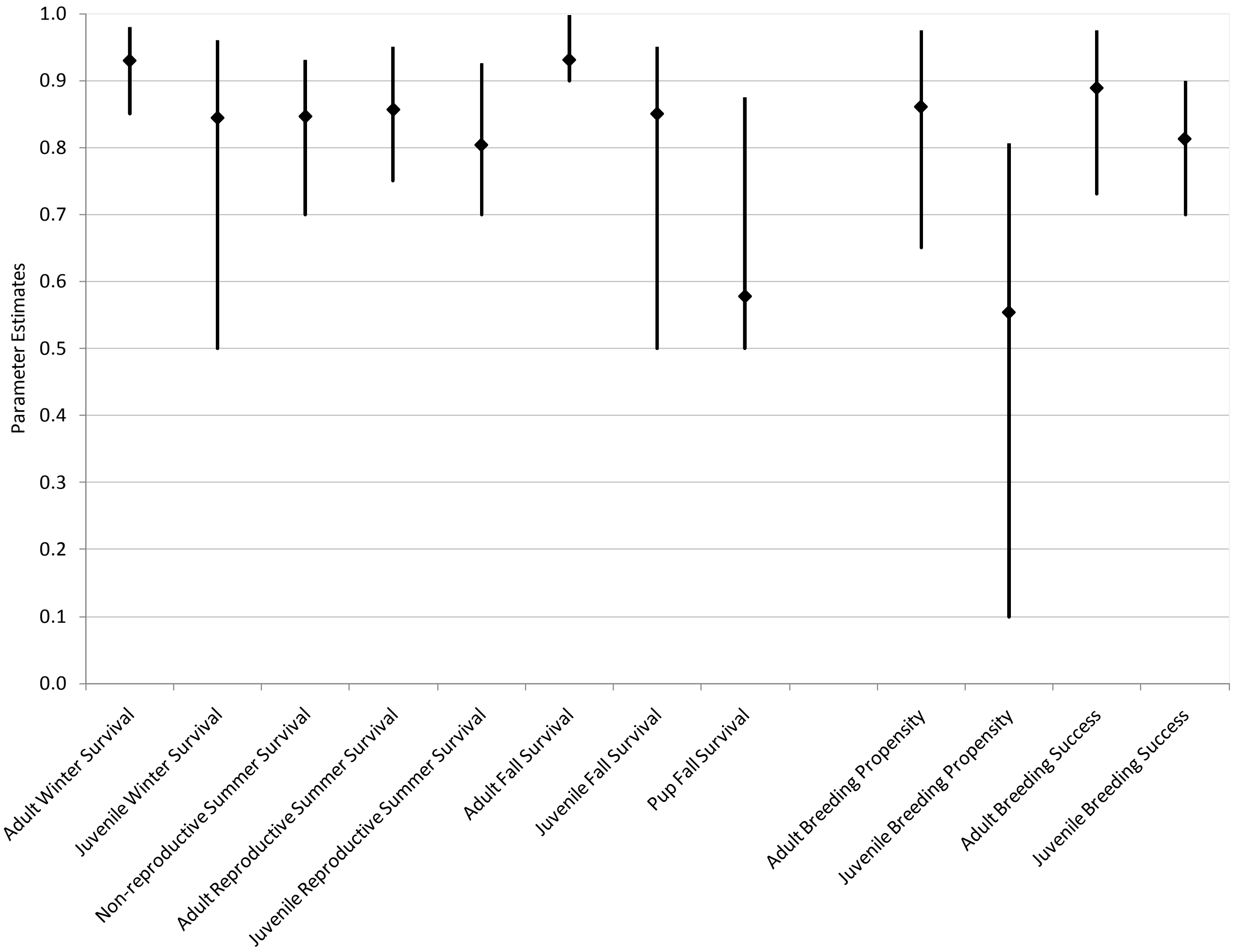

Figure 2. Mean estimates (and range) for parameterizing an Indiana bat demographic model.

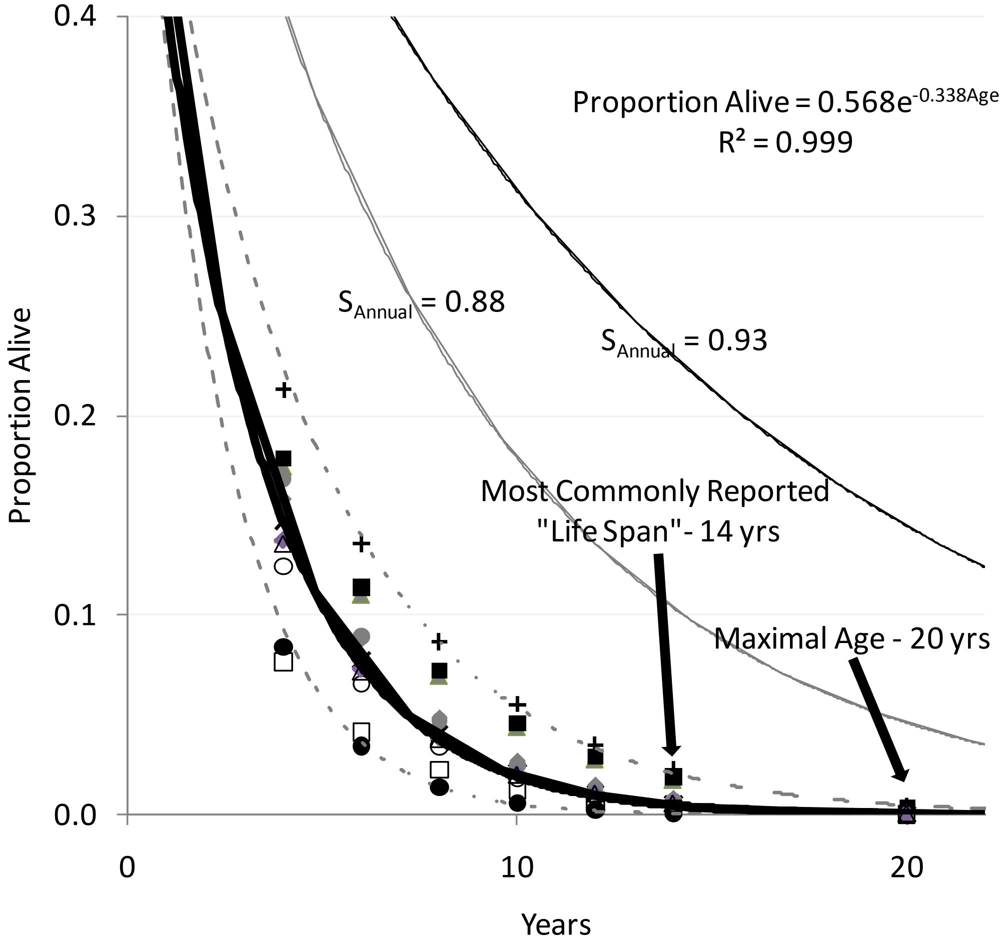

Figure 3. Estimated proportion alive at yearly intervals according to each of the 12 expert estimates for survival (range of expert estimated φ = 0.644–0.799). Annual survival estimates of 0.88 and 0.93 are provided for reference; both of these estimates are above the expert estimates, and are what would be required for Indiana bat populations to consistently increase in size.

PeerJ Preprints | https://doi.org/10.7287/peerj.preprints.2790v1 | CC BY 4.0 Open Access | rec: 8 Feb 2017, publ: 8 Feb 2017

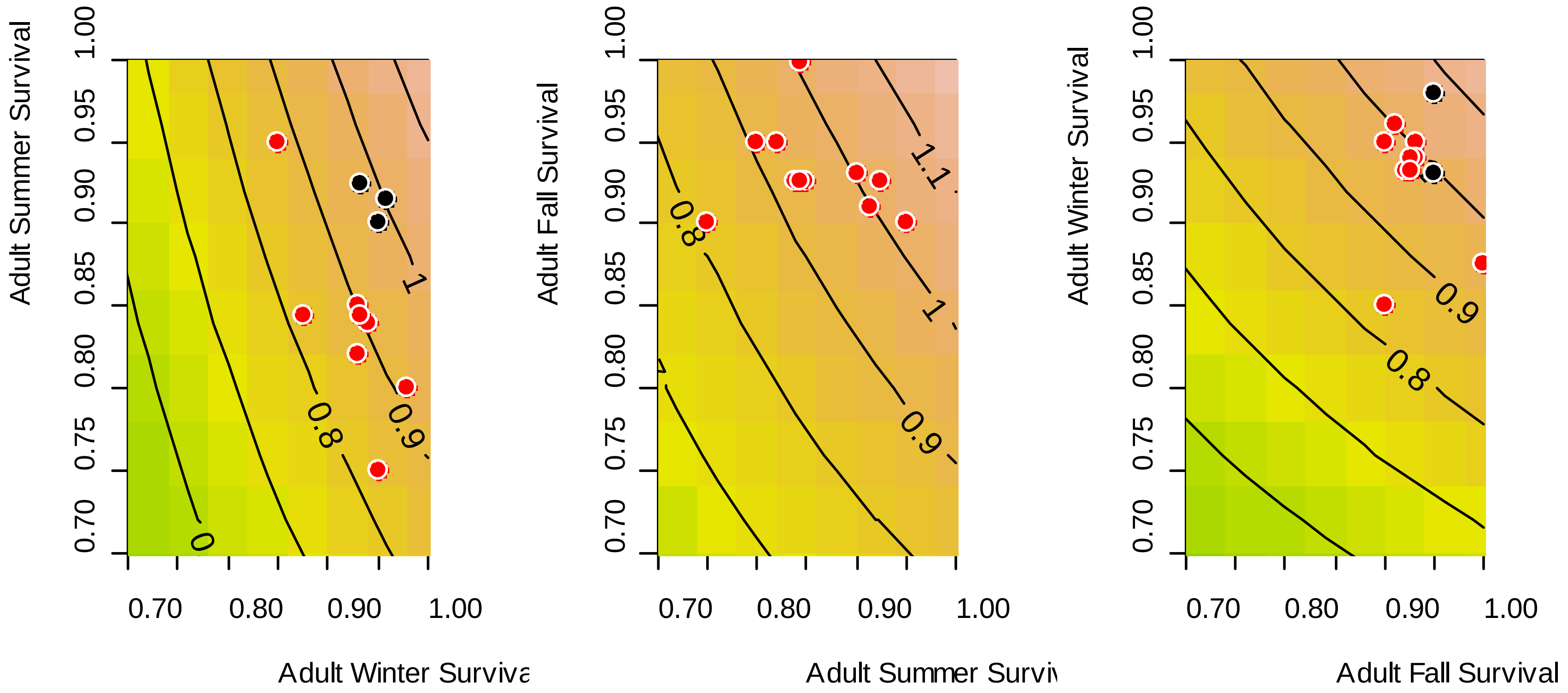

Figure 4. Bivariate contour plots relating the demographic parameters most sensitive to determining population rate of change (λ) from a two-stage matrix model of Indiana bat population demography. The black dots indicate set of expert estimates yielding stationary population dynamics; red dots indicate set of expert estimates indicative of non-stationary dynamics.

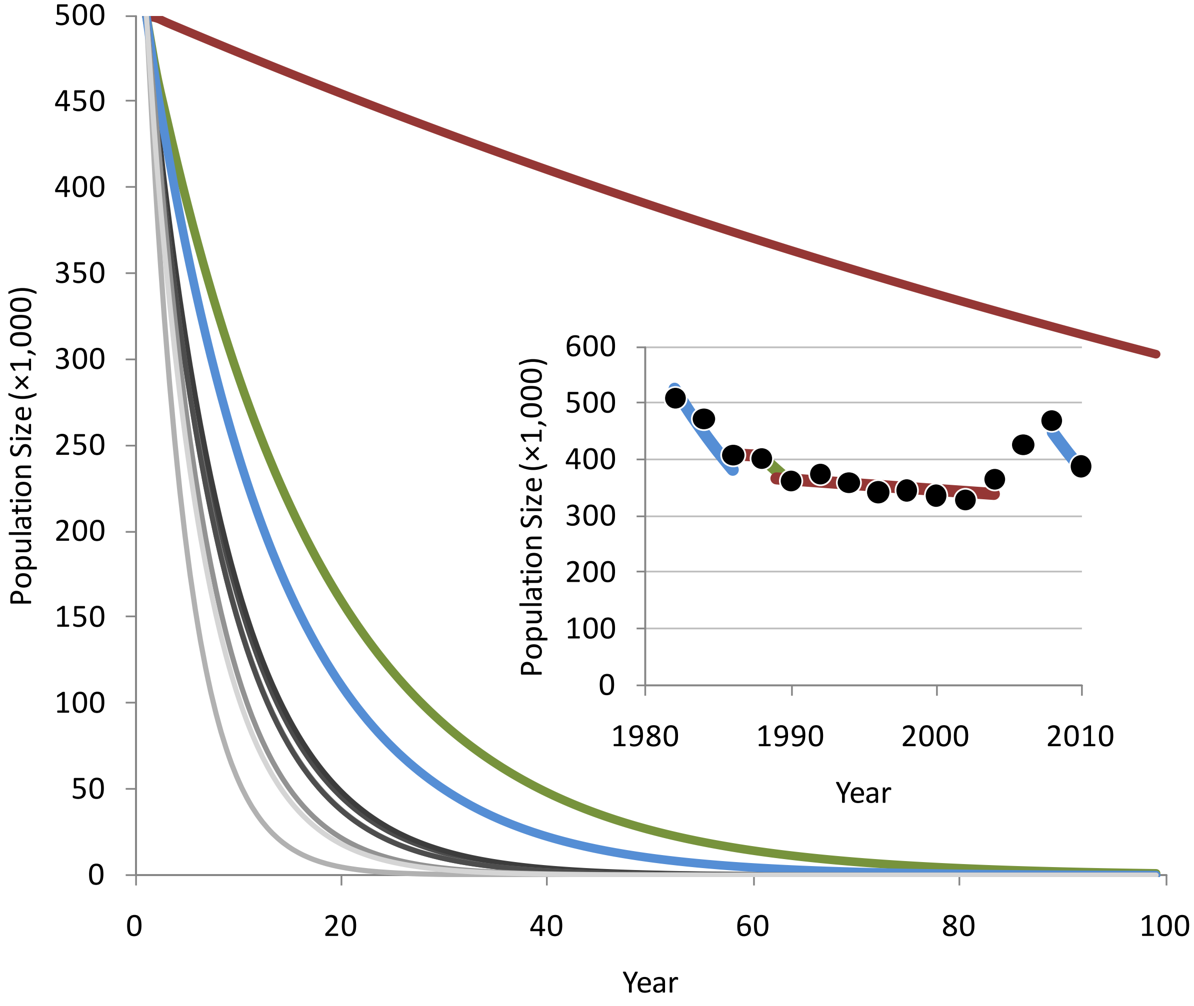

Figure 5. Deterministic projections of population size, starting at 500,000, based on the combination of parameter estimates provided by each of the 12 experts. The inset is historical counts of Indiana bat range-wide population size drawn over best-fitting expert estimates. Colors in the inset match the corresponding deterministic projection.

PeerJ Preprints | https://doi.org/10.7287/peerj.preprints.2790v1 | CC BY 4.0 Open Access | rec: 8 Feb 2017, publ: 8 Feb 2017

Appendix A. Follow-up expert elicitation, submitted to an additional set of 20 experts

Over the past year, US Geological Survey and US Fish and Wildlife Service scientists and biologists have been developing a demographic model for Indiana bats. This model is to help inform the US Fish and Wildlife Service about the potential impact of various perturbations to the population (particularly white-nose syndrome). This model is a multi-stage matrix model following adult and juvenile females through their annual life cycle (see Figure A.1 for a schematic of the modeling process).

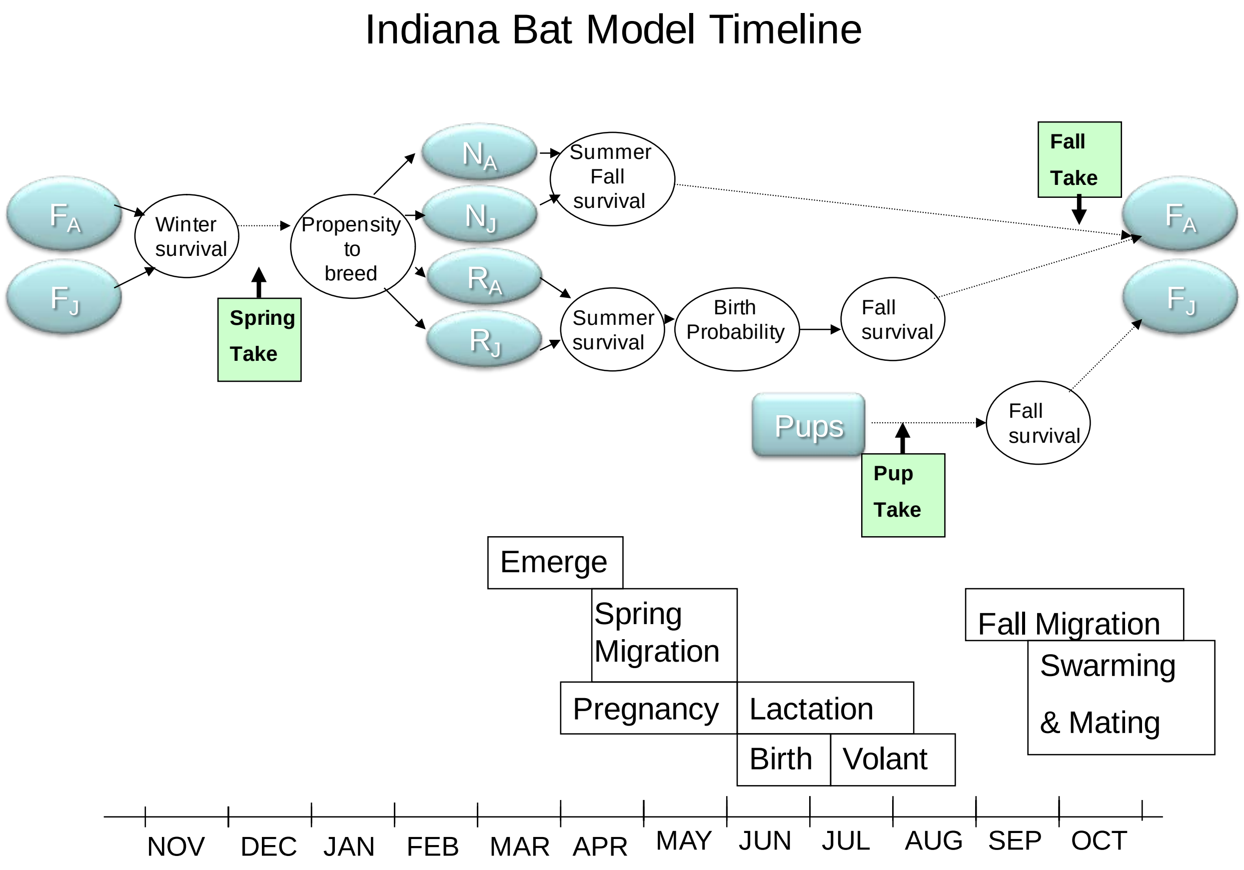

Figure A.1. A conceptual diagram of the timing of varying demographic activities. F_a denotes adult females, F_j, juvenile females, N_a, non-reproductive adult females, N_j, non-reproductive juvenile females, R_a, reproductive adult females, R_j, reproductive juvenile females and pups, which are young of year.

We model only females. The model possesses three age classes, adults (individuals beyond their first year of life), juveniles (individuals experiencing their first period of hibernation), and, in fall only, pups (young-of-the-year, prior to hibernation). For female bats to move from one stage to another (e.g., from winter to spring) the population incurs an age-specific survival rate. These seasonal measures of survival are multiplicatively related to form an annual survival rate (probability of winter survival × probability of summer survival × probability of fall survival). For females entering the breeding period, they exhibit an age-specific propensity to breed and, for those that breed, a probability of successful birthing. The number of pups born each year is a function of the number of individuals in a population and age-specific reproductive parameters (*n* individuals × probability of breeding × probability of successful breeding); we assumed a 50:50 sex ratio.

Because little is known about Indiana bat demography, we convened a small panel of experts to provide initial estimates for these survival and breeding parameter (Table A.1, Figure A.1). Experts were instructed to provide range-wide estimates (rather than estimates specific to their region or state). Further, estimates were to be based on pre-WNS demographics. These experts used their knowledge of available literature (e.g., Humphrey and Cope 1977, Boyles et al. 2007) and general understanding of bat demography to provide these estimates. From the expert-elicited parameters, we determined, for instance, that the maximal annual survival rate for adult females was 0.88 (i.e., 0.98 [winter] × 0.95 [fall] × 0.95 [summer]). The minimal annual survival for adult reproductive females was 0.574 (0.85 × 0.75 × 0.90). For juvenile reproductive females, the minimum survival rate was 0.448 (0.80 × 0.70 × 0.80). The maximal probability of producing a pup was 0.90 for adult females and 0.72 for juvenile females, whereas the minimal probability of producing a pup was 0.52 for adult females and 0.07 for juvenile females.

The question we face now is whether these parameter estimates reasonably characterize the expected demography of a general population of Indiana bats, prior to the onset of white-nose syndrome. We would appreciate your perusal of these estimates (Table B.1) and any input and comments you may have on the validity of these estimates (please complete Table B.2). If you wish to provide estimates for these various parameters, we would much value including them within our pool. Please complete the table and return to Wayne Thogmartin (wthogmartin@usgs.gov) no later than 24 September. If you have any questions regarding this exercise, please contact Wayne Thogmartin (wthogmartin@usgs.gov; 608-781-6309) or Carol Sanders-Reed (carolsr@swcp.com; 505-281-4126).

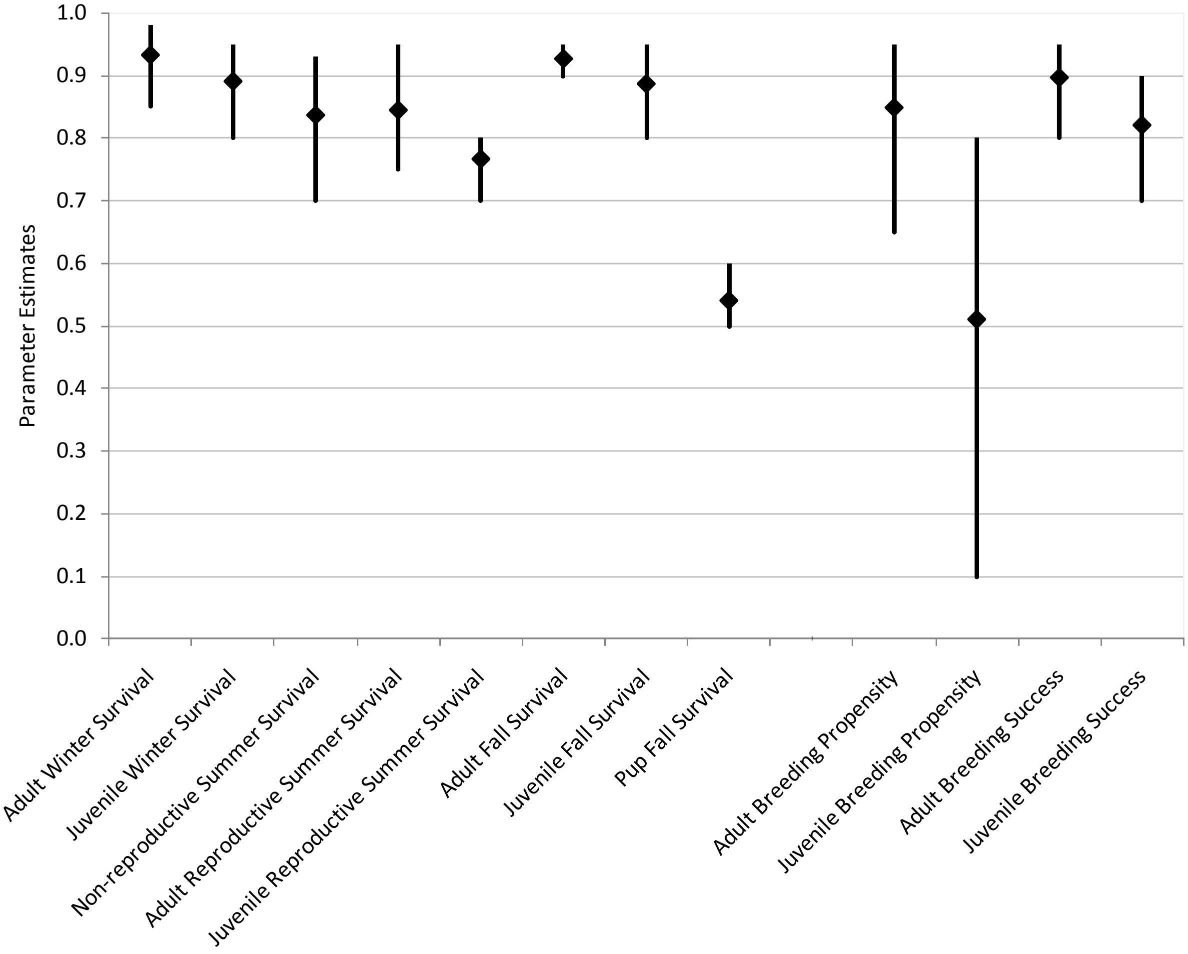

Figure A.2. A graphical depiction of the range among the individual rates as provided by the initial expert panel. The range of values for each of the parameters reflects the magnitude of agreement between experts; for instance, all of the experts we polled believed adult winter survival was generally high. However, there was greater uncertainty for the probability of a juvenile to breed; some believed the probability of juveniles breeding in their first year was low (0.1) whereas others believed as many as 80% bred annually.

Table A.1. Put a checkmark in the "valid interval" column if the interval seems reasonable. Feel free to provide comments on your rationale for assessing the interval. If you have a belief about the appropriate minimum, mean, or maximum parameter estimate, please feel free to provide that as well.

Stage	Rate	Expert-derived Range		Valid Interval (√)	Your Estimate		
		Min	Max		Min	Mean	Max
Adult Reproductive female	Winter	0.85	0.98				
	Fall	0.90	0.95				
	Summer	0.75	0.95				
	Implied yearly survival	0.57	0.88				
Juvenile Reproductive Female	Winter	0.80	0.95				
	Fall	0.80	0.95				
	Summer	0.70	0.80				
	Implied yearly survival	0.45	0.72				
Adult Non-reproductive female	Winter	0.85	0.98				
	Summer / Fall	0.70	0.93				
	Implied yearly survival	0.60	0.91				
Juvenile Non-reproductive female	Winter	0.80	0.95				
	Summer / Fall	0.70	0.93				
	Implied yearly survival	0.56	0.88				
Pup	Fall	0.50	0.60				
Adult Reproductive female	Propensity to breed	0.65	0.95				
	Prob. of successful birth	0.80	0.95				
	Implied yearly birth rate	0.52	0.90				

PeerJ Preprints | https://doi.org/10.7287/peerj.preprints.2790v1 | CC BY 4.0 Open Access | rec: 8 Feb 2017, publ: 8 Feb 2017

Juvenile Reproductive Female	Propensity to breed	0.10	0.80				
	Prob. of successful birth	0.70	0.90				
	Implied yearly birth rate	0.07	0.72				

Appendix B. Changes to the expert-estimated parameter estimates for a stage-based matrix model of Indiana bat demography as the sample of experts increased from 5 to 12.

Stage	ΔMinimum	ΔMaximum	ΔMean
Adult Winter Survival	0.000	0.000	-0.002
Juvenile Winter Survival	-0.300	0.010	-0.046
Non-reproductive Summer Survival	0.000	0.000	0.011
Adult Reproductive Summer Survival	0.000	0.000	0.013
Juvenile Reproductive Summer Survival	0.000	0.125	0.038
Adult Fall Survival	0.000	0.048	0.005
Juvenile Fall Survival	-0.300	0.000	-0.036
Pup Fall Survival	0.000	0.275	0.039
Adult Winter Survival	0.000	0.000	-0.002
Juvenile Winter Survival	-0.300	0.010	-0.046
Non-reproductive Summer Survival	0.000	0.000	0.011
Adult Reproductive Summer Survival	0.000	0.000	0.013
Juvenile Reproductive Summer Survival	0.000	0.125	0.038

PeerJ Preprints | https://doi.org/10.7287/peerj.preprints.2790v1 | CC BY 4.0 Open Access | rec: 8 Feb 2017, publ: 8 Feb 2017

Annual Reproductive Adult Survival	0.000	0.004	0.013
Annual Non-Reproductive Adult Survival	-0.067	-0.062	-0.046
Annual Reproductive Juvenile Survival	-0.313	0.025	-0.007
Annual Non-Reproductive Juvenile Survival	-0.446	-0.116	-0.149
Adult Annual Reproduction	-0.003	0.050	0.005
Juvenile Annual Reproduction	0.000	0.000	0.031

PeerJ Preprints | https://doi.org/10.7287/peerj.preprints.2790v1 | CC BY 4.0 Open Access | rec: 8 Feb 2017, publ: 8 Feb 2017