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## Revisiting old data to answer modern conservation questions: Population modeling of two species in Kingsnakes, *Lampropeltis* sp. in Kansas

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There is increasing interest on the effects of take for the pet trade on reptiles in Kansas, although little data is available to elucidate possible impacts. The Kansas Department of Wildlife, Parks, and Tourism and the Kansas Biological Survey recently partnered on a project to digitize Henry Fitch's nearly 60 years of data collection on Northeast Kansas snake populations. We utilized the mark-recapture data for two species of snakes, the Prairie Kingsnake *Lampropeltis calligaster* and the Milk Snake *L. triangulum* to build population models and identify life history stages most vulnerable to take. Population growth rates for *L. calligaster* were most sensitive to changes in both juvenile and adult female survivorship. *Lampropeltis triangulum* was most sensitive to take of adult females. Sustained take over 20 years exceeding 30% in *L. triangulum* resulted in population extirpation based on population viability models developed here.

*Keywords:* Collections, Milk Snake, pet trade, Prairie Kingsnake, reptiles, survivorship, viability

### INTRODUCTION

The commercial removal of reptiles from wild populations for use as pets is thought to affect reptile populations globally. A study of exports of reptiles from the United States showed that exports for all reptiles increased from 1996-2012 (Robinson et al. 2015). Unfortunately, evidence linking take of reptiles to population declines is lacking as long-term studies on many species have not been conducted (Todd, Willson and Gibbons 2010). The lack of studies for some groups such as snakes are exacerbated by the difficult nature of studying them in the field. Snakes are typically thought of as poor subjects for study due to low recapture rates and high variability in density (Parker and Plummer 1987; Vitt 1987). With an increasing interest in the effects of take on native amphibians and reptiles in Kansas by resource management agencies, the authors revisited the long-term

data on snakes collected by Henry Fitch at his study site in northeastern Kansas. The digitization of nearly 60 years of field data by Henry Fitch (as partially summarized in Fitch 1999) has provided the opportunity to examine the demographic vital rates of two species of kingsnakes, a group that has some commercial relevance within the pet trade. While there is little tracking of native snakes in the pet trade, snakes within the genus *Lampropeltis*, particularly the Common Kingsnake, *L. getula* and Milk Snake *L. triangulum* make up a portion of the trade in reptiles in the United States (Fitzgerald et al. 2004; Enge 2005; Prestridge, Fitzgerald and Hibbitts 2011).

Although not overly abundant on his research sites, Fitch did capture multiple individuals of *L. triangulum* and the Prairie Kingsnake *L. calligaster*. Both species are fairly cryptic and not always easily observable. Richardson, Weatherhead, and Brawn (2006) noted that

individuals of *L. calligaster* spent as much as 73% of their time underground. *Lampropeltis triangulum* also spends considerable time underground, often showing high site fidelity to exposed rock outcrops that are used for thermoregulation (Dyrkacz 1977; Row and Blouin-Demers 2006a,b). Despite their cryptic nature, Fitch made 331 captures of *L. calligaster* and 279 captures of *L. triangulum* between 1949-1997, primarily using funnel traps and drift fence arrays (Fitch 1999). An additional 71 captures of *L. calligaster* and 17 captures of *L. triangulum* were made between 1997-2003, after the publication of Fitch (1999). While the overall captures for both species appear low for a 54 yr time span, they represent the most robust data set for either species in Kansas. Our objective was to subject each updated data set to a more robust analysis of demographic vital rates and identify those life history traits most sensitive to perturbation, such as take. Using these models, natural resource managers can best extrapolate how take might impact populations.

## MATERIALS AND METHODS

Basic population models focus on the interaction between birth rates and mortality, so we focused on female survivorship and fecundity when constructing viability models for the two species of *Lampropeltis* (Pianka 1994). Demographic vital rates were constructed from 402 captures of 286 individuals of *L. calligaster* and 296 captures of 198 individuals of *L. triangulum*. Apparent survivorship ( $\Phi$ ) and recapture probability ( $p$ ) were calculated using Cormack-Jolly-Seber models in Program MARK (White and Burnham 1999). We generated models to test whether  $\Phi$  and  $p$  were best explained by time, group (male, female), or were independent of group level influences. Model selection was based on corrected Akaike Information Criterion ( $AIC_c$ ) values, with lower values denoting greater parsimony (Burnham and Anderson 2002). We then reversed the encounter rates to determine the probability of an individual entering the population (Pradel 1996). Pradel models estimate the realized growth rate ( $\lambda$ ) of a

population minus the influence of fecundity and is here on referred to as Pradel's  $\lambda$ . Pradel's  $\lambda$  was calculated in Program MARK.

Using apparent survivorship values calculated in Program MARK, and reproductive data summarized within Fitch (1999), we developed population viability models in Program Vortex (Lacy and Pollack 2014). Age at first reproduction for *L. calligaster* was 3 yrs and mean clutch size was 9 (range 6-13). Age at first reproduction for *L. triangulum* was 4 yrs and mean clutch size was 7 (range 5-9). Age and clutch size values were used to calculate baseline deterministic rates for each species within Vortex. Deterministic rates used here include population growth rate ( $\lambda$ ), net reproductive rate (average number of age class zero offspring produced by an average newborn during its life time;  $R_0$ ) and mean generation time ( $T$ ). We then hand calculated the reproductive value, or to what extent do members of a given age group contribute to the next generation between birth and death (Fisher 1930). Reproductive value is defined as:

$$v_x = \sum_{t=x}^{\infty} \frac{l_t}{l_x} m_t$$

The term  $l_t/l_x$  represents the probability of living from age  $x$  to age  $t$ , and  $m_t$  is the average reproductive success of an individual at age  $t$  (Pianka 1994).

We then ran a series of sensitivity tests for 3 parameters: percent of females breeding/year, juvenile mortality, and adult female mortality. Sensitivity tests within Vortex work by creating a series of scenarios in which each parameter can be varied. Scenarios were set so that values for each parameter varied from 0-100%. For each scenario a value is randomly chosen for each of the three parameters from across the range specified. Then the mean value of the output variable was graphed in what is referred to as spider plots by Vortex. All models were based on a simulated timespan of twenty years.

Table 1. Demographic parameters ± standard error for *Lampropeltis calligaster* and *L. triangulum* in northeast Kansas. Parameters include weighted mean apparent survivorship ( $\Phi$ ) and recapture probability ( $p$ ) based on AICc weights, Pradel's  $\lambda$  and actual  $\lambda$ , reproductive replacement rate ( $R_0$ ) and mean generation time ( $T$ ).

	$\Phi$	$p$	Pradel's $\lambda$	$\lambda$	$R_0$	$T$
<i>Lampropeltis calligaster</i>	Female	0.13 ± 0.06	1.00 ± 0.003	0.99	0.98	3.52
	0.51 ± 0.09					
	Male	0.09 ± 0.04				
	Juvenile	0.08 ± 0.03				
<i>Lampropeltis triangulum</i>	Female	0.12 ± 0.06	1.02 ± 0.004	1.02	1.13	4.9
	0.56 ± 0.10					
	Male	0.13 ± 0.03				
	0.64 ± 0.05					

**RESULTS**

Apparent survivorship for *L. calligaster* were similar between sexes (Table 1). The most parsimonious model explaining apparent survivorship in *L. calligaster* was constant survivorship and recapture probability independent of group or time interactions (Table 2). Variation between AIC<sub>c</sub> scores were

slight when compared to models with group interactions, but weighted averages and standard errors of the most parsimonious model overlap (Table 1), suggesting the top model truly reflects apparent survivorship and recapture probabilities. Fitch did have enough recaptures of pre-reproductive aged *L. calligaster* to calculate apparent survival, which was calculated independent of adult models. (Table 1).

Table 2. Comparison of Cormack-Jolly-Seber models for apparent annual survival ( $\Phi$ ) and recapture rates ( $p$ ) for *Lampropeltis calligaster* in northeastern Kansas. Models differ in whether  $\Phi$  and  $p$  are assumed to be constant (.), fully time dependent (t), or differ between sexes (g), and whether there are interactions (\*) among these factors. The model with the lowest AIC<sub>c</sub> score is considered the most parsimonious.

Model	AIC <sub>c</sub>	$\Delta$ AIC <sub>c</sub>	AIC <sub>c</sub> Weights	Parameters	Deviance
{ $\Phi$ (.) p(.)}	164.9469	0	0.46734	2	107.3081
{ $\Phi$ (g) p(.)}	166.3505	1.4036	0.23166	3	106.6442
{ $\Phi$ (.) p(g)}	166.4718	1.5249	0.21803	3	106.7656
{ $\Phi$ (g) p(g)}	168.404	3.4571	0.08297	4	106.6072
{ $\Phi$ (t) p(.)}	233.067	68.1201	0	41	73.0694
{ $\Phi$ (t) p(g)}	236.2486	71.3017	0	42	72.8764
{ $\Phi$ (t) p(t)}	277.5817	112.6348	0	59	48.4486
{ $\Phi$ (.) p(t)}	282.8864	117.9395	0	54	74.9079
{ $\Phi$ (g) p(t)}	286.6482	121.7013	0	55	74.5721
{ $\Phi$ (g*t) p(.)}	322.8008	157.8539	0	67	55.9939
{ $\Phi$ (g*t) p(g)}	327.7745	162.8276	0	68	55.8866
{ $\Phi$ (t) p(g*t)}	347.6808	182.7339	0	77	25.7086
{ $\Phi$ (g*t) p(t)}	358.9583	194.0114	0	78	30.8861
{ $\Phi$ (g*t) p(g*t)}	389.6698	224.7229	0	84	22.3834
{ $\Phi$ (.) p(g*t)}	614.7101	449.7632	0	106	50.6643
{ $\Phi$ (g) p(g*t)}	626.2565	461.3096	0	107	50.5244

Table 3. Comparison of Cormack-Jolly-Seber models for apparent annual survival ( $\Phi$ ) and recapture rates ( $p$ ) for *Lampropeltis triangulum* in northeastern Kansas. Models differ in whether  $\Phi$  and  $p$  are assumed to be constant ( $\cdot$ ), fully time dependent ( $t$ ), or differ between sexes ( $g$ ), and whether there are interactions ( $*$ ) among these factors. The model with the lowest AIC<sub>c</sub> score is considered the most parsimonious.

Model	AICc	$\Delta$ AICc	AICc Weights	Num. Par	Deviance
{ $\Phi(g)$ $p(\cdot)$ }	321.0392	0	0.39785	3	251.5396
{ $\Phi(\cdot)$ $p(\cdot)$ }	321.9572	0.918	0.2514	2	254.5112
{ $\Phi(\cdot)$ $p(g)$ }	322.322	1.2828	0.20949	3	252.8224
{ $\Phi(g)$ $p(g)$ }	323.1101	2.0709	0.14126	4	251.5386
{ $\Phi(t)$ $p(\cdot)$ }	346.7685	25.7293	0	49	158.0013
{ $\Phi(t)$ $p(g)$ }	349.3652	28.326	0	50	157.3206
{ $\Phi(\cdot)$ $p(t)$ }	362.9391	41.8999	0	54	157.4083
{ $\Phi(g)$ $p(t)$ }	365.2551	44.2159	0	55	156.2553
{ $\Phi(t)$ $p(t)$ }	377.288	56.2488	0	70	110.9837
{ $\Phi(g*t)$ $p(\cdot)$ }	441.5302	120.491	0	76	149.1373
{ $\Phi(g*t)$ $p(g)$ }	446.0043	124.9651	0	77	149.0617
{ $\Phi(t)$ $p(g*t)$ }	462.3762	141.337	0	91	94.7643
{ $\Phi(g*t)$ $p(t)$ }	467.426	146.3868	0	90	105.3374
{ $\Phi(g*t)$ $p(g*t)$ }	547.5742	226.535	0	105	93.2056
{ $\Phi(\cdot)$ $p(g*t)$ }	585.1879	264.1487	0	104	137.666
{ $\Phi(g)$ $p(g*t)$ }	591.6199	270.5807	0	105	137.2513

Male *L. triangulum* had higher apparent survivorship than females (Table 1), and the most parsimonious model states survivorship varied by group, but recapture probability did not vary by group or time (Table 3). Again, the differences between models was slight, but weighted averages plus standard errors of apparent survivorship between sexes show little overlap, suggesting differences in survivorship between sexes may be real. Since recaptures of pre-reproductive *L. triangulum* were lacking, apparent survival values for *L. calligaster* were substituted for use in population viability models.

When considering population growth rates, a value of  $\lambda=1$  denotes a stable population, while higher or lower values signify increasing or decreasing populations. Pradel's  $\lambda$ , or the number of new animals entering the population, suggest stable populations for both species in this study (Table 1). When survivorship values are coupled with reproductive rates within Program Vortex,

deterministic values also suggest stable populations for both species. Both true  $\lambda$  and the population replacement rate ( $R_0$ ) are near a value of 1. Due to an earlier age of maturity in *L. calligaster* mean generation time was 1.5 yrs shorter than for *L. triangulum* (Table 1).

Based on the reproductive values provided by Fitch (1999) and the deterministic rates provided here, populations for both species of *Lampropeltis* within Fitch's study site appear to be stable. When we ran simulations varying deterministic rates we observed differences in how variation influenced population growth rates. There were strong interactions between female and juvenile mortality and the percent of females breeding in the *L. calligaster* models (Fig. 1). Fitch (1999) noted that dependent on available resources, roughly 1/3 of the female population may not reproduce in a given year. This temporal reduction in reproductive females increases the importance of juveniles transitioning into reproductive age classes.

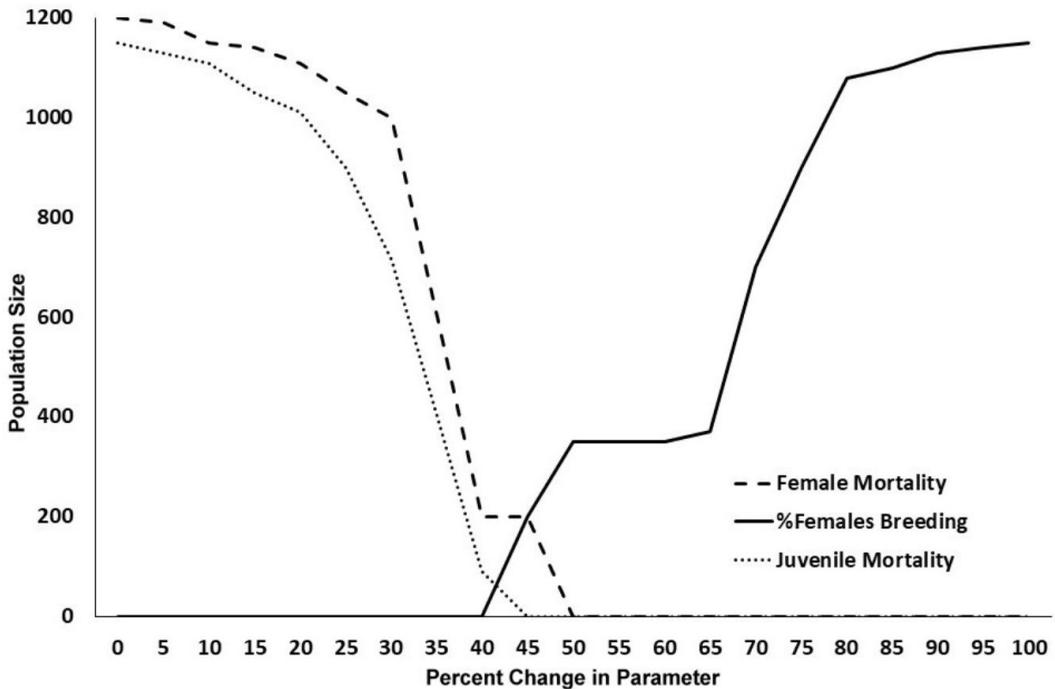


Figure 1. Sensitivity plots showing the influence of percent change in measured parameters on population size for *Lampropeltis calligaster* in northeast Kansas.

The *L. triangulum* models placed more importance on female mortality followed by juvenile mortality (Fig. 2). Considering that *L. triangulum* reach sexual maturity a year later and have slightly smaller clutch sizes as compared to *L. calligaster*, maintaining reproductive age females is important for population maintenance. Sustained mortality or removal of adult females exceeding 30% would result in population extinction.

In all population viability models, particularly those for *L. triangulum*, female mortality played an important role in population persistence. The reproductive value of females (the probability of future offspring offset with age-specific mortality rates) increased with age peaking at 6 yrs for *L. calligaster* and 7 yrs for *L. triangulum* (Fig. 3).

## DISCUSSION

While the populations of the two species of *Lampropeltis* on Fitch's study site in northeast Kansas appear to be stable, adult survivorship for both species was low based on mark-recapture data. Low recapture rates may have been influenced by both species cryptic nature and the fact that Fitch primarily used funnel traps as his sampling method. Even with those considerations, the duration of Fitch's study provided a fairly robust data set for both species, including data on known age cohorts, which allowed for more accurate estimation of timing of important life history stages.

For both species, population persistence was dependent upon the presence of breeding age females within the population. The peak in reproductive value calculated here coincides

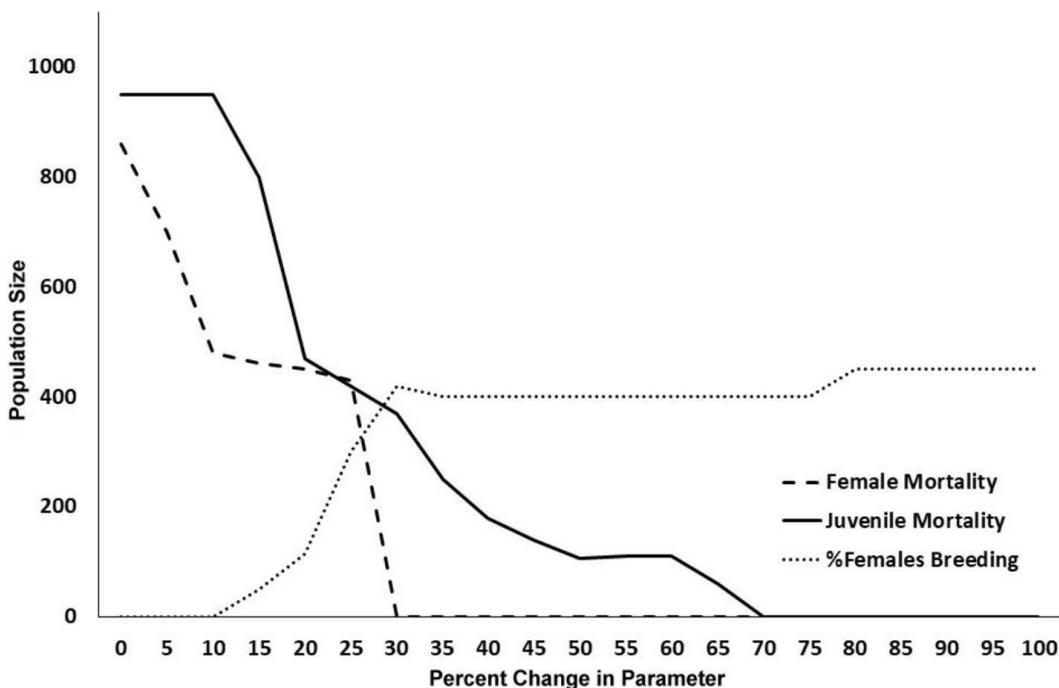


Figure 2. Sensitivity plots showing the influence of percent change in measured parameters on population size for *Lampropeltis triangulum* in northeast Kansas.

with the age at which females reach mean adult size and begin producing larger clutches of eggs before annual mortality rates begin to offset reproductive advantages. It appears that high annual mortality coupled with not breeding every year (*L. calligaster*) or delaying sexual maturity (*L. triangulum*) have the greatest influence on population growth rates. Increasing the number of female snakes' breeding in a given year may offset low adult survivorship in *L. calligaster* but is not as likely to influence population growth rates in *L. triangulum*. Ensuring juvenile snakes transition into reproductive age classes for both species is as important as maintaining female survivorship.

While Fitch's unprecedented work on snake communities took place within the confines of a protected natural area, the demographic information it provides is an important baseline for consideration of the possible impacts of take. A general rule is variation within reproductive constraints influences population growth rates, and it is important to elucidate the sources of

variation between species. Timber Rattlesnakes *Crotalus horridus*, is considered a typical k-adapted species with late age to maturity, and long reproductive life cycles coupled with a low number of life-time reproductive efforts (Brown 2016). On the other end of the spectrum the Northern Water Snake *Nerodia sipedon* grows fast and reach sexual maturity by 3y of age (Brown and Weatherhead 1999). Mortality greatly increases for *N. sipedon* after reaching maturity. The much smaller bodied Ring-necked Snake also exhibits a young age to maturity, with high mortality rates for pre-reproductive individuals and higher survivorship for adults (Riedle 2014). The models presented within this manuscript demonstrated variation between two species of sympatric, congeneric kingsnakes. Both species of kingsnakes studied here are wide ranging, so it is expected that vital rates will vary greatly across their distributions. For the transcontinental rat snake *Pantherophis obsoletus*, latitude appears to play a significant role in growth rates, age at maturity, and life spans (Blouin-Demers et al. 2002).

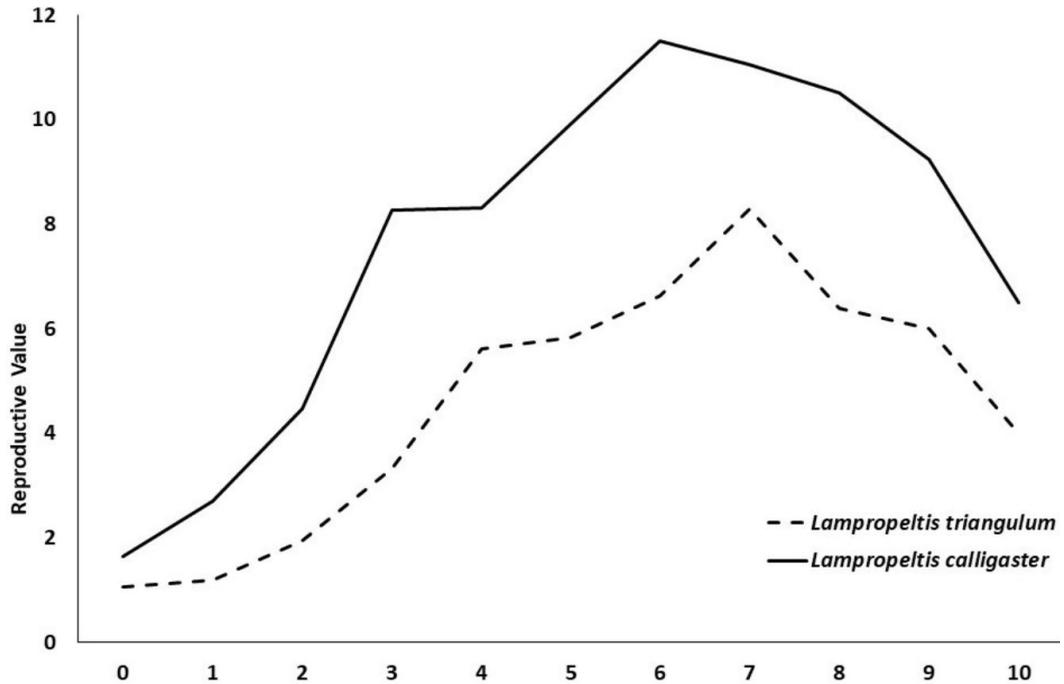


Figure 3. Reproductive value of female *Lampropeltis calligaster* and *L. triangulum* from ages 0-10 in northeast Kansas.

Outside of a few common species, demographic vital rates are lacking to assess possible impacts of trade nor are accurate data available on the trade in many species. Most data have focused on international exports while data on local trade is nonexistent (Schlaepfer, Hoover and Dodd 2005). The near extirpation of the insular snake *Boa constrictor imperator* due to the pet trade has been documented (Wilson and Cruz-Diaz 1993; Reed et al. 2007). Webb et al. (2002) noted dramatic declines in the Australian broad-headed snake *Hoplocephalus bungaroides* due to collection for pets. These declines were disparate between sexes, where 85% of the females disappeared from the population but male declines were much less severe. The authors state collectors were selectively harvesting female snakes.

The two focal species of *Lampropeltis* discussed in this manuscript are common throughout most of the state of Kansas and are most likely not in any danger of extinction in

the state (Collins, Collins and Taggart 2010). Anecdotal information from law enforcement at the Kansas Department of Wildlife, Parks, and Tourism though suggests that *L. triangulum* is a target species for many reptile enthusiasts visiting Kansas. Most of their habitat is found primarily on private lands within the state, which protects many populations from sustained impact. Based on the demographic information presented here though, increased take on the minimal public lands available within the species range could or possibly has resulted in the creation of localized sink populations by reducing breeding females and thus future offspring at specific sites. While neither species may be of immediate conservation concern, long-term data sets, such as those compiled by Fitch, provide important baseline data for demographic analyses and informing future management decisions. We suggest using the baseline demographics described in this paper as a starting point to better understand population trends and trade of *Lampropeltis* in the state.

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## LITERATURE CITED

- Blouin-Demers, G., K.A. Prior and P.J. Weatherhead. 2002. Comparative demography of Black Rat Snakes (*Elaphe obsoleta*) in Ontario and Maryland. *Journal of Zoology* 256:1–10.
- Brown, G.P. and Weatherhead, P.J. 1999. Demography and sexual size dimorphism in Northern Water Snakes, *Nerodia sipedon*. *Canadian Journal of Zoology* 77:1358–1366.
- Brown, W.S. 2016. Lifetime reproduction in a northern metapopulation of timber rattlesnakes (*Crotalus horridus*). *Herpetologica* 72:331–342.
- Burnham, K.P. and Anderson, D.R. 2002. Model selection and multimodel inference. Springer-Verlag, New York, 488 pp.
- Collins, J.T., S.L. Collins and Taggart, T.T. 2010. Amphibians, Reptiles, and Turtles in Kansas. Eagle Mountain Publishing, Eagle Mountain, UT, 318pp.
- Dyrkacz, S. 1977. The natural history of the eastern milk snake (Reptilia, Serpentes, Colubridae) in a disturbed environment. *Journal of Herpetology* 11:155–159.
- Enge, K.M. 2005. Commercial harvest of amphibians and reptiles in Florida for the pet trade. pp. 198–211 in *Amphibians and reptiles: status and conservation in Florida*. Krieger Publishing, Malabar, Florida.
- Fisher, R.A. 1930. *The genetical theory of natural selection*. Clarendon Press, Oxford, England.
- Fitch, H.S. 1999. A Kansas snake community: composition and changes over 50 years. Krieger Publishing, Malabar, Florida. 165 pp.
- Fitzgerald, L.A., Painter, C.W., Reuter, A. and Hoover, C. 2004. Collection, trade, and regulation of reptiles and amphibians of the Chihuahuan Desert Ecoregion. TRAFFIC North America. Washington D.C.: World Wildlife Fund.
- Lacy, R.C. and Pollak, J.P. 2014. Vortex: a stochastic simulation of the extinction process. Version 10.0. Chicago Zoological Society, Brookfield, Illinois, USA.
- Parker, W.S. and Plummer, M.V. 1987. Population ecology. Pp. 253–301 In *Snakes: Ecology and Evolutionary Biology*. Seigel, R.A., J.T. Collins, and S.S. Novak (Eds.). Macmillan, New York, New York, USA.
- Pianka, E.R. 1994. *Evolutionary Ecology*. Harper Collins, New York, New York, USA.
- Pradel, R. 1996. Utilization of capture-mark-recapture for the study of recruitment and population growth rate. *Biometrics* 52:703–709.
- Prestridge, H.L., Fitzgerald, L.E. and Hibbitts, T.J. 2011. Trade in non-native amphibians and reptiles in Texas: lessons for better monitoring and implications for species introduction. *Herpetological Conservation and Biology* 6:324–339.
- Reed, R.N., Boback, S.M., Montgomery, C.E. Green, S., Stevens, Z. and Watson, D. 2007. Ecology and conservation of an exploited insular population of *Boa constrictor* (Squamata: Boidae) in the Cayos Cochinos, Honduras. pp. 389–403 in *Biology of the Boas and Pythons*. Henderson, R.W. and R. Powell (eds.). Eagle Mountain Publishing, Eagle Mountain, UT.
- Richardson, M.L., Weatherhead, P.J. and Brawn, J.D. 2006. Habitat use and activity of prairie kingsnakes (*Lampropeltis calligaster calligaster*) in Illinois. *Journal of Herpetology* 40:423–428.

- Riedle, J.D. 2014. Demography of an urban population of ring-necked snakes (*Diadophis punctatus*) in Missouri. *Herpetological Conservation and Biology* 9:278-284.
- Robinson, J.E., Griffiths, R.A., St. John, F.A.V. and Roberts, D.L. 2015. Dynamics of the global trade in live reptiles: shifting trends in production and consequences for sustainability. *Biological Conservation* 184:42-50.
- Row, J.R. and Blouin-Demers, G. 2006a. Thermal quality influences habitat selection at multiple scales in milksnakes. *Ecoscience* 13:443-450.
- Row, J.R. and Blouin-Demers, G. 2006b. Kernels are not accurate estimators of home-range size for herpetofauna. *Copeia* 2006:797-802.
- Schlaepfer, M.A., Hoover, C. and Dodd Jr., C.K. 2005. Challenges in evaluating the impact of the trade in amphibians and reptiles on wild populations. *BioScience* 55:256-264.
- Todd, R.D., Wilson, J.D. and Gibbons, J.W. 2010. The global status of reptiles and causes of their decline. pp. 47-67 in *Ecotoxicology of Amphibians and Reptiles*, Second Edition. Sparling D.W., C.A. Bishop, S. Krest (eds.). CRC Press, Pensacola, FL, USA.
- Vitt, L.J. 1987. Communities. pp. 335-365 in *Snakes: Ecology and Evolutionary Biology*. Seigel, R.A., J.T. Collins, and S.S. Novak (eds.). Macmillan, New York, New York.
- Webb, J.K, Brook, B.W. and Shine, R. 2002. Collectors endanger Australia's most threatened snake, the broad-headed snake *Hoplocephalus bungaroides*. *Oryx* 36:170-181.
- White, G.C. and Burnham, K.P. 1999. Program MARK: survival estimation from populations of marked individuals. *Bird Study* 46(Suppl.): S120-139.
- Wilson, L.D. and Cruz-Diaz, G. 1993. The herpetofauna of the Cayos Cochinos, Honduras. *Herpetological Natural History* 1:13-23.