Joint estimation of growth and survival from mark-recapture data to improve estimates of senescence in wild populations

Beth A. Reinke[1*], Luke Hoekstra[2], Anne M. Bronikowski[2], Fredric J. Janzen[2], and David Miller[1]

[*]Corresponding Author: bxr389@psu.edu

[1] Department of Ecosystem Science and Management, Pennsylvania State University, University Park, PA 16802.

[2] Department of Ecology, Evolution, and Organismal Biology, Iowa State, University, Ames, IA, 50011

Abstract.

Understanding age-dependent patterns of survival is fundamental to predicting population dynamics, understanding selective pressures, and estimating rates of senescence. However, quantifying age-specific survival in wild populations poses significant logistical and statistical challenges. Recent work has helped to alleviate these constraints by demonstrating that age-specific survival can be estimated using mark-recapture data even

when age is unknown for all or some individuals. However, previous approaches do not incorporate auxiliary information that can improve age estimates of individuals. We introduce a survival estimator that combines a von Bertalanffy growth model, age-specific hazard functions, and a Cormack-Jolly-Seber mark-recapture model into a single hierarchical framework. This approach allows us to obtain information about age and its uncertainty based on size and growth for individuals of unknown age when estimating age-specific survival. Using both simulated and real-world data for two painted turtle (*Chrysemys picta*) populations, we demonstrate that this additional information substantially reduces the bias of age-specific hazard rates, which allows for the testing of hypotheses related to aging. Estimating patterns of senescence is just one practical application of jointly estimating survival and growth; other applications include obtaining better estimates of the timing of recruitment and improved understanding of life-history trade-offs between growth and survival.

Key words: growth, hazard, mark-recapture, painted turtle, senescence, survival

Introduction

Senescence, the deterioration of function with advancing age, can result in varied aging rates within populations. Thus, aging is a fundamental process affecting animals and has important implications for determining population dynamics and the evolution of life-history traits (Ricklefs 2010, Bronikowski et al. 2011, Jones et al. 2014). Despite its seemingly paradoxical existence, the evolution of an age-specific decline in reproduction and survival can occur if traits that cause these declines occur later in life (Medawar 1952). These traits are less subject to selection than traits that occur earlier in life because organisms are increasingly likely to have succumbed to extrinsic causes of mortality (i.e., predation,

conflict) as they age (Medawar, 1952; Williams, Day, Fletcher, & Rowe, 2006). Moreover, this susceptibility itself can also change with age (Williams & Day, 2003). The ubiquity of demographic senescence (i.e., changes in age-specific survival and fecundity due to age-specific deterioration) motivates the need for statistical models that estimate age-specific demography (Siler 1979, Pletcher 1999, Colchero and Clark 2012). We focus here on characterizing age-specific mortality. The ability to measure the relationship between age and mortality is essential for biodemographic modeling (Miller et al. 2014), informs evolutionary theory (Ricklefs 2010), and aids conservation and population management efforts (Lynch & Fagan 2009).

Laboratory experiments and theoretical work on senescence and aging often rely on assumptions and constraints that are unlikely to be true for free-living wild populations (Williams et al. 2006, Nussey et al. 2008). Thus, it is important to measure and understand patterns of senescence in the wild where natural selection occurs. Mark-recapture studies provide data on animals in the wild and these types of longitudinal data sets are necessary for understanding inter- and intra-specific variation in senescence (Nussey et al. 2008). For example, despite it long being thought that turtles senesce slowly or not at all, Warner et al. (2016) detected significant declines in age-specific reproductive success and survival by measuring reproductive output, embryo survival rates, and post-hatching mortality in painted turtles (*Chrysemys picta*) using a 20-year mark-recapture data set.

Mark-recapture methods are a common approach for measuring survival in wild populations. However, estimating age-specific patterns of survival has traditionally required following known-age individuals for long periods of time to track their mortality. This process requires knowledge of the age of individuals, which is often only available for

animals marked as newborns and juveniles, thus necessitating long time-series and large

sample sizes to meet data requirements for accurate estimation. To overcome these

limitations, Colchero and Clark (2012) developed a hierarchical model within a Bayesian

framework to estimate age-specific patterns of survival when some or all individuals within a

population are of unknown age. In doing so, they provided a method to query data that were

previously unusable, consequently reducing the uncertainty typical in these analyses

(Colchero and Clark 2012, Colchero et al. 2012).

The approach outlined by Colchero & Clark (2012) remains an important advance,

but does not incorporate auxiliary information that might augment our understanding of age.

Specifically, the size and growth of individuals is directly related to age for many species,

especially those that have indeterminate or extended periods of growth (Eaton and Link

2011). Here, we present a new mark-recapture estimator that uses continuous, non-linear,

growth equations to incorporate individual variability in growth rate and asymptotic size.

This extends models proposed by others to estimate age dependent survival (Colchero and

Clark 2012, Rose et al. 2018b, Bird et al. 2019) by estimating patterns of growth and

senescence simultaneously within a single joint modeling framework. The von Bertalanffy

(vB) growth curve is a flexible, non-linear function for estimating growth (von Bertalanffy

1938). The vB growth curve is ideal for use in mark-recapture type studies and can be

extended to allow for individual variation in initial size, final size, and growth rates (Fabens

1965, Eaton and Link 2011, Schofield et al. 2013). Modeling individual growth using a vB

function incorporates how size will vary as a function of age, does not require age to be

known, and, critically, allows for age to be estimated for individuals based on size alone

(Eaton and Link 2011, Schofield et al. 2013).

We demonstrate that estimating growth and survival simultaneously improves estimates of age-specific survival. We first describe a hierarchical model that incorporates growth, age-specific hazards, and mark-recapture survival estimates and use simulated data to validate the model. Then, using mark-recapture data sets for males and females in two populations of painted turtles, *Chrysemys picta*, we show how the model can reduce bias in the estimates of the rate of senescence. In doing so, we shed light on an ongoing debate on the generalizability of female advantage in lifespan and survival (e.g., Austad and Fischer 2016). By focusing our case study on this important model taxon, we broaden the comparative landscape of wild aging biodemography and life-history studies.

Methods

Model: We develop a general model for estimating age-specific survival that combines three distinct components: a model to estimate age and associated uncertainty using a mark-recapture version of a von Bertalanffy growth curve model (Fabens 1965, Schofield et al. 2013), an age-specific hazard function to characterize the functional relationship between age and mortality that estimates patterns of demographic senescence (Siler 1979, Pletcher 1999, Colchero and Clark 2012), and a mark-recapture survival model to estimate hazard function parameters dependent on known or estimated ages (Cormack 1964, Seber 1965, Lebreton et al. 1992). We combine the three components into a single hierarchical model to share information and distribute uncertainty among the components. The Colchero and Clark (2012) model estimates age-specific survival when age is unknown for a subset of the population. Our model incorporates additional information available from sizes and growth rates for the unknown-age component of the population. Our goal is to improve estimates by reducing uncertainty in the age-based component of the model.

Growth model: We use a von Bertalanffy growth model to predict size at capture L_{it} for individual i during survey occasion t. We use an age-at-first-capture formulation of the mark-recapture model (Schofield et al. 2013). We denote the initial size at age 0 for individual i as $L0_i$. Similarly, asymptotic size of an individual is denoted as LI_i and represents the maximum size attained by an individual at age infinity. Finally, each individual is assumed to grow at a growth rate K_i, which represents the proportion of growth from $L0_i$ to LI_i that remains after a year of time. The size of individual i at time t is calculated as:

$$L_{it} = L0_i + (LI_i - L0_i)(1 - K_i^{(AFC_i + \Delta_{it})})$$

where AFC_i is the age of the individual at first capture (may be known or unknown) and Δ_{it} is the number of years since first capture. At the first capture, $\Delta_{it} = 0$ and $(AFC_i + \Delta_{it})$ is the age of the individual i at time t.

We allow for individual variation in each of the estimated parameters. For *L0* and *LI*, we assume normal variation where $L0_i \sim Normal(\mu_{L0}, \sigma_{L0}^2)$ and $LI_i \sim Normal(\mu_{LI}, \sigma_{LI}^2)$. For K, we assume logit normal variation where $\text{logit}(K_i) \sim Normal(\mu_K, \sigma_K^2)$. For *AFC*, we assume a negative binomial distribution, which constrains *AFC* to be a positive integer. It is also possible to incorporate *AFC* as a continuous variable, using a distribution such as a log-normal (see Schofield *et al.* 2013). We chose to model *AFC* as discrete since most animals have limited birthing seasons that are amenable to assignment to a year. We also let each parameter vary by sex, though it is additionally possible to vary them by time in the case of *K*, or by other useful covariates that explain within-population growth patterns (e.g., site).

The final component of the growth model relates L_{it}, the expected size of individual i at time t, to the observed size value, $obsL_{it}$. This accounts for sampling error as well as lack-of-fit to the vB function. We assume a normal error structure where $obsL_{it} \sim Normal$ $(L_{it}, \sigma_{sample}^2)$.

When fitting models in subsequent sections, we use uniform priors for μL_o and μL_l across reasonable values for each. For μ_k, we use a uniform prior on the probability scale where logit(μ_k) ~ Uniform(0,1). For the variance parameters $\sigma^2_{L0}, \sigma^2_{LI}, \sigma^2_K$, and σ^2_{sample}, we use a t-distributed prior where σ ~ t(0,0.0004,3) but is constrained to be greater than 0, as in Schofield et al. 2013. Using the t-distribution allows for robust estimates and occasional extreme values (Gelman and Hill 2007). Note that Eaton and Link (2011) provide another formulation to incorporate individual variation into a vB growth function, which has been successfully applied to estimate growth for other mark-recapture data sets (Fellers et al. 2013, Rose et al. 2018a).

Age-specific hazard function: In studies that explore rates of demographic senescence, it is typical to estimate the relationship between age and survival using hazard functions (Bronikowski et al. 2011, Miller et al. 2014). Unlike most estimates of survival using mark-recapture data, mortality is treated as a continuous rather than as a discrete process, such that the hazard is an estimate of the instantaneous ability to an animal to survive at a given time, rather than over a determined time period. In this case, if the mortality rate μ is constant, then survival for one year is given by $e^{-\mu}$ and survival from birth to age T is given by $e^{-\mu T}$.

In the case of senescence, mortality is expected to depend on the age, *a*, of the individual, and is denoted by $m(\mu|a)$. This relationship may be described by Gompertz, Weibull, Siler, and Logistic equations, with or without a constant Makeham mortality term, all of which describe how mortality changes as an animal ages (Siler 1979, Pletcher 1999, Colchero and Clark 2012). If the continuous mortality rate varies as a function of age, then estimating the survival over a given interval requires determining the average mortality during the interval multiplied by the length of that interval. To do so, one calculates the

integral of $m(\mu|a)$ over the interval of interest and as before, takes the negative exponent of the natural logarithm for this value. For example, the probability of surviving, φ, from age a to $a + 1$ is:

$$\varphi[a] = e^{-\int_a^{a+1} m(\mu|a)}$$

The form used for $m(\mu|a)$ is flexible. We focus on exponential (i.e., constant) mortality using a Gompertz function (Gompertz 1825), where:

$$u = e^{\beta 0 + \beta 1 * a_{it}}$$

In most cases, we expect mortality to be high for young individuals and then to fit a Gompertz-type function once animals reproductively mature. In this case, we can separate the early ages and use an exponential mortality function for these younger animals and then use a Gompertz function for older animals; we subsequently call the age at which this separation is made the truncation age. Importantly, truncation age is not necessarily equivalent to the age at maturation, but rather is the age at which a population transitions from exponential to Gompertz mortality. Other functions can be used, as described above, and we include code for a Gompertz-Makeham and Siler function in the supplementary material (Data S3 and S4).

Mark-recapture survival model: Finally, we estimate apparent survival using a standard Cormack-Jolly-Seber (CJS) model that relates observed detections of individuals across time to underlying survival and detection probabilities (Lebreton et al. 1992, Pledger et al. 2003). Note that CJS models are not able to distinguish between dead individuals and individuals that have emigrated. Let $z_{it} = 1$ if individual i is alive at time t and $z_{it} = 0$ if individual i is apparently dead at time t. Let f_i be the year of initial capture and a_{it} be the age of individual i at time t. We can calculate a_{it} as a function of the time and age of first capture where:

$$a_{it} = AFC_i + (t - f_i)$$

The CJS formulation conditions on the initial capture, where $z_{i0} = 1$, which denotes that the individual is alive (i.e., z = 1). The probability $z_{it+1} = 1$ (i.e., the animal is still alive in time $t + 1$ given that it is alive in time t) for all subsequent years is given by $z_{it+1} = $ Bernoulli($z_{it} * \varphi_i[a_{it}]$). The value for $\varphi_i[a_{it}]$ comes from the age-specific hazard function. The probability of observing individual i at time t, y_{it}, is the probability of detecting an animal given that it is alive at time t. We express this probability as $y_{it} \sim$ Bernoulli($z_{it} * \theta_t$). We use θ_t to denote the probability of detecting an individual, given that it is alive at time t, and we allowed θ_t to vary as a function of time, age, sex, or other factors thought to affect capture probabilities in the system.

Simulated data set: We use Monte Carlo simulations to test model performance and to assess whether including information about individual growth increases the accuracy of our approach. We simulate the capture of 25 new individuals (i.e., not previously captured) each year for 20 years where animals still alive in subsequent years were recaptured with a moderate 50% detection probability. Age at first capture (*AFC*) is assumed to come from a negative binomial distribution. Length at birth and asymptotic size for each individual come from normal distributions with means of 30 and 150 and standard deviations of 1 and 10, respectively. Additionally, we ran simulations with varied numbers of animals and a lower detection probability and found that the results are decently robust (Appendix S1).

We use a truncated mortality function for early ages where survival is allowed to vary until age 6, and thereafter follow a Gompertz model where $\text{\ss}_0 = -4$, and $\text{\ss}_1 = 0.2$. We generate 100 data sets and then analyze each data set with and without growth information included in the estimator to determine whether our growth model improved estimates. In addition, we varied the proportion of known ages to estimate the impact of unknown age percentages on

the bias of our model. Our simulations include data sets with 0%, 10%, 50%, and 100%

known ages. Additionally, to account for possible age class constraints in the wild, we

constructed data sets using only newborn individuals (0-1 year-olds) and only old individuals

(>6 year-olds).

Painted turtle data sets: We used two mark-recapture data sets of painted turtles,

Chrysemys picta. One data set consists of a 26-year study (1993-2018) of a population near

Thomson, Illinois, where females were captured on land after nesting, with male captures and

additional female captures supplemented by trapping (Pearse et al. 2001, Warner et al. 2016).

The other data set is an 8-year study (2010-2012, 2014-2018) of a population on Lac Courte

Oreilles, Wisconsin, where most individuals were captured by dip-net. In both populations,

age was estimated using annuli, rings that occur on the plastron scutes each growing season.

Because annuli fade with age, if an individual had greater than 8 annuli when it was first

captured, we recorded it as being of unknown age; approximately 71% of all captures in the

IL population and 32% of all captures in the WI population were of unknown age (see

Appendix S2: Table S1 for more information on data sets). We treated these data as missing

rather than censored because the incorporation of size data effectively defines these

individuals as only of older ages. Many turtle species have high hatchling mortality, likely

due to size-dependent predation (Janzen et al. 2000), so we assumed the years before maturity

were drawn from a different survival distribution than the years after. For both data sets, we

compared models with truncation ages of 6 and 8 years since this is the conservative age

range during which painted turtles reach sexual maturity (Shine and Iverson 1995).

Analysis: We used 5,000 iterations of Markov-chain Monte Carlo algorithms with a burn-in of 2,000 to estimate posterior distributions for our simulations, which was sufficient for convergence and computationally efficient for running a large number of data sets. We used 50,000 iterations of Markov-chain Monte Carlo algorithms with a burn-in of 20,000 for our painted turtle data sets and ran three parallel chains. We used the Gelman-Rubin convergence statistic ($\hat{R}$ ~1) to ensure that all three chains mixed well (Gelman and Rubin 1992). We assessed goodness of fit using a post-predictive check for which we calculated estimated residual error (*obsL$_{it}$-L$_{it}$*) and compared this to the distribution of predicted residual errors for our model. We used these data to identify potential outliers, check for differences in error distributions, and determine whether residual error varied systematically with size (Appendix S2: Figures S1-S2). All models were implemented using the program JAGS (Plummer 2003) through R version 3.4.4 (R Core Team 2016) using the package 'jagsUI' (Kellner 2015).

Results

Simulated data set: Including a growth model in simulated data greatly reduced negative bias when estimating rates of senescence, especially when no individuals were of known age and when the age of only a specific age class of individuals is known (Fig. 1a). The mean squared errors of the models were also lower when the growth model was included (Fig. 1b). When the age of only old individuals is known, incorporating a growth model reduced the bias and lowered the error (Fig. 1).

Painted turtle data set: Actuarial survival declines at approximately the same rate for female and male *C. picta* (Fig. 2a-b; Appendix S2:Figure S3). In the Illinois population, males had an estimated maximum life expectancy (mean cumulative survival <0.05; Fig. 2c-

d) of 27 years whereas females had a life expectancy of 32 years. In Wisconsin, males had an estimated maximum life expectancy of 37 years and females had a maximum life expectancy of only 22 years. For both populations, a truncation age of 8 resulted in a better fit than a truncation age of 6 (Appendix S2:Table S2). Full parameter estimates for both populations are available in Table 1.

Discussion

These results, based on both simulated and empirical field data from wild populations of painted turtles, demonstrate that simultaneously modeling growth along with survival improves precision and reduces the bias of estimates of age-specific mortality. This improvement has important implications for modeling demographic senescence. Especially in the case of long-lived organisms, collecting long-term data sets in the wild for known-age individuals is a significant logistical challenge. The ability to include individuals of unknown age in the analyses provides a significant advance. In addition, combining models of growth and survival may improve estimates of other important parameters, such as annual recruitment rates and the covariation between growth and survival.

Our analysis of two populations of *C. picta* expands on previously published results using 20 years of data on females from the Illinois population (Warner et al. 2016). Warner et al. (2016) found that, contrary to other reports, female painted turtles exhibited mortality senescence. Our results corroborated this finding in an additional population, and found that male mortality also increases with age (Fig. 2). Previous reports on painted turtles have largely studied females because of the ease of capturing them on land while nesting. Our approach here, which incorporates both sexes caught by a variety of methods, has allowed us to broaden the comparative landscape in the long-standing question of whether males

universally age faster than females. Specifically, we found that female and male painted turtles demonstrate similar adult mortality acceleration (Appendix S2: Figure S3), although the amount of uncertainty merits further investigation. Mammals appear to have a general phenomenon of enhanced female life expectancy relative to males, often accompanied by reduced mortality acceleration, whereas birds have a reported male advantage (Bronikowski et al. 2011, reviewed in Austad and Fischer 2016). Interestingly, one of the hypotheses for sex-specific variation in lifespan centers on an advantage to the homogametic sex, with some available data supporting this contention (Tower 2006, Maklakov and Lummaa 2013). Painted turtles, like many species of reptiles, do not have sex chromosomes and sex is determined by the temperature experienced during egg incubation (Janzen and Krenz 2004). Furthermore, across the reptile clade, both forms of genotypic sex determination (i.e., heterogamety and homogamety) occur in addition to environmental sex determination (Janzen and Phillips 2006). Thus, studying sex-specific aging across non-avian reptiles has the potential to disentangle causes of aging from the presence of sex chromosomes.

We find that incorporating growth increases the accuracy of models for estimating senescence in populations of animals of unknown ages. The method is likely to be most effective in species where size is indicative of age; species that reach asymptotic size early in life may not be appropriately fit with the vB function. The general approach used here---simultaneously estimating growth and survival---has many additional applications not highlighted here. The approach allows for improved estimates of age and uncertainty about age, life-span of individuals, average life-span of populations, and size-specific survival rates. In addition, the model could be extended to improve estimates of recruitment as well as covariation between growth and survival. Improved methods for estimating these parameters are necessary not only for understanding the evolutionary ecology of long-lived species, but also for aiding their management and conservation.

Literature Cited

Austad, S. N., and K. E. Fischer. 2016. Sex differences in lifespan. Cell Metabolism 23:1022–1033.

von Bertalanffy, L. 1938. A quantitative theory of organic growth (inquiries on growth laws. II). Human Biology 10:181–213.

Bird, T., J. Lyon, S. Wotherspoon, C. Todd, Z. Tonkin, and M. McCarthy. 2019. Combining capture–recapture data and known ages allows estimation of age-dependent survival rates. Ecology and Evolution 9:90–99.

Bronikowski, A. M., J. Altmann, D. K. Brockman, M. Cords, L. M. Fedigan, A. Pusey, T. Stoinski, W. F. Morris, K. B. Strier, and S. C. Alberts. 2011. Aging in the natural world: Comparative data reveal similar mortality patterns across primates. Science 331:1325–1328.

Colchero, F., and J. S. Clark. 2012. Bayesian inference on age-specific survival for censored and truncated data. Journal of Animal Ecology 81:139–149.

Colchero, F., O. R. Jones, and M. Rebke. 2012. BaSTA: An R package for Bayesian estimation of age-specific survival from incomplete mark-recapture/recovery data with covariates. Methods in Ecology and Evolution 3:466–470.

Cormack, R. M. 1964. Estimates of survival from the sighting of marked animals. Biometrika 51:429–438.

Eaton, M. J., and W. A. Link. 2011. Estimating age from recapture data: Integrating incremental growth measures with ancillary data to infer age-at-length. Ecological Applications 21:2487–2497.

Fabens, A. J. 1965. Properties and fitting of the von Bertalanffy growth curve. Growth 29:265–289.

Fellers, G., P. Kleeman, D. A. W. Miller, B. J. Halstead, and W. A. Link. 2013. Population size, survival, growth, and movements of *Rana sierrae*. Herpetologica 69:147–162.

Gelman, A., and J. Hill. 2007. Data Analysis Using Regression and Multilevel/Hierarchical Models. Cambridge University Press, New York.

Gelman, A., and D. B. Rubin. 1992. Inference from iterative simulation using multiple sequences. Statistical Science 7:457–511.

Gompertz, B. 1825. On the nature of the function expressive of the law of human mortality, and on a new mode of determining the value of life contingencies. Philosophical Transactions of the Royal Society of London 115:513–583.

Janzen, F. J., and J. G. Krenz. 2004. Phylogenetics: which was first, TSD or GSD? Pages 121–130 *in* N. Valenzuela and V. A. Lance, editors. Temperature-dependent sex determination in vertebrates. Smithsonian Books, Washington, DC.

Janzen, F. J., and P. C. Phillips. 2006. Exploring the evolution of environmental sex determination, especially in reptiles. Journal of Evolutionary Biology 19:1775–1784.

Janzen, F. J., J. K. Tucker, and G. L. Paukstis. 2000. Experimental analysis of an early life-history stage: Selection on size of hatchling turtles. Ecology 81:2290–2304.

Jones, O. R., A. Scheuerlein, R. Salguero-Gómez, C. G. Camarda, R. Schaible, B. B. Casper, J. P. Dahlgren, J. Ehrlén, M. B. García, E. S. Menges, P. F. Quintana-Ascencio, H.

Caswell, A. Baudisch, and J. W. Vaupel. 2014. Diversity of ageing across the tree of life. Nature 505:169–173.

Kellner, K. 2015. jagsUI: a wrapper around rjags to streamline JAGS analyses. R Package.

Lebreton, J., K. P. Burnham, J. Clobert, and D. R. Anderson. 1992. Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. Ecological Monographs 62:67–118.

Lynch, H. J., and W. F. Fagan. 2009. Survivorship curves and their impact on the estimation of maximum population growth rates. Ecology 90:1116–1124.

Maklakov, A. A., and V. Lummaa. 2013. Evolution of sex differences in lifespan and aging: Causes and constraints. BioEssays 35:717–724.

Medawar, P. B. 1952. An unsolved problem of biology. H.K. Lewis, London.

Miller, D. A. W., F. J. Janzen, G. M. Fellers, P. M. Kleeman, and A. M. Bronikowski. 2014. Biodemography of ectothermic tetrapods provides insights into the evolution and plasticity of mortality patterns. Sociality, Hierarchy, Health: Comparative Biodemography: Papers from a Workshop:295–313.

Nussey, D. H., T. Coulson, M. Festa-Bianchet, and J. M. Gaillard. 2008. Measuring senescence in wild animal populations: Towards a longitudinal approach. Functional Ecology 22:393–406.

Pearse, D. E., C. M. Eckerman, F. J. Janzen, and J. C. Avise. 2001. A genetic analogue of "mark-recapture" methods for estimating population size: An approach based on molecular parentage assessments. Molecular Ecology 10:2711–2718.

Pledger, S., K. H. Pollock, and J. L. Norris. 2003. Open capture-recapture models with heterogeneity : I. Cormack-Jolly-Seber model. Biometrics 59:786–794.

Pletcher, S. D. 1999. Model fitting and hypothesis testing for age-specific mortality data. Journal of Evolutionary Biology 12:430–439.

Plummer, M. 2003. JAGS : A program for analysis of Bayesian graphical models using Gibbs
    sampling. Proceedings of the 3rd International Workshop on Distributed Statistical
    Computing 124 125.10.

R Core Team. R: A language and environment for statistical computing. 2016. . R Foundation
    for Statistical Computing, Vienna, Austria.

Ricklefs, R. E. 2010. Life-history connections to rates of aging in terrestrial vertebrates.
    Proceedings of the National Academy of Sciences 107:10314–10319.

Rose, J. P., B. J. Halstead, G. D. Wylie, and M. L. Casazza. 2018a. Spatial and temporal
    variability in growth of giant gartersnakes: Plasticity, precipitation, and prey. Journal of
    Herpetology 52:40–49.

Rose, J. P., G. D. Wylie, M. L. Casazza, and B. J. Halstead. 2018b. Integrating growth and
    capture–mark–recapture models reveals size-dependent survival in an elusive species.
    Ecosphere 9:e02384.

Schofield, M. R., R. J. Barker, and P. Taylor. 2013. Modeling individual specific fish length
    from capture-recapture data using the von bertalanffy growth curve. Biometrics
    69:1012–1021.

Seber, G. A. . 1965. A note on the multiple-recapture census. Biometrika 52:249–259.

Shine, R., and J. B. Iverson. 1995. Patterns of survival, growth and maturation in turtles.
    Oikos 72:343–348.

Siler, W. 1979. A competing-risk model for animal mortality. Ecology 60:750–757.

Tower, J. 2006. Sex-specific regulation of aging and apoptosis. Mechanisms of Ageing and
    Development 127:705–718.

Warner, D. A., D. A. W. Miller, A. M. Bronikowski, and F. J. Janzen. 2016. Decades of field
    data reveal that turtles senesce in the wild. Proceedings of the National Academy of
    Sciences 113:6502–6507.

Williams, P., and T. Day. 2003. Antagonistic pleiotropy, mortality source interactions, and the evolutionary theory of senescence. Evolution 57:1478–1488.

Williams, P., T. Day, Q. Fletcher, and L. Rowe. 2006. The shaping of senescence in the wild. Trends in Ecology and Evolution 21:458–463.

Table 1. Full parameter mean estimates for IL (Data S1) and WI (Data S2) painted turtle data sets with standard deviations in parentheses. See Appendix S2: Table S3 for credible intervals.

	Illinois		Wisconsin	
	Female	Male	Female	Male
Growth				
L_I	159.162 (0.31)	134.347 (0.56)	160.512 (1.57)	124.441 (1.63)
Logit(K)	0.382 (0.03)	0.245 (0.05)	1.162 (0.05)	0.459 (0.10)
Senescence				
β_0	-2.108 (0.07)	-2.248 (0.34)	-2.667 (0.88)	-3.176 (1.21)
β_1	0.003 (0.003)	0.026 (0.02)	0.084 (0.07)	0.083 (0.08)
β_{Young}	0.230-0.855	0.324-0.844	0.500-0.823	0.510-0.792
Mark-recapture				
θ	0.083-0.515	0.050-0.447	0.176-0.405	0.154-0.410

Figure Legends

Figure 1. (A) There is a small negative bias in estimates of the rate of senescence (β_1) in simulated data. The estimated mean values of β_1 are closer to truth (dotted line) when a growth model is incorporated (open circles). When growth is not included in the model (closed circles), the bias is severe, especially when the proportion of known age individuals is small or when only individuals of a certain age class are of known age. Error bars are +/- 1 SE of the estimates obtained from Markov-chain Monte Carlo simulations. (B) The mean squared error is lower regardless of what percentage and which age classes are known when a growth model is included.

Figure 2. The (a-b) survival, (c-d) cumulative survival, and (e-f) hazard for male and female *Chrysemys picta* from populations in Illinois and Wisconsin as they age, starting at the truncation age (year 8). Females are shown with blue and males are shown with red. Shaded areas encompass the 95% credible interval. See text and Appendix S2: Table S3 for the parameter estimates for the models.