

Subtle individual variation in indeterminate growth leads to major variation in survival and lifetime reproductive output in a long-lived reptile

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Abstract

1. The consequences of individual variation in life-history traits have been well studied due to their importance in evolutionary ecology. However, a trait that has received little empirical attention is the rate of indeterminate growth. In long-lived ectotherms, subtle variation in growth after maturity could have major effects over the animals' lifetimes.
2. These effects are difficult to measure due to the challenges involved in reliably estimating individual variation in the face of environmental stochasticity, and the need to account for trade-offs among growth, reproduction and survival. However, modelling advances have made such analysis possible if long-term high-quality datasets are available.
3. We used an integrated state-space modelling framework to reveal relationships between indeterminate growth, reproduction and survival in a population of North American snapping turtles (*Chelydra serpentina*) using a 41-year dataset for 298 adult females.
4. A hierarchical version of the von Bertalanffy model fitted to data on carapace lengths showed substantial individual variation in growth trajectories, and hierarchical models fitted to clutch-mass data and recapture histories showed that reproductive output and survival probability increased with size. Integration of these models revealed no detectable trade-offs—i.e., individual growth parameters were not correlated with size-specific survival or reproduction rates, and individual variation in reproductive output did not affect the size-specific survival rate. Consequently, individual variation in growth parameters was estimated to result in >2-fold variation in post-maturity life expectancy and >4-fold variation in expected lifetime reproductive output.
5. These results illustrate that indeterminate growth can have major fitness consequences in long-lived species. We suggest that the individual variation in growth rates reflects variation in environments experienced during development or later life. An understanding of this variation may be essential for predicting the population dynamics of long-lived species under threat and identifying the most important environments to protect.

KEYWORDS

Bayesian hierarchical modelling, indeterminate growth, individual variation, life-history evolution, long-lived ectotherms, survival modelling, von Bertalanffy growth model

1 | INTRODUCTION

Growth rate, size-at-age and life histories vary greatly among individuals in a population (Cam, Aubry, & Authier, 2016; Plaistow, Shirley, Collin, Cornell, & Harney, 2015) as well as among species (Pianka, 1970) and populations (Lindgren & Laurila, 2005). This individual variation is of fundamental importance in evolutionary ecology, hence it has been well quantified and its consequences well studied in some systems (Coulson et al., 2006; Pelletier, Clutton-Brock, Pemberton, Tuljapurkar, & Coulson, 2007). Of primary interest to ecologists is the extent to which individual variation in growth and life-history strategy translate into variation in lifetime reproductive success (Abrams & Rowe, 1996; Pelletier et al., 2007). Indeed, a variety of studies have explored the fitness consequences of life-history variation, often using laboratory (Balshine-Earn, 1995; Creighton, Heflin, & Belk, 2009) and field experiments (Hanssen, Hasselquist, Folstad, & Erikstad, 2005; Visser & Lessells, 2001). Although experiments are ideal for detecting life-history trade-offs (Reznick, 1985) and estimating fitness (Plaistow et al., 2015), the consequences of individual variation in growth and life-history strategy in long-lived species accrue over years and decades, and can only be quantified through long-term studies. To date, most long-term studies that explore the fitness consequences of life-history variation have been conducted on birds and mammals (Rollinson & Rowe, 2015), probably because fecundity and survival can be more-easily quantified than in ectotherms, which are often cryptic and produce many offspring that are not easily linked to particular females. If the goal is to understand to the full suite of traits that contribute to individual variation in lifetime reproductive success, then this taxonomic bias is problematic, as many ectothermic species exhibit traits not usually found in birds and mammals.

One trait that may cause substantial individual variation in lifetime reproductive success is indeterminate growth, i.e. growth that continues after sexual maturity, which occurs in most ectothermic vertebrates and some invertebrates (Heino & Kaitala, 1999). Although indeterminate growth has received little empirical attention, theory suggests it is optimal in seasonal environments, where the prospect of successful reproduction is limited to a specific season, and resources acquired at other times of year cannot be used to increase current reproductive success (Ejsmond, Czarnotęski, Kapustka, & Kozłowski, 2010; Ejsmond, Varpe, Czarnoleski, & Kozłowski, 2015). Thus, indeterminate growth affects fitness by affecting body size, which then translates into variation in future fecundity (McLaren, 1966). Indeed, positive size-dependence of fecundity has become a fundamental pillar of all theories of indeterminate growth (Ejsmond et al., 2010, 2015; Gabriel, 1982; Kozłowski, 2006; Kozłowski & Uchmanski, 1987; Perrin, Sibly, & Nichols, 1993), and many models also assume that rapid growth reduces current survival probability due to reallocation

of resources or risky behaviour (Gabriel, 1982; Perrin et al., 1993; see also Abrams & Rowe, 1996). Interestingly, existing theory on indeterminate growth invariably omits positive effects of current size on adult survival even though such effects are highly plausible (Jørgensen & Fiksen, 2006; Taborsky, Dieckmann, & Heino, 2003). The fitness benefits of indeterminate growth therefore depend both on how growth impacts survival and fecundity through investment of resources and how current size directly affects immediate survival and fecundity. To better understand indeterminate growth and to inform theory, it is therefore important to estimate the consequences of individual variation in indeterminate growth on both survival and reproduction, and to account for possible trade-offs in these rates.

Turtles are an interesting group for exploring these issues due to their extreme life histories in terms of slow growth and long life spans. Turtles show no sign of senescence in most long-term studies (Congdon & Gibbons, 1990; Congdon, Nagle, Kinney, & van Loben Sels, 2001; Congdon et al., 2003), although evidence of senescence has recently been reported in one population (Warner, Miller, Bronikowski, & Janzen, 2016). Although turtles' growth may be imperceptibly slow after maturity, long-term studies have revealed ongoing indeterminate growth over decades (Armstrong & Brooks, 2013; Congdon, Gibbons, Brooks, Rollinson, & Tsaliagos, 2013). Congdon et al. (2013) concluded that this indeterminate growth has a trivial effect on adult fitness due to the tiny increases in size after maturity compared to those occurring before maturity. However, Congdon et al.'s (2013) analysis did not account for individual variation in growth, used an inappropriate growth model (linear regression), and did not consider the potential survival benefits of increased size. It therefore remains possible not only that indeterminate growth could be functionally important to turtles, but that subtle variation in indeterminate growth rates could have major effects over the animals' lifetimes. However, sophisticated analytical methods are needed to measure individual variation in the face of environmental stochasticity, to measure growth-related changes in survival, and to measure relationships among rates while accounting for uncertainties.

We applied an integrated state-space modelling framework to a 41-year dataset for a population of North American snapping turtles (*Chelydra serpentina* L.) to determine the consequences of individual variation in growth among adult females. The dataset is ideal not only for its duration, but because the intensive monitoring regime provided detailed individual histories of growth, reproductive output and survival. In addition, because females in this population begin nesting at a consistent size (Armstrong & Brooks, 2013), subsequent size-related differences in growth and survival are almost entirely attributable to indeterminate growth rather than size at maturity. We specifically addressed the following questions. (1) What is the extent of individual variation in indeterminate growth and reproductive output when

annual variation is accounted for? (2) To what extent do reproductive output and annual survival probability increase as females increase in size? (3) Do faster-growing individuals have low survival probability or reproductive output for their size, and do females with consistently high reproductive output have low survival probabilities for their size? (4) Taking these potential size-effects and trade-offs into account, what are the consequences of individual variation in growth and reproductive output on lifetime reproductive success?

2 | MATERIALS AND METHODS

2.1 | Species and study area

North American snapping turtles are omnivorous predators and scavengers that live in lakes, ponds and slow-moving rivers (Steyermark, Finkler, & Brooks, 2008). Our study was conducted in the Wildlife Research Area (45°35'N, 78°30'W) of Algonquin Provincial Park, near the northern edge of the species' range. Mature females produce annual clutches in spring or early summer, and bury them in sandy soil or gravel near water (Congdon, Greene, & Brooks, 2008). The size at which females become sexually mature appears to be quite consistent within populations (Congdon et al., 2008). Females at Algonquin Park predictably start nesting when their straight-line carapace length reaches 24–26 cm, which is a small range of variation given that they may subsequently reach up to 36 cm (Armstrong & Brooks, 2013). The age at which they first nest is expected to be variable, but ranged from 16 to 19 years for the five known-aged females in the dataset whose first clutches were recorded.

2.2 | Dataset

We used data collected from 1972 to 2012 on growth, reproductive output and survival of mature females. All procedures conformed to the guidelines of the Canadian Council on Animal Care and were approved by the University of Guelph Animal Care Committee.

Throughout each nesting season, usually from late May to late June, we patrolled all likely nesting habitat in the Sasajewun Lake watershed, which included 21 different water bodies over a 20 km² area surrounding the research station. We also patrolled other selected sites in the landscape when possible. Most adult females were encountered while nesting, and were captured by hand once their nests were complete. They were individually marked on first capture by wiring a numbered aluminium tag to the rear edge of the carapace, and by notching the edges of the carapace to enable identification if the tag was lost. We measured growth based on straight-line carapace length, which was measured to the nearest 1 mm using callipers on each capture. We measured annual reproductive output based on clutch masses, which were measured by temporarily excavating each nest shortly after laying. The precision of clutch-mass measurements varied depending on the data recorded (entire clutch weighed to the nearest 5 g, all eggs weighed individually to nearest 0.1 g, and/or a sample of 20 eggs weighed individually to the nearest 0.1 g). We therefore did initial modelling of

these data to obtain an estimate and standard error for each clutch mass, allowing the variation in precision to be accounted for in a state-space framework.

We considered clutch mass to be a better metric than clutch size because both egg size and clutch size are positively correlated with fitness, and both are positively correlated with female body size (Rollinson, Farmer, & Brooks, 2012; Rollinson & Rowe, 2016). However, re-analysis of the data using clutch size showed that the choice of metric had negligible effect on the results.

For analysis, we arranged the data into a set of matrices where rows corresponded to individual females and columns to years. These data are provided in Appendix S1. The matrices for carapace lengths and clutch masses included all females that were captured on at least two occasions over the 41 years ($n = 298$), with missing values (NA) entered for years that a female was not captured. The matrices for survival analysis only included females captured at least twice in the Sasajewun Lake watershed ($n = 195$), with the encounter histories starting at the second encounters. Our rationale was that these females would be unlikely to emigrate from the watershed, an assumption supported by capture data from the wider landscape. These matrices indicated whether or not each female was encountered each year, whether she was found dead (20 of 1,751 encounters), and whether she was last encountered at Sasajewun Lake itself. Females nesting at Sasajewun Lake were easier to monitor due to the nesting site being at the field station, so distinguishing these females allowed the difference in detection probability to be accounted for. Preliminary analysis suggested that detection probabilities were otherwise similar among sites.

2.3 | Modelling

We modelled growth, reproduction and survival simultaneously using OpenBUGS (Lunn, Spiegelhalter, Thomas, & Best, 2009; Spiegelhalter, Thomas, Best, & Lunn, 2014). The code is provided in Appendix S2. The Markov chain Monte Carlo (MCMC) estimation used in Bayesian updating software allows multiple data types to be modelled in an integrated framework while accounting for uncertainty in all parameters (Besbeas, Freeman, & Morgan, 2005; Kéry & Schaub, 2012). Using an integrated state-space framework allowed us to estimate whether individual random effects for growth rate affected size-specific survival and reproduction rates, and therefore whether trade-offs were occurring. It also allowed carapace lengths to be modelled as missing values in years without captures, meaning size-dependent survival probabilities could be calculated for each turtle each year. We also included annual variation in parameters as well as individual variation, and assumed that annual effects were consistent among individuals (hence trade-offs in annual growth, reproduction and survival rates will be reflected in relationships among individual random effects). Annual variation was expected due to changes in conditions, such as mean temperature (Rollinson et al., 2012) and predation events (Brooks, Brown, & Galbraith, 1991), and accounting for such environmental stochasticity is essential when estimating individual variation (Cam et al., 2016).

The growth model took the form

$$L_{ij} = a_i - (a_i - L_{ij-1}) \exp\left(\frac{-k_{ij}}{a_i}\right) + \varepsilon L_{ij} \quad (1)$$

where L_{ij} and L_{ij-1} are the carapace lengths for individual i in the current and previous year, a_i is her asymptotic length, k_{ij} is her growth rate for the past year and εL_{ij} is residual error. This is the standard von Bertalanffy model for recaptures (Fabens, 1965) modified to incorporate both individual variation (Armstrong & Brooks, 2013, 2014) and annual variation in growth parameters. A key feature of the modified model is that the original “ k ” parameter has been replaced by k_{ij}/a_i . In the original model the initial growth rate is actually the product of a and “ k ”, imposing a correlation between these parameters if they are allowed to vary among individuals. The modification eliminates this problem (Armstrong & Brooks, 2013).

This individual and temporal variation was modelled as

$$a_i = a_c + \mu a_i \quad (2)$$

and

$$\log(k_{ij}) = \log(k_c) + \mu k_i + \mu t k_j \quad (3)$$

where a_c and k_c are the average growth parameters for the population, μa_i and μk_i are individual random effects and $\mu t k_j$ is the annual random effect on k .

The reproduction model took the form

$$M_{ij} = \alpha M_c + \beta LM(L_{ij}) + \beta a M(\mu a_i) + \beta k M(\mu k_i) + \mu M_i + \mu t M_j + \varepsilon M_{ij} \quad (4)$$

where M_{ij} is the clutch mass for individual i in the current year, αM_c is the expected clutch of an average 24-cm female, βLM is the effect of additional length on the expected clutch mass, $\beta a M$ and $\beta k M$ are the effects of the female’s individual growth parameters, μM_i is her residual individual random effect, $\mu t M_j$ is the annual random effect and εM_{ij} is residual error.

We used a state-space formulation of the Cormack–Jolly–Seber model (Schofield, Barker, & MacKenzie, 2009) to estimate both survival and recapture probabilities. In this formulation the survival status of each individual is modelled as a series of missing values after it was last recorded unless it was found dead. The survival model took the form

$$\begin{aligned} \text{logit}(\varnothing_{ij}) = & \alpha \varnothing + \beta L \varnothing(L_{ij-1} - 24) + \beta a \varnothing(\mu a_i) + \beta k \varnothing(\mu k_i) \\ & + \beta M \varnothing(\mu M_i) + \mu \varnothing_i + \mu t \varnothing_j \end{aligned} \quad (5)$$

where \varnothing_{ij} is the probability of individual i surviving the past year, $\alpha \varnothing$ is the average annual survival probability of a 24-cm female, $\beta L \varnothing$ is the effect of additional length on survival probability, $\beta a \varnothing$, $\beta k \varnothing$ and $\beta M \varnothing$ are the effects of the female’s individual growth and reproductive output parameters, $\mu \varnothing_i$ is her residual individual random effect and $\mu t \varnothing_j$ is the annual random effect. Recapture probability was also modelled with a logit link, and included a distinction between Sasajewun and non-Sasajewun females as well as random annual variation.

We added additional code to simulate lifetime survival and reproduction histories of hypothetical females from the time they reached 24 cm. This allowed us to estimate how the observed individual

variation in growth parameters translates into lifetime reproductive success based on the parameters estimated from the data, assuming no senescence.

We used uninformative priors for all parameters. Priors for fixed effects were all normally distributed with mean 0, and priors for hyperparameters (standard deviations of random effects) were all uniformly distributed with a minimum of 0. The precisions varied depending on the scale of the effects (Appendix S2). We fitted the model by running three MCMC chains for 50,000 iterations after a burn-in of 20,000 iterations, checking for convergence using standard diagnostics (Kéry & Schaub, 2012).

3 | RESULTS

On average, a female reaching sexual maturity at 24 cm carapace length was estimated to reach an asymptotic size of 30.7 cm and to achieve 95% of this post-maturity growth within 100 years (Figure 1). However, growth trajectories varied greatly due to high levels of individual variation in both asymptotic size and growth rate (Table 1, Parameters 1–4). For example the size increase in the first 10 years after maturity was estimated to range 15-fold, from 0.4 to 5.9 cm (2.5th and 97.5th percentiles).

Clutch masses of turtles clearly increased as they grew, with an average female’s clutch mass estimated to increase from 244 to 505 g as she grew from 24 to 30.7 cm (Table 1, Parameters 7–8; Figure 2). Mean clutch size increased from 28.7 to 39.3 over the same size range. There was substantial individual variation in clutch masses, meaning some females had consistently large and others had consistently small clutches for their size (Table 1, Parameter 11; Figure 2). However, this individual variation was unrelated to the individual variation in growth parameters, as indicated by the 95% credible intervals for $\beta a M$ and $\beta k M$, which were both centred close to zero (Table 1, Parameters 9–10).

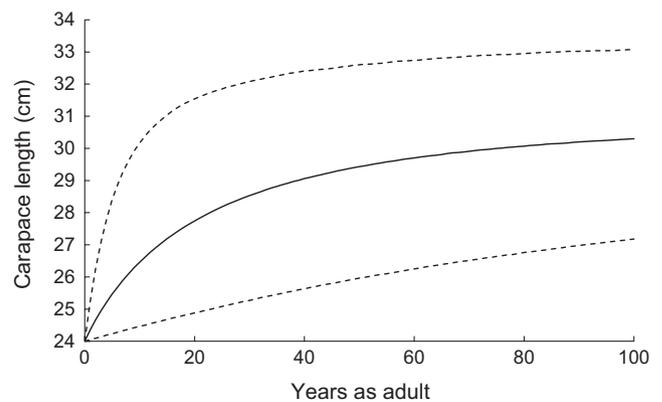


FIGURE 1 Variation in growth trajectories of adult female snapping turtles in Algonquin Park, Canada, estimated using a hierarchical version of the von Bertalanffy model. The solid line shows an average female, and the dotted curved lines show the range of variation among individuals (2.5th and 97.5th percentiles). Most females start nesting when their carapace reaches 24 cm

TABLE 1 Growth, reproduction and survival parameters for 298 adult female snapping turtles in Algonquin Park, Canada, based on 41 years of data on captures, carapace lengths and clutch masses

Parameter	Explanation	Notation	M	SD	95% Credible interval	
					Lower	Upper
1	Mean asymptotic carapace length	a_c	30.700	0.193	30.340	31.100
2	Log of mean growth rate (ak in original von Bertalanffy model)	$\log(k_c)$	0.232	0.116	-0.003	0.449
3	Among-individual variation in asymptotic carapace length	$SD(\mu a)$	1.247	0.155	0.953	1.553
4	Among-individual variation in log growth rate	$SD(\mu k)$	0.639	0.049	0.548	0.739
5	Among-year variation in log growth rate	$SD(\mu tk)$	0.581	0.102	0.411	0.808
6	Residual variation in carapace length	$SD(\epsilon L)$	0.189	0.004	0.181	0.196
7	Mean clutch mass for a 24-cm female	αM_c	244.000	9.975	224.400	263.500
8	Effect of 1 cm increase in carapace length on mean clutch mass	βLM	38.910	1.898	35.230	42.730
9	Effect of individual asymptotic size parameter on clutch mass	βaM	-1.187	3.872	-8.757	6.553
10	Effect of individual growth-rate parameter on clutch mass	βkM	-0.640	6.230	-13.020	11.500
11	Among-individual variation in clutch mass	$SD(\mu M)$	67.870	3.585	61.190	75.290
12	Among-year variation in clutch mass	$SD(\mu tM)$	18.980	2.773	14.280	25.080
13	Residual variation in clutch mass	$SD(\epsilon M)$	50.840	0.957	49.010	52.760
14	Logit of annual survival probability for a 24-cm female	$\alpha \emptyset$	2.582	0.376	1.891	3.363
15	Effect of 1 cm increase in carapace length on logit survival probability	$\beta L \emptyset$	0.137	0.058	0.020	0.251
16	Effect of individual asymptotic size parameter on logit survival probability	$\beta a \emptyset$	0.013	0.098	-0.176	0.207
17	Effect of individual growth-rate parameter on logit survival probability	$\beta k \emptyset$	0.052	0.180	-0.310	0.402
18	Effect of individual clutch-mass parameter on logit survival probability	$\beta M \emptyset$	0.001	0.002	-0.002	0.005
19	Among-year variation in logit survival probability	$SD(\mu y \emptyset)$	1.053	0.249	0.656	1.623
20	Logit of mean detection probability if last found at Sasajewun Lake	αP	1.340	0.149	1.046	1.632
21	Effect on logit detection probability of being found at another site	βP	-0.630	0.114	-0.854	-0.405
22	Among-year variation in logit detection probability	$SD(\mu y P)$	0.771	0.116	0.572	1.025

Parameters were estimated in OpenBUGS using a model integrating three components: (1) a modified version of the von Bertalanffy growth model incorporating individual variation in asymptotic size and growth parameters; (2) a reproductive output model incorporating individual variation in size-specific clutch mass; and (3) a mark-recapture model estimating size-specific survival probabilities. Reproductive output and survival probability are linked to the turtle's individual growth parameters, and survival probability is linked to the turtle's individual reproductive-output parameter. All models include random annual variation.

The estimated annual survival probability also changed significantly with size (Table 1, Parameter 15), increasing from 0.92 for a 24-cm female to 0.96 for a 30-cm female (Figure 3). There was no evidence of individual variation in survival probability, as the posterior distribution for $\mu \emptyset_i$ was concentrated near zero (see Kéry

& Schaub, 2012); consequently this parameter was removed from the model. Other than their effects on size, individual growth parameters had no apparent effects on survival, as shown by $\beta a \emptyset$ and $\beta k \emptyset$ having 95% credible intervals close to zero (Table 1, Parameters 16–17). Survival was also unrelated to individual variation in

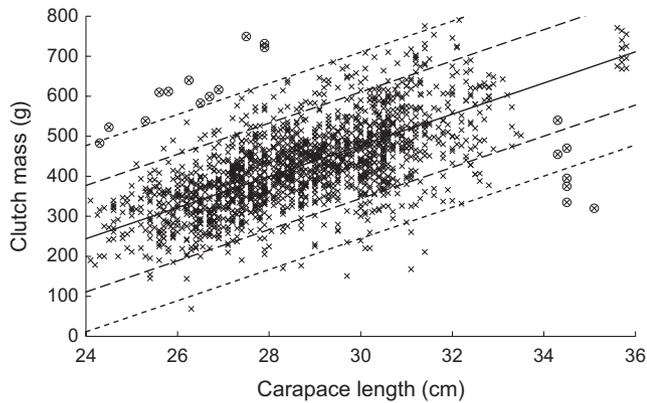


FIGURE 2 Clutch mass in relation to body size for snapping turtles in Algonquin Park, Canada. The crosses show masses of individual clutches, and the lines show a hierarchical general linear model fitted to the data. The solid line shows the estimated increase in clutch mass with growth in an average female. Long-dashed lines show the 95% limits for individual variation among females, and short-dashed lines show 95% prediction intervals accounting for residual error as well as individual variation. The circled crosses show the two females with the largest and smallest clutch masses per body size

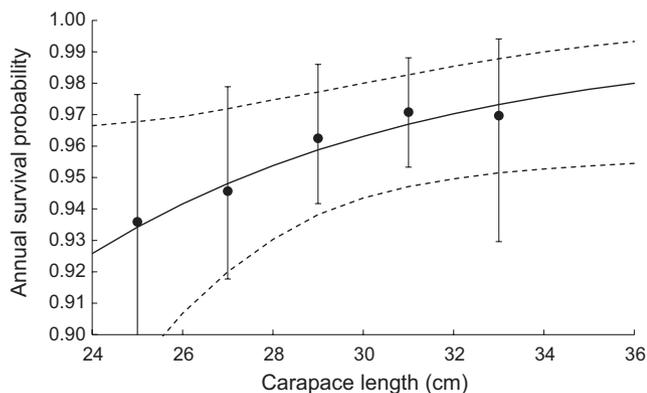


FIGURE 3 Annual survival probability in relation to body size for adult female snapping turtles in Algonquin Park, Canada. The curves show the logit-linear model fitted to the data, with the solid line showing the mean trend and the dotted lines showing the 95% credible intervals. Points show estimates from an alternative model where the relationship between survival and size is treated as a step function (size classes of 24–26, 26–28, 28–30, 30–32 and 32–34 cm), with vertical bars showing 95% credible intervals

reproductive output, as shown by the 95% credible interval for $\beta M\phi$ (Table 1, Parameter 18).

Due to the effects of size on both survival and reproduction, and the absence of trade-offs, individual variation in growth parameters appears to have major consequences on lifetime reproduction. Over the range of individual values estimated for growth parameters a_i and k_i , life expectancy after maturity was estimated to range from 16 to 33 years (Figure 4). The longest adult life expectancies (97.5th percentile) were predicted to be 68 years for slow-growing individuals and 158 years for fast-growing individuals. Over the same range of growth parameters, expected lifetime reproductive output was estimated to range from 4.2 kg of eggs to 17.6 kg of eggs (Figure 4). This four-fold range in reproductive

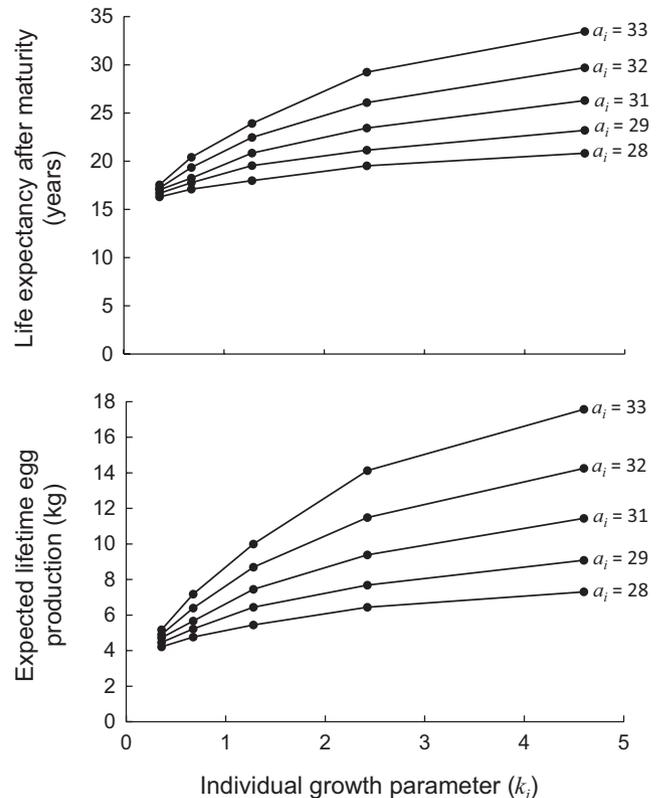


FIGURE 4 Effects of individual variation in growth parameters on post-maturity life expectancy and lifetime reproductive output of female snapping turtles in Algonquin Park, Canada, assuming sexual maturity at 24 cm carapace length. The ranges shown for a_i (asymptotic size) and k_i (growth rate) are the 2.5th and 97.5th percentiles for these parameters, and reflect the range of growth trajectories shown in Figure 1. The other black dots show to the estimated $M \pm SD$ for a_i and k_i , with means corresponding to the 50th percentiles and the SDs encapsulating the 15.9th and 84.1th percentiles

output assumes that females have similar size-specific reproduction rates. It increases to an eight-fold range when individual variation in size-specific reproduction (Figure 2) is accounted for.

Growth, clutch mass and survival all varied over time (Figure 5). However, annual variation in clutch mass was less pronounced than that of the other two rates when considered in relation to their means (Figure 5), and much lower than the variation among individual females (Table 1; Parameters 11–12). Although growth rates varied throughout the study, survival probability was normally fairly high but punctuated by three periods of low survival over the 41 years (Figure 5). Recapture probability also varied among years, being estimated to range from 0.46 to 0.95 for females nesting on Sasajewun Lake and from 0.31 to 0.90 for females nesting at other sites (2.5th and 97.5th percentiles).

4 | DISCUSSION

This study communicates four major findings (Figure 6). First, although adult female snapping turtles grow very slowly, there is great variation among individual females in growth trajectories, and this variation is

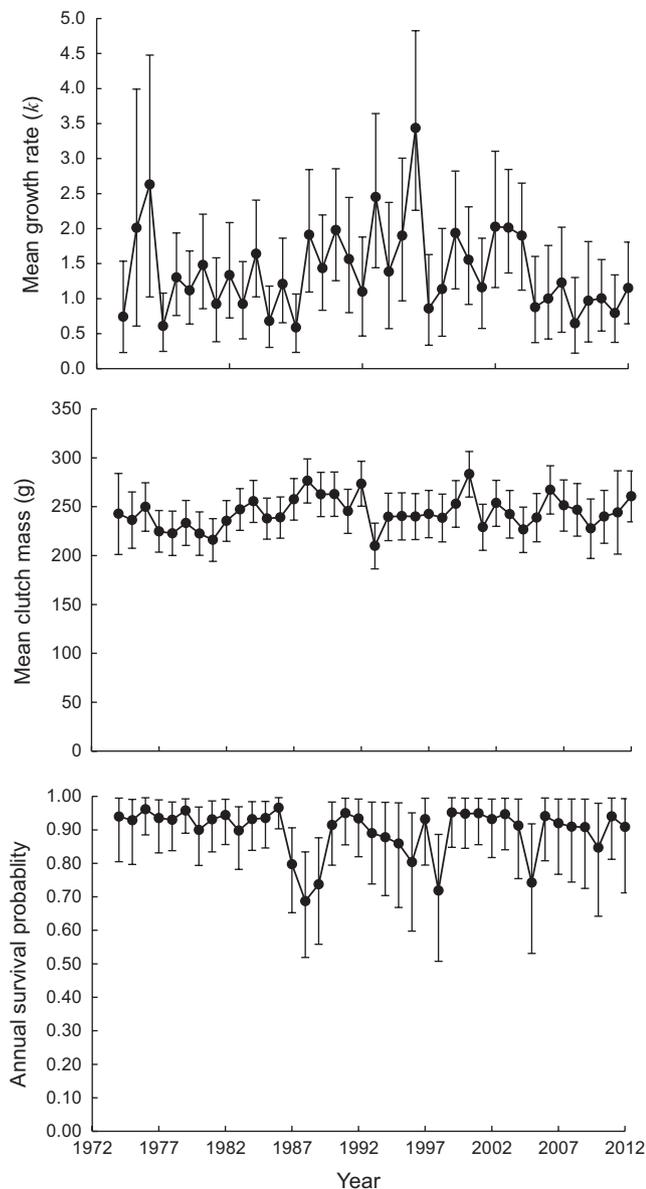


FIGURE 5 Annual variation in mean growth rate, mean clutch mass and annual survival probability of adult female snapping turtles in Algonquin Park, Canada. Estimated clutch masses and survival probabilities are for a 24-cm female. Vertical bars show 95% credible intervals

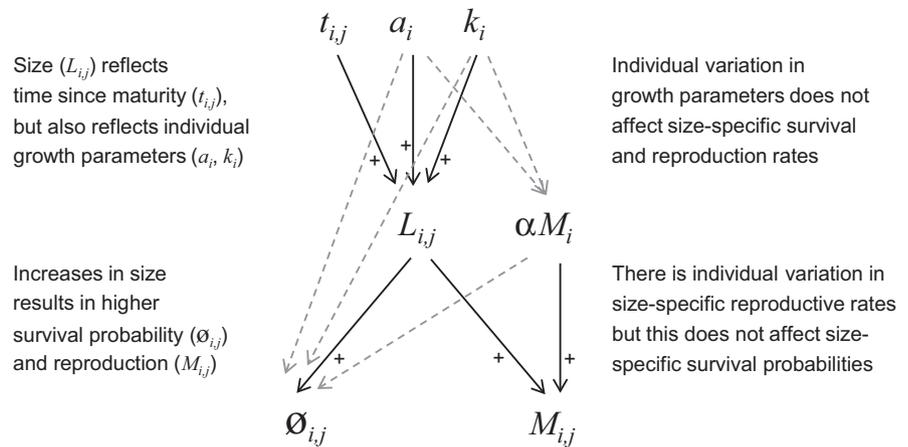
not accounted for by annual variation in environmental conditions. Second, increases in size through indeterminate growth result in significant increases in survival as well as in reproductive output. Third, there are no apparent trade-offs between rates of indeterminate growth and survival or reproduction, or between reproductive output and survival. Fourth, because of the absence of trade-offs, individual variation in growth has major consequences for lifetime reproductive success. These results contradict Congdon et al.'s (2013) conclusion that indeterminate growth was trivial to lifetime reproductive success of turtles, and illustrate the importance of accounting for individual variation in growth rates and using appropriate models to estimate its consequences. Below we frame these findings in the context of life-history theory and implications for population dynamics.

There are two general factors involved in the evolution of indeterminate growth, both of which likely play a role maintaining this trait in local snapping turtles. First, seasonality favours indeterminate growth, as energy should be diverted towards growth at times of year when offspring prospects are poor, provided that larger body size increases future fecundity (Ejsmond et al., 2010; Kozłowski, 2006). Indeed, snapping turtles in our study population are near their species' northern range limit, and inhabit a highly seasonal and time-constrained environment; in fact, many nests exhibit total failure for lack of sufficient thermal energy for embryos to develop and hatch, suggesting that eggs laid early in the season are more likely to be successful (Edge et al., 2017). Second, indeterminate growth tends to be favoured when life expectancy is relatively long (Ejsmond et al., 2010, 2015; Perrin et al., 1993). This is because capital invested in post-maturity growth, which will increase reproductive output later in life (McLaren, 1966), generally has little chance of increasing fitness when life expectancy is short. Snapping turtles may live well over 100 years (Armstrong & Brooks, 2014), so there is potential for indeterminate growth to be highly adaptive in this species.

The extreme longevity of turtles is partly attributable to their carapaces, which are expected to reduce extrinsic mortality. However, the ultimate explanation for this longevity may be their low and stochastic reproductive success, which is expected to drive the evolution of low annual reproductive effort coupled with protracted reproductive life spans (Schaffer, 1974). The clutch masses reported herein, for example, were 8.1% of the female's body mass on average, in comparison to a median of approximately 13% among oviparous squamates that produce one clutch per year (Mesquita et al., 2016; Scharf et al., 2015). The low but protracted reproductive output of turtles increases the probability of encountering conditions with high hatching and juvenile survival rates (Philippi & Seger, 1989; Schaffer, 1974). Furthermore, mature female turtles have high residual reproductive value (Congdon, Dunham, & Van loben sels, 1994; Cunnington & Brooks, 1996), such that adult survival should be prioritized over current reproduction, and growth is not expected to be prioritized unless it enhances survival and future reproduction rather than compromising it (Williams, 1966). This is consistent with the apparent absence of trade-off in snapping turtles (Table 1).

Our results are valuable in demonstrating that indeterminate growth improves future survival. The consistency of size at maturity in the population (Armstrong & Brooks, 2013) means that the size-related increases in survival are almost entirely attributable to indeterminate growth. It is also important to reiterate that our model accounted for the potential confounding effects of individual quality, often referred to as frailty (Cam et al., 2016) or selective appearance and disappearance (Zhang, Vedder, Becker, & Bouwhuis, 2015), so the observed correlation appears to reflect a true effect of size on survival. If such size-dependent survival is common in organisms with indeterminate growth, then it suggests a hitherto overlooked benefit of this trait. Indeed, theoretical models have been developed that incorporate indeterminate growth and allow size-dependent adult survival (Jørgensen & Fiksen, 2006; Taborsky et al., 2003), but to our knowledge these models have never been used to explore how this size-dependent survival affects model predictions. Our study argues for the inclusion of positive size-dependent survival into theoretical

FIGURE 6 Modelled relationships between growth, reproductive output and survival for adult female snapping turtles in Algonquin Park, Canada. Solid lines show effects whose 95% credible intervals did not include zero, whereas dotted lines show effects that were included in the model but had 95% credible intervals that included zero (Table 1)



models of indeterminate growth by providing direct empirical evidence in support of this assumption.

Given the many fitness advantages associated with indeterminate growth, we reiterate Ejsmond et al. (2015: E121) and underscore the question “Why does indeterminate growth so often not exist?” One contributing factor may be that many animal species are not long-lived enough to experience fitness benefits of indeterminate growth, especially if rate of indeterminate growth must be suppressed to avoid affecting current survival or reproductive success. A key feature of many life-history models is indeed that rapid growth reduces current fitness (Dmitriew, 2011; see also Lee, Monaghan, & Metcalfe, 2012a,b), and although we did not detect this trade-off in this study, this does not mean that fast-growing turtles would not experience reduced fitness if all else is held equal. Importantly, trade-offs can be obscured by individual variation in resource acquisition (van Noordwijk & de Jong, 1986).

The amount of individual variation in asymptotic size, growth rate and clutch mass is striking. Given the huge differences in lifetime reproduction associated with the individual variation in growth rates, this variation is probably largely due to environmental conditions experienced (Cressler, Bengtson, & Nelson, 2017), either during early life such as the incubation environment (Dufty, 2002) or resource availability in habitats used later (Reznick, Nunney, & Tessier, 2000). The snapping turtles in our study area differ in their local habitats within a complex system of lakes, rivers and swamps, although such differences are difficult to quantify. However, in our analysis we did control for the direct effects of current body size and year of observation on survival and reproduction, so the estimated individual variation is attributable to either environmental or genetic differences.

Regardless of the source of individual variation, it could potentially affect the dynamics of long-lived reptile populations. As illustrated by this study, populations may be made up on individuals that vary dramatically in their expected longevity and reproductive contributions due to variation in growth trajectories and reproductive output. Such variation is ignored in the stage-based matrix models traditionally applied to long-lived reptiles, where animals are divided into a small number of size-based stages and transition probabilities between stages assumed to be constant (Crouse, Crowder, & Caswell, 1987). Such models are currently being used to predict the long-term fates

of turtle populations threatened by harvesting, road mortality and pollution (Crawford, Maerz, Nibbelink, Buhlmann, & Norton, 2014; Folt, Jensen, Teare, & Rostal, 2016; Salice, Rowe, & Eisenreich, 2014; Zimmer-Shaffer, Briggler, & Millspaugh, 2014). Although it is important to exclude unnecessary detail from population models (Caswell, 1988; Starfield, 1997), it is possible that individual variation could significantly alter the dynamics of populations, although the empirical evidence for this is currently tentative (Cressler et al., 2017; Kendall & Fox, 2002; Lindberg, Sedinger, & Lebreton, 2013; Vindenes, Engen, & Sæther, 2008). It would be useful to determine whether an understanding of individual variation is essential for predicting the dynamics of long-lived reptile populations under threat. Most importantly, the growth and persistence of many populations could potentially be dependent on the best-performing individuals in terms of growth and reproductive output. If these individuals are products of particular environments in terms of development or long-term habitat use, then these will be the most important environments to protect.

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AUTHORS' CONTRIBUTIONS

R.J.B. led the Algonquin Park snapping turtle project from the outset and conceived the ideas for this paper in collaboration with D.P.A. M.G.K. has led the field work since 2009 and contributed to the ideas. N.R. made a major contribution to writing the paper and collecting the data. D.P.A. conceived the ideas for the paper in collaboration with R.J.B., conducted the analysis, wrote the first draft and made a minor contribution to the data collection.

DATA ACCESSIBILITY

The OpenBUGS code and input data are provided in Appendix S1. Data (in spreadsheet format) deposited in the Dryad Digital Repository <https://doi.org/10.5061/dryad.2j05h> (Armstrong, Keevil, Rollinson, & Brooks, 2017).

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