

Estimating ages of long-lived ectotherms from growth data

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1 *Abstract.* Age estimation is important for management of fisheries and wildlife
2 populations, but techniques such as growth ring counts are often impossible or unreliable. An
3 alternative is to estimate age from growth models using Bayesian inference. However,
4 individual variation in growth parameters needs to be incorporated into these models for them
5 to generate realistic prediction intervals. For long-lived ectotherms, it is also important that
6 models allow for changes in growth at sexual maturity, and that the growth models are
7 combined with prior distributions reflecting realistic age structures. We describe how a
8 hierarchical biphasic growth model fitted to a long-term data set of carapace length
9 measurements for North American snapping turtles was combined with prior age
10 distributions generated from survival estimates for the same population. The model was used
11 to generate individual posterior age distributions for turtles captured on two or more
12 occasions, and also for hypothetical turtles of any length that were measured only once.
13 Posterior age distributions for hypothetical turtles were very uncertain at any size due to
14 individual variation in growth parameters, and also very sensitive to the prior used. Using the
15 most realistic prior, the 95% prediction intervals for large hypothetical turtles (38 mm male
16 or 31 cm female) ranged from about 25-170 years with a median of about 70 years. Posterior
17 age distributions for turtles first measured when < 24 cm were insensitive to the choice of
18 prior, and estimation precision was usually greatly improved by individual growth
19 information obtained from recaptures. For example, the 95% prediction interval for a
20 hypothetical 10-cm turtle ranged from 2-14 years using the most realistic prior, whereas the
21 ages of small (< 24 cm) turtles that were recaptured at least once could usually be estimated
22 to within 1-3 years. Similar models could be applied to any data set where measurements and
23 survival data were collected from a large sample of marked individuals, and could potentially
24 be extended to incorporate data on other age indicators.

25 *Key words: Age estimation; Bayesian hierarchical modeling; biphasic growth; prior*
26 *distribution; snapping turtle; survival; von Bertalanffy model; WinBUGS.*

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28

INTRODUCTION

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30 Reliable age estimation is important for management of fisheries (Haddon et al. 2011)
31 and wildlife populations (Lyons et al. 2012). Models used to manage populations often rely
32 on animals being assigned to age classes (Caswell 2001; Williams et al. 2002). Age
33 estimates are also important for advocacy purposes when attempting to conserve long-lived
34 species, as long life spans intuitively illustrate the value of the animals and their potential
35 sensitivity to impacts (e.g. Congdon et al. 1993; Congdon et al. 1994; Towns et al. 2007).

36 Ages of animals can be known precisely if they can be marked a birth, but data are
37 rarely collecting over the lifetimes of long-lived species (Medica et al. 2012). There are
38 numerous methods for inferring age based on anatomical features, but these may be
39 impossible to use on live animals or may suffer from various degrees of unreliability (Eaton
40 and Link 2011; Lyons et al. 2012). For example, although growth ring counts have been used
41 to age turtles in numerous studies, evaluations of the technique have often shown it to be
42 unreliable, particular in mature animals (Wilson et al. 2003).

43 The alternative is to infer age from size based on fitted growth models. Such models
44 can be fitted to measurements taken from known-age animals, but can also be fitted to
45 successive measurements from recaptured animals of unknown age (Fabens 1965). Statistical
46 problems associated with fitting models to recapture data (Sainsbury 1980) have been
47 overcome by estimating individual variation in growth parameters, most recently using
48 Bayesian hierarchical modeling (Zhang et al. 2009). Individual variation is particularly
49 relevant to age estimation, because individuals of the same age can potentially vary greatly in

50 size. Hierarchical modeling allows this variation to be accounted for when estimating age
51 based on size data.

52 Eaton and Link (2011) used a Bayesian hierarchical version of the von Bertalanffy
53 (VB) growth model to infer age distributions for the central African dwarf crocodile
54 (*Osteolaemus tetraspis*) as a function of length. Their modeling approach combined
55 inferences from recapture data for unknown-age animals with data from known-age animals,
56 and generated posterior age distributions that accounted for individual variation in growth
57 parameters as well as uncertainty in parameter estimation. Here we use a similar approach to
58 obtain age distributions as a function of size from a long-term data set for North American
59 snapping turtles (*Chelydra serpentina*), but extend the approach in two ways.

60 First, we use a modification of the VB model that is biphasic as well as incorporating
61 individual variation in growth parameters. For animals with indeterminate growth,
62 reductions in growth are often expected at sexual maturity due to the demands of
63 reproduction, meaning different functions are needed to describe pre- and post-maturity
64 growth (Day and Taylor 1997). Age estimates from uniphasic growth models may therefore
65 be biased, particularly in long-lived ectotherms with slow maturity. That is, ages will
66 overestimated if based largely on data for mature animals, and underestimated if based
67 mainly on data for juveniles. However, methods have been developed for fitting Bayesian
68 hierarchical growth models that allow a change in growth rate at a critical age (Quince et al.
69 2008; Alós et al. 2010a,b) or critical size (Armstrong & Brooks 2013).

70 Second, we combine our growth model with prior information on the expected age
71 distribution. Although prior distributions must be specified in Bayesian inference,
72 “uninformative priors” are typically used in the absence of information (Link and Barker
73 2010). It is questionable, however, whether any prior distribution for age structure could be
74 truly uninformative. Eaton and Link (2011) used a uniform distribution as an uninformative

75 prior for dwarf crocodile age, meaning crocodiles were assumed to have equal probability of
76 being any age between zero and the maximum specified. This is an unrealistic assumption
77 for most populations, and would be typically result in ages being overestimated to some
78 extent. We nominated informative prior distributions for age based on independent survival
79 estimates from our population, and assessed the sensitivity of age inference to the prior for
80 turtles of different sizes.

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METHODS

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Species and Study Area

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86 North American snapping turtles are omnivorous predators and scavengers that live in
87 lakes, ponds and slow-moving rivers (Steyermark et al. 2008). Our data were collected in the
88 Wildlife Research Area (45°35'N, 78 30'W) of Algonquin Provincial Park, near the northern
89 edge of the species' range. Female snapping turtles in this area predictably start egg laying
90 when their straight-line carapace length reaches 24 cm (Armstrong and Brooks 2013). Mature
91 females lay one clutch annually, with these clutches buried in sandy soil or gravel near water
92 (Congdon et al. 2008). Brooks et al. (1997) tested the reliability of growth ring counts in
93 Algonquin Park snapping turtles by analyzing changes in counts between recaptures. They
94 found the counts to be an inaccurate indicator of the number of years between captures for
95 juveniles, and to be completely uninformative for mature turtles.

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Data Set

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100 The data set consisted of 1,996 straight-line carapace length measurements taken from
101 317 individually marked turtles from 1972-2005. Nesting females were usually found by
102 patrolling known nest areas daily from late May to early July, and were caught by hand once
103 their clutches were buried. This patrolling generally resulted in annual recaptures of mature
104 females. Mature males and juveniles were captured less regularly via trapping or
105 opportunistic encounters. Mature turtles can be sexed based on the length of pre-cloacal tail
106 section in relation to the length of the posterior lobe of the plastron (Ernst, 2008), but
107 juveniles cannot be sexed externally. Most (288) of the turtles in the data set were of known
108 sex but unknown age, but there were smaller samples of individuals of known sex and age
109 (5), unknown sex but known age (19), and unknown sex and age (5). Turtles of unknown
110 age were only included if they were measured at least twice. See Armstrong and Brooks
111 (2013) for further details.

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Growth Model

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115 Armstrong and Brooks (2013) fitted a baseline hierarchical VB model to the above
116 data set, then used the Deviance Information Criterion (DIC) to compare its predictive value
117 to that of alternative models. The baseline model was similar to the VB model fitted by
118 Eaton and Link (2011) in that it incorporated random individual variation as well as sex
119 differences in parameters, and integrated inferences from first measurements of known-aged
120 animals with those from recapture data. Minor differences include the use of a VB function
121 for first measurements as well as recaptures (Eaton and Link [2011] used a linear function for
122 the former, as the VB function was expected to approximate linearity up to the first

123 measurements), the substitution of k_i/a_i for k_i in the VB function (see Armstrong and Brooks
 124 [2013] for rationale), and the modeling of individual variation and random error as Normal
 125 rather than Gamma processes. Comparison to alternative models gave strong evidence that
 126 individual variation in parameters should be retained, and that sex-specific biphasic growth
 127 should be incorporated (Armstrong and Brooks 2013).

128 Under the best model, which received unambiguous support, the average growth of
 129 males and females is similar until they reach 24 cm, after which females change trajectory
 130 toward a smaller asymptotic length. For males the model takes the form

$$131 \quad L_{ij} = a_i(1 - \exp(-k_i/a_i(t_j - t_0))) + \varepsilon_{ij} \quad (1)$$

132 for first measurements, and

$$133 \quad L_{ij} = a_i(a_i - L_{i,j-1})(1 - \exp(-k_i/a_i(y_j - y_{j-1}))) + \varepsilon_{ij} \quad (2)$$

134 for recaptures, where L_{ij} is the expected length of individual i at measurement j , a_i is the
 135 individual's asymptotic length, k_i determines its initial growth rate, t_j is its age at
 136 measurement j , t_0 is the theoretical age at which its length would be zero, y is the year of
 137 measurement, and ε_{ij} is random error. Individual variation in parameters a_i and k_i was taken
 138 to be normally and log-normally distributed respectively, with means μ_a and μ_k and variances
 139 σ_a^2 and σ_k^2 , and ε_{ij} was taken to be normally distributed with mean 0 and variance σ_e^2 .

140 For females > 24 cm the model takes the form

$$141 \quad L_{ij} = a_i + \beta_a - (a_i + \beta_a - 24) \exp(-k_i/(a_i + \beta_a)(t_j - t'_i)) + \varepsilon_{ij}, \quad (3)$$

142 for first measurements, and

$$143 \quad L_{ij} = a_i + \beta_a - (a_i + \beta_a - 24) \exp(-k_i/(a_i + \beta_a)(y_j - y'_i)) + \varepsilon_{ij}, \quad (4)$$

144 for recaptures, where β_a is the change in the asymptotic size parameter, and t' and y' are age
 145 and time at which 24 cm was reached. The values of t'_i and y'_i are estimated as part of the
 146 modeling, with their expected values given by

$$147 \quad t'_i = \ln(1 - 24/a_i)(a_i/k_i) + t_0 \quad (5)$$

148 and

$$149 \quad y'_i = \ln[(a_i - 24)/(a_i - L_{i,j-1})](a_i/k_i) + y_{j-1}. \quad (6)$$

150 Consequently, in an individual MCMC iteration a recaptured female's length at measurement
151 j could be predicted by Equation 2, Equation 4, or a combination of the two (see WinBUGS
152 code in Supplement). The model can be used to generate probability distributions for
153 carapace length as a function of age and sex (Armstrong and Brooks 2013, Fig. 2).

154

155 *Age Estimation*

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157 From Bayes' theorem (Link and Barker 2010), the probability of an individual being a
158 particular age (z) based on its length is

$$159 \quad \Pr(t_z | L_{ij}) = \frac{\Pr(L_{ij} | t_z) \times \Pr(t_z)}{\sum_{x=1}^{Max} \Pr(L_{ij} | t_x) \times \Pr(t_x)} \quad (6)$$

160 where $\Pr(L_{ij} | t_z)$ is the likelihood (the probability of the individual being that length at age z
161 based on the model), and $\Pr(t_z)$ is the prior probability of being that age. The discrete form of
162 the theorem is appropriate for our scenario because turtles are measured at about the same
163 time of year, so their ages fall into whole numbers of years. Because the model generates
164 individual distributions for parameters a_i and k_i , it is possible to generate individual posterior
165 age distributions that exploit the information gained from repeated measurements.

166 Alternatively, posterior distributions can be generated for hypothetical individuals of any
167 length by sampling a_i and k_i from distributions incorporating the range of individual
168 variation. Eaton and Link (2011) only attempted the latter, as their data set contained only
169 five observations of animals captured more than twice. In contrast, most of the 317 turtles in
170 our data set were captured more than twice, and 155 were captured at least 5 times. We

171 therefore used the model above to estimate the age at initial capture for all unknown-age
172 turtles in our data set as well as ages of hypothetical males and females of various lengths.

173 Ages are estimated by inserting unknown ages in Equations 1 and 3, and modeling
174 these unknown ages as missing values (Link and Barker 2010). However, the “cut” function
175 in WinBUGS (Spiegelhalter et al. 2007) is applied to all parameters in the relevant lines of
176 code (Supplement) to prevent the parameter estimation being influenced. Bayes’ theorem is
177 implemented by assigning a prior distribution to each unknown age. It is reasonable to
178 assume that survival probability is constant with respect to size and age among mature
179 snapping turtles (Brooks et al. 1988), meaning the age distribution among these large animals
180 is expected to approximate the negative binomial distribution

$$181 \quad t \sim NB(1, 1-S)$$

182 where S is the annual survival probability. This probability was estimated to be 0.966 for
183 large (> 24 cm) snapping turtles in Algonquin Park (Galbraith and Brooks 1987), whereas
184 annual survival of smaller turtles was estimated to be 0.754 (Brooks et al. 1988).

185 We therefore generated separate age estimates using negative binomial priors based
186 on these two survival probabilities, and compared these to assess the sensitivity to the choice
187 of prior. Although it would be desirable to construct an overall age distribution based on
188 both survival probabilities, this would require using our growth model to infer age, meaning
189 the prior would not be based on independent data. We compared the estimates generated
190 using the two negative binomial priors to those generated using the uniform prior

$$191 \quad t \sim U(0, 500)$$

192 which was expected to give unrealistically high age estimates for at least the larger animals.

193 We added the lines of code generating age estimates to the WinBUGS code used to fit
194 the growth model (Supplement), and ran the whole model simultaneously to allow covariance
195 in parameter estimation to be accounted for in age estimation. We used uninformative priors

196 for all parameters and hyperparameters in the growth model (Armstrong and Brooks 2013),
197 and generated posterior distributions from 500,000 MCMC iterations after a burn-in of
198 10,000 iterations.

199

200

RESULTS

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202 Asymptotic carapace length was estimated to have a median value of 38.2 cm in
203 males, and to fall between 35.6 and 40.8 cm in 95% of individuals. For females the estimated
204 median was 30.9, with 95% of individuals falling between 28.3 and 33.5 cm. The largest
205 individuals recorded were 40.7 cm and 35.7 cm for males and females respectively.

206 If a negative binomial prior with 0.966 annual survival is used ($NB[1,0.034]$), as is
207 most realistic for large turtles, the median predicted age of a hypothetical 38 cm male is 73
208 years (95% prediction interval 27-173) and the median predicted age of a hypothetical 31 cm
209 female is 65 years (23-162) (Fig. 1). These rise to 299 years (76-490) and 288 years (63-489)
210 when the uniform prior is used ($U[0,500]$), and fall to 19 (8-37) and 17 (7-34) when a
211 negative binomial prior based on the juvenile survival rate is used ($NB[1,0.246]$). A
212 hypothetical 24 cm turtle (the size when females begin egg laying) of either sex has a median
213 predicted age of 25 years (8-70) when $NB(1, 0.034)$ is used as the prior. This rises to 36
214 years (9-126) when $U(0,500)$ is used, and falls to 11 years (6-24) when $NB(1, 0.246)$ is used.
215 A hypothetical 10 cm turtle has a median predicted age of 6 years (2-14) under the most
216 realistic prior of $NB(1,0.246)$. This rises to 10 years (3-28) using $NB(1,0.034)$ and 11 years
217 (3-37) using $U(0,500)$.

218 Posterior age distributions for real turtles (Fig. 2) were quite different from those for
219 hypothetical turtles, with the degree of difference depending on the prior used and the size of
220 the turtle. The credible intervals for ages of large turtles corresponded fairly closely to the

221 prediction intervals for hypothetical turtles when the uniform prior was used, but were high in
222 relation to the prediction intervals for hypothetical turtles when negative binomial priors were
223 used. For example, when $NB(1,0.034)$ was used as the prior, the estimates for the six males
224 near 38 cm (37-39) averaged 172 years, compared to the median 73 years for a hypothetical
225 38-cm male, and the estimates for the 32 females near 31 cm (30-32) averaged 127 years,
226 compared to the median 65 years for a hypothetical 31-cm female. The credible intervals for
227 ages of small turtles fitted the predicted age distributions for hypothetical turtles when
228 $NB(1,0.256)$ was used as the prior, but were lower and much tighter than the distributions for
229 hypothetical turtles when the other priors were used.

230 The choice of prior had less influence on age estimates for real turtles than those for
231 hypothetical turtles (Fig. 3), as is to be expected given that the former exploit additional data
232 on individual-specific growth parameters. The influence of the prior on individual age
233 estimates was greatest for large turtles, and had negligible effect for turtles first measured
234 when < 24 cm (Fig. 3). Among large turtles, the influence of the prior was highest for turtles
235 estimated to be atypically old for their size (Fig. 2). The influence of the prior was unrelated
236 to the number of captures, but depended on the interval between the first and last capture (i.e.
237 had greater influence if this interval was short).

238 Using age estimates for individual turtles, it is possible to infer individual growth
239 histories in relation to age (Fig. 4). However, such histories are hypotheses that are highly
240 sensitive to estimation uncertainty, particular among the larger turtles.

241

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DISCUSSION

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245 Our results illustrate that it is possible to combine a hierarchical biphasic growth
246 model with informative priors to obtain posterior age distributions as a function of size, either
247 for hypothetical individuals measured once or for recaptured individuals with two or more
248 measurements. However, the results also illustrate the inherent uncertainty involved in
249 attempting to infer age from size, mainly due to individual variation in growth. Uncertainty
250 in parameter estimation and model selection will also be important in many cases. However,
251 the large sample sizes for our case study meant that the standard errors for mean parameter
252 values were quite small in relation to the estimated individual variation, and the choice of
253 model was also unambiguous (Armstrong and Brooks 2013).

254 Our results support the belief of many herpetologists (e.g. Carr and Goodman 1970;
255 Halliday and Verrell 1988; Congdon et al. 2001) that size is weakly related to age. Congdon
256 et al. (2001) state that the relationship between size and age may be strong in juveniles,
257 weaker in adults, and become weakest or absent in the oldest individuals. This trend will
258 occur in any species where animals approach an asymptotic size that varies among
259 individuals, as the effect of the individual variation will progressively overwhelm the effect
260 of age as animals get larger. Our results suggest there is great uncertainty in age estimates
261 even for small turtles if they are only captured once. For example, although the median age
262 prediction for a 10-cm juvenile is more than twice that of a 5-cm juvenile, there is huge
263 overlap in the prediction intervals, and these intervals even overlap with those for mature (>
264 24 cm) individuals. However, there was generally much tighter estimation for juveniles that
265 were recaptured. The initial ages of these animals could be estimated to within 1-3 years as
266 long as they had grown at least 3 cm between the first and last capture.

267 Our results also show the importance of choosing appropriate priors and assessing
268 sensitivity to the choice of prior. Eaton and Link (2011) compared uniform priors with
269 different maxima, and concluded that the lower limits of prediction intervals were robust to
270 the choice of prior. Although we also found lower limits to be less affected than medians or
271 upper limits, even the lower limits differed between the uniform and negative binomial
272 priors, and between the two different negative binomial priors reflecting adult versus juvenile
273 survival rates. We did find that posterior distributions generated using the two negative
274 binomial priors were identical for recaptured turtles first measured when < 24 cm. We
275 therefore suggest that the prior based on the adult survival rate [$NB(1,034)$] is appropriate for
276 all recaptured turtles. The appropriate prior for age estimates of hypothetical turtles is less
277 straight forward because the posterior distribution is sensitive to the prior at all sizes.
278 However, reasonable inferences can probably be made by focusing on $NB(1,034)$ for large
279 turtles and $NB(1,0.256)$ for small turtles, and the combination of the two for intermediate
280 sizes. The ideal prior would be the expected overall age distribution based on age-specific
281 survival and fecundity estimates (Schwartz and Runge 2009), but because ages of most turtles
282 are unknown in our study population, it is impossible to obtain these estimates independently
283 of the growth model.

284 Although size-based age estimation is particularly difficult for large turtles, this is
285 where the information can have most impact, both because it is impossible to age old turtles
286 from growth rings and because age estimates for old animals are valuable for advocacy. The
287 North American snapping turtle is a good example of a species needing such advocacy, as
288 their populations are subject to road mortality, harvesting, and persecution (Brooks et al.
289 1988; Congdon et al. 1994). In Ontario, despite being classified as a species at risk in the
290 province, snapping turtles are still subject to a harvest that is almost certainly unsustainable.
291 Information on the long life spans and slow growth of these animals is critical for

292 highlighting their long-term vulnerability to impacts, and the posterior distributions reported
293 in this paper have already been used for this purpose (Armstrong 2009).

294 The prediction intervals for hypothetical turtles with $NB(1,0.034)$ as prior probably
295 give a realistic guide to the ages of large turtles. That is, the largest male and female
296 snapping turtles in our population are probably 30-190 years old with a best estimate of about
297 80. Ten of the recaptured turtles had median age estimates > 190 years, but the
298 credible intervals all ranged < 190 except for one extremely large (35.7 cm) female that
299 showed no detectable growth over 14 years. In addition, an underlying assumption of these
300 estimates is that the individual variation in growth detected during the study can be
301 extrapolated back throughout the turtles' lives. This assumption may be questionable when
302 the age estimates are many times greater than the duration of the study. Even 190 years may
303 seem an implausibly long life, but it is important to keep in mind that turtles are particularly
304 long-lived animals (Shine and Iverson 1995), and that the study population was at the
305 northern edge of its range where the animals are only active for about 5 months of the year.

306 Future attempts to estimate age from size must continue to account for individual
307 variation in growth parameters, and for long-lived ectotherms should also account for
308 biphasic growth and use appropriate priors for expected age distributions. As noted by Eaton
309 and Link (2011), Bayesian hierarchical modeling frameworks facilitate flexible model
310 structures allowing for individual variation, but also accommodate multi-model inference and
311 assimilation of independent data sets into a single framework. Therefore, an obvious step for
312 advancing size-based aging is to assimilate the data with those from other techniques such as
313 growth ring counts. Given that there are many different methods for aging animals but most
314 of them are problematic, the ideal approach will be to incorporate all relevant data for a
315 species into a unified framework that fully accounts for the error associated with each
316 technique.

317

318

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327

328

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SUPPLEMENT

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416 WinBUGS code for estimating ages of North American snapping turtles from growth

417 data (*Ecological Archives* xxxx-xxx-xx).

FIG. 1. Posterior age distributions for hypothetical snapping turtles of different sizes. Open circles show medians for large (> 24 cm) females, and filled circles show medians for large males or small turtles of either sex. Error bars show 95% prediction intervals. Likelihoods were based on a growth model fitted to data collected from 317 turtles over 34 years, using three different prior distributions: a) a uniform age distribution with maximum age of 500 years; b) an age distribution that would be found in a stable population with annual survival of 0.966 (typical of turtles > 20 cm), and c) an age distribution that would be found in a stable population with annual survival of 0.754 (average annual survival of smaller turtles). Note the different scales on the y-axis.

FIG. 2. Posterior distributions for age at first capture for 293 snapping turtles of unknown age that were captured on at least two occasions. Likelihoods are based on the same growth model as for Fig. 1, but with individual distributions for growth parameters. Open circles show females, and filled circles show males or small (< 20 cm) turtles of unknown sex. Other conventions are for Fig. 1.

FIG. 3. Effect of prior on posterior age distributions for (a) hypothetical turtles captured on one occasion, and (b) real turtles captured on 2-25 occasions. Values show the proportionate reduction in median age when the prior was shifted from $NB(1,0.034)$ to $NB(1,0.256)$ (see Figures 1-2). Open circles show females, and filled circles show males or small (< 20 cm) turtles of unknown sex.

FIG. 4. Reconstructed growth curves for snapping turtles of unknown age. The age of each turtle at first capture was set to the median of the posterior distribution generated using

$NB(1,0.034)$ as the prior distribution (Fig. 2b). Gray lines show females, black lines show males, and dashed lines show turtles of unknown sex.

FIGURE 1

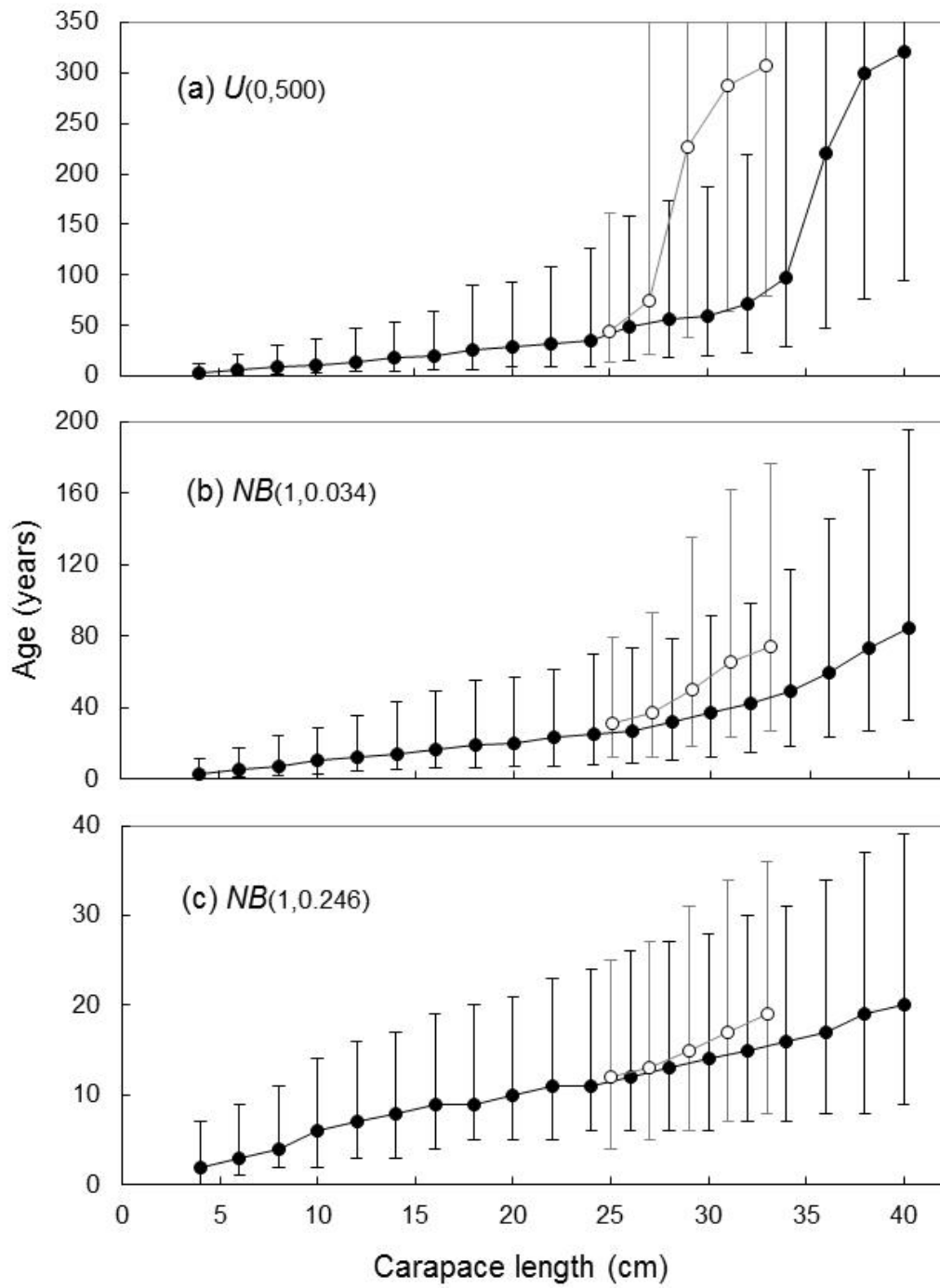


FIGURE 2

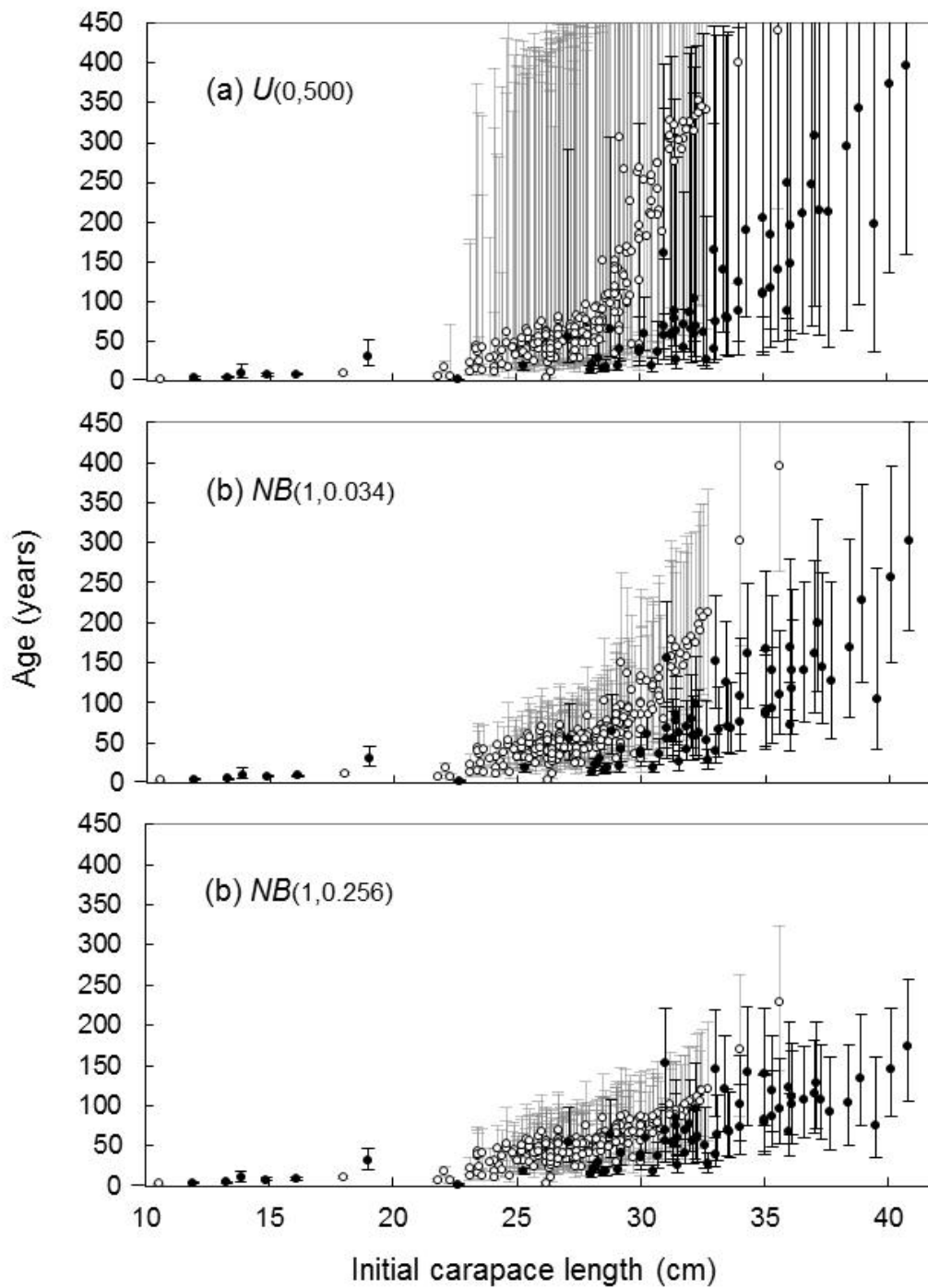


FIGURE 3

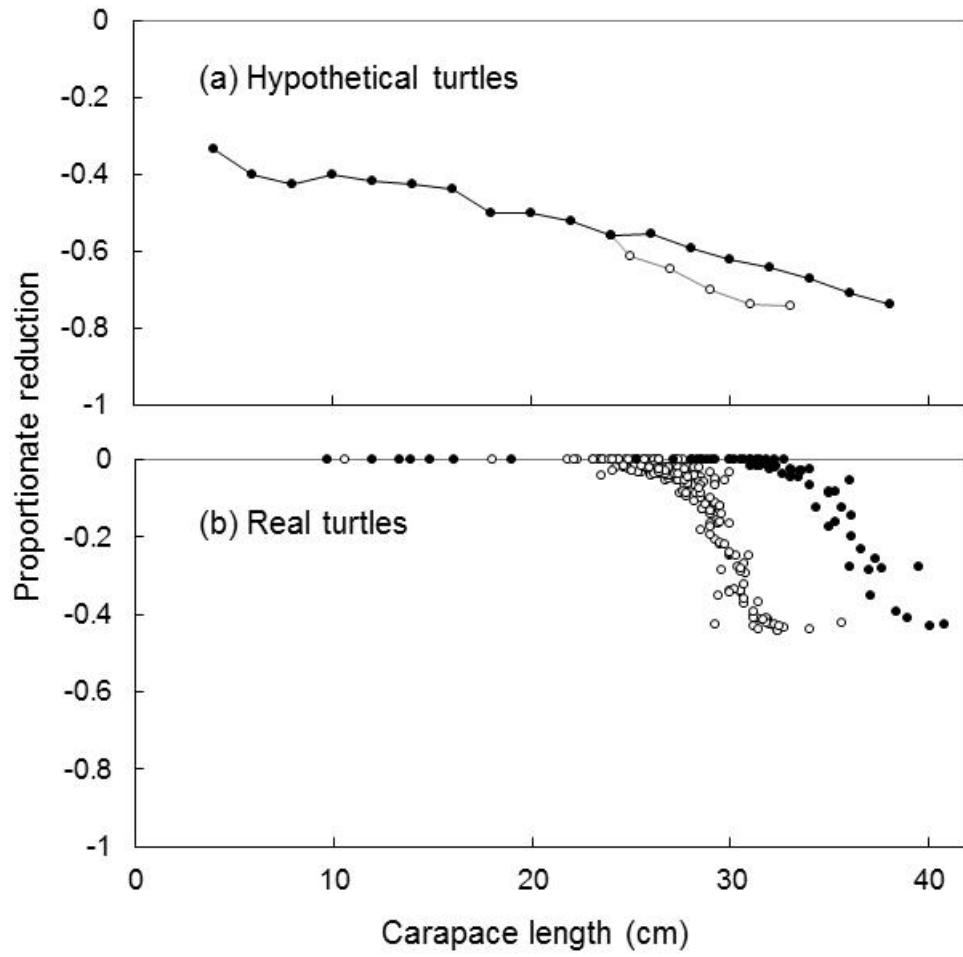


FIGURE 4

