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Growth patterns of two widely distributed freshwater turtles and a comparison of common methods used to estimate age

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Abstract

Turtles are long lived and demographic models requiring estimates of age, growth, fecundity and survival are central for management. Most studies that estimate age and growth of freshwater turtles use annuli as an index of age without estimating its error and very few studies that use growth models include many juveniles, where growth is often large and variable. In this paper, I compare the reliability of growth annuli and common models in determining age and growth of two widely distributed turtles in Australia. Most turtles are carnivorous during the juvenile stage but many species shift to a lower-quality omnivorous diet prior to maturing. Patterns of growth are often characterised by this dietary shift and I compared the growth of a common omnivorous turtle (Emydura macquarii) and a vulnerable sympatric species that is an obligate carnivore (Chelodina expansa). Mark-recapture programs were established in three lagoons on the Murray River. In total, 1218 hatchling E. macquarii were released into two of the lagoons and growth annuli were found to be unreliable in estimating their age by Year 2. The von Bertalanffy and logistic growth models can reliably estimate age of both male and female E. macquarii and C. expansa respectively. Growth is extremely rapid during the juvenile stage of E. macquarii, but is highly variable in C. expansa, with rapid growth occurring only beyond three years of age. Hence growth models fail to predict age when juveniles are excluded from the analyses. Female E. macquarii delay maturity until 9-12 years of age because clutch size is positively related to body size and they can produce only one large clutch per year. Female C. expansa mature later (at ~14 years) than female E. macquarii and both species are sexually dimorphic, as males mature earlier at smaller sizes than females. Common growth models describe the growth of two widely distributed freshwater turtles, but different patterns of growth and age at maturity relate to quality of diet and reproduction.

Introduction

Basic demographic data for many Australian freshwater turtles are scarce and often confined to anecdotal evidence from captive-reared animals (Cann 1998). Understanding the relationship between body size and age is important for the development of demographic models. In most freshwater turtles, body size can have a large influence on parameters such as fecundity because clutch size and frequency are positively related to body size (Iverson 1991; Van Loben Sels *et al.* 1997; Zuffi *et al.* 1999). Similarly, survivorship is positively related to body size, with nest mortality greater than 80% each year in most freshwater species and adult survivorship close to 100% per year (Spencer 2001). Many demographic models of reptiles are based on size rather than age (Crouse 1999), yet these models still require a measure of the growth rate of a species because the components of the model rely on the amount of time spent in each size class (Cochran and Ellner 1992). Age and size at maturity represent an important transitional stage in demographic models, and most studies on freshwater turtles have estimated age at maturity specifically using species that display annuli on epidermal scutes as indicators of annual growth (Wilbur 1975; Iverson 1991). Unless previously evaluated, growth annuli can be

unreliable determinants of age, particularly as the individual ages (Galbraith and Brooks 1987; Cox *et al.* 1991; Congdon *et al.* 2001). Two pioneering studies of Australian freshwater turtles (Parmenter 1976; Chessman 1978) used growth annuli to determine age without evaluating their accuracy, and their estimates of age at maturity for the three most widely distributed freshwater turtles in Australia (*Emydura macquarii, Chelodina longicollis* and *Chelodina expansa*) may be inaccurate.

Australian freshwater turtles generally conform to the typical reptilian growth pattern (Bury 1979) of rapid juvenile growth followed by a decline in growth rates as individuals reach maturity; growth of adult turtles is often irregular and indeterminate (Parmenter 1976; Chessman 1978; Georges 1982; Kennett and Georges 1990; Kennett 1996). However, recent theory suggests that growth patterns may be closely associated with diet (Hailey and Coulsen 1999). The method developed by Fabens (1965) to fit recapture growth data to the von Bertalanffy model and derive age–size curves describes the growth of many freshwater turtles (Jones and Hartfield 1995; Lindeman 1999), including many Australian species (Chessman 1978; Georges 1982; Kennett 1996). However, growth models, and thus estimates of age, are severely distorted if growth data from all size classes are not included in the analyses. Juvenile turtles are cryptic and difficult to capture in many populations; however, the age–growth trajectory of a species is primarily determined by juvenile growth, which is often large and variable (Shine and Iverson 1995). Hence, models that describe the growth of adult populations are redundant and estimates of age at maturity of many species may be erroneous because too few juveniles were included in the analyses.

The three most widely distributed freshwater turtles in Australia inhabit the Murray-Darling system in south-eastern Australia (Cann 1998). All three species (suborder: Pleurodira) belong to the Chelidae, which is the dominant freshwater chelonian family in Australia. In this paper, I compare the reliability of annuli and common models in determining age at maturity and the growth trajectory of two of these species. I also compare the growth of a common omnivorous turtle (Emydura macquarii) and a vulnerable sympatric species that is an obligate carnivore (Chelodina expansa). The Murray short-necked turtle, Emydura macquarii, is currently recognised as a widespread species inhabiting the Murray-Darling drainage system, west of the Great Dividing Range, and with several forms distributed throughout eastern-flowing rivers of coastal New South Wales and Queensland (Cann 1998). Emydura macquarii is omnivorous (Spencer et al. 1998) and suffers high nest mortality on the Murray River (Thompson 1983; Spencer 2002). The broad-shelled turtle, Chelodina expansa, is the largest Australian freshwater chelid and is considered rare and vulnerable (NRE 1999); however, this may reflect its secretive nature and difficulty of capture, rather than its true conservation status. Nevertheless, basic demographic or life-history data for this species are not common. C. expansa is an obligate carnivore, primarily consuming a live prey of fish and crustaceans (Cann 1998).

Materials and Methods

Growth

Study sites were located in the upper Murray River of south-eastern Australia. Three lagoons were selected to evaluate growth in the Albury region of south-eastern Australia (36°08'S, 146°96'E). Hawksview and Snowdon's lagoons are located 12 km east of Albury below Lake Hume, on either sides of the river. The third lagoon, Bankview, is located 20 km west of Albury. A lagoon connected to Lake Mulwala (36°02'S, 146°00'E) and a sheltered bay within the lake were used to evaluate reproductive parameters.

Both species were predominantly captured in hoop traps with a trap entrance in an inward rectangular funnel (300 mm wide and 120 mm deep). Traps were baited predominantly with ox liver and placed into

Growth of freshwater turtles

bait cages in the centre of the trap. Trapping was carried out for 10–18 days each month within the lagoons between September and March of each year from 1996 to 1999. Traps were set near Mulwala throughout October and November 1996–99. Six traps within each lagoon were stretched between two 1.5-m-long wooden stakes in waist-deep water (1.2 m). The back ring of each trap was partially emerged to allow captured turtles within the traps to breathe. Traps were set 10 m apart within each lagoon and were checked twice daily (at 08:00 and 18:00 hours). All captured turtles were removed and traps were reset with fresh bait.

Each captured turtle was sexed (Cann 1998) and weighed to the nearest 25 g using a 10-kg spring balance. Smaller turtles (<500 g) were weighed to the nearest 10 g using a 1-kg spring balance. Curved and straight carapace (CL) and plastron (PL) lengths were measured to the nearest 1 mm with a tape measure and callipers. The vertical distance between the top of the carapace and the plastron was measured with callipers. Each turtle was furnished with a unique combination of notches in the marginal scutes and underlying bone (Thompson 1982) with an angle grinder (Ryobi 10 mm) or bastard file. Marked turtles were released within 12 h at their point of capture. The number of annuli present on the left pectoral plate (Sexton 1959) was initially used to estimate age, but it became clear that annuli were difficult to see, even in small turtles. Gravid female E. macquarii captured in the Mulwala region were induced to drop their eggs. Female turtles were held vertically and palpated by placing both index and middle fingers between the left and right back leg pits to locate oviductal eggs. Gravid female turtles were given a subcutaneous intramuscular injection of 2 mL of oxytocin (Syntocin, Ilium™) in the thigh (Ewert and Legler 1978) and placed in enclosed cardboard containers. Most females began to oviposit within 30 min. Eggs were marked using an HB graphite pencil and placed into a mixture of two parts vermiculite to one part water by weight in foam containers (1000 mm \times 400 mm \times 350 mm). The female's number and the egg number (in order from oviposition) were marked on each egg. All eggs were transported to the University of Sydney within 24 h of collection. An even number of eggs from each clutch were randomly incubated at 25°C (cool nest) or 30°C (hot nest) in vermiculite approximating -370 kPa on the basis of similar vermiculite calibrated using thermocouple psychrometry and a Wescon C52 sample chamber connected to a Wescon KR33T micro-voltmeter. Distilled water was used to compensate for small water losses from the incubation boxes. Hatchlings were toe-clipped with unique combinations that distinguished between clutch and temperature treatments. Only one toe from each foot was clipped (webbing rarely disrupted) and no more than three feet were clipped on each individual. Hatchlings were weighed and their plastron and carapace lengths and widths measured before release. In total, 1218 hatchling turtles were marked and released at the beginning of 1997 and 1998 into Hawksview and Bankview lagoons in the Albury region and I attempted to recapture them over the total trapping period, as well as during a two-week period in February 2001. Each hatchling's carapace and plastron length were measured. Recaptured turtles were remeasured, and the number of growth rings present on the left pectoral plate of the plastron was recorded.

I plotted the plastron lengths of all *E. macquarii* captured in each lagoon during one season (September–April) and determined growth rate (incremental changes in plastron length) if recaptured in the following season, i.e. an index of one growth year. *E. macquarii* hibernates in the Murray River and grows very little over this period (Chessman 1978). I imposed a minimum growth interval of 274 days and a maximum of 427 days to ensure that only one growth period of each turtle was represented. Each turtle's growth was represented once for the analysis, i.e. if turtles were captured in multiple trapping seasons, the growth between the first two seasons was included in the analysis. Adult male and female turtles were analysed separately, but juveniles could not be easily sexed so I assumed that juvenile turtles of both sexes grew at similar rates. From recapturing turtles of unknown age and recapturing the hatchlings released in 1997 and 1998, I determined the relationship between size and growth rate for *E. macquarii*. Regression analyses between plastron length (PL) and the natural log of growth rate (GR) were performed to determine the strength of the relationship. I applied the relationship between age and plastron length is based on known-age hatchling and juvenile growth and the growth of recaptured adult and juvenile turtles.

I tested the growth pattern of both *E. macquarii* and *C. expansa* against common growth models. The von Bertalanffy and logistic models are asymptotic models that describe growth rate as a function of size (Fabens 1965; Schoener and Schoener 1978). The general form of the von Bertalanffy equation is given in the form

$L = a(1 - be^{-kt})$ Equation 1

where L = plastron length (mm), a = asymptotic length, e = base of natural logarithms, b = related to hatchling length, where b = (1 - h)/a (h = hatchling length), k = intrinsic growth rate, and t = is age

Fabens (1965) derived the growth-interval equation of the von Bertalanffy model,

$$L_2 = \mathbf{a} - (\mathbf{a} - L_1) \, \mathbf{e}^{-\mathbf{k} \, (dt)} \qquad \qquad \text{Equation } 2$$

where L_1 is plastron length at first capture, and L_2 is plastron length at recapture, and dt is time in years between capture dates. Growth data of turtles captured one or more trapping season apart were included in the model. Growth trajectories are estimated from plastron lengths of recaptures using non-linear regression of the interval equation to estimate the parameters a (asymptotic size) and k (growth coefficient). The parameter b in Equation 1 (a constant derived from hatchling and asymptotic lengths: Dunham 1978; Schoener and Schoener 1978; James 1991) is calculated using the estimated values of a and k. Mean hatchling plastron length was determined from the 1218 *E. macquarii* released during 1997 and 1998. A hatchling plastron length of 38 mm was used for *C. expansa* (Booth 1998).

The general form of the logistic equation (Schoener and Schoener 1978) is:

$$L = a/(1 + be^{-kt})$$
 Equation 3

and the logistic growth interval equation for recapture data is:

$$L_2 = aL_1/(L_1 + (a - L_1)e^{-k(dt)})$$
 Equation 4

The parameters are defined as for Equations 1 and 2 and the same procedures in solving the von Bertalanffy growth equation were applied to determine growth trajectories using the logistic model. Plastron lengths at capture and recapture of *E. macquarii* and *C. expansa*, and time intervals between capture and recapture, were used to fit to von Bertalanffy and logistic growth-interval equations with JMP (SAS incorporated) non-linear least-squares regression procedures. The model that returned the smallest residual mean-square error (residual sum of squares divided by the number of sample points) was considered to be the one that best fitted the data (Dunham 1978; Schoener and Schoener 1978; James 1991).

Male *E. macquarii* and *C. expansa* were considered mature when their tail was visibly elongated (Cann 1998) and the plastron lengths of the 10 smallest males were used to determine mean size at maturity. Female *E. macquarii* and *C. expansa* lack the elongated and enlarged tails of males (Chessman 1978) and the 10 smallest mature females were determined by palpating females for oviductal eggs throughout the year.

Reproduction

During the spring and summer months, intensive trapping was carried out in the Mulwala region to determine the proportion of adult females that reproduce each year. All females captured were palpated in the inguinal region to detect the presence of oviductal eggs. Females were judged reproductive if (1) they carried oviductal eggs when palpated and/or (2) were nesting or returning to ponds with clear indications of a recent nesting attempt such as soil on the posterior carapace.

I induced female *E. macquarii* in Mulwala lagoon and Lake Mulwala to oviposit to determine the relationship between clutch and body size. Inducing females to oviposit is not a reliable method to determine exact clutch size because females may not oviposit the entire clutch, but relative clutch sizes is a reliable index to determine the relationship between body and clutch size. I collected eggs from reproductive females by inducing oviposition. The total numbers of eggs per female and female plastron and carapace lengths were recorded. Females were again palpated after oviposition to determine whether the female retained some eggs. If eggs were still present in the female's oviducts, that female's clutch size was not included in the analyses. The relationships between body size and clutch size in both populations were compared using regression analysis.

Results

Age estimated from recapture data

Growth annuli were extremely variable by the time the hatchlings were two years old. Twelve of the hatchlings released into Bankview and Hawksview lagoons in early 1997 were recaptured at the beginning of 1998. Ten of these hatchlings had one observable



Fig. 1. The relationship between growth rate and plastron length of juvenile and female *Emydura macquarii* fit to logarithmic least squares.

growth ring on shields of both the carapace and plastron and two hatchlings had no discernible increments. In total, 42 hatchlings from 1997 were recaptured at two years of age in early 1999; 26 had two annuli on their carapace and plastron, 4 had one annulus, 11 had no discernible annuli and one hatchling had three visible annuli. Thus, there is a 17% (2/12) chance of error in aging first-year *E. macquarii* and the error in aging turtles increases to more than 36% (16/42) after two years. For these reasons, growth rates (in PL) of juveniles and females were solely determined from recaptures at intervals of at least one trapping season.

Hatchling *E. macquarii* that were released in 1997 grew 40 ± 1 (s.d.) mm PL during the first year (n = 12), and turtles that were captured in 1999 and two years old, were 68 ± 9 (s.d.) mm PL (n = 42) greater than their original size. The variation in first-year growth rates was extremely small and second-year growth was estimated by applying average first–year growth (40 mm) to the initial PL of each hatchling captured in 1999 and determining the difference between the recaptured length (PL) and the estimated value for 1998. Hatchling and juvenile growth is rapid but declines to less than 5 mm per year in individuals with a plastron length of 200 mm (Fig. 1).

On the basis of recapture data and the relationship between growth and plastron length (PL), growth rate (GR) for females and juveniles is best defined by a logarithmic equation $(R^2 = 0.93)$:

$$\ln(PL) = 5.4 - 0.05(GR)$$
 Equation 5

Growth of male *E. macquarii* declines linearly after maturity and males continue to grow beyond 200 mm PL. Growth varies from 9 mm year⁻¹ to 2 mm year⁻¹ between 170 mm and 180 mm PL respectively and growth after maturity is best described by the linear equation $(R^2 = 0.72)$:

$$PL = 214 - 6.7(GR)$$
Equation 6

The size of one- and two-year-old turtles are known from recapturing hatchlings released in 1997. The relationships between plastron length and growth rate is extremely strong, especially within female turtles ($R^2 = 0.93$). By using Equations 5 and 6, as well as mean

Age	Predicted size (PL)	Known size (PL \pm s.d.)
1	68.3	$67.5 \pm 1 \ (n = 12)$
2	94.3	$95.9 \pm 9 \ (n = 42)$
3	114	$113 \pm 12 \ (n = 6)$
4	130	$132 \pm 5 \ (n = 7)$
5	143	
6	155	
7	165	
8	174	
9	182	
10	189	

 Table 1. Relationship between age and size of female *E. macquarii* predicted from Equation 4 and mean hatchling size (27 mm PL)

 The third column shows the size of hatchlings marked and released in 1997 and recaptured in 1998 and 1999

Table 2. Non-linear regression of recapture data fitted to the von Bertalanffy and logistic equations

a, asymptotic plastron length (±s.e.); *k*, characteristic growth parameter (±s.e.) (Schoener and Schoener 1978); RMS, residual error mean square; MSE, mean square error

Model	а	k	RMS	MSE
For female E. macquarii				
von Bertalanffy $(n = 901)$	214 (2.8)	0.20 (<0.01)	5.0	25.4
logistic $(n = 901)$	206 (2.8)	0.72 (0.02)	14.4	207
For male E. macquarii				
von Bertalanffy ($n = 487$)	208 (2.6)	0.23 (<0.01)	4.1	16.5
logistic $(n = 487)$	195 (1.6)	0.84 (0.01)	7.6	58.2
For female C. expansa				
von Bertalanffy $(n = 54)$	318 (25)	0.07 (0.01)	8.0	63.4
logistic $(n = 54)$	264 (4.4)	0.25 (0.01)	5.3	28.7
For male C. expansa				
von Bertalanffy $(n = 46)$	308 (52)	0.07 (0.01)	8.2	74.4
logistic $(n = 46)$	235 (4.7)	0.29 (0.01)	5.6	32.1

hatchling size (27 mm PL), I developed a relationship between age and size (PL) (Table 1) by assuming that juvenile growth was the same for both male and female turtles, as it is in *Trachemys scripta* (Dunham and Gibbons 1990).

Age estimated from common growth models

Predicted sizes were similar to the actual sizes of turtles that were released in 1997 and recaptured in 1998 (one year old) and 1999 (two years old). The growth data of both male and female *E. macquarii* fit the von Bertalanffy model extremely well. In all cases the von Bertalanffy model has smaller residual mean square than the corresponding logistic model (Table 2), indicating that the former is more appropriate for describing growth of both male and female *E. macquarii* (Frazer and Ehrhart 1985; Frazer 1991; Cox *et al.* 1991).

The von Bertalanffy model produced a curve that was extremely similar to the predicted curve based on recapture data and known-age individuals (recapture/known-age model). For both male and female *E. macquarii*, the curves follow a similar trajectory, except near the asymptote for females, where the rate of growth in the von Bertalanffy model declines



Fig. 2. The relationship between age and size (PL) of juvenile and female *E. macquarii*. Thick solid line, projected age–size curve based on growth rates and size (Equation 4). Diamonds, size of hatchlings recaptured in 1998, 1999 and 2001. Broken line, growth curve of females and juveniles constructed using the von Bertalanffy equation. Thin solid line, growth curve of females and juveniles constructed using the logistic equation. Grey line, growth curve of adult females only constructed from the von Bertalanffy equation.

much faster than the curve based on growth rates and initial hatching size (Fig. 2). The average plastron length at maturity for female *E. macquarii* is 187 mm and the 10 smallest gravid females were 175–195 mm PL in Bankview, 179–192 mm PL in Hawksview and 173–193 mm PL in Snowdon's Lagoons. Thus, according to the recapture/known-age and the von Bertalanffy equations, females mature at 9–12 years (Fig. 2).

Male *E. macquarii* have elongated tails at an average plastron length of 147 mm, based on the 10 smallest males in each lagoon (141–152 mm PL at Bankview, 139–151 mm PL at Hawksview and 147–155 mm PL at Snowdon's lagoons), although some turtles between 135 mm and 141 mm had slightly elongated tails but were considered sub-adults. According to the recapture/known-age equation, male *E. macquarii* begin to mature at 5–6 years (Fig. 3). The tails of two hatchlings (135 and 137 mm PL) released at the beginning of 1997 and recaptured in 2001 (~4 years later) were slightly elongated and were thus considered sub-adult males. The von Bertalanffy equation predicts that male *E. macquarii* mature 4–7 months earlier than does the recapture/known-age equation.

The models were recalculated using only growth data of female and juvenile turtles captured and recaptured throughout the study period, excluding growth data of known-age hatchlings released in 1997 and 1998, to evaluate the importance of growth rates of young (small) turtles to the general shape of the growth curve. Growth trajectories are similar to the full model, except that it fails to predict the large growth rate of hatchling and juvenile turtles (Fig. 2). Hence, asymptotic size (234 mm PL) is much larger and the growth parameter (k) (0.1) is less than half that predicted by the full model.

In contrast, the von Bertalanffy model is a poor descriptor of growth of both male and female *C. expansa*. Growth of *C. expansa* is better described by the logistic equation because juvenile growth is relatively slow before it increases rapidly beyond 5–7 years of age. The smallest gravid female captured was 215 mm but the average length was 219 mm; thus, female *C. expansa* mature at 14–15 years. Males begin to show signs of maturity (tail



Fig. 3. The relationship between age and body size (PL) of male *E. macquarii*. Thick solid line, growth curve of males and juveniles constructed from growth rates (Equation 4.6). Broken line, growth curve of males and juveniles constructed using the von Bertalanffy equation. This solid line, growth curve of males and juveniles constructed using the logistic equation.



Fig. 4. The relationship between age and body size (PL) of female (solid line) and male (grey line) *C. expansa* from growth curves that were constructed from the logistic equation. Broken line, growth curve of female *C. expansa*, excluding juveniles, constructed using the von Bertalanffy equation.

elongation) at 179 mm (mean length 189 mm) or at 9–11 years. Both the logistic (MSE, 6.9; RMSE, 2.6) and von Bertalanffy (MSE, 6.1; RMSE, 2.4) models describe the growth of female *C. expansa* when juveniles are excluded from the analyses and age at maturity is estimated at 10–11 years (Fig. 4).

Reproduction

Clutches comprised 13–36 eggs and clutch size of *E. macquarii* is positively correlated with PL ($R^2 = 0.71$, P < 0.01), increasing by one egg for each 3-mm increase in plastron length. Females generally produce only one clutch per year, with more than 86% of females

Date	Location	Gravid turtles	
October/November 1996	Mulwala lagoon	93%	(125/134)
October/November 1997	Mulwala lagoon	88%	(111/126)
October/November 1998	Mulwala lagoon	94%	(76/82)
December 1996	Bankview/Hawksview	19%	(22/118)
December 1997	Bankview/Hawksview	11%	(8/70)
December 1998	Bankview/Hawksview	20%	(12/59)
January 1996	Bankview/Hawksview	0%	(0/140)
January 1997	Bankview/Hawksview	0%	(0/97)
January 1998	Bankview/Hawksview	0%	(0/90)

Table 3. Proportion of female *E. macquarii* gravid at different locations on the Murray River

gravid each year (Table 3). Some females can produce a second clutch per year, as up to 20.3% of females were gravid in mid-December. Thus, average clutch frequency per year is 1.09; however, this percentage may include some females producing a late first clutch. No gravid turtles were captured after 19 December in any year.

Discussion

The pattern of growth is different between E. macquarii and C. expansa, particularly in the juvenile stage. E. macquarii grows rapidly until maturity, which is a common pattern in most freshwater turtles (Parmenter 1976; Chessman 1978; Bury 1979; Georges 1982; Cox et al. 1991; Kennett 1996), whereas C. expansa grows relatively slowly over the first 3-4 years. Whilst the von Bertalanffy model describes growth for both male and female *E. macquarii*, the logistic model, which describes the growth of some turtles and most squamates, is a better descriptor of the growth of C. expansa (Schoener and Schoener 1978; Frazer and Ehrhardt 1985; Jones and Hartfield 1995). However, this study demonstrates that the exclusion of juvenile growth can distort a model by either overestimating age with turtles showing von Bertalanffy growth patterns or underestimating age in turtles with logistic growth patterns. The von Bertalanffy model failed to predict actual hatchling and juvenile growth (Fig. 2) when only recapture data from adult E. macquarii were included in the model and estimates of female age at maturity would be grossly over-estimated. The absence of smaller size classes underestimates the value of k (growth parameter) and obviously fails to detect juvenile growth that may deviate from the growth model. In contrast, the logistic and von Bertalanffy curves are similar in shape when fitted with data from only the upper size ranges (Fraser and Ehrhardt 1985), failing to detect the slow juvenile growth and underestimating the age of C. expansa.

Growth annuli are unreliable in estimating annual growth and determining age in many turtles (Galbraith and Brooks 1987; Stott 1988; Cox *et al.* 1991) and *E. macquarii* do not have reliable annuli because there is a 36% chance of error in estimating age within two years of hatching. Carapace and plastron annuli can be used to estimate growth and age only when annual periodicity of the annuli is established (Gibbons 1967), a condition that is clearly not met for *E. macquarii*. If conditions are harsh or growth rate declines much earlier than expected, two annuli may appear as one and growth and age is underestimated (Iverson 1991). The adaptation of growth models provides more precise methods of deriving an age–size curve for *E. macquarii* and *C. expansa* when mark–recapture data are available and the individuals cannot be aged. Growth models are robust enough to estimate age of *C. expansa* and *E. macquarii* up until maturity but are of little value beyond maturity

and approaching the asymptotic size (a). Small differences in plastron length (~2 mm) could occur from measurement error or plastron deterioration (Kennett 1996). Large turtles are long-lived and generally grow irregularly when conditions are favourable, thus the relationship between age and size becomes irrelevant for larger-sized animals (Gibbons 1987; Cox et al. 1991; Kennett 1996). In contrast, the growth of first-year E. macquarii was relatively large, but the variation was surprisingly small (Fig. 1). Hatchling turtles may maximise growth over the first year to obtain a size where predation pressures are reduced, as survivorship in turtles is related to age (Shine and Iverson 1995) or, more precisely, size. E. macquarii has a classic Type III survivorship curve, where survivorship increases with age. Mortality rates are extremely high in the egg and hatchling stages of many species, but predation rates generally decrease with increasing size (Tucker et al. 1999). Nest predation is greater than 90% (Thompson 1983; Spencer 2002) and birds are a major source of hatchling mortality (Spencer et al. 2001) in E. macquarii on the Murray River. Predation pressures on two-year-old E. macquarii with a plastron length of over 100 mm is much lower than on a hatchling that is only one third of the size. In contrast, hatchling C. expansa grow relatively slowly compared with older juveniles, which may relate to an ontogenetic dietary shifts. C. expansa feeds primarily on live fish or carrion and hatchling C. expansa may be unable to secure live prey until a certain size, relying instead on lesser-quality food (Chessman 1978). Species with logistic growth patterns, such as C. expansa, are usually obligate carnivores or herbivores, whereas species with the Bertalanffy growth pattern show a marked decrease in diet quality with size and are predominantly omnivores (Hailey and Coulson 1999). Most juvenile turtles are carnivorous despite the adult possibly being omnivorous (Hart 1983), and adult E. macquarii predominantly consume low-quality filamentous algae (Spencer et al. 1998) and aquatic macrophytes (Chessman 1986). E. *macquarii* is less efficient at processing aquatic macrophytes compared with a completely carnivorous diet (Spencer et al. 1998) and the decline in growth rate may reflect a gradual change from a highly digestible carnivorous diet to a much less digestible one. The change in diet may also lead to a habitat shift, as a dietary shift in *Pseudemys scripta* parallels a habitat shift from feeding sites in shallow to deep water (Hart 1983). If diet can influence growth patterns, ontogenetic dietary shifts may influence age of maturity.

Maturity

Female E. macquarii and C. expansa mature at 9–11 and 14–15 years respectively. Male E. *macquarii* and *C. expansa* mature at smaller sizes and much earlier than females (5–6 and 9-11 years respectively). Species that are widely distributed like E. macquarii and C. expansa (Cann 1998) show considerable differences in growth and maturation both between sexes and populations (St Claire et al. 1994). Male painted turtles (Chrvsemvs *picta*) in northern North America mature at similar ages to those in the south, although female turtles in the south mature later and grow quicker than those in the north (St Claire et al. 1994). Similarly, southern female E. macquarii (higher latitude) in the Murray River mature much later than turtles in catchments in northern New South Wales, which mature at much smaller sizes and 3–5 years earlier than the Murray River form (Georges 1982). On both continents, turtles at higher latitudes may be constrained by the number of clutches that can be successfully incubated per year. Northern female painted turtles reproduce at most once per year, whereas southern females can produce several clutches over a summer (St Claire et al. 1994). E. macquarii in the current study generally produced one clutch per year, consistent with other studies of *E. macquarii* on the Murray River (Chessman 1978). Body size influences clutch size in many freshwater turtles and a larger body size and faster

growth may be favoured in females in higher latitudes so that they produce larger clutches but at a much lower annual frequency. Large female *E. macquarii* in the Murray River can produce at least 36 eggs and their average clutch size is far greater than northern *E. macquarii* and *E. krefftii* in Queensland, which produce 3-4 clutches of four eggs throughout spring and summer (Georges 1983). Alternatively, at higher latitudes, winters are usually longer and colder and growing quicker to a larger body size may increase survival and fitness more substantially than a small increase in clutch size.

Female turtles at higher latitudes may mature later and reach larger body sizes than those turtles closer to the equator, but the relative sizes at maturity may not be considerably different. Reproduction is energetically expensive, as it requires resources that would have otherwise been directed into growth (Bernardo 1993), and the reduction in growth rate after maturity is possible evidence of this cost. If turtles are delaying maturity to maximise clutch size, the relationship between size at maturity and maximum size will be close to 1.0. The relationship between size at maturity and maximum size for most freshwater turtles is between 0.72 and 0.75 (see Shine and Iverson 1995) and the ratio for female C. expansa is 0.75, but female E. macquarii delay maturity because the ratio is over 0.80. Delaying maturity and producing a larger clutch may not maximise reproductive potential and would favour only those species with high adult survival. If a long reproductive life is assured, maximising body and, thus, clutch size, will increase reproductive potential despite foregoing smaller clutches that could be produced several years prior to maturity. Survival of *E. macquarii* is described by a Type III survival curve, where hatchling and early juvenile survival is very low but increases significantly throughout the juvenile stage and adult females exhibit extremely high survival, with close to 100% surviving each year (Spencer 2001). Longevity and delayed maturity of E. macquarii on the Murray River increases annual clutch size and possibly maximises reproductive potential. In contrast, male E. macquarii do not delay maturity and grow relatively consistently after maturity, whereas females presumably grow periodically only when conditions are favourable, as the female growth asymptote is closer to the size at maturity (Table 2).

Environmental conditions may also influence age at maturity. If resources are low, growth and reproduction can be reduced. Lack of resources alone does not appear to influence age at maturity of *E. macquarii* because the growth parameters (k) estimated from the von Bertalanffy equation, representing how quickly growth approaches the asymptote for both male (0.23) and female (0.20) turtles, are comparable to those of many other species that mature earlier. For example, female Kinosternum sonoriense (Rosen 1987), Chrysemys picta (Zweifel 1989) and K. subrubrum (Gibbons 1983) all have growth constants between 0.17 and 0.22 (Shine and Iverson 1995), but mature between five and seven years of age. However, growth and age at maturity may be affected by a shift from a high-quality carnivorous diet to a lower-quality omnivorous diet that may coincide with the decline in growth towards the age and size at maturity. The age at maturity of female E. macquarii is at the upper limit of ages for freshwater turtles, which generally mature at 7-9 years: Chrysemys picta, 7-9 years (Wilbur 1975; Mitchell 1988; Iverson and Smith 1993); Trachemys scripta, 8 years (Frazer et al. 1990); K. sonoriense, 7 years (Rosen 1987). C. expansa is the largest chelid in Australia and is a late-maturing turtle, similar to large North American snapping turtles (Chelydra serpentina), which mature at 20 years. Southern species of Chelodina are late-maturing turtles. Two species of Chelodina are sympatric with E. macquarii and both Chelodina longicollis, which is smaller than E. macquarii, and C. expansa mature beyond 10 years (Parmenter 1976). Chessman (1978) estimated that female E. macquarii and C. expansa mature 2-4 years earlier than is

estimated in this study. However, Chessman (1978) solely used annuli to estimate age, which clearly gives erroneous results for *E. macquarii* more than two years old.

Conclusion

In conclusion, turtle populations that experience high adult survival usually delay maturity (see Shine and Iverson 1995) because growth, maturity and reproduction are intrinsically linked. In most turtle populations, the production of eggs may come at the cost of growth and, because clutch size is highly correlated with body size, a species with high survival should delay maturity to maximise lifetime reproductive output. Similarly, if survival of hatchlings and early juvenile *E. macquarii* is functionally linked to body size, rapid growth over the first few years could reduce mortality rates considerably. The von Bertalanffy model for growth predicts that the growth trajectory of juvenile *E. macquarii* is extremely rapid, female maturity is delayed compared with males and growth rate is low after maturity. In contrast, juvenile growth of *C. expansa* is relatively slow over the first few years after hatching, possibly due to diet. This study also shows that common techniques to estimate growth (annuli) and age (growth models) are erroneous when the relationship between age and annuli has not been established and when juvenile growth is not included in the models.

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