

## Population parameters and life-table analysis of two coexisting freshwater turtles: are the Bellinger River turtle populations threatened?

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**Abstract.** Two species of freshwater turtle coexist in the Bellinger River: *Elseya georgesi* is common but limited to the Bellinger River, whereas *Emydura macquarii* is widespread but rare in the Bellinger River. The Bellinger River population of *E. macquarii* has been proposed as a distinct subspecies, so it may be endangered. Survivorship, fecundity, growth, size and age were determined for *El. georgesi* and the finite rate of increase ( $\lambda$ ) was estimated by a life-table analysis using mark–recapture data from surveys between 1988 and 2004. These parameters were compared with those of well studied populations of *E. macquarii* to assess whether modelling the demographic parameters of *El. georgesi* could serve as a surrogate for estimating the influences of these demographic parameters on  $\lambda$  in the Bellinger River population of *E. macquarii*. We estimated that ~4500 *El. georgesi* inhabit the study area and, despite a size distribution strongly biased towards large individuals, the population is increasing ( $\lambda = 1.15$ ) in the best-case scenario, or slightly decreasing ( $\lambda = 0.96$ ) in the worst-case scenario. Comparing *El. georgesi* with *E. macquarii* from the Bellinger River and elsewhere suggests that *E. macquarii* grows faster, attains greater maximum size, has a greater clutch size and a higher fecundity than *El. georgesi*. Hence, *El. georgesi* does not serve as a good surrogate to determine demographic influences on  $\lambda$  in *E. macquarii*.

### Introduction

Management of threatened animal populations is often complicated by a lack of knowledge of the stochastic and/or ecological factors causing decline (Schoener and Spiller 1996; Luisselli *et al.* 1997; Lande 2002). Various modelling techniques are valuable in assessing population decline and may be especially useful in studies of rare species (e.g. Simons 1984; Crouse *et al.* 1987; Heppell and Crowder 1996; Spencer and Thompson 2005). In the absence of reliable empirical data, a conspecific, or a closely related coinhabitant population may be used for predicting survivorship and fecundity and, thus, finite population growth ( $\lambda$ ) of a rare population (Boyce 2002).

In turtles, survivorship and fecundity are linked to size rather than age classes (Crouse *et al.* 1987; Kennett 1996; Spencer and Thompson 2005). Age-structured models are, however, often required in conjunction with stage-structured models to interpret  $\lambda$  in real time (Nisbet and Gurney 1986; Crouse *et al.* 1987; Crowder *et al.* 1994). It is not possible to track individuals of long-lived organisms, such as turtles, throughout their life, so models based on growth rates (e.g. von Bertalanffy, Gompertz and logistic models) are useful tools for understanding population dynamics (Frazer *et al.* 1990a; Kennett 1996; Spencer 2002a). The three prin-

cipal life-history stages utilised in turtle demographic models are the egg–hatchling, juvenile and adult stages (Crouse *et al.* 1987; Heppell *et al.* 1996; Heppell and Crowder 1996; Spencer and Thompson 2005). As a result of their longevity and survivorship pattern, the stable size distribution in turtle populations is usually skewed, having considerably more large adults than juveniles or hatchlings (Thompson 1983; Gibbs and Amato 2000).

Many populations of Australian freshwater turtles are threatened with extinction (Georges *et al.* 1993). Introduced predators (Thompson 1983; Parmenter 1985; Spencer 2002b; Spencer and Thompson 2003) and habitat degradation (Georges *et al.* 1993; Mitchell and Klemens 2000) are implicated as the principal causes for the declines, although the impacts of interspecific and intraspecific competition, and stochastic events, have never been adequately quantified.

Two native short-necked turtles inhabit the Bellinger River, New South Wales, Australia (30°26'S, 152°47'E to 30°27'S, 152°30'E). *Elseya georgesi* is restricted to, but common in, the Bellinger River and *Emydura macquarii* is widespread throughout New South Wales, but rare in the Bellinger River. Specimens of *E. macquarii* from the Bellinger River are morphologically distinct from those of other *E. macquarii*

populations and Bellinger River *E. macquarii* is regarded as a possible subspecies (unnamed: Cann 1998). Despite its uncertain status, and no quantification of population size or projected growth rate, a recovery plan (NSW National Parks and Wildlife Service 2001) was developed for the Bellinger River *E. macquarii*, with fox predation on eggs and nesting females implicated as a threat to this population (Mahon 2001). We performed demographic analyses on all available mark–recapture data taken from 1988 to 2004 to assess: (1) whether the *El. georgesi* population is stable, (2) any negative impacts on it, with an emphasis on foxes, and (3) the applicability of *El. georgesi* as a surrogate population for demographic modelling of *E. macquarii*. The latter was done by comparing *El. georgesi* population parameters with other, well studied, *E. macquarii* populations.

## Methods

### Study site

Turtles were collected from ~30 km of the Bellinger River, where *E. macquarii* has previously been collected (Cann 1998; NSW National Parks and Wildlife Service 2001). The area was partitioned into 21 irregularly spaced suitable capture sites (Cann 1998).

### Sampling methods and measurements

Turtles were captured by hand while snorkeling (~95% of captures), or in traps, between September and February in two distinct periods: 1988–91 (PK only) and 2000–04 (all authors). The date of capture was recorded and each turtle was marked with a unique set of three notches made in the lateral edges of the marginal scutes.

Straight-line carapace length and width, and straight-line plastron length and width were measured on all turtles captured using calipers. Weight was measured to the nearest 0.1 kg (turtles >300 g) or 0.01 kg (turtles <300 g) using an electronic and/or spring balance. Males were identified as having an elongated preloacal length relative to their body length. The minimum size of visually identifiable males (118 mm carapace length) was used as the upper size limit for all juveniles. All turtles were released after marking and measuring. Turtles with discernible growth annuli in the plastral scutes (Sexton 1959) had their annuli counted. Turtles recaptured more than one month after initial capture were measured again.

### Survivorship

#### Egg–hatchling stage

As there were few obvious turtle-nesting sites (Congdon and Gibbons 1990), survivorship of eggs was estimated experimentally. Forty-eight ‘artificial nests’ were constructed, each containing 10 small hen’s eggs (which have been found to attract predators equally as well as turtle eggs: Spencer 2002b; Blamires *et al.* 2003). Two sites, ~2.5 km apart, each contained 24 artificial nests. The two sites had similar surface topology, i.e. a flat riverbank, backed by a steeply sloping (~45–60°) dune, set ~10 m from the water, but one site was more densely vegetated (river shrubs <2 m high and immature and mature *Cuarina* trees) on the riverbank. To assess whether distance from the riverbank and/or elevation influenced predation rate on turtle nests (Stancyk *et al.* 1980; Spencer and Thompson 2003) 12 artificial nests were deposited above the dune and 12 on the riverbank at random distances from each other, at each site. As chelid turtle nests range from ~40 to 180 mm deep (Ewart 1979), half of the nests at each location, at each site, were buried ~40 mm deep and half were buried ~180 mm deep. Artificial nests were monitored for 20 days for signs of predation,

or other forms of destruction. Nests were considered destroyed if found open with eggshells around the nest, trampled on by cattle, or flooded by a raised river level. Results were recorded as 0 for no predation or 1 for predation. Four treatments were used: riverbank, 40 mm deep; riverbank, 180 mm deep; above dune, 40 mm deep; and above dune, 180 mm deep. When predation was found, the predator responsible was identified as fox, goanna, or other, from tracks left in the vicinity of the nest (Triggs 1996). A Chi-square goodness-of-fit test was used to test whether nest depth or site influenced nest destruction by foxes, goannas and other agents.

In addition to the experiment, the riverbanks and dunes at all sampling sites were checked once per survey for any signs of natural nests (e.g. freshly laid nests, depredated nests, hatched nests). Hatched nests were opened and the total clutch size and number of eggs that produced emergent hatchlings were counted.

### Juvenile and adult stages

Survivorship of juveniles and adult females for *El. georgesi* was calculated from mark–recapture. A capture–history matrix, representing 10 secondary capture periods over two primary capture periods (1988–91 and 2000–04), was created. A value of 1 was designated for a capture and 0 for no capture for all individuals in each secondary capture period. Survival probabilities ( $\phi$ ) were estimated from the capture–history matrix by a Jolly–Cormack–Seber goodness-of-fit survival model, the model of best fit determined by Akaike Information Criterion (Burnham and Anderson 1998), using RELEASE. Any turtles found dead were collected, measured, sexed and the marginal scutes examined. Marked turtles found dead were included in capture–history matrices to distinguish mortality from permanent emigration in estimates of  $\phi$  (Barker 1997; Bjørndal *et al.* 2003).

### Fecundity

The breeding season, and the number of females breeding per season, was determined by palpating the inguinal pockets of all females to detect the presence of shelled eggs in the oviducts. The size of the smallest gravid female encountered was considered to be the minimum female breeding size. Clutch size was determined for *El. georgesi* from clutch counts of hatched nests. To compare with *El. georgesi*, maximum carapace length was used to estimate clutch size for the Bellinger River *E. macquarii* from a standard correlation curve between maximum carapace length and mean clutch size among the *E. macquarii* subspecies (data taken from Cann 1998).

### Size distribution and age

Size–distribution curves were generated for adult males and females of each species, using straight carapace length as the standard measure, to enable direct comparison with other species (Cann 1998). The *E. macquarii* calculations included data from 1992–94 published by Cann (1998). Size distributions were tested for normality using a Kolmogorov–Smirnov test.

To assign age to size classes in *El. georgesi* for life-table analysis, the relationship between size and age was estimated by fitting a growth curve from female recapture data, and a combination of recapture data and growth annuli counts (where recapture data were unavailable: Spencer 2002a) in juveniles. Straight plastron length was used as the measure of size for comparison with Spencer (2002a). Growth curves were constructed using the following non-linear regression models (Ratkowsky 1983):

$$\text{von Bertalanffy: } L = a(1 - be^{-kt}),$$

$$\text{logistic: } L = a/(1 + be^{-kt}), \text{ and}$$

$$\text{Gompertz: } L = ke^{-e^{-(a-bt)}}$$

where  $L$  = plastron length,  $a$  = asymptotic length,  $e$  = base of the natural logarithm,  $k$  = intrinsic growth rate, and  $t$  = estimated age.

The model that returned the least residual mean square error was considered the most appropriate fit for the data. The asymptotic length, *a*, and intrinsic growth rate, *k*, calculated from the von Bertalanffy and logistic models, were compared with those of Murray River *E. macquarii* (Spencer 2002a).

*Population estimates*

The study area was considered open to immigration and emigration, so population size (*N*) was estimated for *El. georgesi* using the Jolly–Seber method (Krebs 1989) from recapture histories using Microsoft Excel (McCallum 2000). A series of population estimates pertaining to each sample period (eight per primary capture period) were made. The arithmetic mean of the series estimates was used to estimate the population. Standard errors were estimated for each sample period, with population standard error estimated as the mean of the standard errors of the sample series (Krebs 1989). Given that *E. macquarii* is extremely rare in the Bellinger River, the population size was not estimated. The minimum sample size required to provide demographic parameters with a coefficient of variation under 10% (Cohen 1977) was estimated from the number of *E. macquarii* captured using the program BAND 2.

*Life-table analysis*

Life-table analysis was carried out for female *El. georgesi* (*E. macquarii* being too rare to collect sufficient empirical data) using a stage-based approach (Frazer *et al.* 1990b). Stages were egg–hatchling, juvenile and adult. An age (*x*) was assigned each stage: 1 was assigned to both the egg–hatchling and juvenile stages. The age of reproductive maturity in females was the age attributed to adults. The survivorship and fecundity estimates were used to generate survivorship schedules (the portion of individuals surviving to each stage:  $\ell(x)$ ), and fecundity schedules (the average number of female offspring produced per adult female per breeding season:  $b(x)$ ) (Gotelli 2001). Intrinsic rate of increase (*r*) was estimated by calculating the reproductive rate ( $R_0$ ), the mean number of offspring produced by a female over her lifetime, using the following equations (Gotelli 2001):

$$R_0 = \sum \ell(x)b(x),$$

and

$$r = \ln(R_0) / G$$

where *G* = generation time, which was assumed to be the minimum female reproductive age.  $\lambda$  was calculated using the equation (Gotelli 2001):

$$\lambda = e^r$$

where  $\lambda$  indicates the growth rate of the population ( $\lambda > 1$  indicates population growth,  $\lambda = 1$  indicates stability, and  $\lambda < 1$  indicates decline). If in decline, the size/age distributions were used to assess whether the decline is likely to be due to fox predation on eggs, nesting females, or other causes (Thompson 1983; Spencer 2002b). Using  $\lambda$  and the current population size ( $N_0$ ), the projected population size ( $N_t$ ) after 1, 2, 5, 10, and 20 generations was calculated for *El. georgesi* by the equation (Gotelli 2001):

$$N_t = \lambda^t N_0$$

Eigenelasticity analysis (Caswell 2000; Spencer and Thompson 2005) was carried out to determine the relative influences of growth, fecundity and survival at each stage on  $\lambda$ .

**Results**

In total, 466 *El. georgesi* (221 males, 170 females, and 75 juveniles) and 11 *E. macquarii* (6 males, 4 females, and 1 juvenile) were captured (Table 1). Of these, 76 were recaptured once and 13 were recaptured twice. Adult female *El. georgesi* (203.9 mm) and *E. macquarii* (223.3 mm) had larger mean carapace lengths than adult males (*El. georgesi*, 161.1 mm; *E. macquarii*, 170.7 mm) (Table 1).

*Survivorship*

*Egg–hatchling stage*

Foxes, goannas, trampling cattle and flooding all caused ‘mortality’ in the experimental plots in the artificial nest experiment (Table 2), but there was no significant difference in ‘mortality’ by foxes, goannas, or other sources, across the nest locations and depths ( $\chi^2_{47} = 0.24, P = 0.97$ ).

Predators destroyed 9 of 13 natural nests identified at 5 locations. Two of the 9 were destroyed by foxes, 5 by goannas, and 2 had been visited by foxes and goannas. All nests were within 10 m of the water’s edge and had a mean ( $\pm$ s.e.) depth (surface to base) of  $170 \pm 24$  mm. All of the nest sites were in heavily vegetated areas. Given the location and depth of the natural nests, the results of the artificial nest experiment pertaining to ‘nests’ on the riverbank at 180-mm depth were used in the life-table analysis, the higher value

**Table 1. Mean measurements for Bellinger River *Elseya georgesi* and *Emydura macquarii***  
*n*, sample size; CL, carapace length; CW, carapace width; PL, plastron length; PW, plastron width; F, female; M, male; J, juvenile. Values are mean  $\pm$  s.e. Ranges are shown in parentheses

Species	Sex	<i>n</i>	CL (mm)	CW (mm)	PL (mm)	PW (mm)	Weight (g)
<i>El. georgesi</i>	F	170	203.9 $\pm$ 1.6 (154–231)	161.4 $\pm$ 1.2 (130–215)	165.2 $\pm$ 1.3 (127–185)	75.5 $\pm$ 0.7 (56–91)	977.3 $\pm$ 23.9 (375–1430)
	M	221	161.1 $\pm$ 0.9 (129–212)	125.9 $\pm$ 0.6 (107–167)	128.2 $\pm$ 0.7 (81–146)	57.9 $\pm$ 0.9 (48–73)	462.2 $\pm$ 7.9 (250–1060)
	J	75	120.4 $\pm$ 4.7 (69–130)	104.1 $\pm$ 3.5 (66–113)	97.8 $\pm$ 3.9 (57–115)	44.9 $\pm$ 1.9 (25–66)	218.8 $\pm$ 23.4 (40–520)
<i>E. macquarii</i>	F	4	223.3 $\pm$ 13.7 (189–247)	172.6 $\pm$ 8.6 (151–187)	184.2 $\pm$ 30.8 (153–215)	66.0 66.0	1125.0 $\pm$ 505.0 (620–1630)
	M	6	170.7 $\pm$ 7.9 (148–190)	136.6 $\pm$ 5.5 (113–146)	133.9 $\pm$ 9.2 (118–154)	52.7 $\pm$ 3.3 (46–56)	418.8 $\pm$ 57.2 (300–550)
	J	1	127	117	96	43	400

**Table 2. Results of the artificial-nest experiment showing survival and percentage survival at the two sites for the variables 'location' and 'nest depth'**

Site 1, densely vegetated site; site 2, sparsely vegetated site

Site	Location	Nest depth (mm)	<i>n</i>	<i>n</i> survived	% survival	Cause of mortality
1	Riverbank	40	6	0	0	Goanna, flood, fox
1	Riverbank	180	6	1	17	Goanna, flood, fox
1	Above dune	40	6	0	0	Cattle, flood, fox
1	Above dune	180	6	1	17	Cattle, fox
2	Riverbank	40	6	0	0	Goanna, flood, cattle
2	Riverbank	180	6	4	67	Fox
2	Above dune	40	6	3	50	Cattle, fox
2	Above dune	180	6	4	67	Cattle, fox

(0.67: Table 2) representing a best-case scenario and the lower value (0.17: Table 2) representing a worst-case scenario.

#### *Juvenile and adult stages*

There was no significant difference in survival estimates ( $\phi$ ) between the 1988–91 and 2000–04 capture periods ( $\chi^2 = 1.071$ ,  $P = 0.31$ ), therefore the recapture data from the two periods were pooled to calculate  $\phi$  values representing both primary capture periods with estimates of survivorship throughout each life stage. From the recapture matrices, a  $\phi$  for juveniles of 0.58 (s.e. = 0.02; confidence limit = 0.52–0.63) and a  $\phi$  for adults of 0.86 (s.e. = 0.05; confidence limit = 0.77–0.97) were calculated.

#### *Fecundity*

Female *El. georgesi* were gravid between September and November. Seventeen (16.5%) of 103 females palpated in this period were identified as gravid. The smallest female identified as gravid had a straight carapace length of 154 mm. Mean ( $\pm$ s.e.) clutch size of hatched *El. georgesi* nests was  $13.5 \pm 3.2$  eggs. Of the 4 natural nests that had emergent hatchlings, 3 had 100% hatch success, and 5 of 12 eggs (41%) hatched in the last clutch. Hatching success, in the absence of predation, was thus estimated at 85.4%.

Mean clutch size and maximum body size among the subspecies of *E. macquarii* was positively correlated ( $R = 0.89$ ,  $P = 0.02$ ; predictive equation: clutch size =  $-43.22 + 0.24$  (maximum CL); from data in Cann 1998); accordingly, a mean clutch size of 16.1 eggs was predicted for the Bellinger River *E. macquarii*.

#### *Size distribution and age*

The size distributions of adult *El. georgesi* males (Kolmogorov–Smirnov test, maximum  $D = 0.10$ ,  $P < 0.05$ ) and females (Kolmogorov–Smirnov test, maximum  $D = 0.18$ ,  $P < 0.01$ ) were skewed towards larger individuals (Fig. 1). There were too few data to analyse size distributions of adult male and female *E. macquarii*, although they appear skewed towards larger individuals in both sexes (Fig. 1).

The von Bertalanffy growth model had the least residual mean square (RMS) error (Table 3) and was thus used to

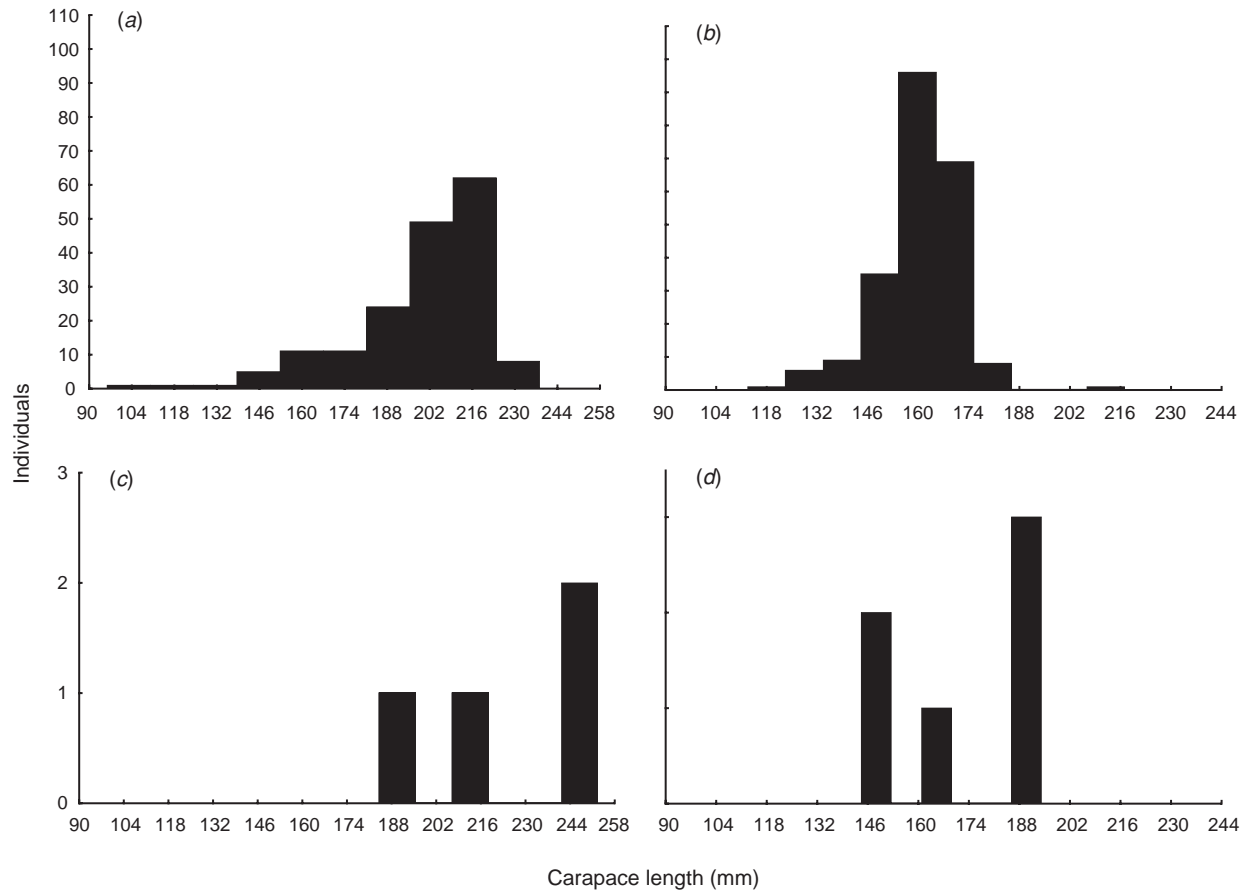
assign age. The von Bertalanffy and the logistic models both revealed a smaller intrinsic growth rate,  $k$ , for *El. georgesi* than for the Murray River *E. macquarii* (Table 3). According to the von Bertalanffy model (Fig. 2), females should attain sexual maturity at  $7.9 \pm 1.2$  years (mean  $\pm$  s.e.) of age, and have a maximum life expectancy of  $28.9 \pm 4.5$  years. Age was not estimated in *E. macquarii* due to lack of recapture data.

#### *Population estimate*

The Jolly–Seber estimate of the population size ( $N$ ) of *El. georgesi* was  $4468 \pm 1409$  individuals (arithmetic mean of sample population estimates  $\pm$  s.e.). Too few *E. macquarii* were captured to be able to make estimates of any population parameters or of  $N$ . Given the data collected on *E. macquarii* over the study period (11 captures, 0 recaptures over 9 years of sampling) it was estimated that over 1000 individuals would be required to achieve a coefficient of variation on the demographic parameters of less than 10%.

#### *Life-table analysis*

Two possible egg–hatchling survivorship estimates were used for the *El. georgesi* life table: 0.17 (the worst-case scenario) and 0.67 (the best-case scenario) (Table 4). Estimates of  $\phi$  for juveniles and adults were used to calculate  $\ell(x)$  in these stages. A  $b(x)$  of 0.96 was estimated from the proportion of the female population breeding, and the number of female hatchlings likely to be produced each season (assuming hatchling sex ratio = 1:1 male:female, 85.4% egg survivorship in non-depredated nests, and a clutch size of  $\sim 13.5$  eggs). The best-case estimation of  $\lambda$  was 1.15 (Table 4), suggesting an increasing population, and the worst-case estimation of  $\lambda$  was 0.96 (Table 4), suggesting a slightly declining population. Extrapolated over 20 generations ( $\sim 160$  years), the best-case scenario shows a population expanding to over 70 000 individuals, while the worst-case scenario shows a population dropping to under 2000 individuals (Fig. 3). Survivorship of adults had higher elasticity values (approximately 7.5: Fig. 4) than any other demographic parameter in any other stage.



**Fig. 1.** Size (straight carapace length; in mm) distribution of (a, c) female and (b, d) male Bellinger River turtles: (a, b) *Elseya georgesi* and (c, d) *Emydura macquarii*.

**Discussion**

The *Elseya georgesi* population in the Bellinger River is, at best, increasing ( $\lambda = 1.15$ ) or, at worst, slightly decreasing ( $\lambda = 0.96$ ). Too few data were collected on *Emydura macquarii* to estimate  $\lambda$ . On the basis of the low capture rate, *E. macquarii* is likely to be exceptionally rare in the Bellinger River. Effective management of this species therefore requires use of a surrogate population, e.g. congeneric

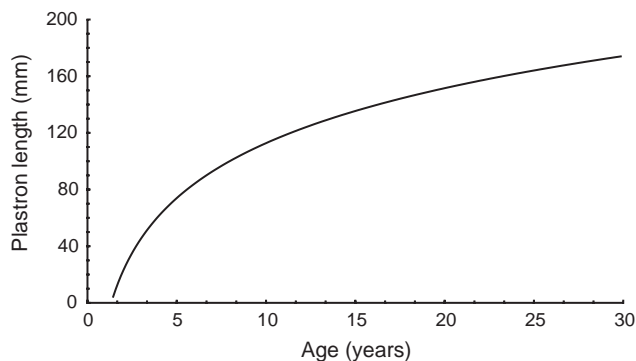
or allogeneric species in similar habitats (Boyce 2002) to predict the influences acting on  $\lambda$ .

*E. macquarii* differed from *El. georgesi* in that *E. macquarii*: (1) attains larger maximum body size (*E. macquarii* = 247 mm carapace length; *El. georgesi* = 231 mm carapace length), (2) grows faster, and (3) lays more eggs per clutch, than *El. georgesi*. Larger body size, through faster growth, results in larger maternal body size, larger clutches and larger

**Table 3.** Residual mean square (RMS) error, asymptotic size (*a*, measured as straight plastron length), and intrinsic growth rate, *k*, for the Bellinger River population of *El. georgesi*, and comparison of *k* with that of the Murray River population of *E. macquarii*<sup>A</sup>

Model	Sex	RMS error	<i>a</i>	<i>k</i>	<i>k</i> for Murray River <i>E. macquarii</i> <sup>A</sup>
Von Bertalanffy	Male	12.0	137.9	0.11	0.23
	Female	18.6	176.1	0.14	0.20
Logistic	Male	15.6	141.5	0.43	0.84
	Female	23.6	186.3	0.33	0.72
Gompertz	Male	18.7	142.9	0.47	
	Female	28.4	184.4	0.40	

<sup>A</sup>Source: Spencer (2002a).



**Fig. 2.** Non-linear regression (von Bertalanffy model) curve used to predict age from straight plastron length measurements for *Elseya georgesi*. The curve is for females only, as these age estimates were the only ones used in the life-table analysis.

hatchlings (Wilbur and Morin 1988), increasing fecundity, and adult and juvenile survival (Werner 1988; Janzen 1993; Shine and Iverson 1995; Heppell 1998). Greater clutch size directly affects fecundity. Since *E. macquarii* and *El. georgesi* grow at a different rate, an assessment of the model that best represents growth in *E. macquarii* needs to be independently elucidated to assign age to size in *E. macquarii*. Thus, survivorship and fecundity schedules calculated for life-table analysis for *E. macquarii* will be different from *El. georgesi*, leading to different values of  $r$  and  $\lambda$ . Hence *El. georgesi* is not a suitable surrogate for modelling *E. macquarii*. A better candidate may be a similar-sized *E. macquarii* from a geographically similar river catchment (e.g. *E. m. gunabarra* from the Hunter River: Cann 1998).

The population of *El. georgesi* is, in the worst-case scenario, declining to ~2000 individuals, and, in the best-case scenario, increasing to ~70000 individuals after 20 generations (~160 years). These figures assume a starting population of 4468 individuals across the study area. A high standard error about the arithmetic mean for the population estimate indicates that the value may be substantially more or less than this. However, the size of the current population is not of interest for management, only the value of  $\lambda$  (Crowder *et al.* 1994). The estimated worst- and best-case  $\lambda$  values of

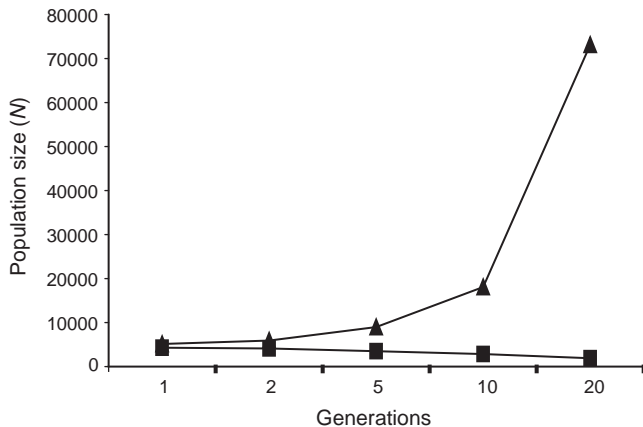
this population indicate that it is not in apparent danger of extinction. Life-table analysis, however, is a retrospective population model; i.e. it predicts the influence of changes in demographic parameters in the past on  $\lambda$ , and says nothing of the influence of future changes in demography (Caswell 2000). Prospective analyses such as sensitivity analyses (Pfister 1998; Mills and Lindeberg 2002) and elasticity analyses (e.g. Pfister 1998; Caswell 2000; Spencer and Thompson 2005) model the influence of future changes in demographic rates on  $\lambda$ . The sensitivity analyses applied to the *El. georgesi* life table indicate that changes in adult survivorship would have the greatest impact on the population growth of *El. georgesi*. This demographic parameter is generally agreed to have the greatest effect on  $\lambda$  estimates in turtle populations (Crowder *et al.* 1994; Heppell and Crowder 1996; Heppell 1998; Spencer and Thompson 2005). The size distribution of female *El. georgesi* (Fig. 2) has a wide range of sizes represented and the high estimates for adult survival are approximately that expected of a stable turtle population (Bjorndal *et al.* 2003; Spencer and Thompson 2005). Thus, the *El. georgesi* size distribution appears to indicate stability. More data on the survivorship of the current cohort of subadults is required, however, to assess any likely changes in population stability (Heppell *et al.* 1996).

Most factors that detrimentally affect survivorship and fecundity in freshwater turtle populations are anthropogenic (Moll and Moll 2000). A major anthropogenic factor affecting numbers of many freshwater turtle populations is introduced predators, e.g. foxes (Thompson 1983; Parmenter 1985; Spencer and Thompson 2005). Foxes (*Vulpes vulpes*) and goannas (*Varanus varius*) destroyed artificial and natural turtle nests along the Bellinger River. The natural nests suffered more predation from goannas than foxes, which may be a result of nesting sites being associated with vegetation; the goanna at this site, *Varanus varius*, is largely arboreal (Cogger 2000). Nest predation from goannas would not be expected to be a major threat to the Bellinger River turtle population as it is likely that, over the time of their coexistence, an equilibrium (Rosenzweig and McArthur 1963) has been reached whereby turtles produce enough offspring to

**Table 4.** Life table for *Elseya georgesi* showing best-case and worst-case scenarios

$x$ , age;  $b(x)$ , fecundity schedule;  $\phi$ , survivorship probability;  $\ell(x)$ , survivorship schedule;  $r$ , intrinsic rate of population growth;  $\lambda$ , finite rate of population growth; E–H, egg–hatchling; J, juvenile; A, adult;  $\Sigma$ , sum of column

Stage	Age (x)	b(x)	Best-case scenario ( $\phi_{E-H} = 0.67$ )			Worst-case scenario ( $\phi_{E-H} = 0.17$ )		
			$\phi$	$\ell(x)$	$b(x)\ell(x)$	$\phi$	$\ell(x)$	$b(x)\ell(x)$
0	0	0	0	0	0	0	0	
E–H	1	0	0.67	0.67	0	0.17	0.17	0
J	1	0	0.58	0.39	0	0.58	0.10	0
A	8	0.96	0.86	0.34	0.33	0.86	0.08	0.08
$\Sigma$					0.33			0.08
r			0.14			0.04		
$\lambda$			1.15			0.96		

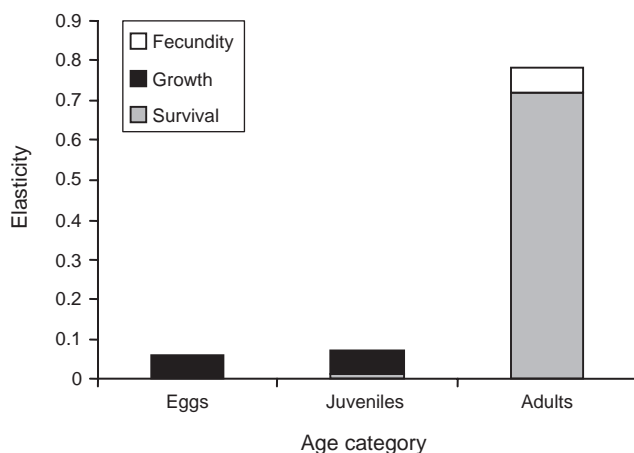


**Fig. 3.** Population size ( $N$ ) of the Bellinger River *El. georgesi* population extrapolated over 1, 2, 5, 10 and 20 generations from the equation,  $N_t = \lambda^t N_0$ , where  $\lambda$  = finite rate of increase,  $N_0$  = population size at generation 0,  $N_t$  = population size after generation  $t$  ( $\blacktriangle$  = population change if  $\lambda = 1.15$  (the best-case scenario) and  $\blacksquare$  = population change if  $\lambda = 0.96$  (the worst-case scenario)).

sustain the population despite nest predation. Introduced foxes, on the other hand, can have enormous impacts on turtle populations through predation on eggs (Thompson 1983; Spencer and Thompson 2003, 2005) or nesting females (Moll and Moll 2000; Spencer 2002b; Spencer and Thompson 2005). As  $\lambda$  is more sensitive to the mortality of adult females than of embryos (Heppell *et al.* 1996; Pfister 1998; Moll and Moll 2000; Spencer and Thompson 2005), predation on nesting females by foxes has the potential to negatively affect population growth in Bellinger River turtles and should be continually monitored.

#### Why is *E. macquarii* so rare in the Bellinger River?

Given that *E. macquarii* is particularly common in other river systems (Cann 1998) it is unusual that the Bellinger



**Fig. 4.** Elasticity values for fecundity, growth and survival across the life-history stages: egg-hatchling (eggs), juvenile, and adult, for the Bellinger River *Elseya georgesi* population.

River population is so small. No estimate of  $\lambda$  was possible in this study because too few individuals were caught, but the small numbers suggest that the population may have fallen below the minimum viable population size, causing the population to decline towards extinction (Lacy 1992).

Exclusive competition, which implies that while one species reaches carrying capacity the other goes extinct (Gotelli 2001), may be a cause of population decline in *E. macquarii* in the Bellinger River. The diets of *El. georgesi* (Allanson and Georges 1999) and *E. macquarii* from other rivers (Chessman 1986; Spencer *et al.* 1998) overlap, implying potential competition. However, competitive exclusion is unlikely to be driving *E. macquarii* to extinction because: (1) considerable cooperative partitioning of resources is implicated between native freshwater turtles (up to 4 species may coexist in a (often small) water body: Legler and Cann 1980; Vogt and Guzman 1988), and (2) both species are facultative omnivores, a strategy implicit in organisms that partition resources (Diehl 2003).

The Bellinger River *E. macquarii* differs morphologically from *E. macquarii* of other rivers of the region (e.g. the Macleay, Clarence, Hunter: Cann 1998). An isolated population of Blanding's turtle (*Emydoidea blandingii*) sustained rapid morphological change under isolation (Herman *et al.* 1994), so morphological divergence does not necessarily indicate that *E. macquarii* did not originate from a nearby river. DNA comparisons between *E. macquarii* in the Bellinger River and *E. macquarii* of nearby rivers (e.g. Macleay, Clarence Rivers) could positively identify whether this population is unique to this river. If the Bellinger River *E. macquarii* is not unique it may be a recent anthropogenic introduction, or a recent expansion of another *E. macquarii* population. The presence of a juvenile and a dead gravid female indicate that the Bellinger River *E. macquarii* population is breeding. It would thus be imperative to monitor the numbers and movements of the Bellinger River *E. macquarii* as, if it is introduced, its continued presence may represent a threat to *El. georgesi*.

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