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

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Running Title: Life table analysis of Bellinger River turtles

Abstract. Two species of freshwater turtle co-exist 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 may be endangered. Survivorship, fecundity, growth, size, and age, were determined for *El. georgesi* and the finite rate of increase (λ) was estimated by a life table analysis using mark-recapture data from surveys between 1988-2004. These parameters were compared to those of well studied populations of *E. macquarii* to assess if modelling *El. georgesi* could serve as a surrogate for estimating the influences of these demographic parameters on λ in *E. macquarii* in the Bellinger River. We estimated that approximately 4500 *El. georgesi* inhabit the study area, and despite a strongly biased size distribution towards large individuals, the population is increasing, λ=1.15, in the best case scenario, or slightly decreasing, λ=0.96, in the worst case scenario. Comparing *El. georgesi* with the Bellinger River and other *E. macquarii* populations suggest 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 influences on λ in *E. macquarii*.

Introduction

Management of threatened animals is often complicated by a lack of knowledge of the causes of decline, with many stochastic (Lande 2002) and ecological factors (Hallam 1986;

Schoener and Spiller 1996; Luisselli *et al*. 1997) causing population decline. 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 2004). In the absence of reliable empirical data, a model population, either a conspecific, a closely related co-inhabitant, or a previously studied population of similar organisms in a similar environment, may be used for predicting the demographic influences on finite population growth, ? (Boyce 2002).

In turtles, demographic parameters are usually linked to size rather than age classes (Crouse *et al.* 1987; Kennett 1996; Spencer and Thompson 2004). Age-structured models are, however, often required in conjunction with stage structured models to interpret ? in real time (Nisbet and Gurney 1986; Crouse *et al.* 1987; Crowder *et al*. 1994). It is not possible to track individuals throughout their life for long lived organisms, such as turtles, 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; Cox *et al.* 1991; Kennett 1996; Spencer 2002a). The three principal 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 2004). As a result of their longevity and survivorship pattern, the stable size distribution in turtle populations are usually skewed, having considerably more large adults than juveniles or hatchlings (Thompson 1983; Gibbs and Amato 2000).

Many populations of Australian freshwater turtle 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. *Elseya georgesi* is restricted to, but common in, the Bellinger River and *Emydura macquarii*, is widespread, but rare, in the river. The Bellinger River *E. macquarii* is morphologically distinct from other *E. macquarii* and is regarded as a 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 foxes implicated as the threatening process (Mahon 2001). Both species are potentially vulnerable to foxes through predation on eggs and nesting females (Cann 1993; Spencer and Thompson 2001). We performed demographic analyses on all available mark-recapture data taken from 1988-2004 to assess: 1) whether the *El. georgesi* population is stable, 2) any negative impacts with an emphasis on foxes, and 3) the applicability of *El. georgesi* as a surrogate population for demographic modelling of *E. macquarii* by comparing *El. georgesi* population parameters with well studied *E. macquarii* populations.

Methods

Study site

Turtles were collected from approximately 30 km of the Bellinger River upstream from Thora, New South Wales (152° 47'E, 30° 26'S to 152º 30' E, 30º 27' S), the only area where the Bellinger River *E. macquarii* has been previously collected (Cann 1993, 1998; NSW National Parks and Wildlife Service 2001; Spencer and Thompson 2001). The area was partitioned into 21 randomly distributed sampling sites.

Sampling methods and measurements

Turtles were captured by hand while snorkeling (approximately 95%) or in traps between September and February in two distinct time periods; 1988-1991 (PK only) and 2000-2004 (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 and curved plastron length and width were measured using calipers (straight-line measurements) and a flexible tape measure (curved measurements) in all turtles. Mass was measured to the nearest 0.1 kg (turtles > 300g) or 0.01 kg (turtles < 300g) using a electronic and/or spring balance. Males were identified by an elongated pre-anal tail length, relative to body length. The minimum size of visually identifiable males was used to determine the minimum size of differentiation of females from juveniles. All turtles were released after marking and measuring. Turtles with discernable 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

Survivorship of eggs was estimated experimentally by constructing 48 “artificial nests” of 10 small hens eggs, which experiments have found attract predators equally as well as turtle eggs (Spencer 2002b; Blamires *et al*. 2003). Two sites, approximately 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 (approximately 45-60°) dune, set approximately 10 m from the water, but one site was more densely vegetated (river shrubs < 2 m high and immature and mature *Cauarina* trees) on the riverbank. As distance from the riverbank and elevation can influence 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 approximately 40 to 180 mm deep (Ewart 1979), half of the nests at each location, at each site, were buried approximately 40 mm deep and half were buried approximately 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, opened by predators or humans, damaged by cattle, or flooded by a raised river level. The predator or agent responsible for destruction was noted. Predators were identified from any tracks in the vicinity of opened nests, (Triggs 1996). Data were analysed using a Chi-squared goodness of fit test, with correction for continuity (Snedecor and Cochran 1980), for predation by foxes, goannas and other causes of mortality, across four treatments: riverbank/40 mm deep, riverbank/180 mm deep, above dune/40 mm deep and above dune/180 mm deep.

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 ten secondary capture periods over two primary capture periods (1988-1991 and 2000-2004), 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 (ϕ) 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 for marks. Marked turtles found dead were included in capture history matrices, to distinguish mortality from permanent emigration in estimates of ϕ (Barker 1997; Bjorndal *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 smallest gravid female encountered was considered 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 1992-1994 published by Cann (1998). Size distributions were tested for normality using a Kolmolov-Smirnov test.

To assign age to size classes, the relationship between size and age was estimated by fitting a growth curve from adult 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:

von Bertalanffy (Fabens 1965; Frazer *et al.* 1990a):

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

logistic (Schoener and Schroener 1978):

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

Gompertz (Winsor 1932; Cox *et al.* 1991) models:

$$L = ke^{-e^{a-bt}}$$

(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). Recapture rate was used to predict whether age could be estimated for *E. macqurii*.

Population Estimates

The study area was considered open to immigration and emigration, so population size (N) was estimated for *El. georgesi* using the Jolly-Cormack-Seber method from recapture histories using Microsoft Excel (McCallum 2000). 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 co-efficient of variation (CV) under 10% (Snedecor and Cochran 1980) was estimated from the number of *E. macquarii* captured using the program BAND 2.

Life Table Analysis

Life table analysis was done 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; l(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):

$$R_0 = \overset{k}{\underset{x=0}{S}}\, l(x)\ b(x)$$

and

$$r = \frac{\ln (R_0)}{G}$$

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

$$?=e^{r}$$

where ? indicates the stability of the population (? >1 indicates population growth, ? =1 stability, and ? <1 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 (Thompson

1983; Spencer 2002b), or other causes. Using ? 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):

$$N_t = ?^t N_0$$

Eigenelasticity analysis (Caswell 2000; Spencer and Thompson 2004) was done to determine the relative influences of growth, fecundity, and survival at each stage on λ.

Results

A total of 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). Seventy-six were recaptured once and 13 were recaptured twice. Adult female *El. georgesi* (203.9mm) 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 by 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 ($?^2_{47}$ = 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 waters edge and had a mean (± s.e.) depth (top to bottom) of 170 ± 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 (0.67; Table 2) representing a best case scenario and the lower value (0.17; Table 2) representing a worst case scenario.

Juuvenile and adult stages

There was no significant difference in survival (ϕ) between primary capture periods ($?^2$ = 1.071, P = 0.31) so calculated ϕ values were taken to represent turtles sampled across the entire study period. A juvenile ϕ value of 0.58 (± 0.02; confidence limit = 0.52-0.63) and an adult ϕ of 0.86 (± 0.05; confidence limit = 0.77-0.97) were calculated from the recapture matrices.

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 (± s.e.) clutch size of hatched *El. georgesi* nests was 13.5 ± 3.2 eggs. All of the eggs hatched in 3 of the 4 nests from which eggs hatched, with 5 of a clutch of 12 eggs, (41%) hatchings in the last clutch. Hatchling emergence 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 significantly positively correlated ($r = 0.89$, $P = 0.02$; predictive equation: clutch size = -43.22 + 0.24 max. CL; from data in Cann 1998) and accordingly, a mean clutch size of 16.1 eggs was predicted for the Bellinger River *E. macquarii*.

Size distribution and age

The size distribution of *El. georgesi* adult males (Kolmogorov-Smirnov; maximum $D = 0.10$, $P < 0.05$) and females (Kolmogorov-Smirnov; maximum $D = 0.18$, $P < 0.01$) was skewed toward larger individuals (Fig. 1). There were too few data to analyse size distributions in *E. macquarii* adult males and females, although they appear skewed toward 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, in *El. georgesi* compared with the Murray River *E. macquarii* (Table 3). Under the von Bertalanffy model, females attain sexual maturity at 7.9 ± 1.2 years (mean ± s.e.) of age, and have a maximum life expectancy of 28.9 ± 4.5 years. Age was not estimated in *E. macquarii* due to lack of recapture data.

Population estimate

The Jolly-Cormack-Seber estimate of *El. georgesi* population size (N) was 4468 ± 1409 individuals. The capture rate of *E. macquarii* was too few to make meaningful estimates of any population parameters or 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 co-efficient 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). Juvenile and adult ϕ estimates were used to calculate $l(x)$ 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% eggs survival in unpredated nests, and a clutch size of approximately 13.5 eggs). The best case estimation of λ was 1.15 (Table 4), suggesting an increasing population, and the worst case estimation of λ was 0.96 (Table 4), suggesting a slightly declining population. Extrapolated over 20 generations (approximately 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. 2). Survivorship of adults had higher elasticity values (approximately 7.5; Fig. 3) than any other demographic parameter in any other stage.

Discussion

The *Elseya georgesi* population in the Bellinger River is, at best, increasing (? = 1.15) or, at worst, slightly decreasing (? = 0.96). Too few data were collected on *E. macquarii* to estimate ?. Based on 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 ?.

Emydura macquarii differed from *El. georgesi*, as *E. macquarii*: 1) attains larger maximum body size (*E. macquari* = 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 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 *E. macquarii* growth 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 ?. 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 around 2000 individuals, and in the best case scenario increasing to around 70,000 individuals after 20 generations (approximately 160 years). Thus, this population is not in apparent danger of extinction, however life table analysis is a retrospective population model; i.e. predicts the influence of changes in demographic parameters in the past on ?, 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 2004) model the influence of future changes in demographic rates on ?. The sensitivity analyses applied to the *El. georgesi* life table indicate that changes in adult survivorship would have the greatest impact on *El. georgesi* population growth. This demographic parameter is generally agreed to have the greatest effect on λ estimates in turtle populations (Crowder *et al.* 1994; Heppell and Crowder 1994; Heppell 1998; Spencer and Thompson 2004). Female size distribution of *El. georgesi* (Fig. 2) has a wide range of sizes represented and the high adult survival estimates are approximately that expected of a stable turtle population (Bjorndal *et al.* 2003; Spencer and Thompson 2004). Thus, *El. georgesi* size distribution appears to be stable. More data on the survivorship of the current cohort of sub-adults is required to assess any likely future changes in population stability however (Heppell *et al.* 1996).

The vast majority of factors that detrimentally impact 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 (Parmenter 1985; Thompson 1983; Mitchell 2000; Spencer and Thompson 2004). 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 co-existance an evolutionary stable strategy (Murphy 1968) has been reached, whereby turtles can produce enough offspring to 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, 2004) or nesting females (Moll and Moll 2000; Spencer 2002b; Spencer and Thompson 2004). As ? is more sensitive to adult female mortality than embryonic mortality (Heppell *et al.* 1996; Pfister 1998; Moll and Moll 2000; Spencer and Thompson 2004), 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 River population is so small. No estimate of ? was possible in this study because too few individuals were caught, but the small numbers suggest the population is likely to have fallen below the minimum viable population size (MVP), causing the population to decline toward extinction (Lacy 1992).

Exclusive competition, which implies that while one species reaches carrying capacity the other goes extinct (Hallam 1986; 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; Spencer and Thompson 2001) and *E. macquarii* from other rivers (Chessman 1986; Cann 1993; Spencer *et al.* 1998) overlap, implying the potential for competition. Competitive exclusion is however unlikely to be driving *E. macquarii* to extinction because: 1) considerable co-operative partitioning of resources is implicated between native freshwater turtles, where up to 4 species may co-inhabit 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. maqcuarii* 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. Only DNA comparisons between *E. macquarii* in the Bellinger River and *E. macquarii* of nearby rivers (e.g. Macleay, Clarence Rivers) can positively identify if this population has been introduced, and from which river. If the Bellinger River *E. macquarii* represents a recent anthropogenic introduction, and the presence of a juvenile represents a breeding population, it is important to determine the affinities of the Bellinger River *E. macquarii* as, if it is introduced, its continued presence may represent a threat to *El. georgesi* and thus should be eradicated.

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Table 1. Mean measurements: Carapace Length (CL), Carapace Width (CW), Plastron Length (PL), Plastron Width (PW), and Mass, and sample size (n) for female (F), male (M) and Juvenile (J) Bellinger River *Elseya georgesi* and *Emydura macquarii*. Values are mean ± 1 standard error. Range is in parentheses. All values are straight-line measuements.

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

Table 2. Results of the artificial nest experiment showing survival and % survival at the sites 2 (1, densely vegetated site, and 2, sparsely vegetated site) for the variables: location (riverbank and above dune), nest depth (40 mm and 180 mm).

Site	Location	Nest Depth (mm)	N	N 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	2	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

Table 3. Residual mean square (RMS) error, asymptotic size (*a*, measured as straight plastron length), and intrinsic growth rate, *k*, for the Bellinger River *El. georgesi* population, and comparison of *k* with the Murray River *E. macquarii* population. *source: Spencer (2002a).

Model		RMS error	*a*	*k*	*k* Murray River *E. macquarii**
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	

Table 4. Life table for *El.georgesi* showing age (*x*), fecundity schedule (b(*x*)), survivorship probability (ϕ), and survivorship schedule (l(*x*)) across the egg-hatchling (E/H), juvenile (J), and adult (A) life history stages (S = sum of column). The intrinsic rate of population growth (r) and finite rate of population growth (?) is calculated for best case ($\phi_{E/H}$ = 0.67) and worst case ($\phi_{E/H}$ = 0.17) scenarios.

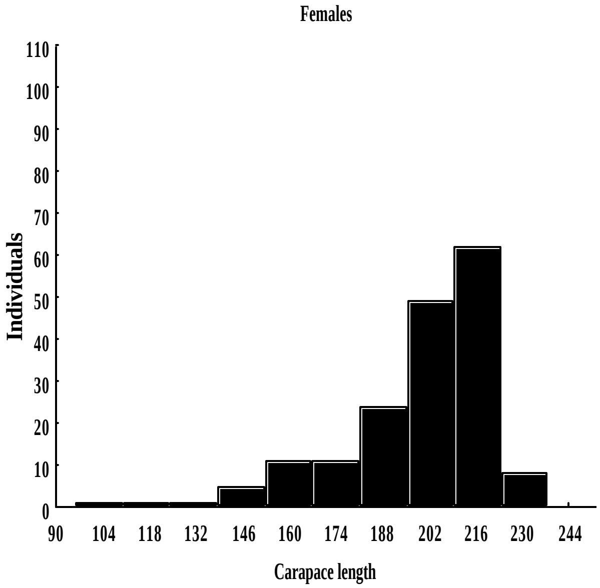
				Best case scenario			Worst case scenario	
Stage	Age (*x*)	b(*x*)	ϕ	l(*x*)	b(*x*)l(*x*)	ϕ	l(*x*)	b(*x*)l(*x*)
0	0	0	0	0	0	0	0	0
E/H	1	0	0.67	0.67	0	0.17	0.17	0
J	1	0	0.58	0.39	0	0.58	0.10	0
A	8	0.96	0.86	0.34	0.33	0.86	0.08	0.08
S					0.33			0.08
r			0.14			0.04		
?			1.15			0.96		

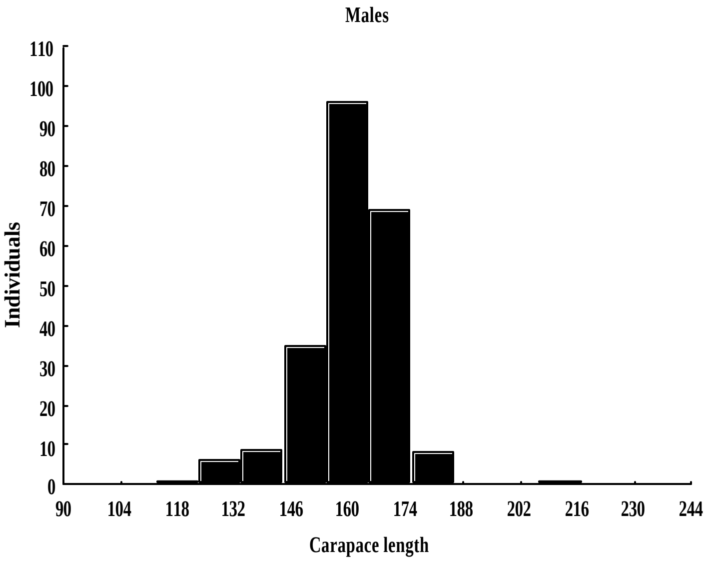
Fig. 1. Size (straight carapace length; in mm) distribution of male and female Bellinger River turtles: *Elseya georgesi* and *Emydura macquarii*.

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

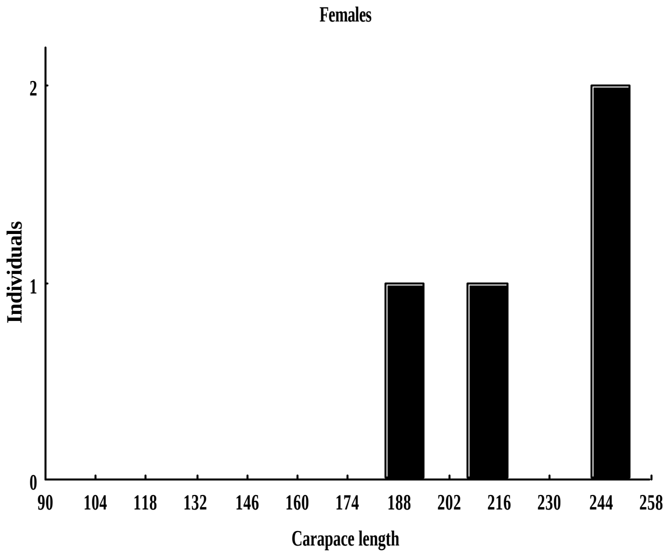
Fig. 3. Elasticity values for fecundity, growth and survival across the life history stages: egg/hatchling (eggs), juvenile, and adult, for the Bellinger River *El. georgesi* population.

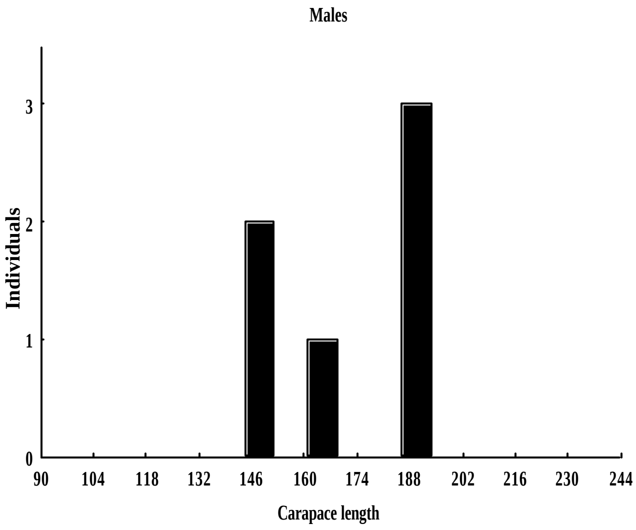
Elseya georgesi:

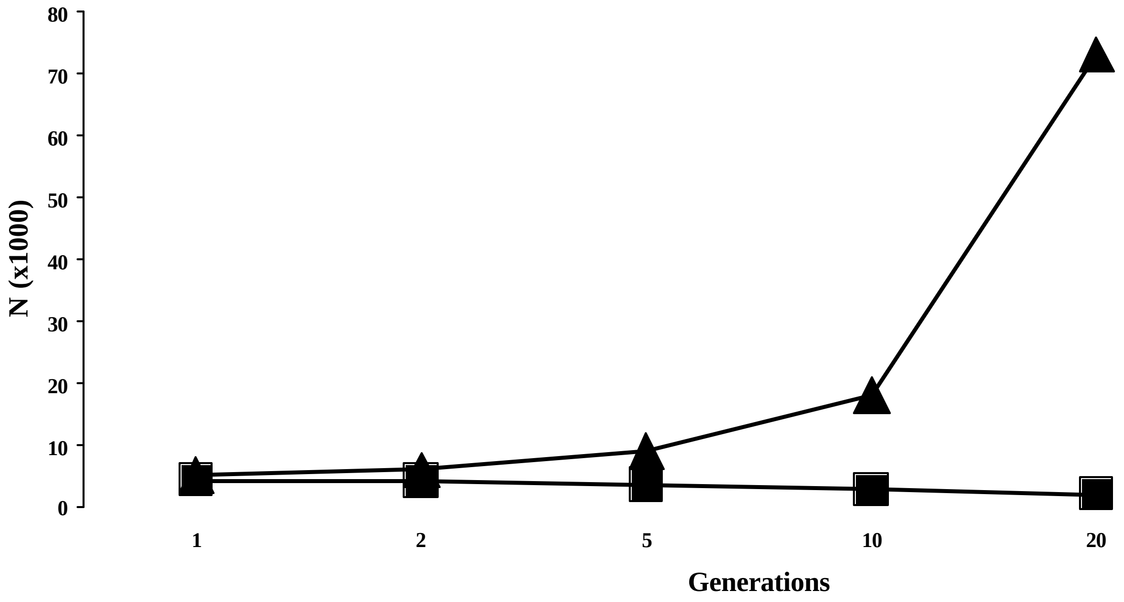


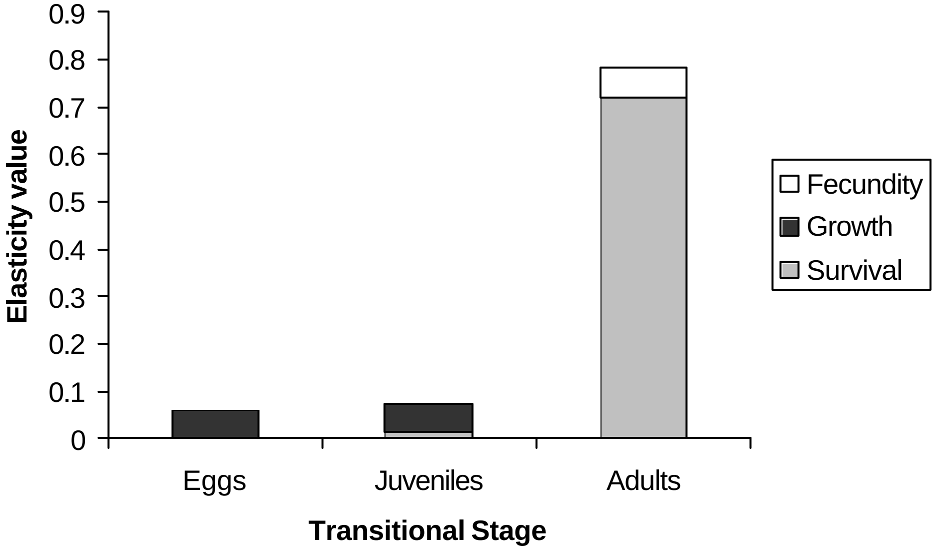


Emydura macquarii:






80
70
60
50
40
30
20
10
0
N (x1000)
1
2
5
10
20
Generations


0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
Elasticity value
Eggs
Juveniles
Adults
Transitional Stage
Fecundity
Growth
Survival