

Response of juvenile growth rate to experimental removal of nest predators in a long-lived vertebrate

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ABSTRACT- Examining the phenotypic and genetic underpinnings of life-history variation in long-lived organisms is central to the study of life-history evolution. Juvenile growth and survival are often density-dependent in reptiles and theory predicts the evolution of slow growth in response to low resources (resource-limiting hypothesis), such as under densely populated conditions. However, rapid growth is predicted when exceeding some critical body size reduces the risk of mortality (mortality hypothesis). Here we present results of paired large-scale, 5-year field experiments to identify causes of variation in individual growth and survival rates of an Australian turtle prior to maturity. To distinguish between these competing hypotheses, we reduced nest predators in two populations (retained a control population) to create variation in juvenile density by altering recruitment levels. We also conducted a complementary split-clutch field transplant experiment to explore the impact of incubation temperature (25°C or 30°C), nest predator level (low or high) and clutch on juvenile growth and survival. Juveniles in high-density populations were not resource limited, growing more rapidly than young turtles in the control populations. Our experiments also revealed a remarkably long-term impact of the thermal conditions experienced during embryonic development on growth of turtles prior to maturity. Moreover, this thermal effect was manifested in turtles approaching maturity rather than in turtles closer to hatching, and was dependent on the population density in the post-hatching rearing environment. This apparent phenotypic plasticity in growth is complemented by our observation of a strong, positive genetic correlation between individual growth in the experimental and control populations ($r_G = +0.77$). Thus, these Australian pleurodiran turtle populations have the impressive capacity to acclimatize plastically to major demographic perturbations, as well as enjoy the longer-term potential to evolve adaptively. These findings suggest that long-lived organisms possess two means for responding to substantial changes to population structure to maintain viability.

Introduction

Life-history traits vary with environmental factors such as predation (Tinkle and Ballinger 1972), food (Dunham 1978; Niewiarowski and Roosenburg 1993; Bernardo 1994; Bronikowski and Arnold 1999), temperature (Schultz et al. 1996), and overall climate (Berven and Gill 1983; Newman 1988). Such

environmentally induced phenotypic variation (phenotypic plasticity) can arise from altered developmental trajectories and embryonic growth rates, particularly in oviparous organisms. Still the ecological and evolutionary significance of plasticity for most traits remains obscure (Via et al. 1995).

Understanding how phenotypic variability arises in response to the environment could help to ascribe trait variability to adaptation (Lorenzon et al. 2001). Phenotypes can be expressed two ways in response to the environment. Different environmental conditions may induce phenotypic variation through its influence on gene expression (phenotypic plasticity) or through differential selection on the traits and their associated genotype (genetic polymorphism) (Lorenzon et al. 2001). Transplant experiments provide a robust technique to assess phenotypic variation caused by plasticity because if two genotypes express the same phenotype in the same environment, phenotypic differences observed under natural conditions result from phenotypic plasticity (Niewiarowski and Roosenburg 1993; Rhen and Lang 1995; Schultz et al. 1996; Sorci et al. 1996). Conversely, if phenotypic differences between genotypes are maintained across different environments, the variability derives from a heritable polymorphism (Lorenzon et al. 2001).

Whether plasticity is locally adaptive is difficult to demonstrate (Smith-Gill 1983; Newman 1992; Gotthard and Nylin 1995) because fitness associated with a trait is difficult to estimate in different environments (Lorenzon et al. 2001). By definition, life-history traits have a large effect on fitness, including juvenile growth and survival rates (Huey and Stevenson 1979; Dunham et al. 1989; Sinervo and Adolph 1994). Variation in juvenile survival can hardly be compensated by variation in other life-history traits, like fecundity or adult survival, to ensure a similar fitness over the entire life cycle (Sorci et al. 1996; Boudjemadi et al. 1999). Body size and growth rate affect fitness directly, as well as indirectly through age and size at maturity, fecundity and/or adult survival (Adolph and Porter 1993; Berrigan and Charnov 1994; Sibly and Atkinson 1994). Thus, juvenile growth and juvenile survival are important fitness components, so that low values will reflect low fitness.

Juvenile growth and survival are often density-dependent in reptiles (Massot et al. 1992) because of competition for food (Wilbur and Collins 1973). Besides resource availability, social interactions can affect

feeding and growth rates of reptiles and amphibians (Andrews 1982): in laboratory-staged dominance interactions, larger Snapping turtles often win contests for food items over smaller Snapping turtles (Froese and Burghardt 1974). Theory predicts the evolution of slow growth in response to low resources (resource-limiting hypothesis), such as under densely populated conditions (Arendt and Reznick 2005). However, rapid growth is predicted when exceeding some critical body size reduces the risk of mortality. For example, predation levels are substantial on small hatchling turtles (Janzen et al. 2000) and theories of density-dependent natural selection suggest that intraspecific competition will favor juveniles of high competitive ability (Svensson and Sinervo 2000); hence rapid juvenile growth would be favored by selection under both conditions (mortality hypothesis).

Both these hypotheses concern different life-history phenotypes with respect to age-specific allocation of energy and yield opposing predictions of potential growth rates. The resource limitation hypothesis concerns a reduction in energy, whereas implicit in the mortality hypothesis is a reallocation of energy, or change in ecological, behavioral or physiological traits, which is conducive to selection and possible life-history evolution. To address the ecological and evolutionary significance of a variation in growth rates, it is necessary to distinguish between the two competing hypotheses.

Freshwater turtles provide an excellent system to experimentally test for local adaptation of growth rates to environment. Firstly, turtles are oviparous and eggs can be distributed across a range of incubation conditions to test for the effect of developmental environment on phenotype (Ewert 1985; Packard and Packard 1988). Secondly, they often inhabit essentially closed populations and produce relatively large clutches of eggs, which is ideal for split-clutch transplants of hatchlings into different environments. Lastly, although population densities are often high (Spencer and Thompson 2005), nest predation rates are also high, meaning that recruitment and juvenile densities are very low (Spencer 2002a, Spencer and Thompson 2005). Thus any reduction in nest predators could lead to a large increase in recruitment levels, which is conducive for density-dependent processes and interactions. However, such experiments are rare because of

the significant long-term effort required to reduce predator populations and to retrieve enough turtles for comparison of life-history traits between environments.

Here we present results of paired large-scale, 5-year field experiments to identify causes of variation in individual growth rates of a long-lived turtle (*Emydura macquarii*) prior to maturity. To distinguish between resource-limiting and mortality hypotheses, we greatly reduced nest predators in two populations (and retained a control population) to create variation in juvenile density by altering recruitment levels. We also conducted a complementary split-clutch field transplant experiment to explore the impact of incubation temperature (25°C or 30°C), nest predator level (low or high) and clutch on juvenile growth. We then interpreted results of these two experiments in the context of findings from a long-term demographic study to assess predictions of the competing hypotheses. Specifically, we would expect reduced individual growth rates if resources are limiting in high-density (low-predator) populations. Alternatively, we would expect rapid individual growth in high-density populations if juvenile survival is positively associated with body size.

Methods

Study sites were located in the upper Murray River of south-eastern Australia (see Spencer 2002a, b for complete descriptions). Four populations (Snowdon's, Hawksview, Bankview and Cook's lagoons) of *Emydura macquarii* on the Murray River in Australia have been studied since 1996. Over 90% of turtle nests are destroyed by introduced foxes (Thompson 1983, Spencer 2002a) and these populations have been part of a large project investigating the full impact of foxes on turtle demography (Spencer and Thompson 2005) and behavior (Spencer 2002a, Spencer and Thompson 2003). *Emydura macquarii* is an omnivorous turtle that is heavily reliant on adult turtles for population stability (Spencer and Thompson 2005). The juvenile population is extremely small and even minor reductions in nest predation rates can potentially increase recruitment significantly.

We used a BACI (Before-After-Control-Impact; Underwood 1997) designed fox removal program to determine the impact of foxes on freshwater turtle population dynamics (see Spencer and Thompson 2005).

Essentially, fox numbers were monitored in all sites from July 1996 to January 1999, using spot-light counts conducted over 4–7 consecutive nights each month between August and November, and every second month between January and May. Foxes were removed, using spotlight shooting and a baiting program, from around two lagoons (fox removal sites- Snowdon’s and Hawksview) after the first nesting season, whereas foxes were continually monitored around another lagoons (control site- Bankview). Each site was chosen randomly as a removal or control site. We monitored nest predation rates around each lagoon and conducted a large capture-mark-recapture (CMR) program of each (except Cook’s) freshwater turtle population to determine stage specific life-history traits between September and March of each year from 1996 to 1999 and in February 2001 and 2002 (growth, fecundity and survival) (see Spencer 2002b; Spencer and Thompson 2005).

Turtles 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 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 and in February 2001 and 2002 (Snowdon’s lagoon was also trapped in January-March 1995). 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 calipers. Each turtle was furnished with a unique combination of notches in the marginal scutes and underlying bone (Thompson 1982) with an electric grinder (Ryobi 10 mm) or bastard file. Marked turtles were released within 12 h at their point of capture.

We developed separate growth curves for each population to determine if juvenile growth varied between populations both before and after fox removal. Changes in juvenile growth have the largest effect on the growth coefficient (k), which can be derived from von Bertalanffy growth equations (Spencer 2002b). Fabens (1965) derived the growth-interval equation of the von Bertalanffy model,

$$L_2 = a - (a - L_1) e^{-k(dt)}$$

where L_1 is straight plastron length at first capture, and L_2 is straight 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 were 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). JMP 5.1 was used for non-linear regression procedures. We compared estimates of growth coefficients (k) and asymptotic growth (a) from each population both before and after fox removal began.

Transplant experiment

Gravid female *E. macquarii* were captured in Mulwala lagoon (~100km downstream of the focal populations) and induced to lay their eggs by a subcutaneous intramuscular injection of 2 mL of oxytocin (Syntocin, Ilium) in the thigh (Ewert and Legler 1978). Injected turtles were placed in enclosed cardboard containers where most 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 (approximating -370 kPa) in foam containers (1000 mm × 400 mm × 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. Clutches were randomly incubated at 25°C or 30°C. Because *E. macquarii* does not have temperature-dependent sex determination (TSD) (Thompson 1988), male and female offspring were produced in both incubation treatment. 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 both Hawkview (Fox removal) and Bankview (Control) lagoons. We designed the experiment such that hatchlings from each clutch were released into both lagoons. Recaptured

hatchlings were identified (from toe clippings) and remarked as part of the general capture-mark-recapture (CMR) program in both lagoons (see Spencer 2002b, Spencer and Thompson 2005).

The data set comprised CMR history profiles in five trapping periods (year) for each population. Survival (ϕ) and capture (p) probabilities were estimated and modeled following the CMR methodology (Lebreton et al. 1992) and the method developed by Pradel (1996) using the program Mark (White and Burnham 1999). Plastron length (mm) at hatching was included as an individual covariate in the model. To select the most appropriate model for describing demographic temporal variation, we used a bias-corrected version of the Akaike's Information Criterion, AICc. We tested for overdispersion and adjusted the AICc value (QAICc) using an estimate of the variance inflation factor (i.e., \hat{c}) (Anderson et al. 1994). Models were compared by QAIC value, and we retained the most parsimonious one (lowest QAIC; Anderson et al. 1994).

We analyzed growth rates of juvenile turtles using ANCOVA with density, incubation temperature, and age as factors and plastron length at hatching as a covariate. We used the Holm-Sidak pairwise multiple comparison procedures to compare between treatment groups. Raw data were ln-transformed. SigmaStat 3.1 and Systat 10.0 were used for these statistical procedures.

Results

Density

Female population sizes of Bankview, Hawksview and Snowdon's lagoons were 615, 587 and 632 respectively and average fecundity was calculated at 24 eggs per annum (Spencer 2002b, Spencer and Thompson 2005). Nest predation rates were between 85-93% at all sites prior to fox removal. After fox removal, nest predation rates fell below 50% in treatment sites but remained above 83% in the control site (Spencer 2002a).

Under high nest predation conditions, potential hatchling recruitment was between 1300-2500 turtles per annum (Fig. 1). After foxes were removed, annual recruitment increased to 7000-8500 hatchlings. Almost 16000 hatchlings entered treatment populations after foxes were reduced in 1998 and 1999, whereas

less than 4000 hatchlings entered control populations during the same period (excluding transplanted hatchlings)(Fig. 1).

Although overall size distributions of turtles captured in both Bankview (low-density) and Hawksview (high-density) lagoons did not significantly differ before (January 1997) and five years after (January 2002) fox removal, the number of captures of turtles 110-150mm in PL spiked in Hawksview lagoon in January 2002 (Fig. 2). This size range corresponds to a turtle age of 3-5 years (Fig. 3).

Growth

The relationship between growth rate and both incubation temperature and population density depended on age (Table 1). A three-way ANCOVA revealed that there was an Age x Inc. Temp. x Density interaction and plastron size of hatchling (PL) had no effect on post-hatching growth. We then removed age as a treatment and PL as a potential covariate and conducted separate two-way ANOVAs for each age group to further explore the meaning of this result. Density at all ages had a significant effect on growth, but incubation temperature became increasingly important as turtles aged (Table 1). At all ages individual growth was generally greater in the high-density population compared to the low-density population, however the relationship depended on incubation temperature at ages four and five (Fig. 3). There was no significant difference in growth at age four between density treatments for turtles incubated under colder conditions during embryonic development. However, turtles incubated under the hotter regime were significantly larger in the high-density population compared to their sibs in the low-density population ($t=6.5$ $p<0.001$). Within the low-density population at age four, there was no difference in growth of turtles incubated at either temperatures (Fig. 3). However, turtles from the hotter incubation temperature were larger than turtles from the colder incubation temperature within the high-density treatment ($t=3.6$ $p<0.01$). At age five, turtles incubated at both hotter ($t=3.5$ $p=0.002$) and colder ($t=6.6$ $p<0.001$) incubation temperatures were larger in the high-density population compared to the low-density population. Although there was a significant difference between growth of hot and cold-incubated turtles in the low-density population at age five ($t=5.6$ $p<0.001$), there was no such difference in the high-density population (Fig. 3).

Regardless of environmental effects on growth, there was a strong genetic (family) correlation of growth patterns between density treatments; however, the precise shapes of the relationships were age-related (Fig. 4). Slopes were significantly different at age five ($b=1.71\pm 0.48$ S.E; $r_G=0.78$, $F_{1,8}=12.1$) compared to age four ($b=0.44\pm 0.15$ S.E; $r_G=0.77$, $F_{1,6}= 8.9$) and age two ($b=0.58\pm 0.16$ S.E; $r_G=0.77$, $F_{1,9}=12.8$), indicating ontogenetic changes in genetic covariance for juvenile growth.

An increase in intrinsic growth is not caused by differences in resources between populations; from a total catch of 1339 juvenile and female *E. macquarii*, individual growth rates (k) at all sites were similar prior to fox removal. After foxes were removed, individual growth rates were greater in fox removal (high-density) populations compared to the control population (Table 2). Asymptotic length (a) decreased in all populations but all estimations were within similar confidence limits (Table 2).

In high-density sites, annual survival of released hatchlings was related to size at hatching ($\phi(PL)p_t$ -QAICc weight= 1.0, $\Delta QAICc= 28.0$) although overall recapture probabilities were low ($p=0.10-0.23$) (Fig. 5). In low-density sites, annual survival was constant at 0.57 (0.12-0.78 C.I.) and unrelated to hatching size (ϕp_t -QAICc weight= 0.95, $\Delta QAICc= 5.9$). Again, recapture rates over the duration of the study were low ($p=0.09-0.28$). Thus, while size at hatching was unrelated to post hatching growth, larger neonates in the high-density sites accrued a survival advantage over smaller individuals and benefited from the fast growth opportunity produced by that presumably competitive post-hatching environment.

Discussion

Our data strongly support a mortality or predation driven pattern of growth in juvenile *E. macquarii* and reject the resource limitation hypothesis. The backwaters of the Murray River are highly productive environments (Shiel 1990) and despite an increase in juvenile density in several populations, growth trajectories and individual growth rates increased. Growth in *E. macquarii* therefore represents adaptive phenotypic plasticity, or a response to size-related differences in juvenile survival. Although plastron length at hatching was not a good predictor of growth rate, it predicted which turtles survived in the high-density population.

Rapid adaptive growth in the high-density population is related to size dependent mortality from competitive interactions or predation. Similarly, most life-history models have assumed that selection should favor a maximization of juvenile growth rate, because individuals with rapid growth have the potential to reach the largest possible size in the shortest possible time (Gotthard 2001). Under this hypothesis, growth rate is directly determined by the quality of the environment, which depends on factors such as food availability and ambient temperature (Gottard 2001). However, there is strong evidence of individuals growing at a lower rate than they are physiologically capable of achieving (Case, 1978; Arendt, 1997; Nylin and Gotthard, 1998; Bronikowski 2000). This sub-maximal pattern of growth is observed in the low-density population because high growth rates may actually be associated with a fitness cost and the optimal growth rate of an individual in this environment is not necessarily maximal (Gotthard 2001). Most models of optimal age and size at maturity have not incorporated the possibility that individuals adaptively adjust their growth by balancing it against juvenile mortality (reviewed in Roff, 1992; Stearns, 1992). Gilliam and Fraser (1987) suggested that the optimal growth strategy of an individual is to choose habitats that minimize the ratio of mortality rate (μ) and growth rate (g) – the ‘minimize μ/g ’ rule. Assuming a mean annual mortality rate of 0.59 and 0.43, the μ/g ratio was 2.95 and 3.07 in high and low-density populations, respectively (using estimated k values). These ratios are very similar, suggesting that growth may be optimal in both environments, at least at the population level.

Both theoretical and empirical studies of adaptive growth imply that high juvenile growth rates are likely to carry fitness costs, and in certain circumstances it is beneficial for individuals to grow more slowly (Gotthard et al., 1994; Skelly, 1994; Anholt and Werner, 1995; Abrams et al., 1996; Abrams and Rowe, 1996; Arendt, 1997; Nylin and Gotthard, 1998; Gotthard, 2000). Consequently, much of the observed variation in growth rate may be the result of an adaptive balancing of costs and benefits associated with growth, which may result in different optima in different environments (Gotthard 2001). The evolution of submaximal growth rates, particularly in environments conducive to rapid growth, suggests the existence of trade-offs with other fitness-related traits. Costs of rapid growth may be developmental, behavioral, or

physiological. Each of these costs implies that there is a direct increase in the amount of energy allocated to growth. Life-history theory predicts that the components of the energy budget (maintenance, growth, storage, and reproduction) compete with one another for available resources (Gadgil and Bossert, 1970). In some ectotherms, rapidly growing genotypes allocate a greater fraction of ingested energy to growth and less to maintenance (Malloy and Targett 1994, Imsland et al. 2000). In other species, rapid growth is achieved through higher rates of energy acquisition (Jonassen et al. 2000, Nieceza et al. 1994). Greater energy acquisition essentially requires changes in feeding behavior or a complete habitat shift, which increases risk taking to obtain food (Werner and Anholt 1993, Skelly 1996). Whereas diverting energy from other somatic processes to growth have long-term impacts on aging and longevity (Jonsson et al. 1992), energy storage (Forsman and Lindell 1991) and resistance to pathogens (Smoker 1986).

For an organism to be optimally adapted to its environment the life-history traits have to be coordinated. This co-ordination is reflected in the genetic and phenotypic correlation matrix, and hence phenotypic and genetic correlations are central to the study of life-history evolution (Charlesworth, 1980; Stearns, 1992; Roff, 1996). A number of life-history studies on neonatal turtle have described a positive link between body size and at least short-term survival, although a handful of experiments have not detected such a relationship (Janzen 1993; Janzen et al. 2000; but see Congdon et al. 1999). Our study highlights the context-dependency of size-related survival in turtles and thus may provide insight into the causes of variable results in these other studies. That is, where there is a premium on size, larger size should be favored by selection (e.g. when larger size minimizes exposure time to predation, maximizes handling time by predators, improves competitive ability during foraging). When turtle or predator density is low or resources are abundant, body size at hatching is unlikely to confer any fitness benefits.

Growth in reptiles is influenced by several factors, including egg size (Congdon and Gibbons 1985; Packard and Packard 1988; Steyermark and Spotilla 2001) and egg quality (Congdon and Gibbons 1985), which comprise maternal effects (Bernardo 1996). Other possible sources of variation in off-spring phenotype include environmental factors such as egg incubation temperature and substrate moisture

potential (Ewert 1985; Packard and Packard 1988). However, variation in post-hatching growth rates of reptiles is largely considered in terms of embryonic incubation conditions, while the potential for variation due to post-hatching developmental conditions and genetic effects has been largely ignored (Steyermark and Spotila 2001). Thermal and hydric conditions during incubation can influence locomotion (Miller et al. 1987, Burger 1990, Van Damme et al. 1992), olfaction (Burger 1991), defense (Burger 1998), growth (Joanen et al. 1987) and survival of hatchling ectotherms (de March 1995). The consequences of the incubation environment for offspring quality can last months (Burger 1989) or even years (Joanen et al. 1987, Roosenburg and Kelley 1996). Our experiments also revealed a remarkably long-term impact of the thermal conditions experienced during embryonic development on growth of turtles prior to maturity. Moreover, this thermal effect was manifested in turtles approaching maturity rather than in turtles closer to hatching, and was dependent on the population density in the post-hatching rearing environment. Why this pattern arose is not clear, but we can rule out one possible explanation. Most turtles have temperature-dependent sex determination, where, warm incubation temperatures yield females and cool incubation temperatures produce males (Ciofi and Swingland 1997). *Emydura macquarii* does not have this sex determining mechanism (Thompson 1988), so incubation temperature cannot be confounded with sex in this study. Hence, our results are not caused by sex-specific growth. We have also assumed males and females are distributed across all treatments, and we will explicitly deal with sex-specific differences in growth, once individuals reach maturity over the next five years.

We speculate that the delayed effect of incubation temperature on post-hatching growth may be linked to temporal changes in gene expression related to both developmental and environmental conditions. Historically, nearly all developmental phenomena were believed to be solely regulated by genes and signals within the embryo, with relatively little input from the environment. However, the environment plays a significant role in the development of most species, and animal genomes have evolved to respond to environmental conditions (Gilbert, 2001; West-Eberhard, 2004). Gilbert (2005) argues that environment can control phenotype during development by at least three major routes: the neuroendocrine system; as an

embryonic inducer; and as a transcriptional modulator. At five years of age, male *E. macquarii* in particular, are rapidly approaching the age of first reproduction (Spencer 2002b) and a whole suite of genes involved in maturity may be activated, some of which could exemplify the “fingerprint” of thermal conditions (e.g. differential methylation) experienced during embryonic development. This view is bolstered by evidence of a change in quantitative genetic architecture underlying growth in this experiment. At all ages we detected a strong positive genetic correlation between density treatments, but the slope of this relationship changed with age. Of particular note, larger turtles in the high-density treatment have slowed growth rates at age five, an indicator of the approaching onset of maturity. Concordantly, the genetic correlation between growth in the two density treatments at age five declined substantially because little variation in growth was present in the high-density turtles.

Although our experimental design cannot rule out possible non-genetic maternal effects on post-hatching growth, their influence is likely to be minimal in this study. In some turtles, the maternal effect of egg mass influences offspring size and subsequent post-hatching growth (e.g. Roosenburg and Kelley 1996, Janzen and Morjan 2002). Similarly, egg size is positively related to hatchling body size in *E. macquarii* (Judge 2001), but such non-genetic maternal effects appear not to affect post-hatching growth: we found that growth in all years was never dependent on hatching body size. Our findings accord with those noted in garter snakes, where maternal effects on body size at birth are important (Bronikowski and Arnold 1999), but negligible on neonatal growth (Bronikowski 2000). In addition, our transplant experiment was designed to minimize the influence of non-genetic maternal effects on among-clutch variation in juvenile growth, because hatchlings were obtained from females that inhabited a common environment.

In conclusion, our experimental populations experienced a dramatic change in demographic structure, as increased numbers of juveniles were recruited. At the same time, juveniles in these high-density populations were not resource limited, growing more rapidly and maturing earlier than young turtles in the control populations. This apparent phenotypic plasticity in growth and age at maturity is complemented by our observation of a strong, positive genetic correlation between individual growth in the

experimental and control populations ($rG = <+0.77$). Thus, these Australian pleurodiran turtle populations seem to have the impressive capacity to acclimate plastically to major demographic perturbations as well as enjoy the longer-term potential to evolve adaptively. These findings suggest that long-lived organisms possess two means for responding to substantial changes to population structure to maintain viability.

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Table 1. Results of two-way ANOVA of the effects of incubation temperature (Inc. Temp), and population density (Density) on growth (plastron length) rate at ages 2, 4 and 5 in *Emydura macquarii*. Significant values are bold.

Age 2	DF	SS	F	P
Inc. Temp	1	0.0	0.0	0.9
Den.	1	0.0	18	<0.001
Inc. Temp x Den.	1	0.0	1.1	0.3
Residual	16	0.0		
Total	19	0.1		

Age 4	DF	SS	F	P
Inc. Temp	1	0.0	0.9	0.4
Den	1	0.0	36	<0.001
Inc. Temp x Den	1	0.0	17	0.006
Residual	6	0.0		
Total	9	0.0		

Age 5	DF	SS	F	P
Inc. Temp.	1	0.0	28	<0.001
Den	1	0.1	53	<0.001
Inc. Temp x Den	1	0.0	7.1	0.013
Residual	24	0.0		
Total	27	0.1		

Table 2. Non-linear regression of recapture data from each control and treatment population (before and after fox removal) fitted to the von Bertalanffy logistic equations. *a*, asymptotic plastron length; *k*, characteristic growth parameter (Schoener and Schoener 1978), CL confidence limits. Growth constants were lower in the control site but increased after fox removal in the treatment sites.

Site	<i>k</i> (pre-fox removal)	<i>k</i> (post-fox removal)	<i>a</i> (pre-fox removal)	<i>a</i> (post-fox removal)
Bankview (control low-density)	0.12 (0.10-0.14 CL) (RMS= 8.1 n=101)	0.14 (0.13-0.16 CL) (RMS= 6.1 n=312)	219 (211-229 CL)	214 (208-224 CL)
Hawksview (treatment high-density)	0.11 (0.10-0.12 CL) (RMS= 6.3 n=115)	0.19 (0.18-0.21 CL) (RMS= 5.9 n=356)	221 (210-232 CL)	215 (206-224 CL)
Snowdon's (treatment high-density)	0.11 (0.09-0.13 CL) (RMS= 6.1 n=123)	0.22 (0.20-0.24 CL) (RMS= 4.9 n=332)	218 (209-227 CL)	212 (206-229 CL)

Fig. 1. Annual hatchling recruitment into low-density (open bars) and high-density (closed) populations bars between 1997-1999. Removal of foxes causes a 400% potential increase in hatchling recruitment.

Fig. 2. Size distribution histogram low-density (grey bars) and high-density (closed) sites from a catch in February 1997 (a) and February 2002 (b). hatchling turtles were released in February 1997 and 1998.

Fig. 3. Interaction between density and incubation temperature on growth at ages 2(a), 4(b) and 5(c) in *E. macquarii*. Plastron length was greater in high-density sites than low-density sites in most years. Incubation temperature affected growth in the high-density site in year four, but turtles incubated in the hot treatment (solid line) were larger than turtles incubated in the cold treatment (dashed line) in both high and low-density treatments.

Fig. 4. Genetic (family) correlation of growth across both density populations. A positive association between populations occurred in all years; however the slope of five year olds was significantly different from other years.

Fig. 5. Annual survival rate of hatchlings in relation to hatching size released into the high-density population (mean \pm 95%CI). Survival was related to hatching size in the high-density population (black), but was constant in the low-density population (grey). Confidence intervals for each population are shown as broken lines.









