

## Population Model Analysis for the Loggerhead Sea Turtle, *Caretta caretta*, in Queensland

Selina S. Heppell<sup>A</sup>, Colin J. Limpus<sup>B</sup>, Deborah T. Crouse<sup>C</sup>,  
Nat B. Frazer<sup>D</sup> and Larry B. Crowder<sup>A</sup>

<sup>A</sup>Department of Zoology, Box 7617, North Carolina State University, Raleigh, NC 27695, USA.  
Present address: Duke University School of the Environment, Marine Laboratory,  
135 Duke Marine Lab Road, Beaufort, NC 28516-9721, USA.

<sup>B</sup>Queensland Department of Environment and Heritage, PO Box 155, Brisbane, Qld 4002, Australia.

<sup>C</sup>Center for Marine Conservation, 1725 DeSales Street NW, Washington, DC 20036, USA.

<sup>D</sup>Savannah River Ecology Laboratory, PO Drawer E, Aiken, SC 29802, USA.

### Abstract

Worldwide declines of marine turtle populations have forced a need for sound conservation policies to prevent their extinction. Loggerhead turtles, *Caretta caretta*, are declining rapidly at eastern Australian nesting beaches, which are visited by females from all feeding areas for the stock. In some feeding areas of eastern Australia, loggerheads have been protected from deleterious anthropogenic effects. Using long-term mark–recapture data from one such protected group of turtles feeding on Heron Island Reef, Queensland, we created a matrix model to analyse loggerhead demography. We also produced a model for the females nesting at Mon Repos, Queensland, a major rookery where the annual nesting population has declined at rates approaching 8% per year. As indicated by a similar model for loggerheads in the USA, our models predicted that small declines in annual survival rates of adult and subadult loggerheads can have a profound impact on population dynamics. A loss of only a few hundred subadult and adult females each year could lead to extinction of the eastern Australian loggerheads in less than a century. Survival in the first year of life is relatively less important in these long-lived and slow-maturing animals. At Mon Repos, nesting female survival is apparently so low that even beach protection efforts resulting in 90% hatchling emergence success would not prevent population decline. Our research suggests that continued mortality pressure on subadult and adult turtles in their dispersed feeding areas of eastern and northern Australia is a major threat to the eastern Australian loggerhead turtle population. Measures that protect adult and subadult loggerhead turtles should be supported, including the use of turtle excluder devices (TEDs) on prawn trawls.

### Introduction

Marine turtles have suffered severe declines worldwide because of a number of human impacts, including over-exploitation through intentional harvest and incidental bycatch mortality in fisheries, habitat loss due to beach development and erosion, marine pollution and boat strikes (Dodd 1988; National Research Council, U.S. National Academy of Sciences 1990; Limpus and Reimer 1994). Unfortunately for most populations there is a dearth of information from which to plan for effective conservation. The marine turtle for which there exists probably the most comprehensive life-history database is the loggerhead turtle, *Caretta caretta*. In particular, loggerhead turtles have been the subject of intense study in Queensland, Australia, as well in south-eastern USA (Frazer 1983, 1986, 1987; Limpus 1985; Limpus and Reimer 1994). Because loggerheads are long-lived and have few natural predators, they are particularly susceptible to

adverse human effects (Crouse *et al.* 1987; Crowder *et al.* 1994). In addition, loggerheads take decades to mature (Frazer and Ehrhart 1985; Limpus 1990; Frazer *et al.* 1994), which makes it difficult to measure the effects of human disturbance on loggerhead population growth.

Significant advances in understanding loggerhead population function and demographics, especially with the eastern Australian population, have provided the present opportunity to re-examine the population dynamics of the species. The loggerhead turtles that breed in eastern Australia are genetically discrete from the Japanese nesting population, the other major nesting population of the Pacific basin (Bowen *et al.* 1995). The loggerhead turtles that nest on the coral cays of the southern Great Barrier Reef and the adjacent mainland beaches form a single interbreeding stock (Limpus *et al.* 1984; Limpus 1985; Gyuris and Limpus 1988). These loggerhead turtles migrate to nest at their eastern Australian rookeries from feeding grounds up to 2600 km distant (Limpus *et al.* 1992). Any one rookery is populated by females from many feeding grounds throughout the feeding range for the stock and females inhabiting any one feeding area will migrate to breed at many different rookeries for the stock (Bustard and Limpus 1971; Limpus 1989; Limpus *et al.* 1992, 1994). The adults share their shallow-water feeding grounds with large immature turtles (Limpus 1985; Limpus *et al.* 1994). The large immature loggerheads display considerable site fidelity to their respective feeding grounds and this fidelity continues even after they reach maturity and commence their breeding migrations (Limpus 1985, 1994). Eastern Australian adult loggerheads make breeding migrations from their feeding grounds to their respective rookeries at intervals of 2–7 years (Limpus 1985, unpublished data).

The annual nesting population of loggerhead turtles in eastern Australia has been declining rapidly over the past decade at all monitored rookeries (Limpus and Reimer 1994). This decline is not the result of mortality occurring only at the rookeries, but includes mortality that occurs over all the habitats that the females utilise, including feeding grounds away from their rookeries. The population changes recorded at the rookeries represent the summation of the changes occurring at all feeding grounds supplying females to the rookeries. At the Mon Repos rookery there has been an average decline in nesting female numbers of 7–8% annually (Limpus and Reimer 1994) with the overall decline in nesting females during an 11-year period (1978–1989) being a staggering 50%.

Because population dynamics of long-lived species are difficult to observe in the field, population models are useful tools for determining key life-history components and guiding conservation management policy. Frazer (1986) developed a life table for loggerheads nesting on Little Cumberland Island, Georgia, USA. Reduced survival rates of large turtles, primarily due to incidental drowning in shrimp trawls, had resulted in an estimated population decline of 3% per year based on censuses of nesting females. The life table was later reduced to a 7-stage matrix model, in which turtles were grouped into size-classes (Crouse *et al.* 1987). A sensitivity analysis of parameters in the matrix model suggested that annual survival of large juvenile turtles was most critical to population growth, while survival of eggs and hatchlings was far less critical. Even when first-year survival was increased to 100%, the model population continued to decline. These results are confirmed in an updated model (Crowder *et al.* 1994) and have influenced management policy for marine turtle conservation in the USA.

In this study, we used deterministic matrix models to analyse the demography of (1) the currently stable group of loggerheads that are resident of Heron Reef and (2) a declining group of nesting females at Mon Repos, Queensland. We identified which parameters have the greatest impact on population growth, then examined the effect of reductions in subadult and adult survival in the Heron Reef model. Finally, because of concern over fox predation of loggerhead eggs on mainland beaches (Limpus and Reimer 1994) we simulated a severe loss of clutches to fox predation and compared the conditions necessary for recovery within the stable and declining population models.

## Methods

### Data Collection and Model Parameterisation

The data used in our first model were collected for Heron Reef loggerheads captured by the turtle rodeo method in February–May 1978–1992 [for a detailed description of the Heron Reef study site and capture methods, see Limpus and Reed (1985)]. Individuals had their gonads examined by laparoscopy to determine sex, maturity and breeding condition. Three classes of turtles were determined by the maturity of reproductive organs, as described for green turtles, *Chelonia mydas* (Limpus and Reed 1985) and hawksbill turtles, *Eretmochelys imbricata* (Limpus 1992): prepubescent immature turtles with immature gonads (SA), pubescent immature turtles undergoing sexual maturation (SP) and adults that had ovulated at least once. We calculated the number of years spent in the SA and SP stages (six and eight years, respectively) by averaging measured stage durations for turtles that were observed changing status. These durations are likely to be underestimates, because the Heron Reef study is less than 20 years old and few individuals have been observed to mature in that time.

To estimate annual survival probabilities for each maturity class, we analysed mark–recapture information from Heron Reef females using the Cormack–Jolly–Seber approach (Pollock *et al.* 1990; Lebreton *et al.* 1992). To approximate the Cormack–Jolly–Seber assumption of no deaths or migrations during the sampling period, we restricted our analysis to captures made during February–May, when more than 80% of recaptures occurred. We estimated annual survival for each reproductive stage (SA, SP and adult) using a computer program (JOLLY) supplied by Dr Ken Pollock, North Carolina State University Department of Statistics. We used mean survival rates estimated by Model A, which assumes that capture probability and survival vary from year to year, because this model provided the best goodness-of-fit tests for all three reproductive stages (Appendix 1) (Pollock *et al.* 1990).

On the nesting beaches of the Woongarra coast, which includes Mon Repos, we used recapture information for tagged adult females from 1979 to 1987. The mean annual survival rate for adult females was estimated from the mean remigration interval for surviving females and the probability of recapture. Annual survival rates for adult females nesting on Mon Repos were calculated from the probability of recapture (the proportion of turtles resighted,  $p$ ) and the mean remigration interval (the mean number of years between breeding seasons,  $n$ ) by taking the  $n$ th root of  $p$  (annual survival =  $p^{1/n}$ ). Monitoring efforts at Mon Repos and adjacent beaches ensured that effectively every nesting female was observed (Limpus 1985) and multiple tagging and the use of titanium tags reduced the possibility of tag loss (Limpus 1992). We limited our calculation to turtles nesting prior to 1987 to reduce bias in the estimate from turtles with particularly long remigration intervals. Thus, we feel that our estimate of annual survival was reliable. We did not use the Cormack–Jolly–Seber approach for these turtles because the probability of recapture was confounded by long remigration intervals.

### Model Development

Our models were square transition matrices that contained survival, growth and fecundity values calculated for a 1-year period. The stage-based models had four classes: pelagic juveniles, subadult prepubescents (SA), pubescents and virgin adults (SP), and adults. There were two major differences between our models and the one used by Crouse *et al.* (1987). First, the Australian loggerhead model stages were based on reproductive condition rather than size; we suggest that this is a more accurate classification (when such information is available), as sea turtles have highly variable growth rates and can mature at a wide range of sizes. Second, our models did not include an egg/hatchling stage. First-year survival was incorporated into the fecundity term; thus, our models described birth-pulse populations with a pre-breeding census (Caswell 1989). In the model simulations, the 'census' took place just before nesting.

Adult fecundity (defined as the number of 1-year-old juvenile females produced per adult female) was calculated on an annual basis from the following relationship:

$$F = \frac{N \times C}{R} \times \sigma_n \times \sigma_n,$$

where  $F$  is the mean annual fecundity,  $N$  is the mean number of nests,  $C$  is the mean number of eggs per nest,  $R$  is the mean remigration interval (the average number of years between nesting seasons) and  $\sigma$  is the survival probability for nests ( $\sigma_n$ ) and hatchlings ( $\sigma_n$ ). We estimated the mean annual fecundity for loggerheads in Queensland to be 32.54 female hatchlings (based on an overall primary sex ratio of 1:1)

**Table 1. Stages used in the models for Australian loggerhead sea turtles, their annual survival estimates and durations**

The number of recaptures used in the Cormack–Jolly–Seber analysis (Heron Reef) or nesting female survival estimation (Mon Repos) appear in parentheses; stages without a specified sample size have survival estimated by matrix analysis (juveniles) or estimation (see text). SP stage includes mature virgin turtles that have not yet bred

Stage	Heron Reef annual survival	Mon Repos annual survival	Stage duration (years)
Juveniles	0.827	0.827	20
Subadults (SA)	0.8295 (81)	0.7127	6
Pubescents (SP)	0.8853 (109)	0.7606	8
Adults	0.9102 (195)	0.782 (557)	No limit

(data from Limpus 1985). Annual survival rates for SA, SP and adult females were taken directly from the Cormack–Jolly–Seber analysis, but the survival rates for pelagic juvenile turtles were unknown. Using a von Bertalanffy growth curve, Frazer *et al.* (1994) estimated the mean age at maturity of loggerheads to be 35 years; thus, we used an estimated duration of the pelagic juvenile stage of 20 years (Table 1) (the first year of life is incorporated into the fecundity term). We estimated annual survival for these juveniles by calculating the survival rate necessary to achieve a population growth rate of 0% per year for the Heron Reef population. This survival rate was assumed to be the same for turtles originating at Mon Repos and for the Heron Reef turtles prior to their arrival at the feeding area because the juveniles for the entire stock were presumed to lead a pelagic life far out to sea.

#### Model Analysis

Details on matrix algebra and sensitivity analyses may be found in Caswell (1989). We provide a brief discussion of parameterisation methods and equations in Appendix 2. The stage-based matrix entries occurred on the diagonal ( $P_i$ , the probability of surviving and remaining in a stage), on the subdiagonal ( $G_i$ , the probability of surviving and growing into the next stage) and on the top row ( $F_i$ , fecundity). We assumed that all individuals within a stage were identical, and that a fixed proportion of individuals grew into the next stage each year. The finite rate of population increase,  $\lambda$ , was the annual multiplication rate for the model population given that mean survival, growth and reproductive rates remained constant, and that the population was at a stable age or stage distribution (constant proportion of individuals in each stage). This population growth term is related to the intrinsic rate of increase,  $r$ , which is often calculated in life-table analyses [ $r = \ln(\lambda)$ ]. The elasticity of a matrix parameter is the proportional change in  $\lambda$  following a per cent increase or decrease in that parameter (Appendix 2). This proportional sensitivity analysis uses the stable stage distribution given by the right eigenvector of the matrix, and the stage-specific reproductive values given by the left eigenvector of the matrix with the first-stage reproductive value set at 1.0. We used the elasticity values to compare the relative impact of stage-specific survival, growth and fecundity on population growth.

#### Simulations Using Age-based Models

After analysing each stage-based model, we expanded the  $4 \times 4$  stage-based matrices into  $35 \times 35$  age-based matrices with each row and column representing a single year in a turtle's life to adulthood. Simulations using age-based matrices (also called Leslie matrices) reveal short-term, transient effects induced by changes in matrix parameters (Crowder *et al.* 1994). In particular, the age-based models show population responses to the long time-lag between birth and reproduction. The final row/column of our  $35 \times 35$  matrices represented the adult stage; thus, unlike a true Leslie model, the adult survival rate appeared in the lower right-hand corner of the matrix. We chose this type of matrix because all adult turtles were assumed to have the same annual survival probability and the lifespan of sea turtles is unknown. Because our simulations did not incorporate annual variability in survival or growth rates, the trajectories represented hypothetical population sizes under constant conditions and should be regarded qualitatively.

We simulated a series of hypothetical harvest regimes on the Heron Reef group to compare the population trajectories as a constant number of SA, SP and adult turtles were removed. For these

simulations, the initial population was assumed to have 5000 adult females (which would approximate to the current size of the eastern Australian *annual* nesting population of about 1200 females). The number of turtles in the remaining age-classes was calculated from the stable age distribution of an 'undisturbed population' represented by the Heron Reef matrix; assuming a constant distribution of turtles in each age-class, the total population size at time zero of each simulation was 946 000 turtles. We simulated harvest quotas of 50, 100, 250, 500 and 1000 female turtles each year. The harvested turtles were split into maturity classes (SA, SP, adult) in a ratio of 3 : 1.3 : 1, as determined by the stable age distribution.

We used the same age-based models to simulate the impacts of fox predation and nest-protection efforts. Each of these factors affected annual fecundity. A 90% loss of nests to foxes for a 10-year period was assumed, to simulate past clutch losses along a significant portion of the mainland nesting beaches near Mon Repos (Limpus and Reimer 1994). Following this period, we assumed that fecundity levels returned to their pre-fox invasion level (32.54 female hatchlings per year) or increased because of beach-protection efforts (43.068 female hatchlings per year; nest protection = 90% of clutches survive). We simulated these changes in fecundity as a hypothetical case for the undisturbed population represented by the Heron Reef model, as well as our current estimates for the declining population represented by the Mon Repos model.

## Results

### *Annual Survival and Population Growth Rate at Mon Repos*

Our estimates were catchability ( $p$ ) = 0.402, remigration interval ( $n$ ) = 3.7 years and annual survival probability = 0.782. This reflects a 14% reduction in survival compared with adult females in the protected population at Heron Reef. For the Mon Repos model, we reduced SA and SP survival by 14% as well, thus assuming that mortality factors affecting adults have a similar effect on pubescent and prepubescent turtles living in the same feeding areas (Table 1).

The Heron Reef model was calculated for a stable population; thus, its intrinsic rate of increase ( $r$ ) is zero [ $r = \ln(\lambda)$ , so  $\lambda = 1.0$ ] (Table 2). The Mon Repos model predicted a population decline of 7.65% per year ( $r = -0.07653$ ,  $\lambda = 0.92633$ ). This decline is similar to the observed 7–8% annual decline of nesting females on Mon Repos from 1978 to 1989 (Limpus and Reimer 1994).

### *Model Results and Elasticity Analysis*

The stable stage distributions and reproductive values of the two populations were slightly different (Figs 1, 2). In particular, there was a greater proportion of prepubescent immatures but fewer adult turtles in the Mon Repos model.

**Table 2. Annual transition matrices for loggerhead sea turtles on Heron Reef and Mon Repos, Queensland**

$\lambda$  = dominant eigenvalue of the matrix;  $\ln(\lambda) = r$  = intrinsic rate of increase of the population. Although both models have the same juvenile survival rate, the first column of the Mon Repos model has slightly different values because of the change in  $\lambda$  (see Appendix)

	From juvenile	From SA	From SP	From adult
Heron Island ( $\lambda = 1.0$ , $r = 0.0$ )				
To Juvenile	0.823	0	0	32.54
To SA	0.004	0.747	0	0
To SP	0	0.082	0.816	0
To adult	0	0	0.070	0.910
Mon Repos ( $\lambda = 0.9263$ , $r = -0.0765$ )				
To juvenile	0.816	0	0	32.54
To SA	0.012	0.657	0	0
To SP	0	0.056	0.717	0
To Adult	0	0	0.043	0.782

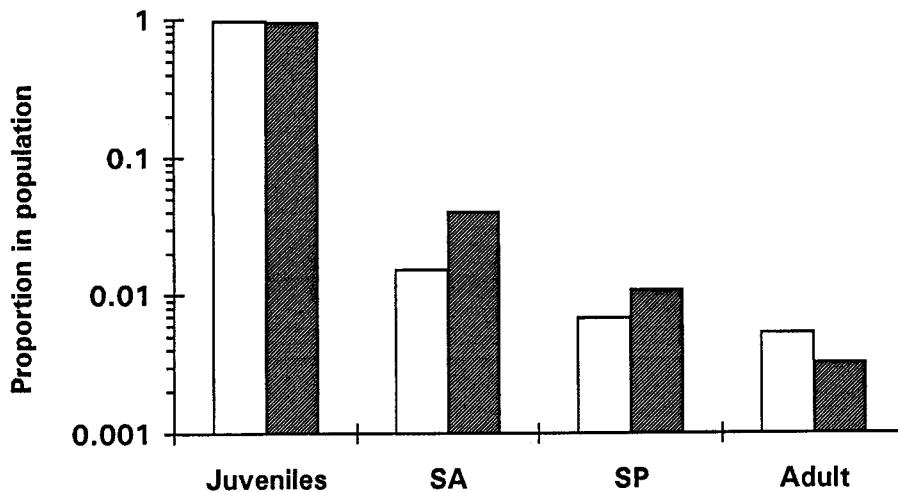


Fig. 1. Stable stage distributions of two matrix population models for Australian loggerhead sea turtles. Models were based on survival rates for turtles feeding at Heron Reef (open bars) or nesting at Mon Repos, Queensland (shaded bars). The stable stage distribution gives the proportion of individuals in each life-history stage once the population has reached a stable distribution and constant growth rate.

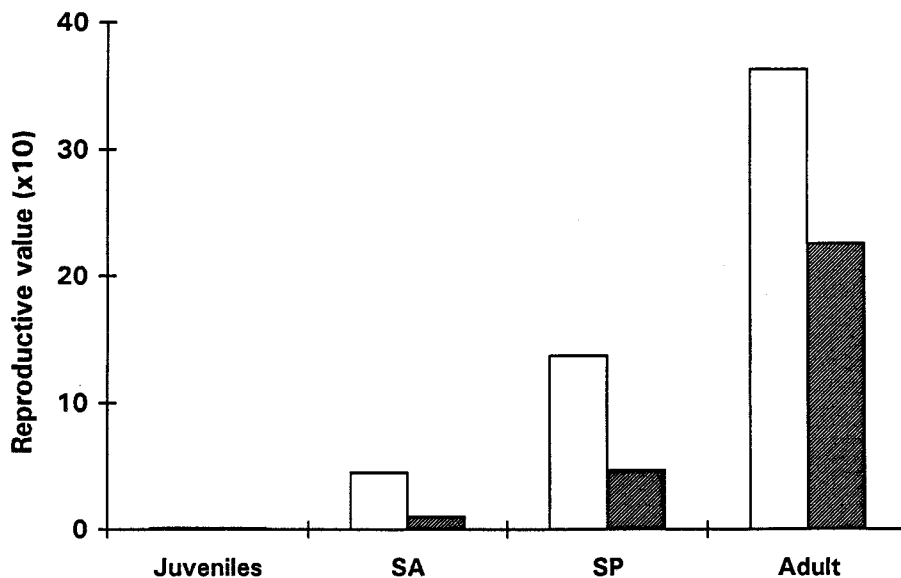


Fig. 2. Stage-specific reproductive values for two matrix population models for Australian loggerhead sea turtles. Models were based on survival rates for turtles feeding at Heron Reef (open bars) or nesting at Mon Repos, Queensland (shaded bars). Reproductive values are determined by survival and fecundity probabilities once the population has reached a stable distribution and constant growth rate.

We calculated the proportional effect of changes in the model parameters on the population growth rate ( $\lambda$ ) using an elasticity analysis (Caswell 1989) (Appendix 2). Differences in the stable stage distributions and reproductive values affected the elasticity values of the two matrices (Fig. 3). As with the US loggerhead population model, the growth rates of both

populations were much more sensitive to the probability of surviving and remaining in a stage ( $P$ ) than growth ( $G$ ) or fecundity ( $F$ ). The peak elasticity shifted from adult survival to pelagic juvenile survival when large turtles were exploited in the Mon Repos model. In both populations, the impact of egg and hatchling survival was minimal (recall that first-year survival is incorporated into the fecundity term). Annual survival for the pelagic juvenile stage had a very high elasticity value in both models, mainly because most of the population is in this stage (Fig. 4). Low survival rates for adults in the Mon Repos population have led to a shift in the relative

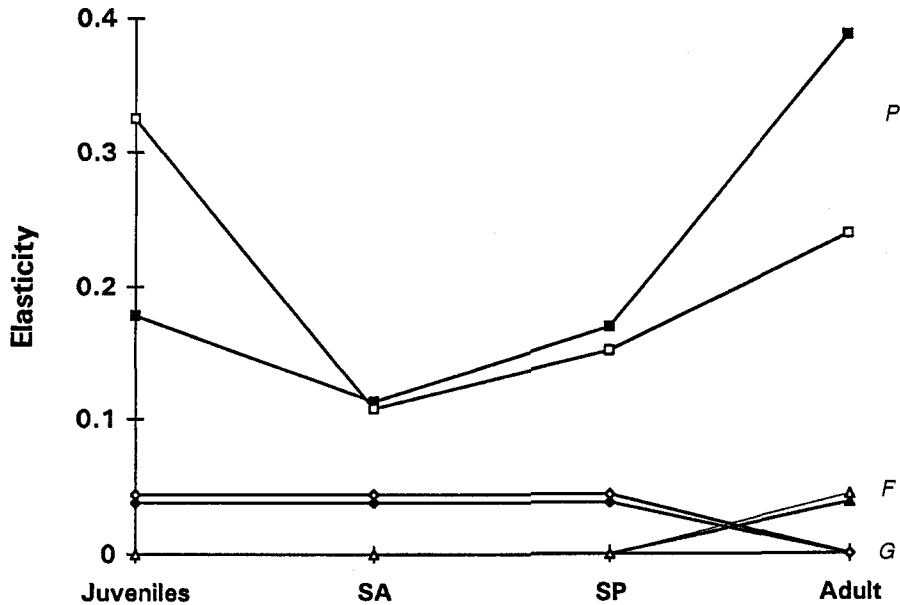


Fig. 3. Elasticities of each matrix parameter in two population models for Australian loggerhead sea turtles. Models were based on survival rates for turtles feeding at Heron Reef (closed symbols) or nesting at Mon Repos, Queensland (open symbols).  $P$  is the probability of surviving and remaining in a stage,  $G$  is the probability of surviving and growing into the next stage and  $F$  is fecundity. Elasticity is the proportional change in the population growth rate ( $\lambda$ ) following a per cent change in a matrix parameter (see Appendix 2).

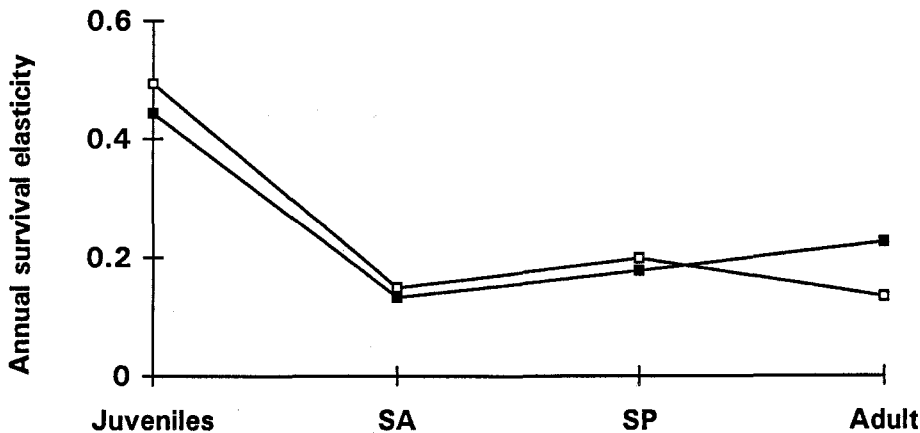
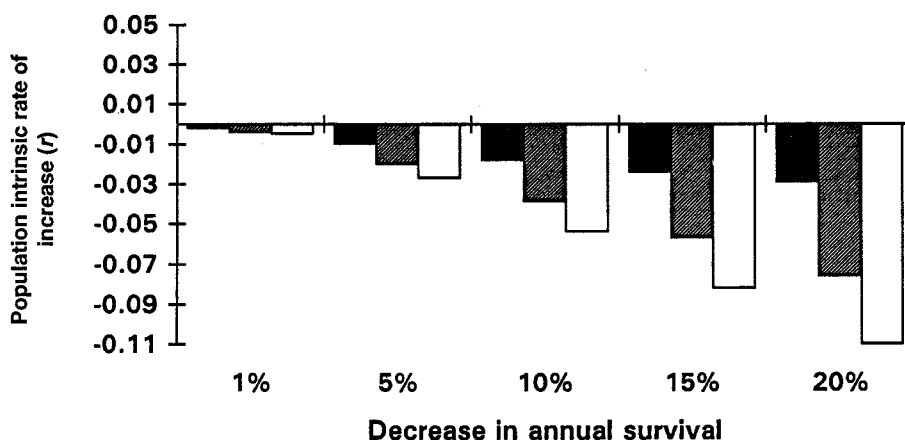


Fig. 4. Annual survival elasticities in two population models for Australian loggerhead sea turtles. Models were based on survival rates for turtles feeding at Heron Reef (■) or nesting at Mon Repos (□), Queensland.

contribution of that stage to population growth. In the unexploited population on Heron Reef, adult survival had a higher elasticity than survival of prepubescent or pubescent immature turtles.

Decreasing the survival rate of large immature (SA, SP) and adult loggerheads in the Heron Reef model led to rapid population decline (Fig. 5). If all three stages were impacted, the population declined by as much as 11% per year with heavy exploitation. When adults were the only affected stage, the reduction in the intrinsic rate of increase was less severe. As shown by the elasticity analysis of the Mon Repos model, when adult survival decreased, its relative impact on population growth decreased. When adult and SP stages were both affected, a decrease in survival of as little as 10% resulted in a model population decline of 4% per year. We estimated that the annual survival rate at Mon Repos was 14% lower than that at Heron Reef.



**Fig. 5.** Changes in the intrinsic rate of increase ( $r$ ) estimated for a model population of Australian loggerhead sea turtles as annual survival rates decreased. Stage-specific reductions in annual survival probability were for adults only (solid bars), adults and pubescents (SP) (shaded bars), and for adults, pubescents and pre-pubescents (SA) (open bars).

### Simulation Results

When a constant number of turtles were removed from the population our age-based model projections showed a 'bump' in the frequency of adult females every 35 years, as a new generation reached adulthood (Fig. 6). Removing a total of 100 SA, SP and adult female turtles each year resulted in a gradual decline. This harvest rate included only 19 adult females, or 0.4% of the initial adult female population of 5000 animals. The estimated sex ratio for loggerheads at Heron Reef was 29% female (Limpus 1985); thus, a harvest of 100 females equalled a total harvest of approximately 345 turtles. Greater harvest rates resulted in severe population declines (Fig. 6).

The impact of fox predation on nests during the 1970s may have created a 'hole' in loggerhead populations originating from mainland nesting beaches. Because loggerheads take about 35 years to mature, we may not see a decline in first-time nesting females for another decade. Our age-based model projections showed the transient effect of a 10-year nest loss on the number of adult females in a simulated population that started with 5000 adult females (Fig. 7). As with the harvest projection, 'waves' occurred in the population as the cohorts affected by predation reached maturity. Egg protection, which increased fecundity, allowed the unexploited turtles (represented by the Heron Reef model) to recover and even increase, but the exploited turtles (represented by the Mon Repos model) did not recover with egg protection.



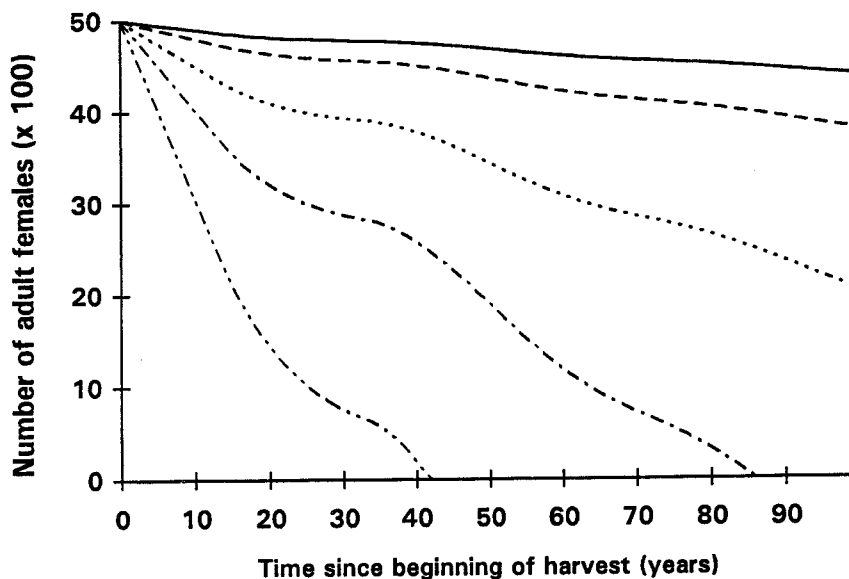


Fig. 6. Changes in the number of adult females with harvest in a model population of Australian loggerhead sea turtles. Simulations were with an age-based model that used survival rates calculated for turtles feeding at Heron Reef. Harvest rates were 50 (—), 100 (---), 250 (.....), 500 (- · - · - ·) and 1000 (- - - - -) female turtles, divided into prepubescent (SA), pubescent (SP) and adult stages according to the stable age distribution given by the model.

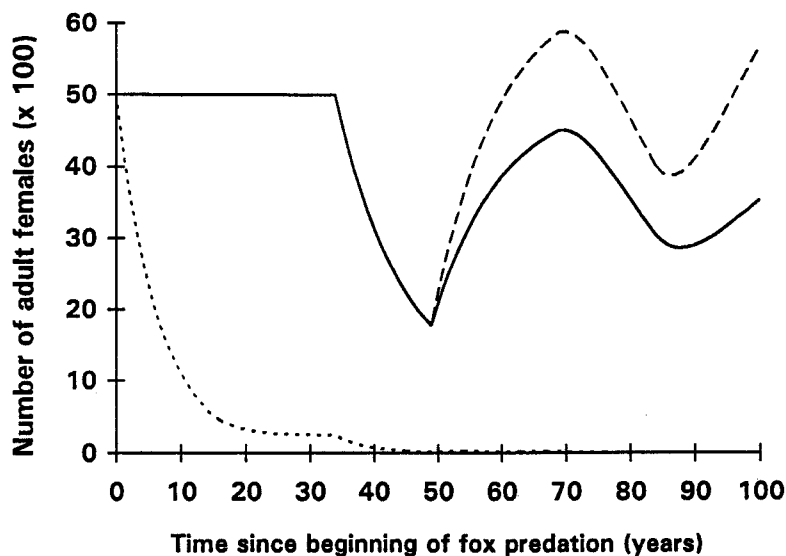


Fig. 7. Simulated changes in the number of adult females following fox predation on nests and subsequent beach protection in two model populations of Australian loggerhead sea turtles. Predation impact of 90% nest loss lasted for 10 years. The age-based model for turtles feeding at Heron Reef gradually stabilised if annual fecundity returned to pre-fox levels (—), or increased if beach protection resulted in a fecundity increase (---). The age-based model for females nesting at Mon Repos showed a decline in adult females in spite of beach protection (.....).

## Discussion

Matrix models, while highly simplified descriptors of population dynamics, are powerful analytical tools that have provided insight in several conservation applications (Simons 1984; Crouse *et al.* 1987; Noon and Biles 1990; Brault and Caswell 1993; Crowder *et al.* 1994; Heppell *et al.* 1994). Our models for Australian loggerheads did not include environmental or demographic stochasticity, nor did they incorporate density dependence. At this time, we do not have enough information to calculate year-to-year variability in survival and growth rates nor the covariance of these parameters; thus, a stochastic model to estimate extinction probability would be highly speculative at best. Instead, we offer these simple models and projections to compare population declines given current conditions and the transient demographic effects that are intrinsic to these slow-maturing turtles. We used the intrinsic rate of increase as an index of population health and sensitivity to change, rather than a predictor of future population size. In a comparison of stochastic and deterministic elasticity analyses, Dixon *et al.* (in press) found that the elasticities of a model that incorporates environmental variability are qualitatively identical to a deterministic model calculated from mean survival and growth rates.

The elasticity analyses presented here yield important information about the kinds of conservation policies that are likely to protect loggerhead populations in Australia. Survival rates affected population growth far more than did fecundity and somatic growth rates, a result obtained by Crouse *et al.* (1987) for US loggerheads. While this does not imply that beach protection efforts are unnecessary, it is unlikely that improving egg and/or hatchling survival will be sufficient to prevent extinction at mainland rookeries. Egg-protection measures on Mon Repos beach (or at other rookeries) or reduction in fox predation on turtle eggs at Wreck Rock Beaches will have little or no effect on the population unless subadult and adult survival is also improved in their dispersed feeding areas.

Life-history theory suggests that, in order to compensate for their extremely long juvenile period, adult loggerhead sea turtles must have high annual survival, be iteroparous and have high fecundity (Congdon and Gibbons 1990; Iverson 1991). Our models showed that small reductions in large turtle survival can have drastic effects on the population growth rate. As the annual survival rate of adults decreased, adult survival elasticity went down. However, this does not mean that adults became 'less valuable'; rather, it indicates that once the population reached a stable state (constant annual decrease) the value of subadult turtles became relatively greater. A similar result was found by Crouse *et al.* (1987) for loggerheads in US Atlantic waters. Because of life-history constraints that include an extremely long generation time, sea turtles are unlikely to compensate for mortality sources that concentrate on maturing and adult turtles.

When stage-specific annual survival rates change systematically over a short time, as with the impact of fox predation or trawler mortality, it becomes difficult to make accurate long-term population projections. The Heron Reef loggerhead study provides the best estimates for survival, growth and fecundity rates in an unexploited population. While other loggerhead populations, such as those in the south-eastern USA, have genetic differences and live in different environments, it is likely that they are capable of the same high survival rates observed in the Heron Reef population (Crowder *et al.* 1994). Reductions in the number of stranded loggerheads in South Carolina, USA, observed since the introduction of Turtle Excluder Devices (TEDs), suggest that these turtles have high natural survival rates (Crowder *et al.* 1995). Finally, a number of freshwater and terrestrial turtle studies have estimated annual adult survival rates of greater than 0.9 (for review, see Iverson 1991).

In the USA, loggerhead population declines have been linked to incidental harvest by trawling industries, most notably shrimp trawlers (Henwood and Stuntz 1987; National Research Council, US National Academy of Sciences 1990). In addition to beach and nest protection, current legislation requires the use of TEDs on all shrimp trawls at all times of the year (Crouse 1993). Further model analysis and population projections indicate that effective use of TEDs in US waters could lead to population recovery in the next 30–40 years, provided that no new mortality

sources appear (Crowder *et al.* 1994). The introduction of TEDs has contributed to a significant decline in sea turtle strandings (dead turtles washed up on shore) in south-eastern USA. Strandings have declined by approximately 44%, although it is far too soon to tell whether this will be a lasting trend (Crowder *et al.* 1995).

Because our models denote stages by sexual maturation instead of body size, a formal comparison with the US loggerhead stage-based model (Crouse *et al.* 1987; Crowder *et al.* 1994) is not feasible. Also, because some turtles exhibit very long remigration intervals, our annual survival estimate for Mon Repos females may be somewhat biased. However, declining adult populations in Australia are probably due to increases in mortality of adult and near-adult loggerheads that live together in the coastal waters of northern and eastern Australia. The trawling industry of these waters could have caused the deaths of many hundreds or possibly thousands of loggerheads annually (Limpus and Reimer 1994; Poiner and Harris 1994). Other sources of mortality would also contribute to the total losses for the eastern Australian stock, including accidental and intentional killing within crab fisheries, boat strike, ingestion of debris and traditional harvests in neighbouring countries. Our study indicated that the combined loss from all sources of only hundreds of adult and subadult loggerheads annually within the eastern Australian nesting stock could be sufficient to cause their extinction within a few generations.

A reduction in hatchling production at the mainland loggerhead rookeries may have far-reaching impacts on population dynamics throughout Queensland. Loggerheads have temperature-dependent sex determination and beach-sand temperatures influence the primary sex ratio (Yntema and Mrosovsky 1980). Mainland beaches tend to be warmer than island beaches, producing a preponderance of female hatchlings (Limpus *et al.* 1985). While the entire Queensland metapopulation is thought to have a 1:1 primary sex ratio, this may become skewed toward males with increased egg mortality at the beaches producing mostly female hatchlings. Evidence for this effect may be apparent already in the sex ratio of prepubescent (SA) turtles arriving to take up residency at Heron Reef. These approximately 20-year-old turtles are likely to be the first of the cohorts impacted by heavy fox predation on mainland beaches in the 1970s. Less than 10% of new turtles observed at Heron Reef are female, and fewer turtles overall have been arriving over the last two years to 1992 (Limpus, unpublished data). Because fox predation may have led to a massive reduction in the number of females born in the 1970s, very small cohorts may be maturing by the turn of the century. The potential for extinction of this loggerhead stock may have been increased by the past intense fox predation of the eggs, particularly if adult and subadult turtle mortality remains high in the feeding areas.

Effective conservation of loggerhead turtles in Australia should include management regimes that give a high priority to eliminating anthropogenic-induced mortality of adult and large immature loggerhead turtles. This action should be directed to the turtles in their dispersed feeding areas, migratory routes and internesting habitats, given that there is no significant adult mortality occurring on the nesting beaches (Limpus and Reimer 1994). The use of TEDs in Australian prawn fisheries has the potential for eliminating annual kills of hundreds of large loggerhead turtles (Poiner and Harris 1994). However, the other sources of anthropogenic-induced mortality of adult and large immature loggerheads should be investigated and appropriate management practices developed and implemented to substantially reduce this mortality.

### Acknowledgments

The field studies in Australia were conducted as part of the Queensland Turtle Research Project of the Queensland Department of Environment and Heritage and have been supported in part by grants from the Australian Nature Conservation Agency and the Great Barrier Reef Marine Park Authority. Assistance in transport and field accommodation has been provided by P&O Resorts, Heron Island and Jim McCutcheon of the Turtle Sands Caravan Park. Computing equipment was provided by Epson Australia and 3M Australia. The capture, tagging and measurement of the turtles was achieved by the assistance of many dedicated staff and

voluntary assistants including Gail Duncan, Alison and Helen Limpus, Valonna Baker, Annette Fleay, Phil Read, Dr Jeff Miller, John Meech, Mark Deakon and the late Darryl Reimer. Graham Rawlins assisted in establishing the computerised database used in the project. For those components of the project undertaken in the USA, funds were provided by the National Oceanic and Atmospheric Administration, National Marine Fisheries Service and University of North Carolina Sea Grant (R/MER-21 and NOAA/NMFS NA90AA-D-S6847). S. Heppell was supported by a National Science Foundation Pre-doctoral Fellowship. Andy Royle provided statistical consulting and initial Cormack–Jolly–Seber results. Thanks are also due to the Center for Marine Conservation (D.T.C.), Greenpeace (N.B.F.) and the Department of Energy (N.B.F.). This assistance is gratefully acknowledged.

## References

- Bowen, B. W., Kamezaki, N., Limpus, C. J., Hughes, G. R., Meylan, A. B., and Avise, J. C. (1994). Global phylogeography of the loggerhead turtle (*Caretta caretta*) as indicated by mitochondrial DNA haplotypes. *Evolution* **48**, 1820–8.
- Brault, S., and Caswell, H. (1993). Pod-specific demography of killer whales (*Orcinus orca*). *Ecology* **74**, 1444–54.
- Bustard, H. R., and Limpus, C. J. (1971). Loggerhead turtle movements. *British Journal of Herpetology* **4**, 228–30.
- Caswell, H. (1989). 'Matrix Population Models.' (Sinauer Associates: Massachusetts.)
- Congdon, J. D., and Gibbons, J. W. (1990). The evolution of turtle life histories. In 'Life History and Ecology of the Slider Turtle'. (Ed. J. W. Gibbons.) pp. 45–54. (Smithsonian Institution Press: Washington, DC.)
- Crouse, D. T. (1993). Victory! TEDs required in all U.S. shrimp trawls. *Marine Turtle Newsletter* **61**, 3–5.
- Crouse, D. T., Crowder, L. B., and Caswell, H. (1987). A stage-based population model for loggerhead sea turtles and implications for conservation. *Ecology* **68**, 1412–23.
- Crowder, L. B., Crouse, D. T., Heppell, S. S., and Martin, T. H. (1994). Predicting the impact of turtle excluder devices on loggerhead sea turtle populations. *Ecological Applications* **4**, 437–45.
- Crowder, L. B., Hopkins-Murphy, S. R., and Royle, J. A. (1995). Effects of Turtle Excluder Devices (TEDs) on loggerhead sea turtle strandings with implications for conservation. *Copeia* **1995**, 773–9.
- Dixon, P., Friday, N., Ang, P., Heppell, S., Kshatriya, M., and Lord, C. (1996). Sensitivity analysis of structured population models for management and conservation. In 'Structured Population Models'. (Eds H. Caswell and S. Tuljapurkar.) (Chapman and Hall: New York.)
- Dodd, C. K. D. (1988). Synopsis of the biological data on the loggerhead sea turtle (*Caretta caretta*) (Linnaeus 1758). US Fish and Wildlife Service Biological Report No. 14.
- Frazer, N. B. (1983). Demography and life history of the Atlantic loggerhead sea turtle (*Caretta caretta*). Ph.D. Thesis, University of Georgia.
- Frazer, N. B. (1986). Survival from egg to adulthood in a declining population of loggerhead turtles (*Caretta caretta*). *Herpetologica* **42**, 47–55.
- Frazer, N. B. (1987). Preliminary estimates of survivorship for wild loggerhead sea turtles (*Caretta caretta*). *Journal of Herpetology* **21**, 232–5.
- Frazer, N. B., and Ehrhart, L. M. (1985). Preliminary growth models for green (*Chelonia mydas*) and loggerhead (*Caretta caretta*) turtles in the wild. *Copeia* **1985**, 73–9.
- Frazer, N. B., Limpus, C. J., and Green, J. (1994). Growth of loggerhead sea turtles in Australian waters. Paper presented at the 14th Annual Symposium of Sea Turtle Biology and Conservation, 2–5 March 1994, Hilton Head, South Carolina.
- Gyuris, E., and Limpus, C. J. (1988). The loggerhead turtle, *Caretta caretta*, in Queensland: population breeding structure. *Australian Wildlife Research* **15**, 197–209.
- Henwood, T. A., and Stuntz, W. E. (1987). Analysis of sea turtle captures and mortalities during commercial shrimp trawling. *Fisheries Bulletin* **85**, 813–17.
- Heppell, S. S., Walters, J. R., and Crowder, L. B. (1994). Evaluating management alternatives for red-cockaded woodpeckers: a modeling approach. *Journal of Wildlife Management* **53**, 479–87.
- Iverson, J. B. (1991). Patterns of survivorship in turtles (Order Testudines). *Canadian Journal of Zoology* **69**, 385–91.

- Lebreton, J. D., Burnham, K. P., Clobert, J., and Anderson, D. R. (1992). Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. *Ecological Monographs* 62, 67–118.
- Limpus, C. J. (1985). A study of the loggerhead sea turtle, *Caretta caretta*, in eastern Australia. Ph.D. Thesis, University of Queensland, Brisbane.
- Limpus, C. J. (1989). Foraging area fidelity following breeding migrations in *Caretta caretta*. NOAA Technical Memorandum NMFS-SEFC-232, pp. 81–3.
- Limpus, C. J. (1990). Puberty and first breeding in *Caretta*. NOAA Technical Memorandum NMFS-SEFC-278, pp. 97–9.
- Limpus, C. J. (1992). The hawksbill turtle, *Eretmochelys imbricata*, in Queensland: population structure within a southern Great Barrier Reef feeding ground. *Wildlife Research* 19, 489–506.
- Limpus, C. J. (1994). The loggerhead turtle in Queensland: feeding ground selection following her first breeding season. NOAA Technical Memorandum NMFS-SEFC-351, pp. 78–81.
- Limpus, C. J., and Reed, P. C. (1985). The green turtle, *Chelonia mydas*, in Queensland: a preliminary description of the population structure in a coral reef feeding ground. In 'Biology of Australasian Frogs and Reptiles'. (Eds G. Grigg, R. Shine and H. Ehmann.) pp. 47–52. (Surrey Beatty and Sons: Sydney.)
- Limpus, C. J., and Reimer, D. (1994). The loggerhead turtle, *Caretta caretta*, in Queensland: a population in decline. In 'Proceedings of the Australian Marine Turtle Conservation Workshop'. (Compiler R. James.) pp. 39–59. (Queensland Department of Environment and Heritage and Australian Nature Conservation Agency: Canberra.)
- Limpus, C. J., Fleay, A., and Guinea, M. (1984). Sea turtles of the Capricornia Section, Great Barrier Reef. In 'Capricornia Section of the Great Barrier Reef. Past, Present and Future'. (Eds W. T. Ward and P. Saenger.) pp. 61–78. (Royal Society of Queensland and Australian Coral Reef Society: Brisbane.)
- Limpus, C. J., Reed, P. C., and Miller, J. D. (1985). Temperature dependent sex determination in Queensland sea turtles: intraspecific variation in *Caretta caretta*. In 'Biology of Australasian Frogs and Reptiles'. (Eds G. Grigg, R. Shine and H. Ehmann.) pp. 343–51. (Surrey Beatty and Sons: Sydney.)
- Limpus, C. J., Miller, J. D., Parmenter, C. J., Reimer, D., McLachlan, N., and Webb, R. (1992). Migration of green (*Chelonia mydas*) and loggerhead (*Caretta caretta*) turtles to and from eastern Australian rookeries. *Wildlife Research* 19, 347–58.
- Limpus, C. J., Couper, P. J., and Read, M. A. (1994). The loggerhead turtle, *Caretta caretta*, in Queensland: population structure in a warm temperate feeding area. *Memoirs of the Queensland Museum* 37, 195–204.
- National Research Council, U.S. National Academy of Sciences (1990). 'Decline of the Sea Turtles: Causes and Prevention.' (National Academy Press: Washington, DC.)
- Noon, B. R., and Biles, C. M. (1990). Mathematical demography of spotted owls in the Pacific Northwest. *Journal of Wildlife Management* 54, 18–27.
- Poiner, I., and Harris, A. (1994). The incidental capture and mortality of sea turtles in Australia's northern prawn fishery. In 'Proceedings of the Australian Marine Turtle Conservation Workshop'. (Compiler R. James.) pp. 127–35. (Queensland Department of Environment and Heritage and Australian Nature Conservation Agency: Canberra.)
- Pollock, K. H., Nichols, J. D., Brownie, C., and Hines, J. E. (1990). Statistical inference for capture–recapture experiments. *Wildlife Monographs* 107.
- Simons, T. R. (1984). A population model of the endangered Hawaiian dark-rumped petrel. *Journal of Wildlife Management* 48, 1065–76.
- Yntema, C. L., and Mrosovsky, N. (1980). Sexual differentiation in hatchling loggerheads (*Caretta caretta*) incubated at different controlled temperatures. *Herpetologica* 36, 33–6.

Year of previous capture	Year of recapture															
	1978	1979	1980	1981	1982	1983	1984	1985	1986	1987	1988	1989	1990	1991	1992	
SA																
1978	0	8	0	0	0	0	0	0	0	0	0	0	0	0	0	
1979	0	0	12	1	0	0	0	0	0	0	0	0	0	0	0	
1980	0	0	0	6	5	0	2	0	0	0	0	0	0	0	0	
1981	0	0	0	0	1	3	1	0	0	0	0	0	0	0	0	
1982	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	
1983	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
1984	0	0	0	0	0	0	0	3	1	0	0	0	0	0	0	
1985	0	0	0	0	0	0	0	0	3	0	0	0	0	0	0	
1986	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	
1987	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
1988	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	
1989	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	
1990	0	0	0	0	0	0	0	0	0	0	0	0	0	2	1	
1991	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	
SP																
1978	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
1979	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
1980	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
1981	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
1982	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0	
1983	0	0	0	0	0	0	5	0	0	0	0	0	0	0	0	
1984	0	0	0	0	0	0	0	6	2	1	0	0	0	0	0	
1985	0	0	0	0	0	0	0	0	7	0	0	0	0	0	0	
1986	0	0	0	0	0	0	0	0	0	9	1	0	0	0	0	
1987	0	0	0	0	0	0	0	0	0	0	10	2	0	0	0	
1988	0	0	0	0	0	0	0	0	0	0	0	8	0	0	0	
1989	0	0	0	0	0	0	0	0	0	0	0	0	9	2	0	
1990	0	0	0	0	0	0	0	0	0	0	0	0	0	6	1	
1991	0	0	0	0	0	0	0	0	0	0	0	0	0	0	6	
Adult																
1978	0	10	4	0	0	0	0	0	0	0	0	0	0	0	0	
1979	0	0	12	1	3	0	0	1	0	1	1	0	0	0	0	
1980	0	0	0	3	6	4	1	0	0	1	0	0	0	0	0	
1981	0	0	0	0	0	1	1	0	0	0	0	0	1	0	0	
1982	0	0	0	0	0	3	4	0	0	1	0	0	0	0	0	
1983	0	0	0	0	0	0	5	1	0	0	0	0	0	0	0	
1984	0	0	0	0	0	0	0	4	1	2	0	0	0	0	0	
1985	0	0	0	0	0	0	0	0	3	1	0	1	0	0	0	
1986	0	0	0	0	0	0	0	0	0	5	0	0	0	0	0	
1987	0	0	0	0	0	0	0	0	0	0	7	4	1	0	1	
1988	0	0	0	0	0	0	0	0	0	0	0	9	0	0	0	
1989	0	0	0	0	0	0	0	0	0	0	0	0	12	2	0	
1990	0	0	0	0	0	0	0	0	0	0	0	0	0	15	0	
1991	0	0	0	0	0	0	0	0	0	0	0	0	0	0	14	

## Appendix 1. continued

The JOLLY program calculates capture and survival probabilities for each annual interval. JOLLY Model A assumes that survival and capture probabilities vary from year to year, whereas Model D assumes that these rates are constant. Because there were no recaptures in some years for the SA and SP females, the JOLLY program was unable to calculate standard errors or goodness-of-fit tests for all models. The following are JOLLY results for annual survival probabilities for each reproductive group and model.

Parameter	Subadults (SA)	Pubescents (SP)	Adults
No. of recaptures	81	109	195
No. of turtles	33	31	48
Survival rate estimate (s.e.)			
Model A	0.83 (–) <sup>A</sup>	0.89 (0.025)	0.91 (0.017)
Model D	0.86 (0.036)	0.88 (0.034)	0.92 (0.018)
95% confidence interval			
Model A	– <sup>A</sup>	0.84–0.94	0.88–0.94
Model D	0.79–0.94	0.81–0.94	0.88–0.95
Goodness-of-fit $\chi^2$			
Model A	3.0857 ( $P = 0.079$ )	– <sup>A</sup>	9.9728 ( $P = 0.076$ )
Model D	30.3466 ( $P < 0.001$ )	– <sup>A</sup>	82.9264 ( $P < 0.001$ )
Model D v. Model A	27.2608 ( $P < 0.001$ )	4.70 ( $P = 0.583$ )	72.9536 ( $P < 0.001$ )

<sup>A</sup>Sample size is too small in certain years to permit an estimate.

The low goodness-of-fit results suggest heterogeneity in sampling. However, this is the only extensive mark–recapture data set available for sea turtles, and we feel that the mean survival estimates from Model A are reasonable given the low standard error of the estimates. Clearly, more data will improve these estimates and should be incorporated into future models.

## Appendix 2. Matrix parameterisation and elasticity analysis

### Matrix Parameterisation

We created a 4-stage transition matrix for each loggerhead population. Each matrix has the form

$$A = \begin{bmatrix} P_1 & 0 & 0 & F_4 \\ G_1 & P_2 & 0 & 0 \\ 0 & G_2 & P_3 & 0 \\ 0 & 0 & G_3 & P_4 \end{bmatrix}$$

where  $P_i$  is the annual probability of surviving and remaining in stage  $i$ ,  $G_i$  is the annual probability of surviving and growing into stage  $i + 1$ , and  $F_i$  is annual fecundity. We calculated  $P$  and  $G$  for each stage using the number of years spent in that stage ( $T$  = stage duration) and the stage-specific annual survival rate ( $\sigma_i$ ), as follows:

$$P_i = \sigma_i(1 - \gamma_i), G_i = \sigma_i\gamma_i, \text{ from}$$

$$\gamma_i = \frac{\left[ \frac{\sigma_i}{\lambda_0} \right]^{T_i} - \left[ \frac{\sigma_i}{\lambda_0} \right]^{T_{i-1}}}{\left[ \frac{\sigma_i}{\lambda_0} \right]^{T_i} - 1},$$

where  $\gamma_i$  is the annual probability of growth for each individual in stage  $i$  and  $\lambda_0$  is an initial estimate of the population growth rate. Thus, a fixed proportion of turtles in each stage grows every year, and the age distribution within a stage is stable. For the Heron Reef population,  $\lambda_0$  was set at 1.0 and the Stage 1 (pelagic juvenile) annual survival rate was adjusted so that the population growth rate from the matrix was equal to 1 (i.e. the dominant eigenvalue of the matrix  $\lambda = 1.0$ ,  $r = 0.0$ ). To calculate the population growth rate after a matrix parameter was manipulated, as in the survival reduction exercise of Fig. 4, we started with  $\lambda_0 = 1.0$  and calculated the dominant eigenvalue through several iterations until  $\lambda_0 = \lambda$ . This iterative procedure was also used to calculate  $\lambda$  for the Mon Repos model. Detail on matrix algebra techniques for population biology may be found in Caswell (1989).

### Elasticity Analysis

A sensitivity analysis looks at changes in the population growth rate,  $\lambda$ , when changes occur in a matrix parameter,  $A_{i,j}$ . The sensitivity calculation takes the form of a differential equation the solution of which is dependent on the stable stage distribution of the population,  $w$ , and the stage-specific reproductive values,  $v$ , as follows:

$$\frac{\partial \lambda}{\partial A_{i,j}} = \frac{v_i \times w_j}{\langle v | w \rangle},$$

where  $\langle v | w \rangle$  is the inner product of the two vectors, or the sum of all  $v_i \times w_i$ . This sensitivity analysis allows us to measure the relative contributions of each matrix parameter to population growth by calculating changes in the population growth rate following small changes in  $P_i$ ,  $G_i$  or  $F_i$ . Elasticity analysis is a slightly modified form of the sensitivity analysis that examines the effects of proportional changes in the matrix parameters (e.g. what the change in  $\lambda$  is if adult survival is decreased by 10%). Elasticities may be calculated by multiplying both sides of the sensitivity equation by  $A_{i,j}/\lambda$ . The matrix elasticities sum to



**Appendix 2.** continued

1.0, thus representing the proportional contribution of each matrix parameter to  $\lambda$ . Because annual survival ( $s_i$ ) affects both  $P_i$  and  $G_i$ , we calculated survival elasticities ( $E$ ), as follows:

$$E = \frac{\lambda_{\sigma_i + \sigma_i \times 0.01} - \lambda_{\sigma_i - \sigma_i \times 0.01}}{\lambda \times 0.02}$$

where  $\lambda_{\sigma_i \pm \sigma_i \times 0.01}$  is the population growth rate calculated for matrix with a stage-specific survival rate increased or decreased by 1% (all  $\lambda$ s were calculated iteratively, as explained above). To get the proportional change in  $\lambda$ , the original matrix  $\lambda$  was multiplied by the total change in survival ( $0.01 + 0.01 = 0.02$ ).

Manuscript received 2 November 1994; revised and accepted 14 July 1995