

Demography of two populations of the Mexican mud turtle (*Kinosternon integrum*) in central Mexico

Rodrigo Macip-Ríos¹, Pablo Brauer-Robleda², J. Jaime Zúñiga-Vega³ & Gustavo Casas-Andreu¹

¹Departamento de Zoología, Instituto de Biología, Universidad Nacional Autónoma de México, Mexico

²Unidad Coordinadora de Delegaciones, Secretaría del Medio Ambiente y Recursos Naturales, Mexico

³Departamento de Ecología y Recursos Naturales, Facultad de Ciencias, Universidad Nacional Autónoma de México, Mexico

Basic demographic information for turtles in tropical and sub-tropical regions is still scarce. As a consequence, prospective management and conservation plans for these long-lived vertebrates lack the necessary quantitative background for successful implementation. In this study, we used capture–mark–recapture techniques in two populations of the Mexican mud turtle (*Kinosternon integrum*) located at different elevations in central Mexico. We estimated stage-specific survival, growth, and fecundity rates and constructed a population projection matrix for each population. In the low-elevation population, the finite rate of population growth (λ) was not significantly different from unity, indicating demographic stability. In the high-elevation population, λ was significantly lower than unity, indicating population decline. Survival of adults was the vital rate that contributed most to population persistence in both populations. We discuss our results in the context of demographic patterns of turtle species, emphasizing the differences between the two populations studied and potential conservation implications.

Key words: capture–mark–recapture, elasticity analysis, freshwater turtles, maximum likelihood estimation, population dynamics, population projection matrices

INTRODUCTION

The vast majority of demographic studies conducted on vertebrates have focused on species that inhabit northern latitudes and temperate habitats (e.g. Pons & Migot, 1995; Coulson et al., 2004; Palstra et al., 2009). Population dynamics of birds and mammals are relatively well known (e.g. Saether & Bakke, 2000; Oli & Dobson, 2003), whereas those of many amphibians and reptiles such as turtles and snakes living in tropical latitudes are still poorly understood. As a consequence, prospective management and conservation plans often lack the necessary quantitative background for successful implementation. For endangered amphibians and reptiles inhabiting tropical and sub-tropical environments, very little is often known about their population dynamics (Frias-Alvarez et al., 2010; Rhodin et al., 2011).

The available demographic studies providing accurate information on population trends for turtles are focused on temperate species and marine turtles nesting on northern beaches (Crouse et al., 1987; Doak et al., 1994; Rouane et al., 2008; Enneson & Litzgus, 2008). Such studies have shown that survival increases with size and age, that population growth rates indicate demographic stability or slight declines, and that adult survival is the most important contributor to population persistence (Heppell, 1998; Mitro, 2003; Enneson & Litzgus, 2008; Eskew et al., 2010). Whether these patterns also occur in turtle species inhabiting tropical regions remains unknown.

This lack of information for tropical turtles is unfortunate, given that the highest levels of disturbance occur in tropical and sub-tropical countries (Gallant et al., 2007).

In addition, several freshwater and terrestrial species are seriously threatened in tropical regions, and no quantitative information is available for such species (Rhodin et al., 2011). In Mexico, one of the two countries with the largest herpetofauna (49 turtle species; Canseco-Márquez & Flores-Villela, 2004; Liner & Casas-Andreu, 2008), no single study has yet attempted to examine the population dynamics of freshwater or terrestrial turtles, and such information is so far only known from lizards (Ortega-León et al., 2007; Zúñiga-Vega et al., 2007; Rojas-González et al., 2008; Zamora-Abrego et al., 2007, 2010; Zúñiga-Vega, 2011).

In this study, we analysed the population dynamics of the endemic Mexican mud turtle, *Kinosternon integrum*, included in the Mexican red list as “under special protection” (SEMARNAT, 2010). We examined the demographic behaviour of two populations located in central Mexico at different elevations, to 1) estimate stage-specific survival, growth and fecundity rates, 2) calculate rates of population increase by means of population projection matrices, 3) examine which vital rates (stage-specific fecundity, growth or survival) contribute the most to population persistence and 4) compare our results between the two study sites.

MATERIALS AND METHODS

Study species

Kinosternon integrum is a small freshwater turtle with a mean carapace length (CL) of 156.3 mm in males and 142.7 mm in females (Macip-Ríos et al., 2009). The species is endemic to the dry tropics of eastern, central and

southern Mexico, where it inhabits ponds, lakes and rivers (Iverson et al., 1998; Iverson, 1999). Reproduction takes place during the rainy season (mid-May to late October); matings occur from early May to late September, females lay eggs from late May to late October and eggs hatch from July to November (Iverson, 1999). Clutch size averages four eggs and the average number of clutches per reproductive season is 2.26 (Iverson, 1999; Macip-Ríos et al., 2009).

Study sites

We surveyed two populations of *Kinosternon integrum* in the localities of Tonatlico and Tejupilco, Estado de México from October 2003 to November 2008 (Fig. 1). Tonatlico is located in the southern limits of the Estado de México in the vicinities of the states of Guerrero and Morelos (18°45'N, 99°41'W), at an elevation of 1640 m. The average annual temperature at this site is 17.7 °C. The low-elevation site (Tejupilco) is located in the western portion of the Estado de México in the vicinity of the state of Michoacán (18°45'N, 100°36'W) at an elevation of 600 m. The average annual temperature at this site is 22.1 °C (INEGI, 2002; Toledo & Bozada, 2002). The distance between the two study sites is approximately 51 km. We considered this distance far enough to assume that gene flow between these populations is negligible. Both sites are characterized by tropical deciduous forest with riparian and secondary vegetation (Rzedowski, 1994). The 1040 m difference in elevation between sites leads to a colder climate at the high-elevation site throughout the year (INEGI, 2002).

Field methods

Tonatlico was visited on 11 occasions: October and November 2003; April, May, June, July, August, September

and October of 2004; August 2007; and September 2008. Tejupilco was visited on six occasions: September and October 2006, July and August 2007; June and September 2008. Turtles were collected in seasonal ponds. Most ponds fill in the rainy season (June–September) and dry out in October–December. During the dry season turtles are mostly inactive, with some activity in small ponds adjacent to permanent streams (Macip-Ríos et al., 2009).

Turtles were collected using seine and fyke nets baited with fresh fish. Upon first capture, turtles were marked by permanent shell notching with an individual number to identify them on subsequent capture occasions. On every capture we measured carapace length, carapace width, plastron length, plastron width (cm) and body mass (g). Repeated visits to the study sites allowed us to obtain recapture (encounter) histories for the marked turtles over the course of this study.

Estimating vital rates

We estimated stage-specific survival, growth and fecundity rates. The populations were structured in five stage/size classes: 1) hatchlings: turtles with plastron length (PL) <6 cm; 2) juveniles: turtles with PL of 6–8 cm; 3) sub-adults: turtles with PL of 8–9.6 cm in the low-elevation population and 8–11.7 cm in the high-elevation population; 4) small adults: reproductive turtles with PL of 9.6–13 cm in the low-elevation population and 11.7–13 cm in the high-elevation population; 5) large adults: reproductive turtles with PL ≥13 cm. The different threshold sizes for sub-adults and small adults were due to differential minimum size at maturity (PL of 9.6 cm at the low-elevation site and 11.7 cm at the high-elevation site; Macip-Ríos et al., 2009; Macip-Ríos, 2010).

Stage-specific survival and growth rates were estimated using maximum-likelihood procedures implemented in the program MARK (Lebreton et al., 1992; White & Burnham, 1999). Based on a multi-state framework (Brownie et al., 1993) and on the observed encounter histories, this computer package estimates three parameters: survival rate (ϕ), capture probability (p) and the rate at which individuals “move” (grow) from one stage to another (ψ = growth or transition probability).

Given that these probabilities may or may not vary among stage classes or across sampling occasions, we constructed different competing models that represented different hypotheses about variation in ϕ , p and ψ . These parameters may vary among stage classes (st), among sampling occasions (oc), or may simply be constant among stages and sampling occasions (\cdot). We did not consider the interaction between stage class and sampling occasion as a source of variation for ϕ , p and ψ , because calculating a different parameter for each combination of stage class and sampling occasion would have required larger sample sizes than those available to us. Taken together, we fitted 27 competing models to our mark–recapture data sets using maximum likelihood routines in MARK. Given that the number of sampling occasions differed between sites, we analysed the mark–recapture data of each population separately.

To select the model with the best fit to the data, we used the corrected Akaike's Information Criterion (AIC_c ;

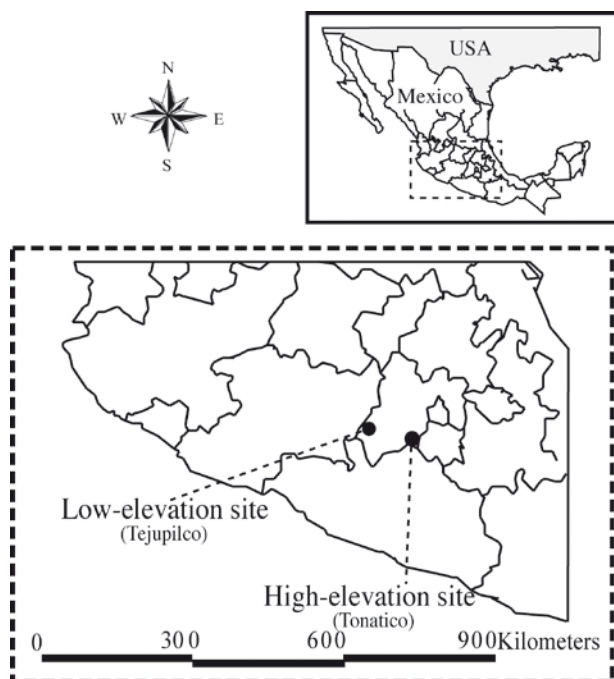


Fig. 1. Map of central Mexico showing the location of the two study populations of *Kinosternon integrum*.

Akaike, 1973). The AIC_c is a measure of model likelihood and parsimony, with the lowest AIC_c score indicating the best-fitting model. A difference in AIC_c scores between two models (ΔAIC_c) larger than two indicates considerable support for a real difference in the fit (Burnham & Anderson, 2002). We also calculated model-specific Akaike weights (w_i), which measure the relative support or weight of evidence for each model in the data (Amstrup et al., 2005). Based on these Akaike weights it was possible to calculate, for each population, weighted averages for the annual survival (ϕ), recapture (p) and transition (ψ) rates of individuals in the different stage classes as per Burnham & Anderson (2002). These model-weighted estimates of ϕ , p and ψ incorporate the uncertainty in the process of model selection by considering the relative support for each competing model. Thus, these weighted average estimates are more robust than those derived from any single model alone (Johnson & Omland, 2004).

We dealt with uneven time intervals between sampling occasions by specifying the relative length of each time interval with respect to one year. MARK uses these specified relative lengths (L_i) as exponents of the parameters of interest during the estimation process (e.g. $\phi_i^{L_i}$), making the parameter estimates between sampling occasions comparable while accounting for the different time lengths between occasions (White & Burnham, 1999). As a result, we obtained stage-specific and model-weighted parameter estimates on a yearly basis (i.e. annual ϕ , p and ψ). To calculate variances and standard errors for these annual estimates, MARK implements the delta method (Seber, 1982).

To estimate average clutch size for small and large adults, we collected females larger than 9 cm PL from both populations. These females were transported alive to the laboratory where they were X-rayed. From X-ray plates we counted the number of eggs present in gravid females. In addition, a 1.5 ml/kg dose of oxytocin was injected to gravid females to induce oviposition (Ewert & Legler, 1978). Again, the number of eggs per female was recorded. Immediately after X-ray tests and oviposition events, females were returned to the field (i.e. they were kept in captivity for only a few days). To compare average clutch size between reproductive stage classes (small vs large adults) and between populations we conducted a two-way ANOVA. Data on the number of eggs per female were square-root transformed to meet assumptions of normality and homogeneity of variances.

Population projection matrices

We modelled population dynamics using a matrix approach (Caswell, 2001). Given that we structured our populations into five size/stage classes, we constructed 5×5 population projection matrices. For each population we constructed only one average annual matrix. These annual demographic matrices are mathematical representations of the annual life-cycle graph (Fig. 2A), because matrix entries summarize the survival, growth and fecundity rates experienced by individuals in the different phases of the life cycle during an average year. The life-cycle graph depicts all the transitions and contributions that can be observed among stage classes from one year

to the next (Fig. 2A). When turtles survive they can either remain in the same stage class (stasis, depicted with an S in both the life-cycle graph and the transition matrix; Fig. 2) or progress to a superior stage class (growth, depicted with a G in Fig. 2). Both adult categories contribute to hatchlings through fecundity (depicted with an F in Fig. 2). Matrix entries (a_{ij}), represent the probability of survival with stasis (in the main diagonal), the probability of survival with growth (in the sub-diagonals) and the contribution to hatchlings through fecundity (in the first row) of an average individual in stage class j (columns) to stage class i (rows) from one year to the next (Fig. 2B; Caswell, 2001).

Stasis and growth entries of the matrices were derived from the annual survival (ϕ) and transition (ψ) rates estimated by MARK (Lebreton et al., 1992; Nichols et al., 1992). The stage-specific probability of survival with

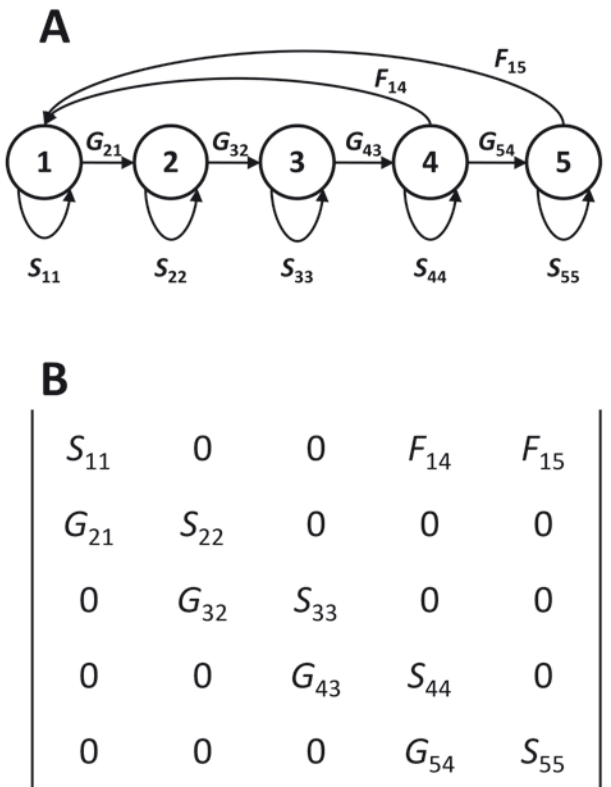


Fig. 2. A) Life-cycle graph of *Kinosternon integrum*. Nodes denote stage classes as follows: 1) hatchlings; 2) juveniles; 3) sub-adults; 4) small adults; 5) large adults. Arrows represent transition probabilities (in the case of growth or stasis) or contributions (in the case of fecundities) made by individuals in a particular stage class to other stage classes from one year to the next. F = fecundity, G = growth, survival with progression to a larger stage class, S = stasis, survival staying in the same stage class. Subscripts (ij) indicate the direction of the transition or contribution, from stage class j to stage class i . B) Population projection matrix for *K. integrum*. Terms in the matrix are equivalent to those in the life-cycle graph. Zero values represent transitions or contributions not observed in our study.

growth to a larger stage class (G_{ij}) was calculated as:

$$G_{ij} = \phi_j \times \psi_{ij}$$

where ϕ_j represents the survival rate of individuals at stage j and ψ_{ij} represents the annual transition probability from stage j to stage i . The stage-specific probability of survival with stasis in the same stage class (S_{ij} , with $i = j$) was calculated as follows:

$$S_{ij} = \phi_j \times (1 - \psi_{ij})$$

The stage-specific fecundity entries (F_{ij}) represent the average number of hatchlings produced by an average reproductive female from the corresponding adult category. These fecundity values were estimated as follows. First, we calculated an overall number of adult females and hatchlings present each year in the populations (N) as:

$$N_j = n/p_j$$

where j represents either small adults, large adults, or hatchlings, n represents the number of individuals captured in stage class j and p is the stage-specific capture probability estimated from MARK (Armstrong et al., 2005). Second, we calculated the total number of eggs produced per year in the populations as:

$$\text{Total number of eggs} = (N_{\text{small adults}} \times \text{clutch size}_{\text{small adults}}) + (N_{\text{large adults}} \times \text{clutch size}_{\text{large adults}})$$

where clutch size represents the average number of eggs produced by females in the two reproductive categories. Third, we calculated the proportion of eggs surviving to hatchlings (ϕ_{eggs}) as:

$$\phi_{\text{eggs}} = N_{\text{hatchlings}} / \text{total number of eggs}$$

Finally, stage-specific fecundity per year was calculated as:

$$F_{ij} = \text{clutch size}_j \times \phi_{\text{eggs}} \times 2.26 \times 0.5$$

The 2.26 included in this expression corresponds to the average number of clutches laid per year by *K. integrum* females (Iverson, 1999), whereas the 0.5 indicates the proportion of females produced in each clutch (assuming a 1:1 sex ratio). Here, we considered only females given that once they reach sexual maturity, they are the ones contributing directly to population recruitment (Caswell, 2001).

The annual finite rate of population increase (λ) was estimated as the dominant eigenvalue of each annual transition matrix. The right (w) and left (v) eigenvectors associated with each λ value represented estimates of the projected stable stage class distribution and the stage-specific reproductive values, respectively (Caswell, 2001). We used χ^2 tests to search for significant differences between observed and projected (vectors w) stage class distributions.

We used elasticity analysis (de Kroon et al., 1986, 2000) to estimate the relative change in λ that would result from relative changes in each matrix entry. Annual elasticity matrices (entries denoted as e_{ij}) were constructed as:

$$e_{ij} = s_{ij} \times (a_{ij}/\lambda)$$

where s_{ij} represents the absolute sensitivity of λ to absolute changes in the matrix entries ($s_{ij} = \partial\lambda/\partial a_{ij}$). As elasticities are standardized sensitivities, they can be used

to compare the relative contribution (i.e. the relative importance) of each matrix entry to the population growth rate (de Kroon et al., 1986, 2000; Benton & Grant, 1999). Given that all the entries in an elasticity matrix sum to unity (Mesterton-Gibbons, 1993), we also quantified the relative contribution of different demographic process (i.e. stasis, growth and fecundity) and of different stage classes to the population growth rate by adding elasticity values corresponding to each process or stage class (Silvertown et al., 1993).

Confidence intervals (95%) for λ and elasticities were constructed using a resampling procedure. MARK estimates survival (ϕ) and growth (ψ) rates along with their standard errors based on likelihood functions (Lebreton et al., 1992; White & Burnham, 1999). We resampled 1000 new random values of ϕ and ψ based on a normal distribution with a mean equal to the point estimate of the corresponding parameter and a standard deviation equal to the standard error of the parameter. We also bootstrapped the reproductive data to obtain 1000 new average clutch sizes per stage and population. From these resampled values of ϕ , ψ and clutch size, we calculated 1000 new values for the matrix entries (G_{ij} , S_{ij} and F_{ij}) and 1000 new values for λ and elasticities. To construct the 95% confidence intervals we used the 25th and 975th sorted values of the resulting distribution of λ and elasticities as the lower and upper limits, respectively.

RESULTS

Model selection

At the low-elevation site, two models had the highest and similar support in the mark-recapture data. The best-fitting model indicated different ϕ and p among stage classes as well as different ψ among sampling occasions ($\phi(st) p(st) \psi(oc)$, $AIC_c = 1715.72$; Table 1). The second best-fitting model indicated constant ϕ , different p among sampling occasions, and different ψ among stage classes ($\phi(.) p(oc) \psi(st)$, $AIC_c = 1716.16$; Table 1). These two models have similar fit to the data ($\Delta AIC_c = 0.44$) and relatively similar support ($w_1 = 0.35$ and $w_2 = 0.28$). Therefore, in this low-elevation population, uncertainty about the real sources of variation for ϕ , p and ψ is high and might be due to the relatively small sample sizes (column n_i in Table 2).

In contrast, in the high-elevation population only one model had strong support in the data. This best-fitting model indicated different ϕ among stage classes as well as different p and ψ among sampling occasions ($\phi(st) p(oc) \psi(oc)$, $AIC_c = 2317.69$; Table 1). The relative support for this model was very high ($w_1 = 0.75$). The difference in AIC_c values between this best-fitting model and the second one indicated a considerable difference in their fit to the mark-recapture data ($\Delta AIC_c = 2.49$), with the second model having weaker support ($w_2 = 0.22$). This second best-fitting model also indicated different ϕ among stage classes and different p among sampling occasions, with the only difference being in ψ : it indicated different ψ among stage classes ($\phi(st) p(oc) \psi(st)$, $AIC_c = 2320.18$; Table 1). The third best-fitting model also indicated differences among stages in ϕ ($\phi(st) p(oc) \psi(.)$, $AIC_c = 2324.31$; Table 1).

Table 1. Model selection results for capture–mark–recapture data from two populations of *Kinosternon integrum*. Survival (ϕ), recapture (p) and transition (ψ) rates may vary among stage classes (st) and sampling occasions (oc), or may be constant among stages and sampling occasions (\cdot). The fit of each model to the observed data was evaluated using a corrected version of Akaike’s Information Criterion (AIC_c). Akaike weights (w_i) measure the relative support in the data for each model fitted. The five models with the strongest support are shown.

Model	AIC_c	ΔAIC_c	w_i
Low-elevation site			
$\phi(st) p(st) \psi(oc)$	1715.72	0	0.35
$\phi(\cdot) p(oc) \psi(st)$	1716.16	0.44	0.28
$\phi(\cdot) p(\cdot) \psi(st)$	1718.55	2.83	0.08
$\phi(oc) p(\cdot) \psi(st)$	1718.85	3.13	0.07
$\phi(\cdot) p(st) \psi(oc)$	1719.87	4.15	0.04
High-elevation site			
$\phi(st) p(oc) \psi(oc)$	2317.69	0	0.75
$\phi(st) p(oc) \psi(st)$	2320.18	2.49	0.22
$\phi(st) p(oc) \psi(\cdot)$	2324.31	6.62	0.03
$\phi(\cdot) p(oc) \psi(oc)$	2331.19	13.50	0.001
$\phi(\cdot) p(oc) \psi(st)$	2339.20	21.51	<0.0001

Survival, recapture and transition rates

Model-weighted estimates of ϕ for the low-elevation population resulted in similar annual survival rates for sub-adults, small adults and large adults (means \pm SE: 0.79 \pm 0.13, 0.78 \pm 0.13 and 0.78 \pm 0.13, respectively; Fig. 3A). Annual survival rates for hatchlings and juveniles were 0.48 \pm 0.14 and 0.59 \pm 0.13, respectively. The rela-

tively high uncertainty in the estimation process for this population resulted in wide 95% confidence intervals for these parameters, which in turn indicated no statistical differences among stage classes in ϕ (Fig. 3A).

In contrast, model-weighted estimates of ϕ for the high-elevation population resulted in clear statistical differences among stage classes in annual survival rates (Fig. 3A). Hatchlings notably experienced the lowest annual ϕ (0.04 \pm 0.06). Juveniles and sub-adults experienced similar annual ϕ (0.54 \pm 0.10 and 0.56 \pm 0.05, respectively). Large adults experienced higher annual ϕ (0.77 \pm 0.04). Small adults at this high-elevation site strikingly experienced the highest annual ϕ (0.97 \pm 0.08). The main difference between the two study populations occurred in the annual survival rate of hatchlings. At the low-elevation site hatchlings had a higher survival probability (0.48 \pm 0.14) in comparison with the high-elevation site, where their survival rate was markedly lower (0.04 \pm 0.06). According to their 95% confidence intervals this difference appears to be statistically significant (Fig. 3A).

In the low-elevation population, the stage-specific transition rates (ψ) were higher in hatchlings, juveniles and sub-adults (0.38 \pm 0.10, 0.30 \pm 0.09 and 0.37 \pm 0.10, respectively) in comparison with the transition rate of small adults (0.17 \pm 0.09; Fig. 3B). However, the 95% confidence intervals for these parameters indicated a lack of statistical differences among stage classes. In the high-elevation population, the annual transition rates were relatively similar among stage-classes (hatchlings: 0.20 \pm 0.09, juveniles: 0.16 \pm 0.06, sub-adults: 0.13 \pm 0.05, small adults: 0.15 \pm 0.05). Again, the 95% confidence intervals indicated no statistical differences among stages in annual ψ (Fig. 3B). For hatchlings, juveniles and sub-adults the point estimates of ψ were higher for the low-elevation site compared to those for the high-elevation site. However, these differences were not significant according to their confidence intervals (Fig. 3B).

Table 2. Population projection matrices and main demographic results derived for two populations of *Kinosternon integrum*. Values for the finite rate of population increase (λ) are shown above each matrix (95% confidence intervals are given within parentheses). n_i = total number of turtles marked per stage class, w = projected stable stage-class distribution, v = stage-specific reproductive values.

	Hatchlings	Juveniles	Sub-adults	Small adults	Large adults	n_i	w	v
Low-elevation site		$\lambda=0.89$ (0.74–1.04)						
Hatchlings	0.30	0	0	1.17	1.53	81	0.50	1.00
Juveniles	0.18	0.41	0	0	0	12	0.19	3.24
Sub-adults	0	0.18	0.50	0	0	13	0.09	8.67
Small adults	0	0	0.29	0.65	0	37	0.10	11.83
Large adults	0	0	0	0.13	0.78	16	0.12	13.30
High-elevation site		$\lambda=0.83$ (0.68–0.99)						
Hatchlings	0.03	0	0	0.43	0.70	26	0.43	1.00
Juveniles	0.008	0.46	0	0	0	27	0.01	95.34
Sub-adults	0	0.08	0.49	0	0	83	0.002	418.17
Small adults	0	0	0.07	0.83	0	22	0.15	1976.64
Large adults	0	0	0	0.14	0.77	73	0.40	12.84

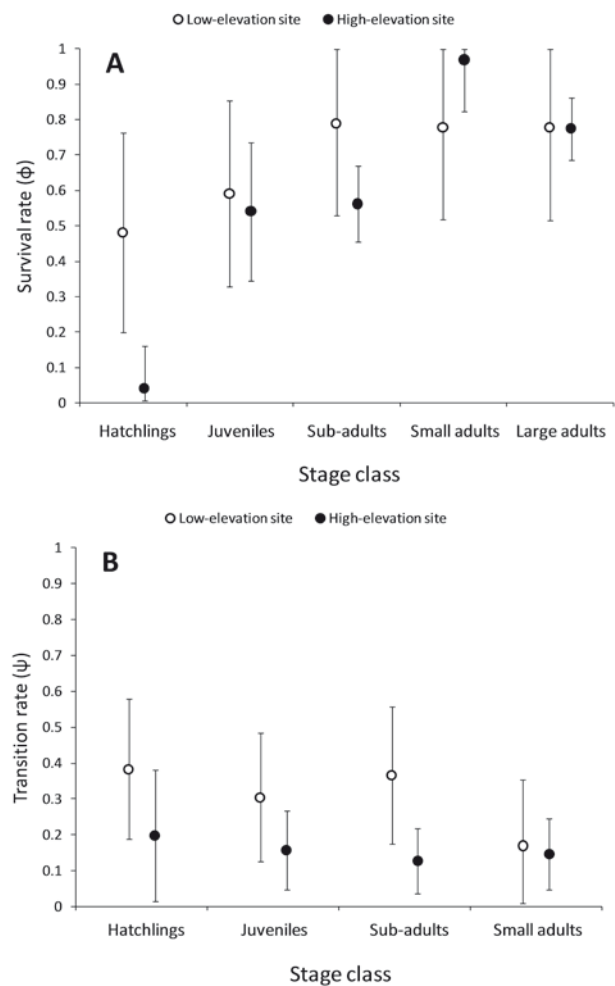


Fig. 3. Model-weighted estimates of A) survival (ϕ) and B) transition (ψ = growth) probabilities for two populations of *Kinosternon integrum*. Estimates are shown per stage class. Vertical bars denote 95% confidence intervals.

Model-weighted average recapture rates (p) at the low-elevation site were 0.35 ± 0.21 for hatchlings, 0.31 ± 0.14 for juveniles, 0.23 ± 0.09 for sub-adults, 0.23 ± 0.08 for small adults and 0.14 ± 0.11 for large adults. At the high-elevation site, no apparent differences among stage classes existed in their recapture probabilities as indicated by the five best-fitting models, which all included an occasion effect rather than a stage effect on p (Table 1). The average recapture rate for turtles of all stage classes in this high-elevation population was 0.18 ± 0.04 . Note that p is higher for most stage classes at the low-elevation site. However, p was more precisely estimated at the high-elevation site (i.e. smaller SE), which resulted in more accurate estimates of ϕ and ψ in this latter population (i.e. narrower confidence intervals).

Clutch sizes

Average clutch size differed significantly between stage classes ($F_{1,41} = 9.39$, $P = 0.004$). However, no significant differences were detected between populations ($F_{1,41} = 1.76$, $P = 0.19$). The interaction between stage class and source population was not significant either ($F_{1,41} = 0.61$, $P = 0.44$). In the low-elevation population average clutch sizes were 3.63 ± 0.47 and 4.75 ± 0.66 eggs for small adults ($n = 8$) and large adults ($n = 4$), respectively. In the high-elevation population average clutch sizes were 2.78 ± 0.44 and 4.50 ± 0.27 eggs for small adults ($n = 9$) and large adults ($n = 24$), respectively.

Population dynamics

The finite rate of population growth (λ) calculated for the low-elevation site was 0.89 and not statistically different from unity as indicated by its 95% confidence interval (0.74–1.04, Table 2). In the high-elevation population, the finite rate of population growth was 0.83 and significantly lower than unity as indicated by its 95% confidence interval (0.68–0.99, Table 2).

The population projection matrices of the two study populations exhibited three main differences (Table 2). First, the proportion of individuals growing to the following stage class from one year to the next was higher for all stage classes in the low-elevation population compared to the high-elevation population (the sub-diagonals of the matrices). Second, both the stasis and growth of hatchlings were lower at the high-elevation site (entries G_{11} and G_{21} in the matrices). Third, fecundities were also lower at the high-elevation site (entries F_{14} and F_{15} in the matrices). This latter difference was due to a lower estimate of egg survival (ϕ_{eggs}) at the high-elevation site in comparison with the low-elevation site (0.14 and 0.29, respectively).

In both populations, the projected stable stage structure was significantly different from the observed population structure (low-elevation site: $\chi^2_4 = 212.1$, $P < 0.0001$; high-elevation site: $\chi^2_4 = 11240.0$, $P < 0.0001$), indicating that population structure changes drastically from year to year. Reproductive values at the low-elevation site for most stage classes were notably lower than at the high-elevation site (Table 2). At the low-elevation site, the greatest reproductive value corresponded to large adults (13.30), with small adults having a relatively high reproductive value as well (11.83). At the high-elevation site, the greatest reproductive value corresponded to small adults (1976.64), and this value was strikingly higher than that for large adults (12.84; Table 2).

Elasticity patterns

At the low-elevation site, the highest elasticity value corresponded to the stasis of large adults (0.29) followed by small adults (0.19; Fig. 4A). The lowest elasticity values corresponded to the fecundity of both small (0.03) and large (0.04) adults, the stasis of hatchlings (0.04) and the growth of small adults (0.04). The 95% confidence intervals for the stasis of all stage classes indicated high uncertainty and poor precision in these estimates (Fig. 4A). At the high-elevation site, only one vital rate made a considerable contribution to the finite rate of population

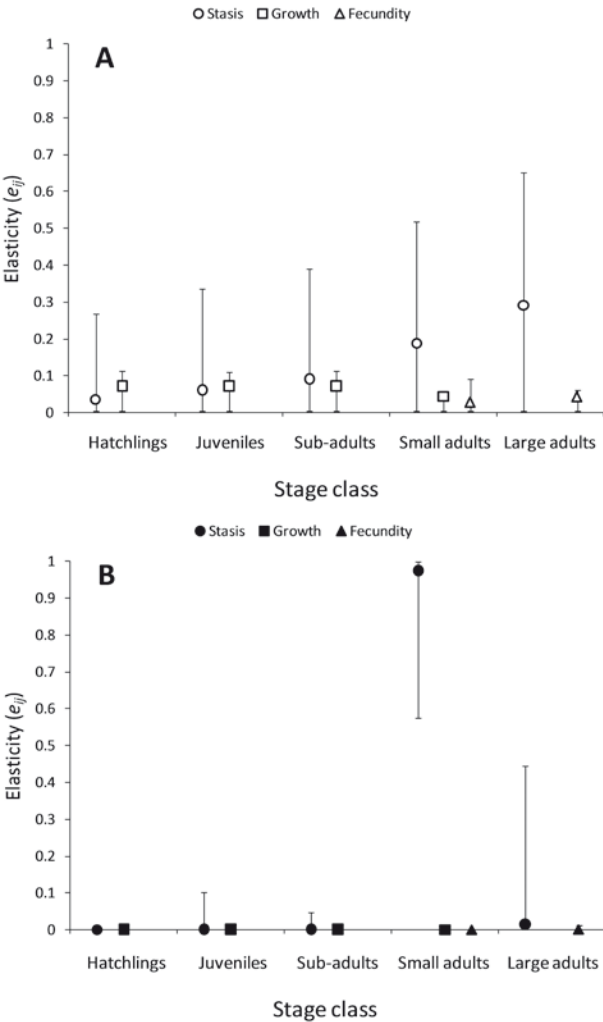


Fig. 4. Relative contribution of every entry in the population projection matrices to the finite rate of population increase as determined by elasticity values (e_{ij}). A) Low-elevation population; B) high-elevation population. Vertical bars denote 95% confidence intervals.

increase. The stasis of small adults had the highest elasticity value (0.97; Fig. 4B). All other vital rates had elasticity values <0.02 . However, the wide confidence intervals associated with the elasticities for the stasis of both adult categories indicate high uncertainty and relatively poor precision in these estimates (Fig. 4B).

Summing up the elasticity values corresponding to different demographic processes, we found that stasis made the greatest contribution to λ in both populations (0.67 at the low-elevation site and 0.99 at the high-elevation site; Fig. 5A). Fecundity made the lowest contribution to λ in both populations (0.07 at the low-elevation site and 0.001 at the high-elevation site; Fig. 5A).

When analysed at the stage-class level, in the low-elevation population the highest elasticity value corresponded to large adults (0.33), followed by small adults (0.26), sub-adults (0.16) and juveniles (0.13), with the lowest

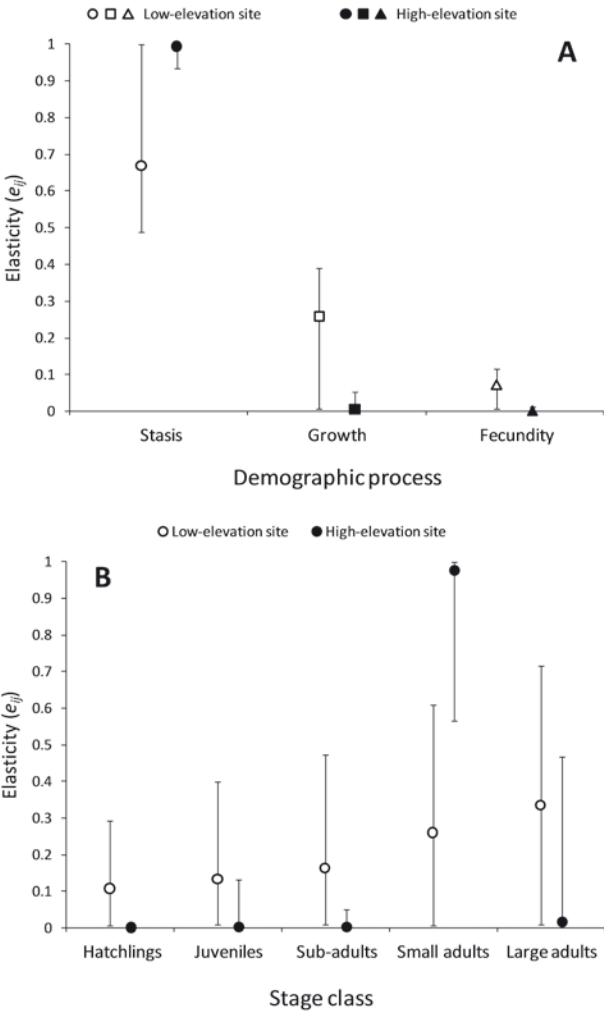


Fig. 5. Relative contribution of A) each demographic process (stasis, growth and fecundity) and of B) each stage class to the finite rate of population increase as determined by elasticity values (e_{ij}). Elasticities are shown per population (low vs high elevation). Vertical bars denote 95% confidence intervals.

elasticity observed in hatchlings (0.11). Their wide 95% confidence intervals did not allow us to detect statistical differences among these estimates (Fig. 5B). In the high-elevation population, the elasticity value for small adults (0.98) was significantly greater than those for all other stage classes (Fig. 5B). Elasticities for hatchlings, juveniles, sub-adults and large adults were <0.02 , again with high uncertainty in the elasticity estimates for small and large adults (Fig. 5B).

DISCUSSION

Demographic patterns of *Kinosternon integrum*
In the two populations studied, *K. integrum* exhibited key demographic traits that are consistent with those observed in other freshwater turtles. Annual survival probabilities are lowest early in life and increase as individuals grow

and age (Fig. 3A). Our results indicate that hatchling survival rates may vary between 0.04 and 0.48, consistent with what has been registered in other freshwater turtles: 0.105 in *Trachemys scripta* (Frazer et al., 1990), 0.23 in *Chelydra serpentina* (Congdon et al., 1994), 0.26 in congeneric *K. subrubrum* (Frazer et al., 1991) and 0.19 in *K. flavescens* (Iverson, 1991). In general, turtles experience the highest annual survival probabilities late in life as reproductive adults. In *K. integrum*, adult survival rates varied between 0.77 and 0.97. These high adult survival probabilities have also been documented in other freshwater turtles such as *Chelydra serpentina* (0.97; Congdon et al., 1994), *Malaclemys terrapin* (0.96; Mitro 2003), *Chrysemys picta* (0.95; Eskew et al., 2010) and *Podocnemis expansa* (0.93; Mogollones et al., 2010). This corresponds to a type III survivorship curve in which mortality is highest early in life and then decreases considerably for older individuals (Gotelli, 2008).

The point estimates of the finite rate of population growth (λ) were below unity in both populations. Values of λ below unity indicate declining populations (Metcalf & Pavard, 2007). At the low-elevation site, λ was not significantly different from unity, suggesting population stability. At the high-elevation site, λ was statistically below unity, suggesting a population decline. Relatively low population growth rates are a common demographic pattern in late-maturing organisms such as turtles, with long generation times, relatively low reproductive effort and notably high adult survival (0.945 for *Caretta caretta*, Crouse et al., 1987; between 0.875 and 0.982 for *Gopherus agassizii*, Doak et al., 1994; and 0.93 for *Podocnemis expansa*, Mogollones et al., 2010). Long periods with low population recruitment can result in periods of demographic decline, followed by population growth due to a more favourable year resulting in population stability (e.g. Mandujano et al., 2001; Dodd et al., 2006). However, drastic or prolonged periods of population declines do not have the immediate potential for recovery. Such species are thus more prone to local extinction (Gårdmark et al., 2003; Jenouvrier et al., 2009; Eskew et al., 2010) and suffer from more conservation problems than short-lived organisms with high levels of reproductive investment and a greater potential for population recovery (Congdon et al., 1993, 1994; Gibbs & Amato, 2000; Ruane et al., 2008).

Elasticity patterns in *K. integrum* were consistent with those observed in other turtles. High elasticity values corresponded to the stasis of both adult categories (Fig. 4). At the high-elevation site, the only vital rate making a significant contribution to λ was the stasis of small adults (97%; Fig. 4B). In other freshwater turtles, survival rates of reproductive categories also account for the highest contribution to population persistence (elasticities for adult survival: 0.64 in *Malaclemys terrapin*, Mitro, 2003; 0.715 in *Clemmys guttata*, Enneson & Litzgus 2008; and approximately 0.90 in *Podocnemis expansa*, Mogollones et al., 2010). The relative importance of fecundity and early survival (hatchling and juvenile stasis) for population growth rate was much lower in both studied populations (elasticity values as low as 0.0001 for the stasis of hatchlings and as low as 0.0003 for the fecundity

of small adults at the high-elevation site; Fig. 4), consistent with studies on *M. terrapin* (between 0.04 and 0.09; Mitro, 2003) and *C. guttata* (ca. 0.04; Enneson & Litzgus 2008). Stasis made the highest and fecundity the smallest contribution to population growth rate at both study sites (Fig. 5A). Both an early review of elasticity patterns in turtles (Heppell, 1998) as well as recent demographic studies have shown that stasis is indeed the most important demographic process for population persistence, whereas fecundity does not seem to contribute significantly to population growth rates (Mitro, 2003; Enneson & Litzgus, 2008; Mogollones et al., 2010).

Differences between low and high elevation

Increases in altitude are usually associated with decreases in temperature (Jackson, 1977). For ectothermic organisms such as reptiles, changes in the thermal regime have predictable demographic consequences. First, warmer temperatures at low-elevation sites result in longer activity periods (both daily and yearly; Rose, 1981). Such environments, with longer favourable periods, should cause higher mortality rates, because individuals spend more time active and are therefore at increased risk of predation in comparison with individuals living in environments with restricted favourable seasons (Adolph & Porter, 1993, 1996; Rojas-González et al., 2008). Second, warmer temperatures at low-elevation sites should promote faster rates of body growth (Adolph & Porter, 1993, 1996; Angilletta et al., 2004; Lu et al., 2006).

Our demographic data agreed only partially with the first prediction. At the high-elevation site, we indeed observed the highest annual survival rate for reproductive individuals (0.97 for small adults). However, the annual survival rate of hatchlings was notably lower in this high-elevation population compared to that in the low-elevation population (Fig. 3A). Differences between populations in predator composition, resource availability, or in the proportion of suitable habitats for hatchlings might explain the low survival rate at the high-elevation site (Litzgus & Mousseau, 2004; Dodd et al., 2006; Gerlach, 2008; Eskew et al., 2010; Hensley et al., 2010). Alternatively, permanent emigration of hatchlings could be higher at the high-elevation site. Given that multi-state models do not distinguish death from permanent emigration when estimating ϕ , this parameter represents only “apparent survival” and might include individuals that leave the population (Lebreton et al., 1992; Brownie et al., 1993; Amstrup et al., 2005).

In spite of relatively high uncertainty in parameter estimation, the maximum-likelihood estimates for the transition rates between stages (ψ) were higher at the low-elevation site for hatchlings, juveniles and sub-adults (Fig. 3B). This result is consistent with theoretical predictions (Adolph & Porter, 1993, 1996; Angilletta et al., 2004). Immature individuals are growing at faster rates in the low-elevation population, presumably due to warmer temperatures. These faster rates of body growth translate into a higher contribution of growth to population growth rate in this low-elevation population in comparison with the relative importance of growth at the high-elevation site (Fig. 5A).

Conservation implications

The low-elevation population appears to be demographically stable. In contrast, the high-elevation population appears to be declining because λ was significantly lower than unity ($\lambda=0.83$, $0.68-0.99$). Indeed, in this latter population we observed fewer individuals each year. The average number of individuals observed per sampling occasion was 46 in 2003, 44 in 2004, 30 in 2007 and only 24 in 2008. Both populations have clear signs of human-induced disturbance. In both localities, turtles were found in shallow and highly eutrophicated ponds adjacent to rural human settlements, but no information is available on whether disturbance is higher in the high-elevation population. The latter site might be part of a source-sink metapopulation system characterized by emigration (Hanski & Gaggiotti, 2004; see Dodd et al., 2006 for an example in freshwater turtles).

Our demographic model might serve as a guide for future management plans. As indicated by our elasticity analysis, actions increasing adult survival would yield the highest positive impact on population growth, similar to other endangered species of turtles (Doak et al., 1994; Heppell, 1998; Mitro, 2003; Enneson & Litzgus, 2008; Mogollones et al., 2010; Rhodin et al., 2011). Particularly for the high-elevation site, reversing the observed negative population trend would require enhancing the stasis of small adults, which is the phase of the life cycle with a strikingly high reproductive value and the highest contribution to population growth rate (Figs 4B and 5B).

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