## Estimating potential reproductive costs in the survival of a xenosaurid lizard

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Both females and males may suffer from increased mortality risk as a result of the activities and physiological processes associated with reproduction. In this study I estimated sex-specific reproductive costs in the survival rates of a viviparous and territorial lizard (*Xenosaurus grandis grandis*), accounting for the potential effects of population density, population growth rate and the size of individuals. I used a multi-model inference framework to test the following hypotheses: 1) female survival rate should decrease when they experience the late phases of embryo development and immediately after births take place; and 2) male survival rate should decrease when they search and compete for potential mates. Capture–mark–recapture data supported the first hypothesis but not the second. Female survival appeared to decrease right before and after parturition events. In contrast, male survival did not decrease during the mating season. I discuss the potential causes and implications of this sex-specific trade-off between reproduction and survival.

Key words: capture-mark-recapture, life-history, multi-model inference, trade-off, Xenosaurus grandis grandis

### INTRODUCTION

Reproduction is costly. In all living organisms the time, resources and energy invested in reproductive processes and activities impose several types of costs (Stearns, 1992; Roff, 2002; Harshman & Zera, 2007). One of the most documented adverse effects of reproductive investment is a potential decrease in survival probability (e.g. Hadley et al., 2007; Jervis et al., 2007; Kitaysky et al., 2010). This life-history trade-off between reproduction and survival is assumed to operate in both sexes (Svensson, 1988; Dijkstra et al., 1990). On the one hand, females allocate vast amounts of resources to the production of offspring. These resources are depleted from ingested food and lipid reserves, negatively affecting their body condition and their chances of surviving to future reproductive events (Golet et al., 2004; Persson, 2005; Cox & Calsbeek, 2010). In addition, reproductive females might be more susceptible to predation (Miles et al., 2000; Veasey et al., 2001; Hoogland et al., 2006). Males, on the other hand, allocate time and energy to searching for, securing and defending potential mates. Such energy expenditure might similarly impoverish their physical condition and decrease their survival probabilities (Fleming & Nicolson, 2004; Schubert et al., 2009). Hence, males might be more susceptible to predation during the reproductive season (Koga et al., 2001; Pavlová et al., 2010).

In viviparous and territorial organisms reproductive costs in survival probabilities are usually noteworthy. On the one hand, viviparous females experience a considerable increase in volume and weight during embryo development (Ghalambor et al., 2004; Shine, 2005). This size increase may represent a tough physical burden that impairs their locomotor abilities, making them easy prey for predators (Van Damme et al., 1989; Shaffer & Formanowicz, 1996; Webb, 2004). Furthermore, after the production of live young, their physical condition may be impoverished and female mortality rates might increase (Weeks, 1996; Lourdais et al., 2004; Hoffman et al., 2008). On the other hand, territorial males exhibit aggressive behaviour against conspecific males during the reproductive season (Hyman & Hughes, 2006; Kemp, 2006). Hence, male mortality could potentially increase during these periods because of diminished physical condition and (or) because they become easy prey during the time period when they attempt to secure and defend their mates (Neuhaus & Pelletier, 2001; Low, 2006; Briffa & Sneddon, 2007).

Nevertheless, an increased risk of mortality as a result of reproductive investment may or may not occur depending on a large set of extrinsic and intrinsic factors (Bell, 1980; Galimberti et al., 2007). For instance, population density may determine whether a reproductive cost actually occurs. In crowed sites or years with limited resources both males and females may experience a higher cost in their survival when producing offspring in comparison with sites or years where resources are abundant and population density is lower (Festa-Bianchet et al., 1998; Brouwer et al., 2009). Similarly, density-independent conditions such as temperature and moisture may also influence reproductive trade-offs. Under unfavourable environmental conditions, offspring production might be more costly in comparison with less harsh conditions (Orzack & Tuljapurkar, 2001; Barbraud & Weimerskirch, 2005). The size or age of individuals may also influence the mortality risk associated with reproduction. Either young, small and inexperienced individuals or old, large and weakened ones might suffer higher costs during reproductive processes (Tatar et al., 1993; Moyes et al.,

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2006). Hence, the study of a trade-off between reproduction and survival must explore the potential effects of these important factors as well.

In this study, I estimated potential reproductive costs in the survival probabilities of a crevice-dwelling, viviparous and territorial lizard (*Xenosaurus grandis grandis*). In particular, I tested two main predictions. 1) Female survival should be lower during the months in which they suffer the highest increase in size due to embryo development (May and June) as well as immediately after parturition events (July and August), in comparison with the months in which they are either non-pregnant or experiencing early phases of embryo development (the rest of the year). 2) Male survival should be lower during the months in which they are searching and competing for mates (October and November), in comparison with the months in which they are not involved in reproductive activities (the rest of the year).

Additionally, I addressed three supplementary questions concerning some extrinsic and intrinsic factors that may influence this life-history trade-off. 1) Is this sort of reproductive cost density-dependent? In other words, does an increased risk of mortality associated with reproductive processes depend on the presence of a relatively large number of individuals in the population? 2) Does the trade-off between reproduction and survival occur only under unfavourable conditions? More specifically, I examined whether this cost is higher or more evident in years with negative population growth given the fact that population growth rate summarizes the effects that the environmental conditions had upon all the individuals in the population (Ebert, 1999). 3) Does the intensity of this trade-off between reproduction and survival depend on the age or size of individuals? My results demonstrate that in the study population, reproduction entails a noteworthy cost in terms of survival probabilities.

## MATERIALS AND METHODS

#### Study system and field methods

Xenosaurus grandis grandis is a knob-scaled lizard that inhabits only a few mountains in eastern Mexico (Ballinger et al., 2000a). It belongs to the family Xenosauridae, which is composed of strictly crevice-dwelling lizard species whose females give birth to live young during spring and summer (Ballinger et al., 2000b; Zamora-Abrego et al., 2007). In X. g. grandis, individuals are highly territorial and two individuals share a single crevice (a male-female pair) only during the mating season (October-November). The rest of the year adult lizards (both males and females) are found alone within a crevice. Gestation lasts on average nine months (October through June). Births occur in July and early August and the average litter size is 5.1 offspring ( $\pm 0.2$  SE). Sizes at maturity are 100 and 95 mm snout-vent length (SVL), for females and males, respectively (Ballinger et al., 2000c; Smith et al., 2000; Zamora-Abrego et al., 2007).

The study site is located in the vicinity of the town of Cuautlapan, in the central portion of the Mexican state of Veracruz (18°52'N, 97°01'W). Vegetation corresponds to a semi-deciduous tropical forest (Rzedowski, 1978). In a 5 ha plot I implemented a capture-mark-recapture experiment from May 2000 through October 2004 (Zúñiga-Vega et al., 2007). During this period I visited the population approximately once every month for a total of 51 capture occasions. On each visit I surveyed all the rock crevices in the study plot (approximately 280), attempting to collect as many individuals as possible. Once located, lizards were extracted from their crevices, sexed (by the presence or absence of hemipenes), measured and marked individually by toe-clipping (only on first capture). After data collection lizards were released in the same crevice that they were occupying. Repeated visits to the study

**Table 1.** Number of individuals of *Xenosaurus grandis grandis* captured per year, sampling occasion (month), sex, and stage (juveniles, small adults and large adults). The number of recaptures (previously marked individuals) on each sampling occasion is shown within parentheses. Estimates of total population density (number of individuals/5 ha, rounded to the next integer) for each sampling occasion are also shown (see text for details on how these estimates were calculated). Every year, late gestation occurred in May and June, births in July and August, and matings in October and November. Missing months (e.g. March 2001) correspond to those in which no sampling effort was conducted.

			Fen	nales	Males		_	
Year	Month	Juveniles	Small	Large	Small	Large	Total	Estimated population density
2000	May	2 (-)	-	2 (-)	1 (-)	2 (-)	7 (-)	50
	Jun	3 (0)	3 (0)	1 (0)	2 (0)	1 (0)	10 (0)	63
	Jul	3 (0)	0 (0)	1 (0)	3 (0)	0 (0)	7 (0)	44
	Aug	4 (2)	4(1)	0 (0)	2 (0)	2 (0)	12 (3)	75
	Sep	6 (0)	0 (0)	1(1)	0 (0)	3 (1)	10 (2)	63
	Oct	24 (6)	8 (1)	10(1)	7(1)	8 (1)	57 (10)	357
	Nov	20 (7)	3 (2)	10 (6)	5 (4)	5 (3)	43 (22)	269
	Dec	11 (8)	0 (0)	8 (5)	3 (2)	1 (0)	23 (15)	144

		_	Fen	nales	Males			
Year	Month	Juveniles	Small	Large	Small	Large	Total	Estimated population density
2001	Jan	16 (10)	7 (2)	3 (0)	2 (2)	4 (2)	32 (16)	200
	Feb	15 (7)	1 (0)	5 (2)	2(1)	6 (3)	29 (13)	182
	Mar	-	-	-	_	_	-	_
	Apr	10 (6)	7 (4)	6 (5)	3 (1)	4 (4)	30 (20)	188
	May	16 (12)	3 (3)	7 (6)	5 (3)	11 (6)	42 (30)	263
	Jun	17 (11)	6 (5)	9 (8)	6 (4)	5 (4)	43 (32)	269
	Jul	23 (14)	5 (4)	5 (5)	7 (4)	5 (4)	45 (31)	282
	Aug	17 (6)	3 (2)	11 (9)	4 (2)	9 (8)	44 (27)	276
	Sep	23 (8)	5 (4)	1(1)	4 (0)	6 (4)	39 (17)	244
	Oct	15 (9)	8 (6)	6 (5)	7 (6)	8 (6)	44 (32)	276
	Nov	19 (11)	5 (3)	5 (2)	6 (5)	11 (5)	46 (26)	288
	Dec	14 (8)	10 (9)	8 (8)	4 (3)	10 (6)	46 (34)	288
2002	Jan	14 (11)	4 (3)	7 (7)	6 (4)	9 (6)	40 (31)	251
	Feb	_	_	_	_	_	_	_
	Mar	22 (11)	3 (3)	9 (6)	7(1)	11 (9)	52 (30)	326
	Apr	11 (7)	4 (2)	11 (8)	4 (2)	7 (5)	37 (24)	232
	May	12 (9)	4 (4)	13 (9)	5 (5)	9 (6)	43 (33)	269
	Jun	14 (10)	3 (1)	13 (10)	6 (6)	13 (11)	49 (38)	307
	Jul	19 (6)	3 (2)	8 (6)	7 (6)	6 (6)	43 (26)	269
	Aug	13 (6)	3 (3)	7 (6)	6 (6)	14 (14)	43 (35)	269
	Sep	16 (8)	0 (0)	10 (10)	4 (3)	10 (10)	40 (31)	251
	Oct	17 (10)	0 (0)	13 (7)	7 (5)	10(7)	47 (29)	295
	Nov	20 (13)	2(1)	7 (6)	8 (5)	8 (7)	45 (32)	282
	Dec	18 (7)	1(1)	3 (3)	11 (7)	12 (10)	45 (28)	282
2003	Jan	14 (8)	4 (3)	6 (5)	2 (2)	7 (6)	33 (24)	207
	Feb	19 (11)	4 (4)	9(7)	6 (5)	8 (7)	46 (34)	288
	Mar	20 (14)	1(1)	11 (11)	1(1)	11 (11)	44 (38)	276
	Apr	_	_	_	_	_	_	_
	Mav	10(7)	6 (5)	10 (9)	2 (2)	12 (11)	40 (34)	251
	Jun	18 (9)	5 (3)	11 (10)	6 (2)	8 (4)	48 (28)	301
	Jul	12 (2)	8 (8)	14 (13)	8(7)	9 (9)	51 (39)	319
	Aug	22 (11)	7(7)	9 (9)	8 (5)	4 (4)	50 (36)	313
	Sep	15 (10)	8 (8)	9 (8)	11 (10)	7 (6)	50 (42)	313
	Oct	16 (13)	4 (4)	9 (9)	7 (7)	9 (9)	45 (42)	282
	Nov	19 (16)	1(1)	9 (9)	8 (6)	9 (9)	46 (41)	288
	Dec	7 (7)	3(3)	11 (11)	7 (6)	4 (4)	32 (31)	200
2004	Jan	8 (5)	3 (3)	7(7)	12 (9)	4 (4)	34 (28)	213
2001	Feb	12(10)	2(2)	5 (5)	6(5)	5 (5)	30 (27)	188
	Mar	12 (10)	$\frac{2}{5}(4)$	9 (8)	4(3)	2(2)	32 (26)	201
	Apr	12(9) 10(9)	4 (4)	6 (6)	3(3)	$\frac{2}{3}(3)$	26 (25)	163
	May	$\frac{10}{4}(4)$	3(3)	$\frac{0}{4}(4)$	1(1)	3(3)	15(15)	94
	Iun	13(11)	5 (5) 6 (6)	6 (6)	7 (7)	9 (9)	41 (39)	257
	Inl	15 (9)	4 (3)	6(6)	4 (3)	8(7)	37 (28)	237
	Δ11σ	9(7)	5 (4)	8 (6)	- ( <i>J</i> )	7(7)	34 (28)	232
	Sen	9(4)	2 (7) 2 (2)	7 (6)	5 (3)	6 (6)	29 (21)	182
	Oct	16 (10)	$\frac{2}{3}$ (2)	, (0) 4 (4)	7 (7)	9 (9)	$\frac{29}{21}$	244
	000	10(10)	5 (5)	(ד) ז	(()	7(7)	57 (55)	

site allowed me to obtain individualized recapture (encounter) histories for each marked lizard over the course of this study (i.e. data on when lizards were seen or not seen). In total, I marked and followed 570 lizards during the study period (i.e. 570 individual encounter histories for a 4.5-yr period). Of these, 281 were females and 289 were males. A detailed description of sample sizes per sampling occasion is shown in Table 1.

#### Capture-mark-recapture analysis

I calculated survival rates for adult males and females by means of maximum likelihood procedures implemented in program MARK (White & Burnham, 1999). I did not include juveniles in the analysis since reproductive costs should be apparent only after maturation (Stearns, 1992). Based on a multi-state framework (Brownie et al., 1993) and on the observed encounter histories, this computer package estimates three parameters: survival rate ( $\phi$ ), capture probability (*p*) and the rate at which individuals move from one stage (state) to another ( $\psi$  = transition probability). MARK estimates all these parameters by finding the values that maximize the following likelihood function:

$$L(\theta|\text{data}) = K(\theta_1^{n_1}\theta_2^{n_2}\dots\theta_m^{n_m})$$

In general, this function calculates the likelihood (*L*) of certain parameters ( $\theta$ ) given the data (Lebreton et al., 1992). In the particular case of multi-state mark–recapture data, the  $\theta$  parameters represent different combinations of  $\varphi$ , *p* and  $\psi$  (Brownie et al., 1993). More specifically, each  $\theta_i$  represents the probability of a certain encounter history, which in turn is a particular function of the individual's chances of surviving ( $\varphi$ ), of being recaptured (*p*) and of moving from one state to another ( $\psi$ ). These  $\theta_i$  parameters are raised to the number of animals observed with that particular encounter history (*n<sub>i</sub>*). *K* represents a multinomial coefficient and *m* the number of different encounter histories observed (Lebreton et al., 1992; Amstrup et al., 2005).

For testing the predictions that guided this study, I constructed different competing models that represented different hypotheses about variation in  $\varphi$ , *p* and  $\psi$  (i.e. such competing models differed in how  $\varphi$ , *p* and  $\psi$  were constrained). I placed the main focus on  $\varphi$ , given my interest in the trade-off between reproduction and survival. In this sense, six main types of models were constructed:

1) Cost of reproduction for females: to test the prediction that female survival should have been lower during the late phase of embryo development and after parturition, I constrained  $\varphi$  for females during May, June, July and August (months when the late phases of embryo development and births occurred) to be different from  $\varphi$ during all other months. In this type of model I kept the survival rate of males constant throughout the year and different from that of females.

2) Cost of reproduction for males: to test the prediction that male survival should have been lower during the mating season, when they must have searched and competed for females, I constrained  $\varphi$  for males during October and November (mating season) to be different from  $\varphi$  during all other months. In this type of model I kept the survival

rate of females constant throughout the year and different from that of males.

3) Cost of reproduction for both sexes: in this type of model I combined the previous two types of model, allowing  $\varphi$  for females to vary depending on the lategestation/birth season and  $\varphi$  for males depending on the mating season.

4) Lower survival during May–August and October– November for both sexes with no apparent reproductive cost: in this type of model I constrained  $\varphi$  for both sexes to be equal and lower during these periods in comparison with the rest of the year. This scenario suggested no reproductive cost because the survival rate of both sexes decreases similarly during such months instead of only females suffering the reproductive cost in May–August and only males suffering the reproductive cost in October–November. Therefore, this type of model indicates that other unknown factors besides reproductive processes might be responsible for higher and sex-independent mortality during these periods.

5) Different survival between sexes with no apparent reproductive cost: this type of model tested for a sex effect on the survival rate although constant throughout the year.

6) Constant and similar survival (null model): in this type of model  $\phi$  was constrained to be equal between sexes and constant throughout the year.

To address the additional questions that I posed concerning extrinsic and intrinsic factors that may influence the expression of a trade-off between reproduction and survival, I included different explanatory factors for  $\varphi$ within the different types of model. First, to examine whether the trade-off between reproduction and survival depended on population density, I included an estimate of monthly population density as a continuous covariate for  $\varphi$ . Density for each sampling occasion ( $N_i$ ) was calculated by accounting for the capture probability ( $p_i$ ) on each occasion *i* as:

$$N_i = n_i / p_i$$

where  $n_i$  represents sample size at occasion *i* (Armstrong et al., 2005). These monthly estimates of population density are shown in Table 1. Henceforth, I refer to this covariate as "density".

Second, to test for an effect of the overall demographic conditions, I included the factor "annual transition" within the different types of model. My interest was in comparing annual transitions (from the summer of one particular year to the summer of the following year; Zúñiga-Vega et al., 2007) with positive population growth (annual transitions with favourable environmental conditions) against annual transitions with negative population growth (annual transitions with unfavourable environmental conditions). Zúñiga-Vega et al. (2007) conducted a demographic study on this population and found that the annual transitions 2000-2001, 2001-2002 and 2002-2003 resulted in a slight potential for numerical growth (i.e. finite population growth rates above unity:  $\lambda$  values = 1.29, 1.32 and 1.13, respectively). In contrast, the annual transition 2003-2004 was an unfavourable year that resulted in negative population growth (i.e. a finite population growth rate below unity:  $\lambda$ =0.85). Therefore, I expected a considerable effect of "annual transition" on  $\varphi$ , with a higher reproductive cost during the unfavourable annual transition.

Third, to examine whether the trade-off between reproduction and survival depended on the size (or age) of individuals I included the factor "stage" within all types of model. To do so, I classified adult individuals of both sexes into two stages: small and large adults. Small adults were all those lizards with sizes between the minimum size at maturity (100 and 95 mm SVL for females and males, respectively) and 112 mm SVL. Large adults were all those lizards larger than 112 mm SVL. According to Zúñiga-Vega et al. (2005, 2007), after reaching 112 mm SVL, adult individuals of X. g. grandis decrease the amount of resources that are allocated to body growth and are therefore considered as non-growing or asymptotic adults. Individuals smaller than 112 mm SVL still invest in body growth along with investment in offspring production. These size-based stages also reflect age given the documented relationship in this species between size and age (Zúñiga-Vega et al., 2005). The category "small adults" includes younger lizards, whereas the category "large adults" includes older ones.

The use of these two stage classes was the reason for using multi-state models to analyse the mark–recapture data, given that during the study period (2000–2004) some males and females grew and "moved" from the small adult stage to the large adult stage. This biological phenomenon imposed the need to estimate the rate at which this transition occurred ( $\psi$ ) along with the survival ( $\phi$ ) and recapture rates (*p*). However, in this particular exploration of a trade-off between reproduction and survival, I placed no focus on the transition probability other than calculating it as accurately as possible to get accurate estimates of  $\phi$ .

In addition to the exploration of potential effects of population density, annual transition and stage, I also examined whether the reproductive cost for females was higher before or after parturitions. I did this by including a factor named "before/after births", which contrasted  $\varphi$  for females during May and June (the months when the last phases of embryo development occurred immediately before parturitions took place) against  $\varphi$  for females during July and August (the months when parturitions occurred; Ballinger et al., 2000c). This factor was included in models that suggested a cost of reproduction for females.

Accurate estimates of survival rely on accurate estimates of both recapture and transition probabilities (Lebreton et al., 1992; Brownie et al., 1993; Amstrup et al., 2005). Therefore, before I evaluated the support for all the biologically meaningful models described above, I constructed and tested a set of preliminary models to explore variation in p and  $\psi$ . The objective of these models was to select the type of variation in these two parameters with strongest support in the mark–recapture data. In this way, I avoided fitting an unnecessarily large number of models. For both p and  $\psi$  I tested the effect of time (a different parameter for each sampling occasion), month (a different parameter for each month regardless of the particular year), sex (different recapture and transition probabilities for males and females), stage (different recapture probability for small and large adults) and their interactions. The effects of time and month along with their interactions with sex and stage on p and  $\psi$  had weak support in the data. Similarly, an effect of stage alone on p was not very likely according to the mark-recapture data for X. g. grandis. Thus, I decided to avoid models with a time or month effect on these parameters as well as models in which p varied only between small and large adults. In contrast, an effect of sex on both p and  $\psi$  had stronger support in the data, as did the interaction between sex and stage over p (i.e. the difference between sexes in the recapture probability depended on the stage). Therefore, I used "sex" and the interaction between sex and stage ("sex  $\times$  stage") as the only meaningful sources of variation for p and "sex" as the only meaningful source of variation for  $\psi$ .

The combinations among the main six types of model, the different factors that may affect the trade-off between reproduction and survival, and the meaningful sources of variation for *p* (sex and sex × stage) and  $\psi$  (sex), resulted in a set of 50 candidate models. These models represent biological hypotheses of variation in the demographic parameters of interest ( $\varphi$ , *p* and  $\psi$ ). I used maximum likelihood routines in MARK to fit all these models to the mark–recapture data for *X. g. grandis* as well as to obtain monthly estimates of  $\varphi$  for males and females. Table 2 lists all 50 models fitted.

To select for the most likely biological scenario, that is, for the model that best supports the process that gave rise to the data, I relied on Akaike's information criterion (AIC; Akaike, 1973), whereby the smaller the AIC, the better the model. Specifically, I used a corrected version of the AIC (AIC<sub>c</sub>) that is appropriate for small sample sizes:

 $AIC_{c} = -2 \log (L) + 2P + [(2P (P + 1))/(n - P - 1)]$ 

where *L* is the maximized likelihood for the model, *P* is the number of estimated parameters and *n* is the sample size (Burnham & Anderson, 2002). This AIC<sub>c</sub> is a measure of model likelihood and parsimony and the lowest AIC<sub>c</sub> score indicates the model with the best fit to the data. A difference in AIC<sub>c</sub> scores between two models ( $\Delta$ AIC<sub>c</sub>) larger than two indicates considerable support for a real difference in the fit of such two models (Burnham & Anderson, 2002). From MARK, I also obtained model-specific Akaike weights (*w<sub>i</sub>*), which measure the relative support or weight of evidence for each model in the data (Amstrup et al., 2005). Given the data and the set of *R* candidate models, these Akaike weights are calculated as:

$$w_i = \exp(-\Delta/2)/\Sigma[\exp(-\Delta/2)]$$

where  $\Delta_i$  is the difference in the AIC<sub>c</sub> score between model *i* and the model with the lowest AIC<sub>c</sub> and *r* represent any model in the set. Thus, the denominator in this expression represents the sum across all *R* models being fitted. Based on these Akaike weights it was possible to calculate weighted averages for the survival ( $\varphi$ ), recapture (*p*) and transition ( $\psi$ ) rates of both males and females, as follows:

average 
$$(\theta) = \Sigma w_i \theta_i$$

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**Table 2.** Model selection of 50 competing models testing for distinct hypotheses concerning variation in monthly survival rate of female and male *Xenosaurus grandis grandis*. Models are described in the text. The fit of each model to the observed data was evaluated using a corrected version of Akaike's information criterion (AIC<sub>c</sub>). The model with the lowest AIC<sub>c</sub> score best fitted the data. Hence, models are listed according to the AIC<sub>c</sub> (from lowest to highest, from best to worst).  $\Delta$ AIC<sub>c</sub> represents the difference between the corresponding model and the best-fitting model. Models with  $\Delta$ AIC<sub>c</sub> <2 are considered to have support comparable to the best model. Akaike weights (*w<sub>i</sub>*) measure the relative support in the data for each fitted model. In all models the probability of transition from small to large adults ( $\psi$ ) differed between sexes.

	Source of variation for:		-		
Type of model – biological hypothesis	φ	р	$AIC_{c}$	$\Delta AIC_c$	$W_{i}$
Cost of reproduction for females	Before/after births	Sex	19293.68	0	0.194
Cost of reproduction for females	-	Sex	19293.95	0.27	0.170
Cost of reproduction for females	Annual transition	Sex	19295.00	1.32	0.101
Cost of reproduction for females	Density	Sex	19295.33	1.65	0.085
Cost of reproduction for both sexes	Before/after births	Sex	19295.72	2.03	0.070
Cost of reproduction for both sexes	-	Sex	19295.98	2.30	0.062
Cost of reproduction for females	Before/after births	$\text{Sex} \times \text{stage}$	19296.27	2.59	0.053
Cost of reproduction for females	-	$\text{Sex} \times \text{stage}$	19296.30	2.62	0.052
Cost of reproduction for females	Annual transition	$\text{Sex} \times \text{stage}$	19297.53	3.85	0.028
Cost of reproduction for both sexes	Density, annual transition	Sex	19297.75	4.07	0.025
Cost of reproduction for both sexes	Annual transition	Sex	19297.81	4.13	0.025
Cost of reproduction for females	Density	$\text{Sex} \times \text{stage}$	19297.87	4.19	0.024
Cost of reproduction for both sexes	Before/after births	$\text{Sex} \times \text{stage}$	19298.31	4.63	0.019
Cost of reproduction for both sexes	-	$\text{Sex} \times \text{stage}$	19298.34	4.66	0.019
Cost of reproduction for females	Stage	Sex	19299.84	6.16	0.009
Lower survival during May-August and October-November	Density	Sex	19299.85	6.17	0.009
for both sexes with no apparent reproductive cost					
Cost of reproduction for females	Density, Stage	Sex	19300.20	6.52	0.007
Cost of reproduction for both sexes	Annual transition	$\text{Sex} \times \text{stage}$	19300.41	6.73	0.007
Cost of reproduction for both sexes	Density, annual transition	$\text{Sex} \times \text{stage}$	19300.83	7.15	0.005
Cost of reproduction for females	Density, annual transition	$\text{Sex} \times \text{stage}$	19300.98	7.30	0.005
Cost of reproduction for both sexes	Density, stage	Sex	19301.48	7.80	0.004
Cost of reproduction for both sexes	Density	Sex	19301.50	7.82	0.004
Cost of reproduction for both sexes	Stage	Sex	19301.53	7.85	0.004
Cost of reproduction for females	Density, annual transition	Sex	19301.60	7.92	0.004
Lower survival during May-August and October-November	Density	$\text{Sex} \times \text{stage}$	19302.49	8.81	0.002
for both sexes with no apparent reproductive cost					
Cost of reproduction for females	Density, stage	$\text{Sex} \times \text{stage}$	19302.77	9.09	0.002
Cost of reproduction for females	Stage	$\text{Sex} \times \text{stage}$	19302.86	9.18	0.002
Cost of reproduction for both sexes	Density, stage	$\text{Sex} \times \text{stage}$	19303.87	10.19	0.001
Cost of reproduction for both sexes	Density	$\text{Sex} \times \text{stage}$	19304.06	10.38	0.001
Lower survival during May–August and October–November for both sexes with no apparent reproductive cost	_	Sex	19304.32	10.64	0.001
Cost of reproduction for both sexes	Stage	$\text{Sex} \times \text{stage}$	19304.50	10.82	0.001
Different survival between sexes with no apparent reproductive cost	-	Sex	19304.92	11.24	0.001
Cost of reproduction for males	Density, stage	Sex	19306.16	12.48	< 0.001
Lower survival during May-August and October-November	-	$Sex \times stage$	19306.57	12.89	< 0.001
for both sexes with no apparent reproductive cost					
Cost of reproduction for males	Stage	Sex	19306.61	12.93	< 0.001
Different survival between sexes with no apparent reproductive cost	Stage	Sex	19306.81	13.13	< 0.001
Cost of reproduction for males	-	Sex	19306.95	13.27	< 0.001
Cost of reproduction for males	Density	Sex	19307.06	13.38	< 0.001
Different survival between sexes with no apparent	_	Sex × stage	19307.48	13.80	< 0.001
reproductive cost		2			
Cost of reproduction for males	Annual transition	Sex	19307.65	13.97	< 0.001
Cost of reproduction for males	Density, annual transition	Sex	19308.02	14.34	< 0.001
Cost of reproduction for males	Density, stage	$\text{Sex} \times \text{stage}$	19308.47	14.79	< 0.001
Constant and similar survival (null model)	_	Sex	19308.85	15.17	< 0.001
Cost of reproduction for males	Stage	$\text{Sex} \times \text{stage}$	19309.12	15.44	< 0.001

	Source of variation for:			
Type of model – biological hypothesis	φ	р	AIC	$\Delta AIC_c  w_i$
Different survival between sexes with no apparent reproductive cost	Stage	$Sex \times stage$	19309.29	15.61 < 0.001
Cost of reproduction for males	_	$\text{Sex} \times \text{stage}$	19309.52	15.83 < 0.001
Cost of reproduction for males	Density	$\text{Sex} \times \text{stage}$	19309.62	15.94 < 0.001
Cost of reproduction for males	Annual transition	$\text{Sex} \times \text{stage}$	19310.28	16.60 < 0.001
Cost of reproduction for males	Density, annual transition	$\text{Sex} \times \text{stage}$	19310.70	17.02 < 0.001
Constant and similar survival (null model)	_	$\text{Sex} \times \text{stage}$	19311.10	17.42 < 0.001

Table 2 (cont.)

In this case,  $\theta$  represents any sex-, time- or size-specific survival, recapture or transition parameter,  $\theta_i$  represents the corresponding parameter derived from model *i*,  $w_i$ represents the Akaike weight for model *i* and the sum is across all fitted models. These model-weighted estimates of  $\varphi$ , *p* and  $\psi$  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).

#### RESULTS

The four models that best-fitted the mark-recapture data of X. g. grandis indicated a cost of reproduction for females (Table 2). The best-fitting model also indicated that survival of females differed between late gestation and immediately after births (it included the factor "before/ after births" affecting  $\varphi$ ; AIC = 19293.68). The second best-fitting model indicated that this cost was constant throughout the years (no additional factor affecting  $\varphi$ ; AIC = 19293.95), whereas the third best-fitting model suggested differences among years in the trade-off between reproduction and survival (it included the factor "annual transition" affecting  $\varphi$ ; AIC = 19295.00). Finally, the fourth best-fitting model suggested an effect of population density on the expression of this cost, although not variable among years (it included the covariate "density" affecting  $\varphi$ ; AIC = 19295.33). These four models had comparable support in the mark-recapture data (i.e.  $\Delta AIC_{2} < 2$ ) and their relative support (w) was 0.194, 0.170, 0.101 and 0.085, respectively (Table 2). All other models had lower support and different fit from that of the four best-fitting models (i.e.  $\Delta AIC_{c} > 2$ ).

Weighted averages calculated for the monthly survival rates of females clearly evidenced this cost of reproduction in their survival probabilities. During May and June of all years, the months when the late phases of embryo development occurred, female  $\varphi$  was the lowest: between 0.81±0.06 SE and 0.87±0.07 SE (Fig. 1). During July and August of all years, the months in which parturition events took place, female  $\varphi$  was still low: between 0.85±0.06 SE and 0.91±0.05 SE, although not as low as during May and June. In contrast, during all other months of all annual transitions, female  $\varphi$  was the highest: between 0.97±0.03



**Fig. 1.** Estimated monthly survival rates ( $\phi$ ) of female *Xenosarus grandis grandis.* A) Small females. B) Large females. Female survival was lowest during May and June of all annual transitions, when embryos were in late stages of internal development. Female survival was also low during July and August of all annual transitions, when parturition events occurred. Survival estimates were calculated by accounting for the relative support of each model fitted to the mark-recapture data (i.e. weighted average survival estimates). Vertical bars denote 95% confidence intervals.

SE and 0.98±0.02 SE. The 95% confidence intervals calculated for female  $\varphi$  during May and June of all years did not overlap with those calculated for female  $\varphi$  during September through April (non-reproductive and early gestation months), whereas those calculated for female  $\varphi$  during July and August of all years overlapped only slightly with those calculated for  $\varphi$  during September– April (Fig. 1). This lack of clear overlap indicates a statistical difference in female  $\varphi$  between late gestation/ parturition months and non-reproductive/early gestation months.

Models including an effect of stage on female  $\varphi$  had weak support in the data ( $\leq 0.009$ ; Table 2). Thus, both small and large females appeared to suffer the same



**Fig. 2.** Estimated monthly survival rates ( $\phi$ ) of male *Xenosarus grandis grandis.* A) Small males. B) Large males. The vertical axis is shown in the same scale as in Fig. 1 for comparative purposes. Survival estimates were calculated by accounting for the relative support of each model fitted to the mark-recapture data (i.e. weighted average survival estimates). Vertical bars denote 95% confidence intervals.

amount of decrease in their chances of survival during the period between May and August (Fig. 1).

Even though both "density" and "annual transition" factors had a considerable effect on female  $\varphi$  as indicated by the third and fourth best-fitting models, their effect was not quite clear. In no single annual transition was the observed decrease in  $\varphi$  during late gestation/parturition months notably different (Fig. 1), despite the fact that the transition 2003–2004 resulted in a tendency towards population decrease ( $\lambda$ =0.85) and despite the temporal variability observed in population density (Table 1).

Models suggesting a reproductive cost for males (lower survival during October and November) had remarkably low support in the data ( $\leq 0.001$ ; Table 2). Weighted averages calculated for the monthly survival rates of males clearly evidenced constant  $\varphi$  within and among years, without an apparent decrease in their survival probability during the mating season (October and November) of any year (Fig. 2). Estimates of male  $\varphi$  for all months and for all years varied only between 0.95±0.02 SE and 0.96±0.01 SE with complete overlap of their 95% confidence intervals. Similar to females, the survival rate of males was not affected by the factor "stage": both small and large males had equal  $\varphi$  (Fig. 2).

Figure 3 depicts weighted averages for the probability of recapture (*p*) and the rate of transition ( $\psi$ ) for both sexes along with their 95% confidence intervals. Recall that time variation in these parameters was not a likely scenario given the data. Thus, it was not necessary to calculate one parameter for each sampling occasion. However, both parameters differed notably between sexes. Small and large females had higher *p* (0.19±0.02 SE and 0.18±0.01 SE, respectively) compared to that of small and large males (0.15±0.01 SE for both stages). Similarly, females exhibited a higher monthly rate of transition ( $\psi$ ) between small and large stages (0.11±0.02 SE) compared to males (0.05±0.01 SE; Fig. 3).

### DISCUSSION

# The trade-off between reproduction and survival occurred only in females

Female Xenosaurus grandis grandis experienced a reproductive cost in their survival probability. Female survival rate was notably lower (an approximately 8% decrease) when they experienced the late phases of embryo development and immediately after parturition events (May through August). This trade-off between reproduction and survival was evident every year during more than four years. The energy invested in the production of live young was the likely cause of the observed decrease in survival. In general, females of viviparous species suffer from a remarkable increase in weight and volume (Ghalambor et al., 2004; Shine, 2005). Such an increase may represent a burden that makes them easier prey, more available to predators (Van Damme et al., 1989; Shaffer & Formanowicz, 1996; Webb, 2004). Furthermore, the late phases of embryo development deplete lipid reserves and impoverish their physical condition, notably increasing the risk of mortality (Lourdais et al., 2004; Winne & Hopkins, 2006; Hoffman et al., 2008). In fact, the



**Fig. 3.** Estimated recapture (*p*) and transition ( $\psi$ ) rates for Xenosaurus grandis grandis. Circles depict recapture rates and squares depict transition rates. These parameters were calculated by combining data from 4.5 years and accounting for the relative support of each model fitted to the mark-recapture data (i.e. weighted averages). Vertical bars denote 95% confidence intervals.

highest risk of mortality for females of *X. g. grandis* occurred just before parturition (i.e. during May and June), although female mortality was also relatively high right after births (i.e. during July and August), presumably because females were in poor condition following offspring production. This trade-off between reproduction and survival experienced by viviparous females has been widely documented in numerous taxa (e.g. Bonnet et al., 2002; Descamps et al., 2009; Hamel et al., 2010a). This is the first study that provides clear evidence of this trade-off in a xenosaurid lizard.

Contrary to what I expected, male survival did not decrease during the mating season in comparison with the rest of the year. In October and November of all years I observed male-female pairs sharing the same crevice. In fact, during these months every year, most adult males were found sharing a crevice with a female. During the remaining months, only one adult individual was observed per crevice. Moreover, male-female pairs were recorded within crevices that were originally occupied by females. These observations, along with data on the gestation period (Ballinger et al., 2000c), indicate that in October and November males must leave their individual crevices (safe refuges) to search for mates. Despite this behavioural change in the mating season, male recapture probability did not vary throughout the year because they could still be found at the same rate, but in different refuges. In the process of searching for mates, males may be involved in aggressive interactions with conspecific

males due to competition for females. Both the documented sexual dimorphism in head shape (in *X. g. grandis* males have wider and larger heads than females; Smith et al., 1997) and the observed aggressive behaviour of two males against each other when caged together (Ballinger et al., 1995; Rojas-González, 1999; Zúñiga-Vega, 2005) support the existence of male–male competition for mates. Together, these facts led me to predict greater male mortality during the mating season given the time and energy that males have to invest in searching and fighting for mates (Neuhaus & Pelletier, 2001; Low, 2006; Briffa & Sneddon, 2007).

However, male mortality appeared to be relatively similar throughout the year. Time outside their refuges might not be long enough to increase their risk of being preved upon. This scenario is supported by a time-invariant recapture probability for males. Moreover, intrasexual competition events might not be intense enough to cause a considerable decline in their physical condition. If the observed male-male aggressiveness does not usually result in severe injuries or in the death of one male, then these interactions might not be costly in terms of mortality. Thus, aggressiveness may be only a mechanism by which males demonstrate their quality and the potential to get mates relative to other males (Cox & Le Boeuf, 1977; Krebs & Davies, 1993). This scenario is supported by similar mortality during the mating season in comparison with the rest of the year. Unfortunately, for xenosaurid lizards no information is available about the consequences of this male-male aggressive behaviour under natural conditions.

#### The effect of extrinsic and intrinsic factors

In addition to examining the existence of a trade-off between reproduction and survival for these lizards, I also aimed to explore the potential effects of some extrinsic and intrinsic factors that might have affected the expression of this reproductive cost. I found that population density exerted some effect on female survival and, as a consequence, on the lower survival associated with reproduction. Previous studies focused on disentangling the causes of a negative relationship between current reproduction and future survival have documented a greater cost of reproduction under high population density conditions given the concomitant decrease in resource availability (Festa-Bianchet et al., 1998; Hamel et al., 2010b). However, even though my 4.5 years of mark-recapture data suggested this sort of density-dependent effect, it was not as intense as expected given that the yearly variation in this reproductive cost was not drastic. Perhaps the fluctuations in population density were not high enough or perhaps my sample sizes did not allow me to detect finescale differences among years.

I also expected a more intense trade-off between reproduction and survival during the unfavourable annual transition. Zúñiga-Vega et al. (2007) documented a negative population trend during 2003–2004 ( $\lambda$ =0.85) as a result of warmer environmental conditions. My markrecapture data suggested differences among years in the expression of this trade-off, with the lowest female survival during May and June of 2004 (Fig. 1). Possibly, the harsh environmental conditions experienced by these lizards during 2003–2004 resulted in more costly reproductive events for females. However, the difference between this unfavourable annual transition and the remaining years in the expression of the reproductive cost was not as high as expected. Either the trade-off between reproduction and survival is fairly constant among years independently of the environmental conditions, or the differences in survival among favourable and unfavourable years are only slight and undetectable with relatively small sample sizes.

A potential intrinsic factor that might promote a higher cost of reproduction is the life-history stage. Several studies in a wide variety of viviparous species have documented that either small, young and inexperienced females or large, old and weakened ones might suffer a greater trade-off between reproduction and survival (e.g. Hutchings, 1994; McElligott et al., 2002; Descamps et al., 2009). However, this was not the case in *X. g. grandis*. Both small (presumably younger) and large (presumably older) females suffered a similar decrease in survival during the months in which late gestation and parturition occurred. This result demonstrates that, in these crevice-dwelling lizards, the high reproductive investment associated with viviparity and the concomitant risks do not vary with size or age.

## Implications for the demography and life-history of *Xenosaurus grandis*

Among xenosaurid lizards, X. g. grandis exhibits one of the largest litter sizes (Zamora-Abrego et al., 2007). Females produce an average of 5.1 offspring. However, they can produce up to eight young (Ballinger et al., 2000c). This litter size is considerably larger than that of other species of the genus (2.5 young in X. platyceps, 2.6 young in X. newmanorum, 2.7 young in X. g. agrenon; Ballinger et al., 2000c; Zamora-Abrego et al., 2007; Rojas-González et al., 2008). Moreover, the relative litter mass of X. g. grandis (percentage of the female mass that is devoted to offspring production = 35%) is notably higher when compared to other xenosaurid species such as X. phalaroanthereon (16%), X. g. rackhami (23%) and X. platyceps (23%; Zamora-Abrego et al., 2007; Rojas-González et al., 2008). Given the relatively lower female reproductive effort in other xenosaurids, I expect to observe a lower cost of reproduction in female survival of the other species listed above (i.e. a less marked difference in survival during late gestation and birth seasons compared to the rest of the year). What are the factors that promote such increased reproductive effort in X. g. grandis, with the concomitant increased risk of mortality for females, in comparison with other xenosaurids? Additional work will be required to address this question. However, the benefits in terms of fitness of this high investment in reproduction must be large enough to offset the observed cost of decreased survival. Testing this hypothesis would require comparing measures of individual fitness, such as the total number of offspring produced during their lifetime, among females with different levels of reproductive investment (e.g. Coulson et al., 2006). This sort of comparison would be worth doing among female X. g. grandis

and among females of different xenosaurid species, both in their natural populations and under controlled conditions. This topic represents indeed a fertile field for future research.

What consequences may the observed sex-specific mortality patterns in the demographic and life-history characteristics of the species have? First, increased female mortality at the end of the reproductive season may skew the population sex ratio towards males. However, adult sex ratio in the study site is no different from 1:1 (Zúñiga-Vega et al., 2007). Thus, newborn sex ratios might be compensating for this lower female survival by producing more females. This hypothesis still needs a formal test. Second, this relatively high cost of reproduction for female survival might explain why the reproductive cycle in X. g. grandis is biennial (Ballinger et al., 2000c). After giving birth to a large number of young in July or early August, the physical condition of females is apparently not good enough to begin a new reproductive cycle in the following October (only two months after). If they did so, their chances of dying would probably increase even more. Instead, females appear to need a whole year to recover, store lipid reserves again and start producing new vitellogenic follicles. Therefore, the combination of viviparity (a process that demands large amounts of resources; Thompson & Speake, 2002), a remarkably long gestation period (nine months; Ballinger et al., 2000c), and the increased mortality risk right before and after parturition might have favoured females that reproduce every other year, from an evolutionary standpoint.

#### Conclusion

Here I have documented a trade-off between reproduction and survival for a xenosaurid lizard. This trade-off was only evident in females. Their risk of mortality was highest during late gestation and still high after births took place. Apparently, males did not suffer from a reproductive cost in survival. During the mating season in all years, when the highest investment in reproduction should have occurred in males, their survival rate remained the same as throughout the rest of the year. This female-specific reproductive cost occurred every year during my study period (2000-2004), regardless of yearly variations in extrinsic conditions such as population density or population growth rate. It is likely that this observed sex-specific trade-off has shaped the evolution of reproductive effort in these lizards. How this process has occurred and how it differs among xenosaurid species deserves future research. These results prove that viviparity requires large amounts of energy and that its benefits are not always as clear as its costs. I have confirmed here that for females of Xenosaurus grandis grandis reproduction is costly.

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