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Determinants of survival in juvenile *Psammodromus algirus* lizards

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Abstract Theories posit that the relative mortality rate of adults and juveniles is a major determinant of population dynamics and life history evolution. Moreover, differential survival of pre-reproductive individuals may be an important source of variation in lifetime reproductive success, and characters that influence survival of juveniles are likely to be under strong selection. We examined survival from hatching to maturity in a natural population of *Psammodromus algirus* lizards using data from a capture-mark-recapture study. We found that mortality from hatching to maturity was high: only 8% of males and 14% of females that hatched in 1996 survived the entire study period until maturity in spring 1998. The probability of survival was 75% during both the first and second overwinter periods when lizards were inactive most of the time, and about 25% during their first spring to autumn activity season. Our analyses further revealed significant associations between survival and snout-vent length, body condition, sex and microhabitat use. However, the relationship between survival and morphological characters varied among time periods, presumably because the sources of mortality during the activity season were different from those during hibernation. The association between survival and body condition also varied within time periods, both between large and small individuals and between the two sexes. This suggests that the relative importance of different selective agents may change during the life of individuals and vary between males and females due to differences in body size and behaviour.

Key words Life history · Body condition · Snout-vent length · Microhabitat · Mortality

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Introduction

There is both theoretical and empirical evidence to suggest that probability of survival is a major determinant of life history evolution (e.g. Charlesworth 1980; Jayne and Bennett 1990; Laurie and Brown 1990; Roff 1992; Janzen 1993). Accurate assessments of survivorship are therefore necessary to differentiate among competing hypotheses concerning the nature of selective forces driving life history evolution (e.g. Stearns 1977; Charlesworth 1980; Gibbs and Grant 1987; Jayne and Bennett 1990; Sinervo and Huey 1990). In particular, information on juvenile mortality rates in the field is, for several reasons, very important for examining life history evolution. First, life history theories posit that the relative mortality of adults and juveniles may play an important role in the evolution of age and size at first reproduction, reproductive expenditure and the partitioning of energy among the different offspring within a clutch or litter (e.g. Reznick et al. 1990). Second, only those individuals that live to maturity may contribute offspring to the next generation, and differential survival of individuals at the pre-reproductive stage may therefore be an important determinant of variation in lifetime reproductive success (Clutton-Brock 1988). Consequently, characters that influence survival of juveniles are likely to be under strong selection. Third, the particular ways in which mortality differs according to size, body condition, sex and growth rate may have important consequences for population structure and dynamics (Bacon 1982; Smith and Sibly 1985; Forsman 1993).

Several attempts have been made to quantify and identify sources of variation in the survival of lizards. Studies of the effects of body size on survivorship of juvenile lizards have shown that larger individuals have a survival advantage over smaller ones (e.g. Ferguson et al. 1982; Ferguson and Fox 1984). Other characters that may affect survivorship are growth rate and body condition. Growth rate may indirectly influence survival because of its effect on body size. Individuals that grow quickly have also been hypothesized to display reduced survival because of the risks involved in foraging and the physiological costs associated with rapid growth (e.g. Calow and Townsend 1981; Sibly and Calow 1986; Forsman 1997). One such physiological cost is the trade-off between growth rate and energy storage or body condition (Forsman and Lindell 1991, 1996). Body condition (body mass adjusted for body length) may be used as an indicator of previous food intake rate, amount of stored energy and general health, and hence individuals in high body condition may be less susceptible to starvation (Pond 1981; Wong 1985; Laurie and Brown 1990; Millar and Hickling 1990; Forsman and Lindell 1996). However, a high body condition may also incur costs because it impairs agility and increases the energy demands of locomotion (Pond 1978, 1981), and decreases endurance capacity and speed (Garland and Arnold 1983; Garland 1985).

Differential survival among lizards may result not only from variation in the phenotypic properties of the individuals themselves but also from differences in their microhabitat. Some microhabitats may supply better refuges against predators or provide more or higher-quality food (Martin and Salvador 1992; Martin and Lopez 1998) and, thus, microhabitat use may have a direct effect on survival (Tracy 1982). For example, Fox (1978) showed that the home ranges of surviving juvenile *Uta stansburiana* had more diverse microhabitats with access to more food and shelter holes, compared to non-survivors. However, home range size and quality may also be associated with the phenotypic quality of the individual. For example, body size and social factors, such as aggressiveness, fighting ability and relative dominance influence the home range size and microhabitat use of some lizards (Stamps 1977; Rose 1982; Schoener and Schoener 1982). Conversely, properties of the home range such as food abundance and basking opportunity may influence phenotypic quality and, hence, survival.

Here, we examine survival from hatching to maturity in a natural population of *Psammodromus algirus*, a medium-sized, terrestrial, diurnal, oviparous lizard inhabiting the Iberian Peninsula, southern France and northwestern Africa (Böhme 1981). The data derive from a capture-mark-recapture study of a cohort of lizards that hatched in autumn 1996 and attained maturity in 1998. We estimate and compare survival of lizards during the first hibernation period, the first complete activity season and the second hibernation period. To examine whether differential survival of individuals was random or associated with morphology, behaviour or microhabitat use, we use logistic regression analysis to test for relationships between survival and sex, snout-vent length (SVL), body condition, growth rate and microhabitat characteristics. Because the relative importance of different selective agents may vary during the life of an individual and among time periods (e.g. activity season versus hibernation), we performed separate analyses on data from each of the two autumn to spring periods and the spring to autumn period.

Materials and methods

Study species and study area

In our study population inhabiting a mountain area in central Spain (see below), *P.algirus* enters hibernation in late October and emerges in early March. During the mating period, beginning shortly after emergence, males defend territories and fight with other males for access to females (Salvador et al. 1995). Furthermore, juvenile individuals of this species actively defend their territory against intruding conspecific juveniles (E. Civantos, unpublished data). Females produce one clutch per season and carry the eggs for approximately 6–8 weeks before ovipositing in July. The eggs hatch between late August and early October, with variation among years depending on weather conditions. The SVL of hatchlings is 24–29 mm. Individuals become sexually mature in their second spring when SVL is 65–70 mm (E. Civantos, unpublished data). Adult body size varies among populations, but SVL seldom exceeds 90 mm.

We performed a capture-mark-recapture study of a cohort of hatchlings born in autumn 1996, from September 1996 through April 1998, when lizards attained sexual maturity. The study population inhabited a deciduous oak forest near Navacerrada (40°44' N, 4°00' W, altitude 1,300 m), a mountain area in central Spain. The vegetation in the study area is characterised by deciduous trees and a well-developed low sapling scrub of oaks (*Quercus pyrenaica*) and less abundant and dispersed perennial evergreen bushes (*Cistus laurifolius*). Some isolated patches of large rocks are present in the forest. Possible predators on *P. algirus* present in our study area are the ocellated lizard (*Lacerta lepida*), snakes (*Malpolon monspessulanus*, *Elaphe scalaris* and *Coronella girondica*), mammals and birds.

In spring 1996, we delimited a plot of 1.5 ha that was divided into a grid with markers every 10 m. We performed four capture and recapture periods: autumn 1996, spring 1997, autumn 1997, and spring 1998. The capture and recapture periods ranged between 3 and 6 weeks. During these periods, we visited the plot every day between 0930–1330 hours and between 1600–1730 hours, and systematically searched for lizards by walking through the plot a routine path to ensure equal sampling effort in all areas. We did not visit the plot during days of bad weather (rain and cold) nor in the cooler months when lizards were inactive. We captured hatchlings by hand, and juveniles and adults by noose, while walking slowly across the study plots. For each individual, we recorded date and place of capture (to the nearest 10-m marker), sex, SVL to the nearest 0.5 mm, weight to the nearest to 0.01 g, and tail condition (entire or broken). The sex of hatchlings was determined from the number of femoral pores, number of ventral scales and number of spots on the right side (Civantos et al. 1999). All individuals were marked by toe clipping for permanent identification. The position where individuals were first sighted was recorded.

Lizards captured in a given period were classified as survivors or non-survivors depending on whether or not they were recaptured in one or more of the subsequent capture periods. Individuals not recaptured were assumed to be dead. To assess the validity of our classification of survivors and non-survivors, we analyzed the data of the first period (autumn 1996–spring 1997) with a probabilistic model for capture-recapture analysis (Lebreton et al. 1992). The estimated capture probability (±SD) was 0.84±0.55 (95% confidence interval 0.70–0.92). This shows that we were able to recapture the vast majority of the surviving individuals. Some individuals nevertheless may have survived and remained in the study area without being recaptured. This will have confounded the results only if lizard with different phenotypes were not equally likely to be caught. However, the difference in morphology between recaptured and non-recaptured individuals shifted among time periods (see below). This may reflect the possibility that a given morphology may make an individual relatively easy to capture during one time period, but relatively difficult to capture during another time period; however, we consider this unlikely. In addition, some individuals may have survived but moved out of our study plot. To search for emigrating individuals, we surveyed a 20-m-wide zone surrounding the study plot for 1 day every week from September to October 1996, March to June 1997 and September to October 1997. Moreover, in an area contiguous to the study plot that was surveyed intensively for 1 day every week from March 1997 to June 1997, we searched for individuals that may have moved between 20 m and 90 m from the border of the study plot. We cannot distinguish mortality from emigration out of our study area. However, the short distances moved between recaptures (Civantos et al. 1999), the low number of recaptures (two individuals) in the 20-m zone surrounding the study plot and the lack of recaptures in the area adjacent to the study plot suggest that individuals that were not recaptured did not emigrate out of the study population.

To examine the influence of microhabitat features on hatchling survivorship, we measured microhabitat characteristics at the point where individuals were first sighted. Due to time constraints and because the method used to quantify microhabitat structure (see below) did not cover the total home range of individuals older than 1 year, this was done only in the spring 1997 capture period. To quantify microhabitat structure, we took four 5-m transects, one at each of the four cardinal orientations radiating from where the lizard was first sighted. Using a scored stick held vertically, we recorded the number of contacts with the stick of grass, leaf litter, bare soil, or rocks at substrate level, at 1-m intervals. Using the same procedure, we recorded plant contacts with the stick at heights of 5, 10, 25, 50, and 100 cm, and then summed the number of vegetation contacts across the five different heights. This procedure provided 20 sample points per observation, allowing us to calculate the value of five habitat variables: the relative abundance of the four different substrate categories, and vegetation cover above ground level (Noon 1981; Scheibe 1987). By using this procedure, we sampled an area similar in size to the mean home range area of an individual during its first spring (E. Civantos, unpublished data).

Statistical analyses

To test for relationships between survival and morphological variables (i.e. sex, SVL and body condition) we used logistic regression analysis, available under the procedure CATMOD in SAS (SAS 1988). Logistic regression is suitable for dichotomous dependent variables (e.g. alive versus dead), and can handle both categorical and continuous independent variables. Hosmer and Lemeshow (1989) give a thorough description, including several examples, of the procedure of logistic regression analysis. SAS provides a likelihood-ratio statistic as a goodness-of-fit for the model, and maximum-likelihood estimators (β, a slope coefficient that represents the change in the logit for a change of one unit in the independent variable) and standard errors of the independent parameters. To assess the significance of the independent variables, we calculated the difference in deviance for a model with and without the variable of interest. We then compared this value (G) against a χ^2 distribution to test the hypothesis that omission of a given variable from the model significantly decreases the support for the model, given the data (Hosmer and Lemeshow 1989; Collett 1991).

The inclusion of SVL as an independent variable in a logistic regression analysis of survival provides a test for a linear relationship (on a logit scale) between body size and the probability of survival. To test if individuals intermediate in size have a higher (or lower) survival rate than large or small individuals, we also examined the effect of squared individual deviations from the SVL means on survival. This was accomplished by including a quadratic term of SVL in the model. Similarly, to test if individuals intermediate in body condition have a higher (or lower) survival rate than individuals in either poor or good condition, we included a quadratic term of condition. A negative value of the maximum-likelihood estimate associated with the quadratic term would imply stabilising selection, whereas a positive estimate would imply disruptive selection.

We started with a saturated model considering effects of all the independent variables sex, SVL, squared SVL, condition, squared condition as well as all interactions between independent variables on survival, and assessed its fit (Hosmer and Lemeshow 1989). We then reduced the number of explanatory variables included in the model in an attempt to find a more parsimonious model that still provided a good representation of the data. This was done by first omitting all high-order interactions, keeping only the main effects and the two-way interactions between sex and SVL, sex and condition, and SVL and condition. We then assessed the fit of this reduced model and determined whether omission of the other interactions significantly decreased the support for the model, as explained above. The interactions between sex and body size and between sex and condition were included in the reduced model to determine whether the relationship between these independent variables and probability of survival was different in males and females. Similarly, the interaction between body size and condition was included to examine whether the relationship between body condition and probability of survival was different in large and small individuals. If any of these three interactions was not significant, a simpler model without the interaction was fitted to the data. To determine whether differences in morphology among hatchlings were associated with long-term survival, we performed one analysis of survival over the entire study period, that is from hatching in autumn 1996 to sexual maturity in spring 1998. In addition, because the relationship between survival and the various morphological variables may change with age or over time, we performed separate analyses of data for each of the periods autumn 1996 to spring 1997, spring 1997 to autumn 1997, and autumn 1997 to spring 1998.

To test for a relationship between relative growth rate and subsequent survival we calculated individual relative growth rates and compared these between surviving and non-surviving individuals. This was done only for the period spring 1997 to autumn 1997 because of limited data for the remaining time periods and because in this time period, the lizards reach their mature body size. We obtained data on growth rate for 75 individuals (37 males and 38 females) that were captured on two separate occasions in early spring 1997. Growth rates were calculated as the increments in SVL between two capture events in spring separated by a mean of 73±13.91 days, with a range 48–134 days. Relative growth rates were calculated as the residuals from the least-squares linear regression of growth rate on SVL at first capture. Residuals thus represent size-independent measures of growth rate relative to other individuals in the sample, and positive and negative residuals represent individuals with fast and slow growth rates for their SVL, respectively. The sexes were analysed separately because the relationship between growth rate and body size is different in males and females (see below).

Finally, we examined whether probability of survival was associated with differences in the microhabitat characteristics of the home ranges of individuals. For this purpose, we first reduced the number of variables used to describe microhabitat by performing a principal-component analysis (PCA) based on a correlation matrix of the five microhabitat variables described above using procedure PRINCOMP (SAS 1988). The principal component scores were not standardised to unit variance but have variances equal to their corresponding eigenvalue. We then tested for a relationship between the first principal component and survival using logistic regression analysis.

Results

The number of recaptured and non-recaptured males and females, and their mean body size, body mass and body condition are presented for each time period in Table 1. The proportion of individuals that were recaptured varied significantly among time periods for both females (χ^2=53.18, *df*=2, *P*<0.001) and males (χ^2=56.60, *df*=2, *P*<0.001).

Table 1 Snout-vent length (SVL), body mass and body condition (measured as residuals from regression of body mass on SVL) of recaptured and non-recaptured *Psammodromus algirus* lizards that hatched in autumn 1996 (*Nr* number of individuals that were recaptured, *Nt* number of captured individuals, *Diff* mean of recaptured minus mean of non-recaptured individuals)

	Sex	Nr/Nt	All		Recaptured		Non-recaptured		Diff
			Mean	SD	Mean	SD	Mean	SD	
Autumn 1996–spring 1997									
Snout-vent length (mm)	M	81/110	27.84	2.64	27.90	2.91	27.67	1.65	0.23
	F	87/117	28.55	2.63	28.85	2.74	27.67	2.05	1.18
Body mass (g)	M	81/110	0.52	0.22	0.52	0.24	0.52	0.11	0.00
	F	87/117	0.54	0.22	0.52	0.08	0.49	0.13	0.03
Body condition	M	81/110	0	0.068	–0.003	0.072	0.069	0.055	–0.072
	F	87/117	0	0.073	–0.004	0.076	0.012	0.063	–0.016
Spring 1997–autumn 1997									
Snout-vent length (mm)	M	18/85	34.55	3.13	34.19	2.37	34.64	3.32	–0.45
	F	33/100	35.00	2.94	35.74	3.32	34.64	2.69	1.10
Body mass (g)	M	18/85	0.95	0.51	0.70	0.97	1.02	0.29	–0.32
	F	33/100	1.00	0.44	1.05	0.68	0.97	0.25	0.08
Body condition	M	18/85	0	0.376	–0.213	0.756	0.057	0.128	–0.270
	F	33/100	0	0.253	–0.039	0.405	0.019	0.124	–0.058
Autumn 1997–spring 1998									
Snout-vent length (mm)	M	14/19	67.89	2.54	68.28	2.01	66.80	3.73	1.48
	F	26/33	68.01	3.14	68.04	3.40	67.93	2.15	0.11
Body mass (g)	M	14/19	7.59	1.17	7.83	0.77	6.89	1.86	0.94
	F	26/33	6.74	0.99	6.70	1.05	6.90	0.82	–0.20
Body condition	M	14/19	0	0.569	0.089	0.564	–0.250	0.564	0.339
	F	26/33	0	0.459	–0.049	0.463	0.182	0.426	–0.231
Autumn 1996–spring 1998									
Snout-vent length (mm)	M	9/110	27.84	2.64	27.58	1.19	27.86	2.73	–0.86
	F	16/117	28.55	2.63	29.28	3.07	28.43	2.55	0.85
Body mass (g)	M	9/110	0.52	0.22	0.55	0.11	0.52	0.23	0.03
	F	16/117	0.54	0.22	0.60	0.26	0.53	0.21	0.07
Body condition (residuals)	M	9/110	0	0.068	0.047	0.075	–0.004	0.066	0.051
	F	16/117	0	0.073	–0.0007	0.0722	0.0001	0.074	–0.0008

Survival in relation to morphological characters

The results from the logistic regression analysis of survival on morphological variables are summarised in Table 2. Note that to allow comparisons across the different time periods, some variables that were not included in the final models are listed in the table. Calculations of differences in deviance between saturated and reduced models revealed that none of the large number of possible interactions that are not included in Table 1 significantly influenced survival, and this was the case for all time periods (all $P>0.25$). Overall, our analyses revealed significant associations between survival and SVL, body condition and sex. These associations were complicated, and varied between time periods, sexes, and between large and small individuals. Below we present the results in greater detail for the entire study period and then for each of the time periods.

Autumn 1996–Spring 1998

We obtained data on survival from autumn 1996 to spring 1998 for 227 individuals (Table 1). Only 8% of males and 14% of females that hatched in 1996 survived the entire study period, that is until they reached sexual maturity. Logistic regression analysis revealed a nearly significant effect on survival until maturity of the interaction between sex and body condition shortly after hatching (Table 2), suggesting that the relationship between condition and survival was different in the two sexes. Separate analysis of the two sexes revealed that survival significantly increased with increasing hatchling body condition in males ($\beta=11.26\pm5.34$, $G=4.45$, $P<0.05$). In females, however, survival was not associated with hatchling body condition ($\beta=-0.17\pm3.69$, $G=0.001$, $P>0.9$).

Autumn 1996–Spring 1997

We obtained data on survival of hatchlings from autumn 1996 to spring 1997 for 227 individuals. In both males and females, 74% of the hatchlings survived this time period (Table 1). Logistic regression analysis revealed a significant quadratic effect of SVL on survival, indicating that hatchlings that were intermediate in size survived less well than either smaller or larger hatchlings

Table 2 Results of logistic regression analysis of survival on sex, snout-vent length (*SVL*) and body condition in *P. algirus* lizards that hatched in autumn 1996. Body condition was measured as residuals from linear regression of body mass on SVL. *SVL2* and *Condition2* represent squared deviations from the mean and test for a quadratic relationship between survival and SVL and body condition, respectively. Non-significant variables are included to allow comparisons among time periods (n number of individuals, β maximum-likelihood estimate with the associated SE)

	β	SE	*G*	*P*
Autumn 1996–spring 1997 (n=227)				
Sex			0.03	>0.75
SVL	0.04	0.11	0.12	>0.75
SVL2	0.116	0.0398	13.73	<0.001
Condition	–6.35	3.43	3.49	$0.05<P<0.1$
Condition2	109	47.83	7.17	<0.01
Sex×SVL			0.29	>0.5
Sex×condition			1.07	>0.25
SVL×condition	6.84	2.237	15.92	<0.001
Spring 1997–autumn 1997 (n=185)				
Sex			2.13	>0.10
SVL	0.12	0.12	0.98	>0.25
SVL2	–0.009	0.027	0.12	>0.50
Condition	–0.68	1.86	0.14	>0.50
Condition2	24.80	9.50	18.66	<0.001
Sex×SVL			2.55	>0.10
Sex×condition			0.02	>0.75
SVL×condition	1.36	0.57	10.31	<0.005
Autumn 1997–spring 1998 (n=52)				
Sex	–0.21	0.38	0.30	>0.50
SVL	0.09	0.15	0.60	>0.25
SVL2			0.22	>0.50
Condition	–0.03	0.85	0.01	>0.90
Condition2	1.56	1.66	0.61	>0.25
Sex×SVL			0.11	>0.50
Sex×condition	1.80	1.14	3.22	$0.05<P<0.1$
SVL×condition	–0.33	0.32	1.24	<0.25
Autumn 1996–spring 1998 (n=227)				
Sex	–0.41	0.25	2.94	$0.05<P<0.1$
SVL	0.04	0.07	0.48	>0.25
SVL2			0.64	>0.25
Condition	5.54	3.24	2.98	$0.05<P<0.1$
Condition2			0.09	>0.75
Sex×SVL	–0.08	0.08	1.68	>0.10
Sex×condition	5.71	3.24	3.22	$0.05<P<0.1$
SVL×condition			0.005	>0.90

(Table 2). Similarly, there was a significant quadratic effect of condition on survival, indicating that hatchlings that were in poor or good body condition survived better than hatchlings in intermediate condition. There was also a significant effect of the interaction between SVL and body condition on survival, showing that the relationship between condition and survival was dependent upon SVL (Table 2). We therefore conducted two separate analyses of the effect of condition on survival, based on data for individuals with a SVL that was smaller than the mean and larger than the mean. Among small hatchlings, survival significantly decreased with increasing body condition ($\beta=-12.24\pm4.48$; $G=7.44$, $P<0.001$). Among large hatchlings, however, the relationship between condition and survival was positive, albeit not significant ($\beta=1.64\pm4.49$, $G=0.13$, $P>0.5$).

Spring 1997–Autumn 1997

We obtained data on survival from spring 1997 to autumn 1997 for 185 juveniles. Of those individuals that had survived their first winter, only 21% of the males and 33% of the females survived during their first activity season (Table 1). Logistic regression analysis again revealed a significant quadratic effect of condition on survival, indicating that juveniles that were in poor or good body condition survived better than juveniles in intermediate condition. As in the previous time period, there was a significant effect of the interaction between SVL and body condition on survival (Table 2). Among small individuals, survival tended to decrease with increasing body condition ($\beta=-4.22\pm3.08$, $G=1.88$, $P>0.1$), but among large individuals, survivorship instead tended to increase with increasing condition ($\beta=2.44\pm2.48$, $G=0.97$, $P>0.25$).

Autumn 1997–Spring 1998

We obtained data on survival from autumn 1997 to spring 1998 for 52 individuals. The proportion of individuals that survived their second winter was 74% in males and 79% in females (Table 1). Logistic regression analysis uncovered a close to significant effect on survival of the interaction between sex and body condition, as was the case also for the entire study period (Table 2). Among females, survival tended to decrease with increasing body condition, albeit not significantly ($\beta=-1.13\pm0.96$, $G=1.36$, $P>0.1$). Among males, the probability of survival instead tended to increase with increasing body condition, but again this relationship was not statistically significant ($\beta=1.14\pm1.01$, $G=1.29$, $P>0.25$).

Survival in relation to microhabitat characteristics

PCA revealed that differences among individuals in microhabitat are adequately represented in two dimensions, judging by the magnitude of their respective eigenvalues; the first two components cumulatively accounted for 84% of the total variance in microhabitat variables. Principal component 1 (PC1) explained 60% of the variance and the first eigenvector showed high positive loadings on aboveground vegetation cover and leaf litter, a high negative loading on grass, and low positive and negative loadings on rock and bare soil, respectively. PC2 explained 24% of the variance and the second eigenvector had high positive loading on grass and aboveground vegetation cover, a high negative loading on leaf litter, and low loadings on rocks and bare soil.

There were no differences in the microhabitats used by males and females, either when microhabitat was measured as PC1 (males, mean±SD: -0.61 ± 4.92, $n=78$; females: 0.52 ± 4.86, $n=84$; $t=-1.4762$, $df=160$, $P=0.14$) or as PC2 (males: -0.21 ± 3.20, $n=78$; females: 0.08 ± 3.15, $n=84$; $t=-0.58$, $df=160$, $P=0.56$). A positive correlation between SVL of individuals in spring 1997 and the PC1-value of their home range (r=0.26, P<0.001, n=162) suggests that body size and microhabitat characteristics were associated. However, there was no association between PC1 and body condition of individuals in early spring (r=–0.08, P=0.29, n=162) nor between PC1 and the rate of growth of individuals until autumn 1997 (r=0.13, P=0.51, n=28). No correlation was evident between PC2 and either SVL, body condition or growth rate (all P>0.25)

The characteristics of the microhabitat used by individuals in spring 1997 was significantly associated with the probability of survival during the activity season until autumn 1997. Thus, survival decreased significantly with increasing values of PC1 (β=–0.12±0.053, G=4.69, P<0.05), suggesting that mortality increased with increasing aboveground vegetation cover. Interestingly, this relationship between survival and PC1 remained unchanged when we statistically controlled for the effects of condition, SVL and their interaction on survival by also including these variables in the model (effect of PC1, β=–0.14±0.058, G=6.01, P<0.05). There was no relationship between PC2 and survival (β=–0.03±0.069, G=0.19, P>0.5).

Survival in relation to growth rate

The relationship between growth rate and body size at first capture differed significantly between the sexes, with males growing faster than females (ANCOVA, comparison of slopes: $F_{1,71}$=0.21, P=0.64; comparisons of least-squares means: $F_{1,72}$=7.58, P<0.01). We therefore computed relative growth rates as residuals from separate regressions of growth rate on initial SVL in males and females. Comparisons of relative growth rates between individuals that were recaptured in autumn 1997 and individuals that were not recaptured yielded no evidence for an effect of growth rate in spring on subsequent survival, either in males (recaptured, mean±SD of residuals: –0.00176±0.0338, n=27; non-recaptured: 0.00476±0.0272, n=10; t=0.55, df=35, P=0.59) or in females (recaptured: 0.00279±0.0300, n=26; non-recaptured: –0.0060±0.0208, n=12; t=0.92, df=36, P=0.36). Logistic regression analysis also revealed no association between the relative growth rate of individuals and their probability of survival (β=–1.86±8.65, G=0.02, P>0.75).

Discussion

Overall, our results show that mortality from hatching to maturity of *P. algirus* lizards was high: only 8% of males and 14% of females that hatched in 1996 survived the entire study period until maturity in spring 1998. The probability of survival varied among time periods, being as high as 75% during both the first and second fall to spring periods when lizards were inactive for most of the time, and about 25% during their first spring to autumn activity season (Table 1). Unfortunately, our mark-recapture data do not enable us to identify the sources of mortality, but the lizards may have either frozen to death during hibernation or died from starvation, infectious diseases, or predation imposed by large lizards, snakes, mammals and birds (see above). In fact, juvenile *P. algirus* lizards may even have been preyed upon by larger conspecifics (E. Civantos, personal observation). Our analyses further revealed significant associations between survival and SVL, body condition, sex and microhabitat use. However, these associations between survival and morphological characters were complex and varied among time periods (Table 2), presumably because the sources of mortality during the activity season differed from those during periods of low activity and hibernation. Another possible explanation for this variability is that the relative importance of different selective factors, such as predation and starvation, may have changed during the life of the individual as a consequence of increments in body size and changes in behaviour.

Survival in relation to body condition, SVL and sex

Body condition was significantly associated with survival during all three time periods, although the effect of condition on survival was sometimes linear, sometimes quadratic, and sometimes dependent upon the sex and body size of the individuals (Table 2). Body condition indices (length-mass relationships) offer a good indicator of previous food intake rate and the size of energy reserves in reptiles (Bonnett and Naulleau 1994; Forsman and Lindell 1996) and are associated with both direct and indirect costs and benefits that may influence survival. A high body condition may enhance survival during periods of food shortage, and during and shortly after emergence from hibernation (Pond 1981). In line with this, the positive relationship between body condition and survival in larger *P. algirus* individuals suggests that a high condition favours survival of hatchlings during winter and periods of inactivity. However, a high body condition may also negatively influence survival. First, large fat deposits increase the metabolic costs of locomotion, and impair locomotor performance (Taylor et al. 1980), possibly leading to increased predation risk and reduced foraging efficiency (Huey et al. 1984). Second, the high foraging activity required to achieve and maintain a high condition may result in increased exposure to predators. Third, because there is a trade-off between somatic growth and accumulation of energy reserves (Forsman and Lindell 1991, 1996), individuals in high condition may not enjoy the survival advantages associated with an increased body size. Individuals in poor condition will avoid these three potential costs, and this may possibly offset their higher susceptibility to starvation and explain why survival decreased with increasing body condition during the first time period. But why did individuals with low and high condition survive better than individuals in intermediate condition during the first two periods (Table 2)? Keeping with the line of arguments presented above, individuals in intermediate body condition may have suffered predation costs of activity without enjoying the benefit of reduced starvation risk.

The associations between survival and some of the morphological characters differed also within a given time period, both between the sexes and between small and large individuals. Thus, during the first two time periods, the relationship between body condition and survival differed in large and small individuals, and during the third time period it was different in males and females (Table 2). We cannot identify the mechanisms responsible for these complex patterns. One possible explanation, however, is that the sources of mortality were different for large and small lizards, and in males and females, depending on behavioural differences between these lizard categories.

Our analysis of data for the entire study period (autumn 1996–spring 1998) revealed that survivorship until maturity significantly increased with increasing body condition shortly after hatching in males but not in females. This association between body condition and survival in males probably does not reflect a causal effect of early condition on subsequent long-term survival. More likely, body condition early in life is simply an indicator of the ability to acquire good territories and a high foraging success.

Survival in relation to microhabitat characteristics

During the activity season from spring to autumn 1997, juvenile survival decreased with increasing aboveground vegetation cover in early spring. The fact that this relationship remained unchanged when we statistically controlled for the effects of condition, SVL and their interaction on survival emphasises that microhabitat characteristics are indeed important sources of variation in juvenile survival. In early spring, aboveground vegetation cover is provided primarily by dispersal perennial *Cistus* bushes. These *Cistus* bushes harbour a high density of invertebrate prey (Diaz and Carrascal 1991), and are frequently used by adult *P. algirus* lizards as well as by important predators on *P. algirus*, such as the snakes and the ocellated lizard (*L. lepida*) (E. Civantos, personal observations). *P algirus* juveniles that use these bushes may thus suffer elevated mortality due to predation both by older conspecifics and interspecific predators, thereby yielding a negative relationship between survival and vegetation cover.

Differences in microhabitat use between juvenile and adult *P. algirus* have been previously described and attributed to intraspecific agonistic interactions and predator avoidance (Mellado 1980; Carrascal et al. 1990). However, differential responses to predation might be an additional factor contributing to age class differences in habitat use (Stamps 1983). Compared to adults, the antipredator behaviour of juvenile *P. algirus* is less dependent on fleeing to a refuge (Martin and Lopez 1995). During spring, juveniles may also occupy microhabitats more or less at random because they are able to find safe refuge in smaller and thinner patches of leaf litter than are larger adults. During late spring, summer and autumn, however, hatchlings and juvenile *P. algirus* lizards select microhabitats that are similar to those used by adults.

Survival in relation to growth rate

Individuals that grow quickly have been suggested to suffer reduced survival because of the risks involved in foraging and the physiological costs associated with rapid growth (e.g. Sibly and Calow 1986). However, our results revealed no significant association between relative growth rate and subsequent survival. Forsman (1993) arrived at similar conclusions when studying growth rate in relation to survival in a natural population of adders, *Vipera berus*. What might be the reason for this apparent lack of effect of growth rate on survival?. One possibility is that the proposed costs accruing to individuals that grow rapidly are offset by survival benefits associated with increments in body size. Small individuals may be more vulnerable to predation than large individuals, and so small juveniles that grow quickly to a larger size may obtain refuge against certain predators and older potentially cannibalistic conspecifics (e.g. Werner and Gilliam 1984). To reach a large size quickly may also be advantageous because body size influences dominance relationships, and hence the ability to acquire resources, in several species of lizards (e.g. Philibosian 1975; Tokarz 1985), including *P. algirus* (Martin and Forsman 1999; E. Civantos, unpublished data). In addition, individuals that grew relatively fast may have been able to do so simply because they were in possession of high-quality territories that provided not only good foraging and basking opportunities but also protection against predators. It should also be emphasised, however, that in our study, the relationship between growth rate and body size at first capture was significantly different in the two sexes, with males growing faster than similar-sized females. This faster growth of males, together with the lower overall survival from hatching to maturity of males (8%) compared to females (14%), suggests that rapid growth, or behaviours associated with rapid growth, may nevertheless negatively influence the survival prospects of *P. algirus* lizards.

In conclusion, our analyses show that the probability of survival to maturity in juvenile *P. algirus* lizards was relatively low, variable among time periods, and associated with both phenotypic characters (sex, body condition and SVL) and microhabitat use. The heterogeneity of the relationship between survival and morphological characters among time periods, between large and small individuals and between the two sexes illustrates that caution is required when making inferences and predictions based on short-term selection studies. Our results further suggest that the relative importance of different selective agents may change in response to environmental variation and during the life of individuals, and differ between males and females.

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