

Fitness of juvenile lizards depends on seasonal timing of hatching, not offspring body size

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Abstract To understand how selection shapes life-history traits, we need information on the manner in which offspring phenotypes influence fitness. Life-history allocation models typically assume that “bigger offspring are better”, but field data paint a more complex picture: larger offspring size sometimes enhances fitness, and sometimes not. Additionally, higher survival and faster growth of larger offspring might be due to indirect maternal effects (e.g., mothers allocate hormones or nutrients differently to different-sized eggs), and not to offspring size per se. Alternative factors, such as seasonal timing of hatching, may be more important. We examined these issues using 419 eggs from captive jacky dragon lizards (*Amphibolurus muricatus*). The mothers were maintained under standardized conditions to minimize variance in thermal and nutritional history, and the eggs were incubated under controlled conditions to minimize variance in offspring phenotypes due to incubation temperature and moisture. We reduced the size of half the eggs (and, thus, the size of the resultant hatchlings) from each clutch by yolk extraction. The hatchlings were marked and released at a field site over a 3-month period, with regular recapture surveys to measure growth and survival under natural conditions. Growth rates and

survival were strongly enhanced by early-season hatching, but were not affected by hatchling body size.

Keywords *Amphibolurus muricatus* · Body size · Jacky dragon · Growth rate · Offspring survival

Introduction

Ever since Smith and Fretwell's (1974) seminal paper on the evolutionary pressures that optimize offspring size, biologists have attempted to clarify the fitness consequences of offspring size variation. The simplistic notion that “bigger is better” (i.e., larger offspring are more likely to survive and grow rapidly than are their smaller siblings) has been supported by many empirical studies (Janzen 1993; Einum and Flemming 2000; Webb et al. 2006) and is easily incorporated in resource-allocation models, but several field-based studies suggest more complex situations. For example, larger body size may enhance survival rates in some populations but not in others (Sinervo et al. 1992; Heath and Blouw 1998), in some years but not others (Ferguson and Fox 1984; Sinervo et al. 1992; Olsson and Madsen 2001; Warner and Andrews 2002), and in offspring of one sex but not the other (Langkilde and Shine 2005). In other cases, fitness is not linked with body size at all (Congdon et al. 1999; Husak et al. 2006; Dibattista et al. 2007).

Much of the empirical work that has addressed this issue has been conducted with reptiles because these animals are particularly well-suited to addressing the “bigger is better” hypothesis. Offspring size is easily quantified because most reptile species do not have maternal nutrient input after hatching or birth, which is an issue that complicates such quantification in most endothermic vertebrates. Also, “allometric engineering” methods allow

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direct experimental manipulation of offspring size (e.g., by yolk removal from eggs), so that researchers can decouple offspring size from maternal investment (Sinervo 1998). This ability is critical, because otherwise correlations between offspring size and fitness might arise not through causal relationships, but because mothers differentially allocate other fitness-affecting factors (such as yolk hormones) to eggs of different sizes (Schwabl et al. 1997; Gil et al. 2006). In addition, the early life-history stages of most reptile species are subject to high levels of mortality (Tinkle 1967; Wilbur and Morin 1988), so that this stage offers a logistically convenient timeframe over which researchers can identify the phenotypic targets of natural selection (Janzen et al. 2000a, b). Moreover, neonates of most reptile species can be easily marked, released, and recaptured in the field, thereby facilitating fitness measurements under ecologically relevant conditions (Sinervo et al. 1992; Janzen 1993, 1995; Andrews et al. 2000; Warner and Andrews 2002; Miles 2004; Brown and Shine 2006).

Despite these advantages, however, few field studies have used these methods to disentangle the roles of body size versus other traits in determining the fitness of neonate reptiles. Of these “other traits”, perhaps the most plausible involves the seasonal timing of offspring production (Perrins 1967; Olsson and Shine 1997). In some species, the advantages of early-season hatching may outweigh those of larger size at birth (Qualls and Shine 2000). Early hatching may provide offspring with a “head start” and permit faster growth and higher survival than can be achieved by individuals hatching later because of more favorable environmental conditions and/or reduced competition from larger conspecifics (Perrins 1967; Olsson and Shine 1997; Ferguson and Bohlen 1978; Qualls and Shine 2000). Hence, variation in the timing of hatching may have major fitness consequences for offspring (Daan et al. 1996; Warner and Shine 2005).

To evaluate the relative importance of offspring body size versus hatching date on offspring survival in a lizard, we obtained eggs and the resultant hatchlings from female jacky dragon lizards (*Amphibolurus muricatus*), a multiple-clutching species, kept under standard conditions over a prolonged reproductive season. Prior to incubating eggs under standard conditions, we manipulated egg size (and hence offspring body size) by removing yolk from newly laid eggs, thereby enabling us to assess causal rather than correlational links between hatchling size and survival. Our release–recapture study in the field then allowed us to evaluate the relative importance of body size and the timing of hatching for offspring survival under natural conditions.

Materials and methods

Study species

The jacky dragon (*Amphibolurus muricatus*) is a medium-sized agamid lizard that inhabits coastal heathland habitat of southeastern Australia (Cogger 2000). This species has an extended reproductive season ranging from October to February, and females can produce up to four clutches of eggs (three to nine eggs per clutch) during a single season (Harlow and Taylor 2000). Because jacky dragons have a 3- to 4-month-long reproductive season, variation in hatching dates is substantial. Moreover, jacky dragons can reach sexual maturity within 1 year of hatching depending on how early they hatched in the previous season. This species consequently is an ideal model organism for evaluating the fitness consequences of hatching date (Warner and Shine 2005). Despite our previous studies of this species in outdoor enclosures, however, very little is known about the ecology of jacky dragons under field conditions. The present study therefore provides the first data on juvenile growth and survival under natural field conditions for this species.

Source of hatchlings

Hatchling lizards were obtained from eggs produced from a captive colony of wild-caught jacky dragons. Adult females nested from 14 October 2004 to 11 January 2005. During this time, we obtained 419 eggs from 83 clutches produced by 37 females. After the females nested, their eggs were removed from the nests and brought to the laboratory for incubation. Details on captive husbandry and egg collection can be found in Warner and Shine (2005) and Warner et al. (2007).

All eggs were weighed less than 24 h after oviposition. We manipulated the size of hatchlings by extracting yolk from half the eggs within each clutch using a sterile syringe (24-gauge needle). This yolk removal reduced egg mass by an average of 12.8% (SD = 8.7). Although a procedural control was not used in this study, puncturing eggs with a syringe (without yolk removal) is likely to have minimal, if any, impact on offspring phenotypes or survival (Sinervo 1998; Warner and Andrews 2002; Warner et al., unpublished data). Following removal of the yolk, the eggs were reweighed and half buried in moist vermiculite (−200 kPa) for incubation. Each egg was incubated individually in a glass jar (125 ml), and jars were covered with plastic wrap (sealed with a rubberband) to prevent desiccation. Egg jars were placed in one of three incubators and were rotated among and within the incubators three times weekly. Because jacky dragons have temperature-dependent sex determination, we incubated eggs at a constant temperature

known to produce both sexes (28°C; Harlow and Taylor 2000).

Hatchling husbandry

After the eggs had hatched, each hatchling was weighed, measured [snout–vent length (SVL) and tail length (TL)], and sexed by manual eversion of hemipenes on males (Harlow 1996). Each hatchling was given a unique toe-clip for individual identification. Hatchlings were housed in outdoor enclosures (1.3 m long \times 0.75 m wide \times 0.55 m deep) for approximately 2 weeks. No more than 15 hatchlings were housed in a single enclosure at a given time. Enclosures contained sand substrate and several branches used by the hatchlings as perching and basking sites. Small tiles and vegetation provided shelter for the hatchlings. Hatchlings were fed three times weekly (crickets and roaches dusted with vitamin/mineral mix), and water was always available. At approximately 2 weeks of age, the hatchlings were reweighed and remeasured (SVL and TL) to obtain growth data while in captivity and subsequently released at our field site.

Release–recapture in the field

The release–recapture study took place at Royal National Park, 32 km south of Sydney, Australia, at a site where this species is common. Our 9600-m² study site consisted of open scrub heathland with scattered trees (typical of jacky dragon habitat; Cogger 2000). Our site was triangular in shape, bordered on two sides by dirt roads and by a forest on the third side.

Twice per week, hatchlings were released in groups of 13–30 individuals from 28 December 2004 to 15 March 2005. All hatchlings were released in the center of the main study site within a 5-m diameter circle. By releasing lizards in the same general location, we minimized any potential confounding effects of spatial habitat variation on our survival analyses. In addition, our weekly releases of hatchlings at the same general location mimicked natural increases in hatchling densities as the hatching season progresses. To estimate survival in the field, we returned to the study site to search for hatchlings on a weekly basis from 6 April to 10 May 2005. During the winter months (mid-May to August) we did not survey the study site because jacky dragons are inactive during this time. Recapture surveys continued after the winter from 10 September 2005 to 22 January 2006. During each survey, we walked in random directions in search of lizards, covering the entire study area. We searched beyond the borders of our study site at least twice per month to evaluate potential dispersal off the site. When sighted, hatchlings were captured with a noose or by hand, and each individual was identified, weighed,

measured (SVL and TL), and released. Overall, a total of 274 person hours was spent searching for lizards. Of the individuals recaptured, only four individuals (5.8%) were found beyond the boundary of our study site, suggesting that most disappearances from our site were due to death rather than dispersal.

Statistical analyses

Statistical analyses were performed with SAS software, ver. 9.1 (SAS Institute 1997). We evaluated sex differences and the effects of yolk removal (independent variables) on hatchling phenotypes using two-factor mixed model analyses of variance (ANOVA) or covariance (ANCOVA) with maternal identity defined as a random factor. To avoid pseudo-replication, we used clutch mean values in cases when siblings of the same sex were allocated to the same yolk-removal treatment. For analyses of hatchling body size, SVL and mass were evaluated in two separate analyses, both using egg mass (prior to yolk removal) as a covariate. Hatchling body condition was evaluated with body mass as the dependent variable and SVL as the covariate. SVL was used as a covariate for the analyses of tail length. The effects of sex and yolk removal on these same variables were evaluated again at 2 weeks of age, just before hatchlings were released in the field. Growth rate over the 2-week period in captivity was evaluated as the change in hatchling size (in mass and SVL) divided by the number of days between measurements. In additional analyses that were used to control for maternal identity effects, paired *t*-tests were performed to evaluate the effects of sex and yolk removal on offspring phenotypes. All results from these paired comparisons were consistent with those from the mixed model ANOVAs, hence we report only the ANOVA results.

Preliminary analyses indicated that maternal identity and clutch had no effect on recapture success in the field (logistic regression: $\chi^2 = 40.4$, $P = 0.37$), suggesting that recapture success was evenly distributed among clutches. Thus, we treated individual hatchlings as our unit of analysis for the field data, rather than using clutch mean values. If individuals were recaptured multiple times, we used only body size measurements at their final recapture in our growth estimates. Because offspring growth rates were influenced by hatchling size at release, the interval between release and recapture (days), and date of hatching, we considered all three of these factors in our analyses of growth rate in the field. All body size measurements were natural log transformed to linearize relationships. Hatchling size at release (SVL and mass) and the interval (days) between release and final recapture were used as independent variables in a multiple regression with body size at final capture (SVL or mass) as the dependent variable. Residual scores from this multiple regression provided an index of growth rate in the field.

Residual scores (indices of growth relative to days prior to recapture) were used as dependent variables in subsequent analyses. We used multiple regression to evaluate the relationships between hatching date, body size, body condition, and growth in captivity (independent variables) on growth in the field (dependent variable). We used ANOVA to evaluate the effect of sex and yolk removal on growth in the field.

Hatchling survival was evaluated at two time periods, survival prior to winter (i.e., individuals that survived to 6 April 2005) and survival after winter (i.e., individuals that survived to 10 September 2005). Our recapture efforts extended well beyond these two time periods (to January 2006), thereby providing ample opportunities to recapture individuals that were ‘missed’ during previous recapture surveys. Individuals recaptured after the cut-off dates were considered alive at each previous time period in our analyses, and hatchlings that were never recaptured were considered dead. Prior to analyses, predictor variables were standardized to a mean of 0 and variance of 1 (i.e., z -scores). We used multiple logistic regression to evaluate relationships between hatchling phenotypes (body size at the time of release, growth rate, and hatching date) and survival (dependent variable expressed as ‘yes’ or ‘no’ at both time periods), as well as associations between offspring sex and yolk removal (and interactions) with survival. We used the method of Janzen and Stern (1998) to transform the logistic regression coefficients to obtain selection gradients, using the average gradient of the estimated selection

surface (i.e., probability of survival). This method results in selection coefficients (β_{avggrad}) that are interpreted in the same way as those obtained from multiple linear regression (Lande and Arnold 1983). Because selection gradients cannot be estimated for categorical variables, we conducted separate logistic regression analyses for each sex and treatment to calculate sex- and treatment-specific selection coefficients for hatchling SVL, growth rate, and hatching date.

As date of hatching was the only variable associated with survival (see Results), we explored this variable in more detail than the others. To evaluate the relationship between hatch date and survival, we used a cubic spline technique developed for visualizing fitness functions (GLMS ver. 4.0 software; Schluter 1988). Standard errors for the spline were calculated by bootstrapping the data 100 times. Because hatchlings released at different time periods were exposed to different durations of time in the field prior to our first recapture efforts, we included this variation in subsequent analyses. For example, individuals that hatched late were in the field for a shorter duration prior to winter than those that hatched early; consequently, late-hatched individuals had fewer opportunities to die before winter than those that hatched early. To account for this variation, we divided our release events into ten weekly cohorts to evaluate the proportion of survivors (up to both before and after winter) from each release cohort. We chose 10 weeks because this was the time period over which hatchlings were released in the

Table 1 Effect of yolk removal, hatchling sex, and their interaction on morphology and growth of hatchling jacky dragons (*Amphibolurus muricatus*)

Trait	Covariate	Yolk-removal effect	Sex effect	Interaction
Incubation duration (day)	–	$F_{1,35} = 5.1, P = \mathbf{0.031}$	$F_{1,30} = 2.3, P = 0.139$	$F_{1,17} = 0.6, P = 0.465$
Snout–vent length (SVL, mm)				
At hatching	Egg mass (g)	$F_{1,35} = 38.5, P < \mathbf{0.001}$	$F_{1,30} = 3.1, P = 0.091$	$F_{1,17} = 1.9, P = 0.186$
At release	Egg mass (g)	$F_{1,33} = 16.9, P < \mathbf{0.001}$	$F_{1,30} = 3.4, P = 0.077$	$F_{1,17} = 1.0, P = 0.331$
Body mass (g)				
At hatching	Egg mass (g)	$F_{1,35} = 76.3, P < \mathbf{0.001}$	$F_{1,30} = 0.9, P = 0.348$	$F_{1,17} = 0.7, P = 0.400$
At release	Egg mass (g)	$F_{1,33} = 11.4, P = \mathbf{0.002}$	$F_{1,30} = 1.0, P = 0.338$	$F_{1,17} = 1.0, P = 0.328$
Tail length (mm)				
At hatching	SVL at hatching (mm)	$F_{1,35} = 4.7, P = \mathbf{0.038}$	$F_{1,30} = 2.2, P = 0.145$	$F_{1,17} = 0.1, P = 0.747$
At release	SVL at release (mm)	$F_{1,33} = 2.6, P = 0.118$	$F_{1,30} = 1.1, P = 0.303$	$F_{1,17} = 0.6, P = 0.468$
Body condition (mass, g)				
At hatching	SVL at hatching (g)	$F_{1,35} = 15.9, P < \mathbf{0.001}$	$F_{1,30} = 0.3, P = 0.582$	$F_{1,17} = 0.2, P = 0.677$
At release	SVL at release (g)	$F_{1,33} = 0.0, P = 0.861$	$F_{1,30} = 0.9, P = 0.355$	$F_{1,17} = 0.1, P = 0.752$
Growth rate in captivity (Δ size/days)				
In SVL	Hatch date	$F_{1,35} = 0.1, P = 0.930$	$F_{1,30} = 2.2, P = 0.152$	$F_{1,17} = 0.0, P = 0.822$
In mass	Hatch date	$F_{1,35} = 0.2, P = 0.889$	$F_{1,30} = 1.3, P = 0.264$	$F_{1,17} = 0.5, P = 0.477$

Analyses were carried out with two-factor mixed model analyses of variance or covariance, with maternal identity as a random effect. P -values in bold denote statistical significance

field; this also corresponds to the time period over which eggs hatched. For each cohort, we then calculated the percentage of mortality per week that individuals were at large in the field prior to our first recapture survey (6 April 2005).

Results

Hatching dates ranged from 3 December 2004 to 4 March 2005. Egg mortality (9.3%) was minimal and was not affected by yolk removal ($\chi^2 = 1.4$, $P = 0.230$). A total of 380 hatchlings were produced, and only four died in captivity prior to release. Thus, 376 hatchlings were used in the release–recapture study, and 69 individuals were recaptured during the study (18.4% recapture success).

Effects of yolk removal and sex on hatchling phenotypes

Yolk removal from eggs strongly affected hatchling morphology (Table 1; Fig. 1). Hatchlings from the yolk removal treatment were significantly shorter in SVL and weighed less than those from eggs without a portion of the yolk removed. Removal of yolk from eggs also produced hatchlings with shorter tail lengths relative to their SVL and a lower body condition compared to individuals from unmanipulated eggs. Despite these effects on morphology, hatchling growth rates were unaffected by yolk removal. The effect of yolk removal on hatchling size (mass and SVL) persisted up to 2 weeks of age (when lizards were released; Fig. 1), but the effects did not persist this long for any of the other phenotypic traits that we measured. We found no significant morphological differences between males and females, nor any significant interactive effects between yolk removal and hatching sex. Yolk removal had a small but significant effect on incubation duration (Table 1); on average, eggs with a portion of the yolk removed hatched about 1 day earlier than unmanipulated eggs (mean incubation duration: 51.6 vs. 52.3 days). In captivity, those offspring which hatched earlier grew more rapidly during the 2-week period prior to release than those which hatched later (date of hatching vs. growth increment: $r^2 = -0.09$, $P = 0.014$).

Growth and age at maturity in the field

Growth rates in the field were not influenced by yolk removal ($F_{1,64} = 0.0$, $P = 0.963$), sex ($F_{1,64} = 1.0$, $P = 0.329$), or their interaction ($F_{1,64} = 0.1$, $P = 0.779$), nor were they significantly related to any hatchling phenotypic traits (all P -values > 0.05). However (as for growth in captivity), growth rate in the field was negatively related to the date of hatching ($r^2 = 0.25$, $P < 0.001$; Fig. 2).

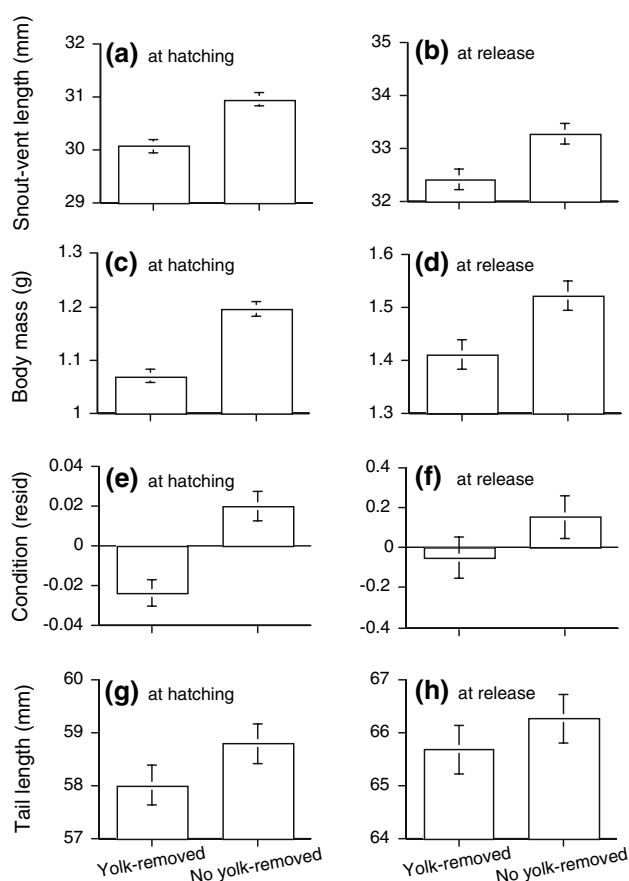


Fig. 1 Effect of yolk removal on the morphology of hatchling jacky dragons (*Amphibolurus muricatus*). *Graphs on the left* show phenotypes measured at hatching, and *graphs on the right* show the same phenotypes measured at release. **a** Snout–vent length at hatching (least-square means \pm 1 SE). **b** SVL at release (least-square means \pm 1 SE). **c** Body mass at hatching (least-square means \pm 1 SE). **d** Body mass at release (least-square means \pm 1 SE). **e** Body condition at hatching (residual scores of regression of mass vs. snout–vent length; means \pm 1 SE). **f** Body condition at release (residual scores of the regression of mass vs. snout–vent length; means \pm 1 SE). **g** Tail length at hatching (least-square means \pm 1 SE). **h** Tail length at release (least-square mean values \pm 1 SE). Statistics are reported in Table 1

Early hatching and rapid growth also influenced age at sexual maturity. Because of their head start and rapid growth rates, early-hatched individuals were larger in body size by the following spring than were late-hatched individuals. Ten individuals were greater than the minimum size at sexual maturity (SVL: 72 mm; Harlow and Taylor 2000) when recaptured during December 2005 and January 2006 and these individuals all had hatched within the first half (47%) of the hatching season in the previous year. Three of these sexually mature individuals were gravid when recaptured at approximately 1 year of age, and all produced viable eggs between 13 December 2005 and 5 January 2006; these individuals were brought back to the laboratory where they oviposited and their eggs incubated.

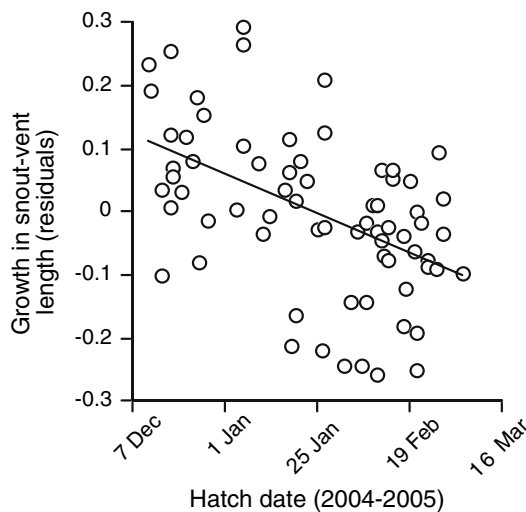


Fig. 2 Relationship between the date of hatching and growth rate of jacky dragons. Growth rate was calculated as the residual scores from the multiple regression of snout–vent length at last recapture (dependent variable) versus body size at release and number of days between release and recapture (independent variables)

Survival in the field

Despite its substantial impact on hatchling body size, yolk removal did not affect recapture probability (Table 2). Rates of hatchling survival did not differ significantly between males and females, nor were they correlated with any of the phenotypic traits that we measured. Date of hatching was the only significant predictor of survival in the field (Table 2). In terms of absolute numbers known to be alive at a fixed time period, individuals that hatched late had a higher probability of survival than those that hatched early (Fig. 3) at both time periods (i.e., survival before and after winter); these same patterns were evident based upon the selection coefficients (Table 3), and also when hatchlings were grouped by weekly release cohorts (Fig. 4a, b). However, the opposite

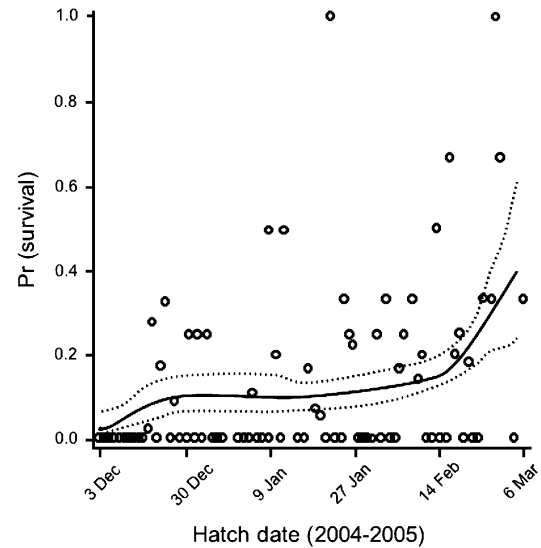


Fig. 3 Probability of survival in relation to hatching date for juvenile jacky dragons. The selection function was derived from cubic spline algorithm (adapted from Schluter 1988). Dashed lines represent standard errors calculated by bootstrapping the data 100 times. This graph represents survival prior to winter; the same pattern was evident for survival after winter

trend was revealed by analyses that accounted for the number of weeks that hatchlings were in the field prior to the first recapture event. On a survival-per-week basis, cohorts released early (i.e., early-hatched individuals) had lower mortality rates than those released late (Fig. 4c, d).

Discussion

Our manipulation of hatchling body size via yolk removal did not affect the probability of recapture for hatchlings nor the growth rates of the young lizards. Because our manipulation generated a large range of body sizes, this

Table 2 Predictors of survival in the field at two time periods (before and after winter 2005) for hatchling jacky dragons

Analyses were carried out with multiple logistic regression. Due to strong correlations among morphological traits, snout–vent length (SVL) at release was the only morphological variable used in the model. Growth in SVL represents growth measured over the 2-week period in captivity, prior to release in the field. *P*-values in bold denote statistical significance

Independent variable	Pre-winter survival	Post-winter survival
Sex	$\chi^2 = 2.395, P = 0.122$	$\chi^2 = 0.008, P = 0.927$
Yolk removal	$\chi^2 = 0.012, P = 0.914$	$\chi^2 = 0.911, P = 0.763$
Sex \times yolk removal	$\chi^2 = 0.027, P = 0.870$	$\chi^2 = 0.036, P = 0.849$
Hatching date	$\chi^2 = 9.982, P = \mathbf{0.002}$	$\chi^2 = 5.882, P = \mathbf{0.015}$
Hatching date \times sex	$\chi^2 = 0.424, P = 0.515$	$\chi^2 = 0.783, P = 0.376$
Hatching date \times yolk removal	$\chi^2 = 0.307, P = 0.579$	$\chi^2 = 0.433, P = 0.511$
Snout–vent length	$\chi^2 = 0.180, P = 0.671$	$\chi^2 = 0.768, P = 0.381$
Snout–vent length \times sex	$\chi^2 = 0.127, P = 0.722$	$\chi^2 = 0.085, P = 0.770$
Snout–vent length \times yolk removal	$\chi^2 = 1.185, P = 0.276$	$\chi^2 = 0.718, P = 0.397$
Growth in snout–vent length	$\chi^2 = 0.095, P = 0.758$	$\chi^2 = 1.382, P = 0.240$
Growth \times sex	$\chi^2 = 0.001, P = 0.973$	$\chi^2 = 1.056, P = 0.304$
Growth \times yolk removal	$\chi^2 = 0.042, P = 0.838$	$\chi^2 = 0.045, P = 0.831$

Table 3 Summary of selection analyses of body size, growth rate, and hatching date (independent variables) on the survival (dependent variable) of hatchling jacky dragons using logistic regression

	Snout–vent length (mm)		Growth rate (Δ mm/day)		Hatch date (Julian day)	
	β_{avggrad}	SE	β_{avggrad}	SE	β_{avggrad}	SE
Both sexes (treatments combined)	0.098	0.194	−0.032	0.195	0.351**	0.141
Yolk-removed treatment	−0.089	0.294	−0.079	0.298	0.409**	0.213
No yolk removed treatment	0.284	0.284	−0.013	0.286	0.329*	0.196
Male hatchlings (treatments combined)	−0.022	0.301	−0.042	0.297	0.274	0.208
Yolk-removed treatment	−0.031	0.420	−0.266	0.418	0.248	0.283
No yolk removed treatment	0.030	0.472	0.221	0.473	0.330	0.321
Female hatchlings (treatments combined)	0.191	0.262	−0.039	0.263	0.426**	0.195
Yolk-removed treatment	−0.208	0.447	0.121	0.453	0.636	0.359
No yolk removed treatment	0.458	0.371	−0.187	0.363	0.307*	0.249

* $P < 0.05$, ** $P < 0.01$

Selection coefficients (β_{avggrad}) and standard errors (SE) were calculated using the method of Janzen and Stern (1998). Because selection gradients cannot be estimated for categorical variables, we report the results of analyses for each sex and treatment separately. This table shows results for survival analyses prior to winter; the same patterns were evident for survival after winter. Note that selection coefficients were much greater for hatch date than for hatchling snout–vent length or growth rate

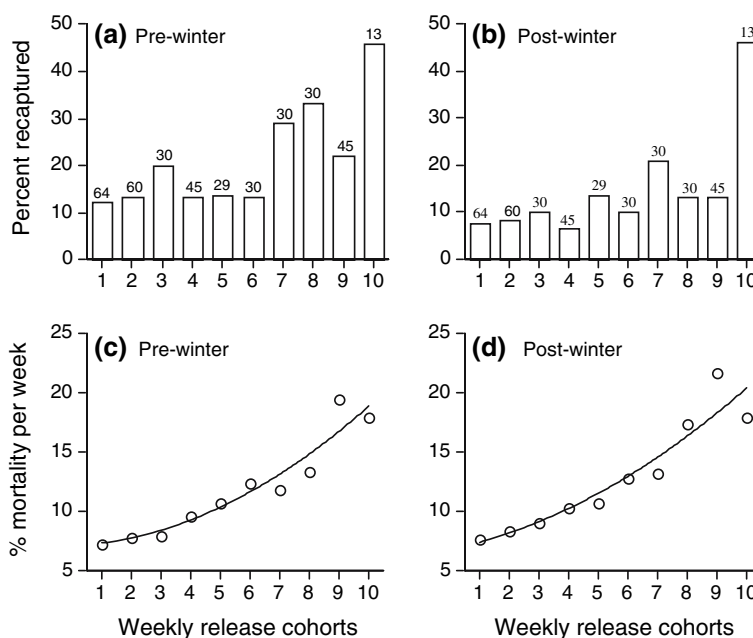


Fig. 4 Relationship between weekly release cohorts and survival. Week 1 represents the cohort released on the week of 28 December 2004–3 January 2005, and the following weeks represent subsequent weekly releases thereafter. Numbers above bars represent the number of hatchlings released at each weekly time period. **a** Percentage of individuals recaptured prior to winter (i.e., 6 April 2005) as a function of

the week of release. **b** Percentage of individuals recaptured after winter (10 September 2005) as a function of the week of release. **c** Mortality rates per week prior to winter (6 April 2005) as a function of week of release date (second-order regression: $r^2 = 0.91$, $P < 0.001$). **d** Mortality rates per week after winter (10 September 2005) as a function of week of release (second-order regression: $r^2 = 0.89$, $P < 0.001$)

result strongly suggests that body size is of little importance to hatchling survival or rate of growth in the field. Overall analyses (i.e., with yolk removal treatments pooled) also indicated that body size was not associated with growth or survival in the field. Our results contrast with those of previous studies demonstrating that

offspring body size can be an important predictor of survival (Packard and Packard 1988; Forsman 1993; Sorci and Clobert 1999; Janzen et al. 2000a, b). Thus, bigger may indeed be better sometimes – but not always (Sinervo et al. 1992; Congdon et al. 1999; Husak 2006; Dibattista et al. 2007).

We have treated growth rates and survival probabilities as separate indices of offspring fitness, but the two may be causally linked. Several studies have suggested that faster growing individuals are less likely to survive (Forsman 1993; Olsson and Shine 2002). For example, growth rate may depend upon risky foraging activity (Gerwien and John-Alder 1992; Lorenzon et al. 1999; Olsson and Shine 2002; Warner and Andrews 2002). We found no such association between growth and survival, but our data are weak in this respect because we could not calculate growth rates of individuals that were not recaptured (i.e., non-survivors). Instead, we evaluated the relationship between field survival and prior growth rates that were measured while animals were in captivity. Because animals were given abundant food in captivity, their growth at this time probably did not accurately reflect variation in individual foraging activity. Nevertheless, growth in the laboratory was positively associated with dispersal distance (Warner and Shine, unpublished data), suggesting that rapidly growing hatchlings may be more active (or move faster) than slow-growing individuals.

Our data suggest that the timing of hatching is an important contributor to variation in offspring growth and survival under natural field conditions. This result agrees well with a previous study that we conducted on this species in predator-free outdoor enclosures: individuals that hatched early in the season grew substantially faster than those that hatched late (Warner and Shine 2005). We previously interpreted this rapid growth of early-hatched individuals as an environmental effect (early-hatching lizards face warmer conditions with few competitors for food; Warner and Shine 2005), but the current study questions that interpretation. We still detected a negative relationship between hatching date and growth rate during the 2-week period in captivity, when all individuals were exposed to similar levels of competition and food supply. The persistence of this pattern hints at some intrinsic growth advantage associated with early hatching.

The timing of hatching was also an important predictor of survival, although the relationship between hatch date and survival depended upon the type of analysis employed. Almost by definition, an individual born late in the season is more likely to be alive at the end of autumn because it has to survive only a brief period to qualify in this respect (Fig. 3). Biologically, the more meaningful question is mortality rate per week of exposure to field conditions; and when the data are analyzed in this way, it is clear that early-hatched lizards fared better than their later-hatched counterparts. Such a pattern may place selective pressures in favor of hatching early in the season, and hence on the timing of maternal oviposition. Similar findings have been demonstrated in a wide range of animals, including birds (Perrins 1967), amphibians (Ryan and Plague 2004), insects (Myers

1981), and other lizard species (Olsson and Shine 1997; Andrews et al. 2000; Qualls and Shine 2000).

We have argued previously that early clutches are disproportionately important to maternal fitness in jacky dragons because these clutches hatch early enough for offspring to reach sexual maturity within 1 year (Warner and Shine 2005). The present study extends these conclusions to natural conditions, as several early-hatched individuals reproduced within their first year of life. The greater survival rates of early-hatched offspring provide further benefits to hatching early in the season. Overall, then, early clutches provide greater fitness returns than clutches produced later in the season. This pattern may impose selection pressure on maternal traits such as reproducing as early as possible and allocating more resources toward early versus late clutches. In keeping with this prediction, relatively large clutch sizes (even if this means a reduction in egg size) early in the season have been reported for multiple-clutching lizard species with life histories similar to that of the jacky dragon (Tinkle 1967; Sinervo 1998; Shanbhag et al. 2000; Radder and Shanbhag 2003) and may well occur in natural populations of jacky dragons as well.

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