From metamorphosis to maturity in complex life cycles: equal performance of different juvenile life history pathways

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Abstract. Performance in one stage of a complex life cycle may affect performance in the subsequent stage. Animals that start a new stage at a smaller size than conspecifics may either always remain smaller or they may be able to "catch up" through plasticity, usually elevated growth rates. We study how size at and date of metamorphosis affected subsequent performance in the terrestrial juvenile stage and lifetime fitness of spadefoot toads (*Pelobates fuscus*). We analyzed capture–recapture data of >3000 individuals sampled during nine years with mark–recapture models to estimate first-year juvenile survival probabilities and age-specific first-time breeding probabilities of toads, followed by model selection to assess whether these probabilities were correlated with size at and date of metamorphosis. Males attained maturity after two years, whereas females reached maturity 2–4 years after metamorphosis. Age at maturity was weakly correlated with metamorphic traits. In both sexes, first-year juvenile survival depended positively on date of metamorphosis and, in males, also negatively on size at metamorphosis. In males, toads that metamorphosed early at a small size had the highest probability to reach maturity. However, because very few toadlets metamorphosed early, the vast majority of male metamorphs had a very similar probability to reach maturity. A matrix projection model constructed for females showed that different juvenile life history pathways resulted in similar lifetime fitness. We found that the effects of date of and size at metamorphosis on different juvenile traits cancelled each other out such that toads that were small or large at metamorphosis had equal performance. Because the costs and benefits of juvenile life history pathways may also depend on population fluctuations, ample phenotypic variation in life history traits may be maintained.

Key words: age-specific breeding probability; amphibian; cohort iteroparity; compensatory growth; complex life cycle; life history transition; maturity; metamorphosis; Pelobates fuscus; sex-specific life histories; size; survival.

Introduction

Maturation divides a life history into preparation and fulfillment (Stearns 1992). In species with complex life cycles, metamorphosis is a further major life history transition that divides the "preparation" stage (Wilbur 1980). Yet, neither metamorphosis nor maturity are new beginnings because performance in one stage can affect performance in later stages. Variation in environmental conditions often creates variation among individuals in growth and size (Lindström 1999, Beckerman et al. 2002, Cam et al. 2003). Animals that start a new life stage at a smaller size than conspecifics may either always remain smaller or they may be able to "catch up" in some way such that they reach a later life cycle stage at the same size as the conspecifics that were initially

larger (Lindström 1999, Metcalfe and Monaghan 2001). Small individuals of many species sometimes compensate for a start at a small size through enhanced growth (Metcalfe and Monaghan 2001) or smaller individuals may allocate resources differently during adulthood such that they can compensate for poor conditions earlier in life (Auer 2010). While the mechanism underlying compensation in most studies is based on plasticity in growth rates or energy allocation, we describe a different mechanism. Studying the juvenile life history of an amphibian, we test whether small and large individuals follow different life history pathways where the effects of different metamorphic traits on maturity cancel each other out (Dobzhansky 1956). Such a "cancelling out" may lead to equal performance such that there are no long-term effects of a bad start.

Recent theory shows that a full understanding of the evolutionary ecology of complex life cycles requires that we better understand the juvenile stage. Population models converged on the conclusion that the juvenile stage is most important because it largely determines

population growth rate (Lampo and De Leo 1998, Hels and Nachman 2002, Conroy and Brook 2003). Our interest was to comprehensively analyze and quantify the effects of variation in metamorphic phenotype (i.e., date of and size at metamorphosis) on first-year juvenile survival, patterns of maturation and fitness (as measured by population growth rate λ). We focus on the juvenile stage of amphibians where we can build upon a substantial body of previous research (e.g., Smith 1987, Semlitsch et al. 1988, Berven 1990, Goater 1994, Scott 1994, Morey and Reznick 2001, Altwegg and Reyer 2003); we note that similar effects of larval performance on subsequent performance have been reported in wide variety of invertebrates (Benard 2004, Pechenik 2006). As previous studies showed, performance in the larval aquatic environment, as measured by the metamorphic phenotype, is likely to affect performance in later terrestrial stages. This relationship is not universal, however, or it may be limited to a short period of time (McPeek and Peckarsky 1998, Boone 2005, De Block and Stoks 2005, Chelgren et al. 2006). In amphibians, long periods of post-metamorphic growth are the rule; maturity is often delayed and attained at different ages by individuals from the same cohort (Bell 1977, Werner 1986). This may allow the growth trajectories of individuals of large and small size at metamorphosis to partially or fully converge (Goater 1994, Boone 2005).

We quantify the effects of date of and size at metamorphosis on juvenile first-year survival and maturation in the spadefoot toad, *Pelobates fuscus* (see Plate 1). We include in our analysis all the traits that were previously identified as being important and we do the analysis separately by sex. In order to learn whether effects of metamorphic phenotype and different trait combinations lead to lasting performance differences or whether effects of different metamorphic traits on maturity cancel each other out (Dobzhansky 1956), we calculate the probability to attain maturity and use a Leslie matrix approach to assess the fitness consequences of different combinations of metamorphic traits (Caswell 2001). We show that date of and size at metamorphosis had effects on subsequent performance but ultimately has no lasting effects because it led to different life history pathways with similar fitness. This contrasts with the widely held view that larval conditions have lasting effects on post-metamorphic performance (Lindström 1999, Pechenik 2006).

Materials and Methods

The spadefoot toad Pelobates fuscus

The European spadefoot toad (*Pelobates fuscus fuscus* Laurenti 1768) is a pelobatid toad found primarily in the lowlands of central and eastern Europe. Outside the breeding season, it is mainly fossorial and emerges from its underground burrows at night for foraging. Unlike North American spadefoot toads (*Spea* sp. and *Scaphiopus* sp.), which prefer temporary ponds, *Pelobates*

fuscus congregate during spring in permanent ponds for reproduction (Van Buskirk 2003). *Pelobates fuscus* is an explosive breeder (Hels 2002). Breeding usually occurred in April and/or May with a peak breeding activity that lasted for about one month (Hödl et al. 1997).

Study site and data collection

We captured juvenile and adult spadefoot toads using a drift fence that completely encircled a permanent pond on an island of the Danube river near Vienna, Austria, during nine consecutive years from 1989 to 1997 (Hödl et al. 1997). The fence was checked daily throughout the year, and captures were made both when toads entered the pond and when they left the pond. The drift fence was placed very close to the pond edge (~1 m). There are other small ponds on the island, but they were only constructed in 1994 and only a single female *P. fuscus* marked at the study site was ever found at another pond (Hödl et al. 1997). Thus, emigration has a negligible effect on our results.

In total, we captured 3113 individuals of *P. fuscus*. At the time of first capture and marking, 2758 were metamorphs and 355 were adults (165 males and 190 females). Metamorphs emerged from the pond long after all adults had left the pond. Of the metamorphs, 467 were recaptured as adult toads (261 males and 206 females) whereas 2291 individuals captured shortly after metamorphosis were never seen again and remained unsexed. Each individual was photographed for later identification. Some toads were marked with a PIT tag as adults (Jehle and Hödl 1998, Gibbons and Andrews 2004). An analysis of double marked adult toads showed that there was no misidentification (R. Jehle, *personal communication*).

Body mass was measured to an accuracy of 0.1 g, and snout–vent length (size) was measured to an accuracy of 0.1 cm. Because the pit falls at the drift fence were checked daily, the date of first capture of the metamorphs was considered to be the date of metamorphosis. Many metamorphs had not yet fully resorbed the tail when they were captured. For metamorphs, we analyzed data from five annual cohorts of metamorphs (years 1989–1993) to ensure that all individuals had a nonzero chance to mature and to be recaptured during the study period. The number of captured individuals varied between years (for metamorphs, 1989, 134; 1990, 235; 1991, 1373; 1992, 603; 1993, 413; for adults, 1989, 93; 1990, 40; 1991, 26; 1992, 26; 1993, 20; 1994, 49; 1995, 59; 1996, 14; 1997, 28). Further details of the methods and additional data are given in Appendix A, Jehle et al. (1995), Hödl et al. (1997), and Jehle and Hödl (1998).

Correlations between metamorphosis and body condition at maturity

Body mass and size at metamorphosis were highly and positively correlated ($r = 0.81$). We used the scores of the first axis of a principal component analyses of body

mass and size as an index of metamorph body condition (PC_{meta}; Altwegg and Reyer 2003). PC_{meta} explained 95% of the variance and both mass and size had positive loadings (0.32 and 0.94, respectively). We used model selection based on regression analysis (Burnham and Anderson 2002) to study the relationship between date and body condition at metamorphosis and body condition at maturity, treating each sex separately (Appendix B: Table B1).

Analysis of mark–recapture data

We used multistate mark–recapture models to estimate apparent survival and age at first reproduction (Clobert et al. 1994, Pradel and Lebreton 1999, Cam et al. 2005, Lebreton et al. 2009) with two states: metamorph and breeder. All individuals that were captured at metamorphosis are in the state "metamorph," and all individuals that were either recaptured or that were initially captured as breeder are in the state "breeder." Once an individual has been captured as a breeder, it will remain in that state even if it skips breeding in some years. The transition probabilities between states are the age-specific probabilities of first time reproduction (*a*), i.e., the transition from state "metamorph" to the state "breeder." Besides the usual assumption of multistate mark–recapture models (Lebreton et al. 2009), the model assumes that survival during the first year after metamorphosis differs from survival later. Hence, we assume that all individuals older than 1 year have the same survival probability irrespective of whether they have started to reproduce (this is the pattern of survival that McCaffery and Maxell [2010] reported for a pond-breeding frog). Moreover, the model assumes a fixed age where all individuals have started to breed. We used model selection to evaluate at which age full reproduction is reached (Clobert et al. 1994).

The model has three different parameter types: $\phi_{m,i}$ is the probability that an individual of age m that is alive at sampling occasion i is still alive and has not permanently emigrated from the population at sampling occasion $i +$ 1, $\alpha_{m,i}$ is the probability an individual of age m years reproduces for the first time at sampling occasion i (i.e., the age-specific transition probability from state "metamorph" to state "breeder"), and p_i is the probability that a marked individual in the state "breeder" that is alive at sampling occasion i is at the pond and recaptured at sampling occasion i. See Appendix C for the matrix notation of the model. The most general model that we considered had different survival probabilities (ϕ) for each of the two age classes, for each time period and for each sex. The probabilities of age-specific first time reproduction (α) differed between sexes, and we initially fixed the age of full breeding to age of 6 years. The recapture probabilities of breeders (p) were time and sex specific. We denote this model as $\{\phi[a2 \times sex \times t], \alpha[a6 \times sex], p[sex \times t]\}$, where ax refers to an age effect with x

age classes, t refers to time dependence (different years), and sex refers to a sex effect.

No goodness-of-fit (GOF) test is available for our model. However, a model with time-specific survival and recapture probabilities for a cohort does in fact account for all heterogeneity introduced by age- and time-specific variation in survival, time of first reproduction, and recapture. Thus, we conducted a goodness-of-fit test with program U-CARE (Choquet et al. 2009) for the model $\{\phi[cohort \times sex \times t], p[cohort \times sex \times t]\}$ for all toads first marked as metamorphs and for the model $\{\phi[sex \times t], p[sex \times t]\}$ for all toads first marked as breeder. The fit of this model was acceptable (for metamorphs, $\chi^2_{13} = 14.89$, $P = 0.314$; for breeders, $\chi^2_{22} = 33.60$, $P = 0.054$; overall, $\chi^2_{35} = 48.49$, $P = 0.064$). Yet, the GOF revealed some overdispersion, and we used a variance inflation factor ($\hat{c} = 1.385$) to adjust model selection criteria and standard errors of the parameters (Burnham and Anderson 2002).

Because of the complexity of the model, the analysis was performed in several steps. Within the first modeling step, we evaluated the most parsimonious structure of recapture, age-specific probability of first breeding, age when all toads have started to breed, and survival; candidate models are shown in Tables B2–B10 in Appendix B. The most complex model for recapture probability allowed for effects of sex and time. To estimate the age at which all individuals started to reproduce, we fitted models in which this age varied from 1 to 6 years; we also tested for variation among cohorts in the age when all individuals have started to reproduce. The most general structure for survival probabilities considered sex- and time-specific variation in first-year juvenile and adult (i.e., after first-year) survival.

The goal of the second modeling step was to assess whether and how date of and body condition at metamorphosis correlated with age-specific breeding probabilities and juvenile first-year survival. While modeling individual covariates, we kept all parameters but the focus parameter at the best structure determined in step one (details are given in the table captions), and only modeled the key parameter.

Because our intention was to estimate sex-specific first-year juvenile survival, we had to know the sex of metamorphs that were never recaptured. Because toads could not be sexed at metamorphosis, we only know the sex of individuals that were captured as adults. We estimated the probability that a given individual is a male by using information about sex-specific differences of size and body mass at metamorphosis (see *Results*), and under the assumption that the sex ratio at metamorphosis is even. We conducted a logistic regression in which sex was the dependent variable and size and body mass the independent variables. The regression coefficients (intercept $= -1.655 \pm 1.749$ [mean $\pm$ SE], size $= 0.040 \pm 0.072$, body mass $= 0.130 \pm 0.179$, $n = 467$ individuals) were used to calculate the

probability that the unsexed individual j with size s_j and body mass bm_j was a male [$p(m_j)$], or a female [$p(f_j) = 1 - p(m_j)$]. Because the morphological differences among sexes were small, these regression slopes were rather shallow and had large standard errors. Consequently the probability that a metamorph of unknown sex was a male was often predicted to be close to 0.5. We also included the assumption that the sex ratio at metamorphosis was even using the following calculation. The total number of metamorphs in cohort i was R_i, of which a subset was later recaptured as males m_i and females f_i, respectively. Thus, of the $R_i - m_i - f_i$ unsexed individuals $0.5(R_i - m_i)$ individuals must be males and $0.5(R_i - f_i)$ must be females if the sex ratio is even. The number of unsexed males at metamorphosis of cohort i based on the logistic regression is $\Sigma p(m_j)$, but should be $0.5(R_i - m_i)$. Hence, the probability that individual j is a male is $M_j = p(m_j)[0.5(R_i - m_i)]/\Sigma p(m_j)$, and that it is a female $F_j = 1 - M_j$. A simulation study showed that unequal sex ratios (11:13) cause small relative bias in first-year juvenile survival estimates ($\pm \sim 8\%$; Appendix E). Only strong sex ratio bias (1:2) caused substantial relative bias ($\pm \sim 30\%$) in estimates of first-year juvenile survival. Juvenile first-year survival of the rarer sex was overestimated whereas juvenile survival of the commoner sex was underestimated (Appendix E). Adult survival and probability of first time reproduction were always unbiased. We are unaware of published evidence for sex ratio bias at metamorphosis in anurans under natural conditions.

We used program MARK (White and Burnham 1999) to conduct the capture–recapture analyses, and performed model selection using AIC_c (Burnham and Anderson 2002). All estimates derived from mark–recapture analyses were subject to model averaging.

Probability to mature and population growth rate

Based on the estimated age-specific survival probabilities (ϕ[age, PC_{meta}, date]) and age-specific probabilities to reproduce for the first time (α[age, PC_{meta}, date]), we calculated the probability (p_m) that a male metamorph with body condition (PC_{meta}) and date of metamorphosis (date) would survive to maturity:

$$p_m[PC_{meta}, date]$$
$$= \phi[1y, PC_{meta}, date]$$
$$\times \left[\alpha[1, PC_{meta}, date] \right.$$
$$+ \sum_{i=2}^{z} \left(\phi_{ad}^{i-1} \alpha[i, PC_{meta}, date] \right.$$
$$\left. \left. \times \prod_{j=1}^{i-1} (1 - \alpha[j, PC_{meta}, date]) \right) \right] \qquad (1)$$

where α[z, PC_{meta}, date] = 1 and ϕ_{ad} is adult annual survival.

To estimate fitness in relation to body condition at metamorphosis and date of metamorphosis, we formulated a post-breeding census, female-based, matrix projection model with five age classes (toadlet, 1 year old, 2 year old, 3 year old, more than 3 years old) and a projection interval of one year to calculate the dominant eigenvalue of the projection matrix as an estimate of the asymptotic population growth rate, and thus of fitness of females (Caswell 2001).

To parameterize the model, we used survival probabilities and probabilities to start reproduction estimated in this study, whereas for tadpole survival and clutch size we used values from the literature on *Pelobates fuscus* (Hels 2002, Hels and Nachman 2002). While tadpole survival is density-dependent (Hels and Nachman 2002), clutch size is positively correlated with body mass of females, and older females have larger clutches than young females (Hels 2002). We calculated population growth rate (i.e., fitness) for females with low, medium, and high body condition (index -2, 0, 2) and early, medium and late timing of metamorphosis (14 July, 8 August, 12 September). The model assumes equal survival during the larval stage for small and large metamorphs and for those that metamorphose early and late. The model therefore compares the fitness of individuals that metamorphose early or late and at small or large size. Given that the fate of juveniles determines the fate of spadefoot toad populations (Hels and Nachman 2002), this approach seems justified. We estimated confidence intervals for the probability to reach maturity and population growth rate in R (R Development Core Team 2009) using simulation code available in the electronic appendix to Schaub et al. (2009). Further details are provided in Appendix D.

RESULTS

Metamorphosis

Across all years, average mass of metamorphic spadefoot toads ($n = 2758$) was 4.46 g (SD 0.89 g), mean length was 32.18 mm (SD 2.24 mm), and mean date of metamorphosis was 15 August (SD = 13.16 d, Fig. 1). Date of metamorphosis and mass at metamorphosis were positively correlated in both males and females (Fig. 1). Metamorphs recaptured as male adults ($n = 261$) had an average mass at metamorphosis of 4.65 $\pm$ 0.86 g (mean $\pm$ SD), a length of 32.61 $\pm$ 2.13 mm, and metamorphosed on average on 16 August (SD = 14.12 d). The corresponding values for metamorphs recaptured as females ($n = 206$) were 4.49 $\pm$ 0.87 g, 32.23 $\pm$ 2.20 mm, and 15 August (SD = 13.82 d). Because the spawning seasons lasted about one month (Hödl et al. 1997), some of the phenotypic variation in date of metamorphosis probably originated because not all tadpoles hatched on the same day.

Differences between males and females were significant when statistically controlling for among-year variation for mass and size (ANOVA including year;

mass $F_{1,461} = 8.12$, $P = 0.004$; size $F_{1,461} = 7.06$, $P = 0.008$), but not for date ($F_{1,461} = 0.66$, $P = 0.418$).

Correlations between metamorphic traits and size at maturity

Across all years, mass and size of spadefoot toads at maturity (defined as first capture as a breeder) differed significantly between sexes. Females were larger and heavier than males (male body mass = 10.14 ± 2.39 g [mean $\pm$ SD], female body mass = 18.75 ± 6.01 g, $t_{256.67} = 19.38$, $P < 0.001$; male length = 42.69 ± 3.63 mm, female length = 50.12 ± 5.75 mm, $t_{329.08} = 16.17$, $P < 0.001$). To describe body condition at maturity, we performed a principal component analysis from body mass and size for each sex separately. The first axis explained >95% of the variance of size and body mass in both sexes and the scores were positively correlated with size and body mass in both sexes (loadings were 0.85 and 0.53, respectively, for males; 0.72 and 0.69, respectively, for females). In males, body condition at maturity (PC_{mat}) was a nonlinear function of date of metamorphosis (Appendix B: Table B1; Fig. 1); predicted body condition at maturity was highest when metamorphosis occurred on 28 August (regression equation: $PC_{mat} = -194.0 + 1.652(date) - 0.0035(date^2)$, where the standard errors of the regression coefficients are 38.3, 0.327, and 0.0007, respectively; $n = 261$). In females, body condition at maturity (PC_{mat}) depended positively on body condition at metamorphosis (PC_{meta}), and negatively on date (regression equation: $PC_{mat} = 37.7 + 1.71[PC_{meta}] - 0.17[date]$, where the standard errors of the regression coefficients are 11.60, 0.50, and 0.05, respectively; $n = 206$; Fig. 2). Yet, the best models only explained little of the observed variation (males, $r^2 = 0.083$; females, $r^2 = 0.055$).

Recapture, age-specific breeding probabilities, and apparent survival

Recapture probabilities.—Recapture probability was best represented by a time-dependent model (Appendix B: Table B2), which we used for subsequent steps, followed by a model that included also an additive sex effect. Other models clearly had no support. Annual recapture probabilities ranged from 0.55 ± 0.05 (mean $\pm$ SE) to 0.98 ± 0.02.

Age-specific breeding probabilities.—Modeling the age at which the probability of an as-yet-inexperienced breeder to reproduce is 1 clearly showed that full reproduction was at the age of 2 years in males, and 4 years in females (Appendix B: Table B3). These ages were used for further modeling.

Age-specific probabilities to reproduce for the first time were cohort dependent in males, but not in females (Appendix B: Table B4). When we inspected the estimates of the best model, we noted two unusual estimates. First, the probability of first-time breeding at age 1 year of the 1989 cohort of males was 0.68 ± 0.29, while the same parameter for males from cohorts 1990–1993 was in the
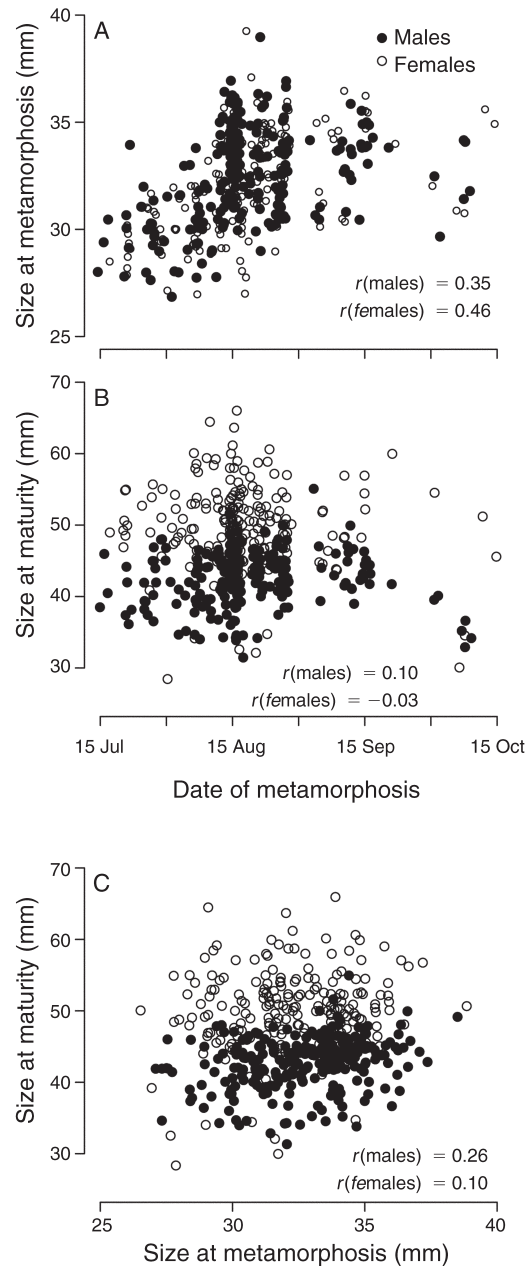

FIG. 1. The relationship between date of and size at metamorphosis and size at maturity. Only toads recaptured as adults, and thus with known sex, are included. Shown also is the correlation coefficient of each sex (r). (A) Date of metamorphosis in relation to size at metamorphosis. (B) Date of metamorphosis in relation to size at maturity. (C) Size at metamorphosis in relation to size at maturity.

range of 0.00–0.12 (with SE in the range of 0.00–0.05). Second, the first-year survival probability of females of cohort 1989 was 1.00 ± 0.00 (profile likelihood confidence interval: 0.60–1.00), and in the range from 0.37 to 0.57 for females from cohorts 1990 to 1993 (SE of 0.08 to 0.12). Since the deviance of the models changes when these two parameters are fixed to some arbitrary values,
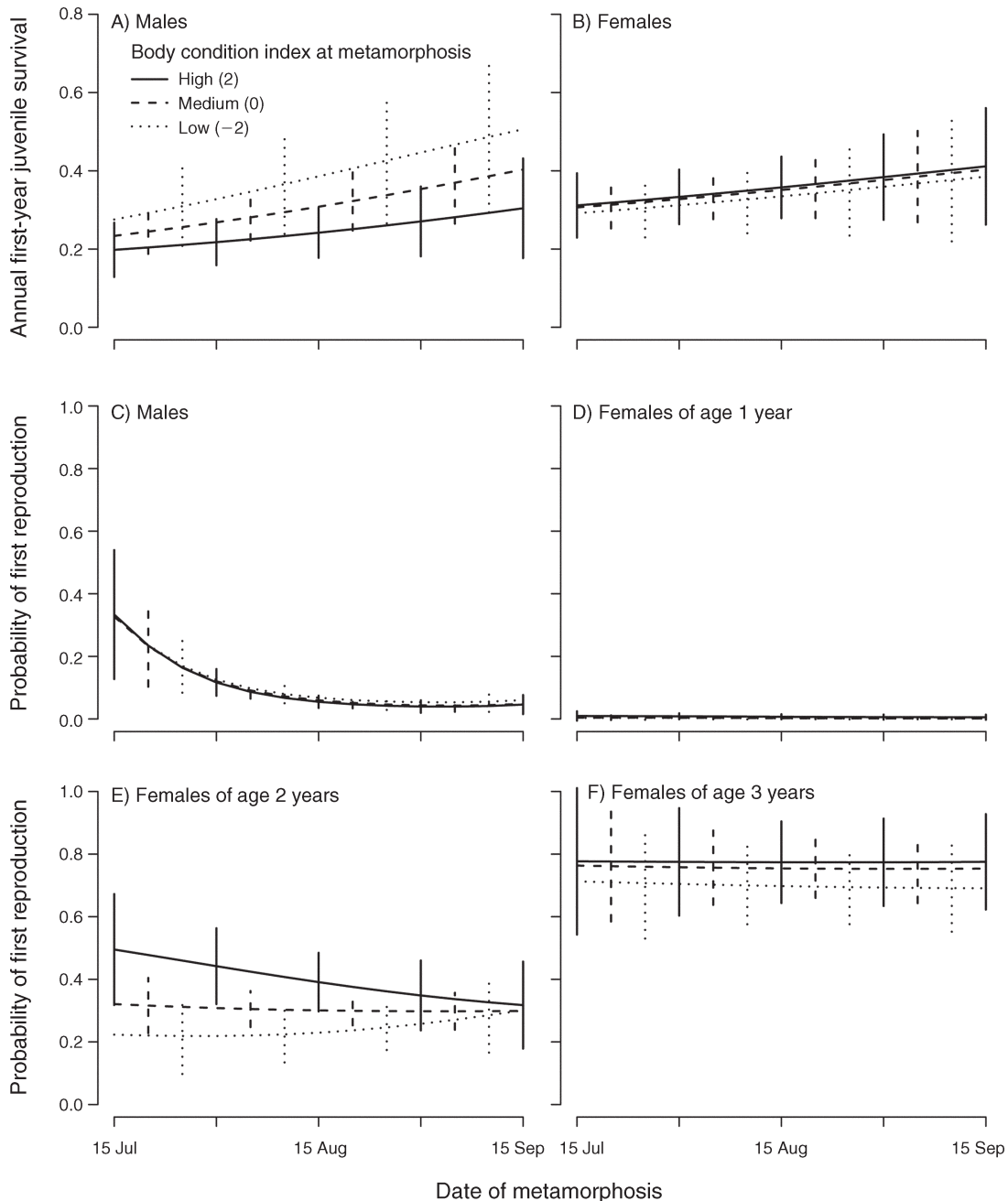
Fig. 2. Juvenile life history traits. All estimates are model-averaged probabilities. The vertical lines represent standard errors of the estimates. (A, B) Estimates of (A) male and (B) female toad first-year survival as a function of the date of and body condition at metamorphosis (PC$_{meta}$). Estimates are for the year 1990. Results for other years are similar, as year is an additive effect on date and body condition at maturity (Appendix B: Table B10). (C) Probability of first reproduction one year after metamorphosis for male toads in relation to body condition at and date of metamorphosis. (D) Probability of first reproduction one year after metamorphosis for female toads in relation to body condition at and date of metamorphosis. (E) Probability of first reproduction two years after metamorphosis for female toads in relation to body condition at and date of metamorphosis. (F) Probability of first reproduction three years after metamorphosis for female toads in relation to body condition at and date of metamorphosis.

the parameters were estimable. As these odd estimates can have an impact on model selection if they are included in models with specific constraints, we rerun the analysis allowing these two parameters to vary freely and modeling only the other parameters.

The a posteriori model selection (Appendix B: Table B6) showed that the age-specific breeding probability of males at age 1 year was the same for all cohorts (1990–1993). Very few males reproduced in the first year after metamorphosis (0.08 ± 0.03); all reproduced at the

latest at age 2. In females, no female reproduced at age 1. Thereafter, age-specific breeding probabilities increased to 0.32 ± 0.05, 0.74 ± 0.08, and finally 1.00 with age 4.

Apparent survival.—Model selection of survival revealed that first-year juvenile survival varied among years and differed between the sexes (Appendix B: Table B5). Adult (i.e., after first-year) survival was also variable among years, but the sex effect was additive. Because the estimates of juvenile first-year and adult survival were very close, we evaluated a posteriori whether they differ (Appendix B: Table B6). The model where juvenile first-year and adult survival were identical received the highest support from the data. Survival varied among years and was consistently higher in females than in males (difference on logit scale: 0.34 ± 0.08).

Impact of body condition and date of metamorphosis on age of first reproduction

We modeled the impact of body condition at and date of metamorphosis on the age-specific probabilities of first time reproduction separately for each sex. In males, model selection showed that the probability to reproduce for the first time at age of 1 year was best described by a non-linear function of the date at metamorphosis (Appendix B: Table B7; Fig. 2B). Models including body condition at metamorphosis had very little support. Males that metamorphosed very early in the season had the highest probability to breed at age 1 year; but then the age-specific breeding probability was almost constant over a wide range of different dates of metamorphosis (Fig. 2B).

In females, the probability of first reproduction at ages 1 and 3 years depended only weakly on body condition or date of metamorphosis; in fact, only the second-best model included body condition at metamorphosis (Appendix B: Table B8). At age 2, a model including body condition at metamorphosis and date of metamorphosis was best supported by the data; this model was almost tied with a model that included only body condition at metamorphosis (Appendix B: Table B8). We then modeled body condition and date of metamorphosis as additive effects across all ages. Model selection revealed that body condition had an effect on the probability of first reproduction (Appendix B: Table B9). Model-averaged estimates for each age showed however that the effect of individual covariates on the probability of first time breeding was rather weak (Fig. 2).

Impact of body condition and date of metamorphosis on first-year juvenile survival

We modeled the effects of individual covariates as additive effects to the time-dependent first-year juvenile survival probabilities. In males, the best model contained the additive effects of date and body condition (Appendix B: Table B10), whereas in females the best model contained only an effect of time. Model-averaged estimates show that juvenile first-year survival was higher when toads metamorphosed later in the season. This effect was stronger in males than in females. In males, it is also apparent that a higher body condition resulted in lower survival probabilities, an effect that was most pronounced at late metamorphosis (Fig. 2A). First-year juvenile survival is survival from metamorphosis to the next year. Early and late metamorphosing toads may simply differ in juvenile survival because early metamorphosing spend more time in the terrestrial environment (i.e., daily survival may be the same but the number of days in the terrestrial environment differs).

Probability to survive to maturity and population growth rates

Males with low body condition at metamorphosis had a higher probability to survive to maturity than males with high body condition (Fig. 3A). The model predicted that early and late dates of metamorphosis were better for survival than average dates. However, there was a positive correlation between date of and size at metamorphosis (Fig. 1A). Hence, only few combinations of date and body condition occurred: early metamorphosis at low condition, metamorphosis at an intermediate date and body condition and late metamorphosis at high condition. There was a tendency (considering the width of the confidence interval), that males that underwent metamorphosis early at a low condition had the highest probability to reach maturity. All other combinations of date of metamorphosis and size at metamorphosis that occurred had lower, but similar probabilities to reach maturity (Fig. 3A). Because few toad metamorphosed very early in the season (15 July, see Fig. 1A), the vast majority of metamorphs had similar probabilities to reach maturity.

The population growth rates (i.e., fitness of females in relation to size at and date of metamorphosis) decreased with decreasing body condition and increased with increasing date of metamorphosis (Fig. 3). There was a tendency (given the width of the confidence intervals) that female toads metamorphosing early in the season at a low body condition had the lowest predicted population growth rate. Other typical combinations of body condition at and date of metamorphosis had similar predicted population growth rates. Since few toads metamorphosed early in the season (15 July, see Fig. 1), the vast majority of metamorphs had similar probabilities to reach maturity.

DISCUSSION

There was substantial variation in the metamorphic phenotype, as measured by size at and date of metamorphosis. This variation caused variation in post-metamorphic life history traits of juvenile spadefoot toads that depended on the sex of the toadlet (Fig. 2, 3). Phenotypic variation in metamorphic phenotype was similar to the variation observed in other field
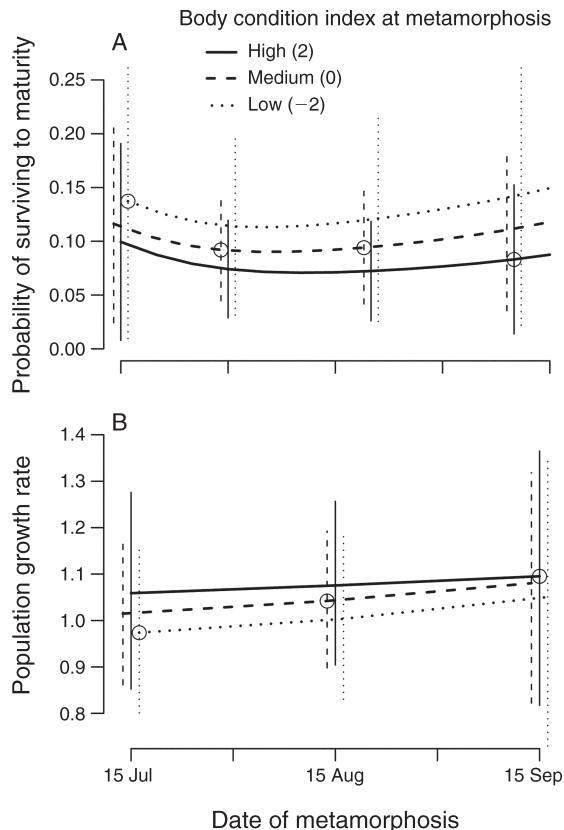
FIG. 3. Integrative measures of juvenile performance. (A) Probabilities of male spadefoot toads to survive to maturity (i.e., to reproduce at least once) in relation to body condition at (PC_{meta}) and date of metamorphosis, calculated from the model-averaged survival probabilities and age-specific probabilities to reproduce for the first time (from Fig. 2). The open circles indicate typical body conditions at metamorphosis (PC_{meta}) for a given date of metamorphosis (note that there is a significant positive correlation between body condition at metamorphosis and timing of metamorphosis). (B) Estimated population growth rates (fitness) of female spadefoot toads in relation to body condition (PC_{meta}) at and date of metamorphosis. Early metamorphosis corresponds to 14 July, medium metamorphosis to 8 August, and late metamorphosis to 12 September. Details about the model are provided in Appendix D. The open circles indicate the most frequent combinations of metamorphic traits (note that there is a significant positive correlation between body condition at metamorphosis and timing of metamorphosis). The vertical lines show the limits of the 95% confidence intervals.

studies (Smith 1987, Semlitsch et al. 1988). The previously described positive phenotypic correlations between metamorphic, juvenile, and adult life-history traits (Smith 1987, Semlitsch et al. 1988, Berven 1990, Goater 1994, Scott 1994, Morey and Reznick 2001, Altwegg and Reyer 2003, Chelgren et al. 2006) were only confirmed when we looked at one trait at a time. Yet, because disadvantages in one trait can be cancelled out by other traits (Dobzhansky 1956), more integrative fitness measures, such as the probability to reach maturity and population growth rate, are necessary

(McPeek and Peckarsky 1998). These fitness measures yielded a different insight than the analysis of single traits. In males, toads that metamorphosed very early at a small size had a higher probability to survive to maturity than toads that metamorphosed at a later date and larger size (Fig. 3). Female toads that metamorphosed early at a low body condition had the lowest predicted population growth. However, because very few male and female toads metamorphosed very early in the season (15 July, see Fig. 1), differences in metamorphic phenotype led to different life history pathways but in the end individuals that followed different life history pathways had equal population growth rates (females) or probabilities to reach maturity (males; Fig. 3). Thus, starting post-metamorphic size at a small size, a "bad start," did not lead to lower overall probability to reach maturity (males) or population growth rates (females).

Date of metamorphosis and size at metamorphosis correlated with the life history traits of juveniles in a sex-specific manner (Fig. 2). In male juvenile spadefoot toads, there was a positive relationship between late metamorphosis and the survival to the next year; the reason may be that early metamorphosing toads spent more time in the terrestrial environment. Male metamorphs with high body condition had lower juvenile first-year survival, whereas early metamorphosis resulted in early maturity, a result that is in line with previous studies. This resulted in a pattern of directional selection on body condition at metamorphosis and disruptive selection on timing of metamorphosis, the latter is determined by both growth and developmental rate.

Female juvenile life histories differed from males (Fig. 2). Predicted population growth rate of female metamorphs with high body condition was higher than predicted life time fitness of female metamorphs with an average or low body condition (Fig. 3). Survival was independent of body condition. Timing of metamorphosis had a weak effect on the age of maturity but was correlated positively with survival. Late metamorphosis resulted in higher life time fitness. Because there was a positive correlation between the size at and date of metamorphosis (Fig. 1A), the effects of body condition on population growth rate and the effect of date of metamorphosis on population growth rate largely cancelled each other out (Fig. 3B). As a consequence, different metamorphic phenotypes performed equally well.

Similar to our results, a number of authors report that larger size at or earlier date of metamorphosis did not lead to enduring increased postmetamorphic performance (e.g., Beck and Congdon 1999, Boone 2005). A possible explanation for this is plasticity in growth rates where small individuals have elevated growth rates (Beck and Congdon 1999, Boone 2005). This would then lead to similar performance of individuals with different starting conditions (i.e., date of and size at metamorphosis). We found that large and small metamorphs had similar performance but the mecha-

PLATE 1.   A spadefoot toad (*Pelobates fuscus*) undergoing metamorphosis. Photo credit: B. Thiesmeier.

nism was not plasticity in growth rates. Different starting conditions led to different life history pathways of similar performance where the effects of different dates of and sizes at metamorphosis cancelled each other out. Thus, there are multiple mechanisms how equal performance despite different dates of and sizes at metamorphosis may be attained. Most life history traits trade off (Dobzhansky 1956, Stearns 1992), so equal performance of different life history pathways may be also common. Many studies of compensatory growth have revealed some costs (Metcalfe and Monaghan 2001). In our case study, small individuals can cancel the effects of a bad start but there may be no costs because growth may not have to be accelerated.

If different combinations of date of and size at metamorphosis lead to different life history pathways with similar performance (probability to reach maturity and population growth rate), then this can contribute to the maintenance of phenotypic variation in metamorphic traits. Such phenotypic variation is known to abound in natural populations of species with complex life cycles (Wilbur and Collins 1973). We believe that natural selection may be more likely to maintain phenotypic variation in size at and timing of metamorphosis rather than to reduce it. We offer two non-mutually exclusive explanations.

The first explanation is based on the notion that the benefits of early and late maturity depend on population dynamics. Put simply, in a growing population, early maturity is favored whereas delayed maturity is favored in shrinking populations (Stearns 1992). Amphibian populations are notorious for strong fluctuations in size (Semlitsch et al. 1996, Meyer et al. 1998, Pellet et al. 2006). In years when the population is about to grow, early metamorphosis at a small size may be favored because it leads to early maturity. In other years when the population is about to become smaller, later metamorphosis at a larger size may be better because it leads to later maturity. Given the fact that amphibian populations fluctuate widely and different trait values are favored in different metamorphic cohorts, abundant phenotypic variation may persist. This scenario may suggest that small metamorphs pay a cost of being small at metamorphosis in shrinking populations because early maturity is disadvantageous. In contrast, large metamorphs may pay a cost of being large in growing populations because late maturity is disadvantageous.

The second explanation is based on the idea of "cohort iteroparity" (Wilbur and Rudolf 2006). In amphibians, there is often substantial variation in recruitment among years (Semlitsch et al. 1996). If there is strong variation in larval survival, then there is selection for decreased annual reproductive effort and higher adult survival (Seger and Brockmann 1987). An alternative to lengthening the adult life span may be to have offspring attain maturity in different years, a phenomenon termed "cohort iteroparity" by Wilbur and Rudolf (2006). This phenomenon is well-known for seed banks (Evans and Dennehy 2005). It may be an explanation as to why some amphibians have remarkably low adult survival despite high variability in reproductive success (Church et al. 2007). In conclusion,

spreading offspring maturity may be beneficial and may explain why so much variation in metamorphic (and maturity) life history traits is maintained.

In agreement with previous studies, our results show that metamorphic phenotype correlated with postmetamorphic performance. However, different life history pathways converged to similar population growth rates (for females) and probability to reach maturity (for males). This result could only be detected through the use of integrative measures of performance. An analysis of one trait at a time would not have made evident that the effects on late and early metamorphosis at large or small size on postmetamorphic life history traits cancel each other out. We suggest that the similar performance of different life history pathways can be understood if a population dynamics perspective is included in the rationale. This perspective may explain how ample phenotypic variation may be maintained.

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SUPPLEMENTAL MATERIAL

Appendix A

Tables showing the number of first captures and recaptures of metamorphs, males, and females for the years 1989–1997 and body mass at metamorphosis, size at metamorphosis, and date of metamorphosis of male and female spadefoot toads for the years 1989–1993 (*Ecological Archives* E093-057-A1).

Appendix B

Tables showing model selection results for intermediate steps of the mark–recapture analysis (*Ecological Archives* E093-057-A2).

Appendix C

Description of the multistate mark–recapture model in matrix notation (*Ecological Archives* E093-057-A3).

Appendix D

Description of the projection matrix model (*Ecological Archives* E093-057-A4).

Appendix E

Results of a simulation study exploring the effects (i.e., absolute and relative bias) of an uneven sex ratio at metamorphosis on juvenile survival, adult survival, recapture probability, and probability to reproduce at an age of 1 year (*Ecological Archives* E093-057-A5).

Ecological Archives **E093-057-A1**

Benedikt R. Schmidt, Walter Hödl, and Michael Schaub. 2012. From metamorphosis to maturity in complex life cycles: equal performance of different juvenile life history pathways. *Ecology* **93:657–667.**

Appendix A. Tables showing number of first captures and recaptures of metamorphs, males and females for the years 1989 to 1997 and body mass at metamorphosis, size at metamorphosis and date of metamorphosis of male and female spadefoot toads for the years 1989 to 1993.

TABLE A1. Number of first captures (newly marked) and of recaptures of spadefoot toads in each year. Note that the metamorphs cannot be sexed and can only be recaptured as adults. Individuals may appear multiple times in the table (first capture and recaptures).

Year	First captures			Recaptured	
	Metamorphs	**Adult males**	**Adult females**	**Adult males**	**Adult females**
1989	134	46	47	-	-
1990	235	19	21	17	10
1991	1373	9	17	13	9
1992	603	17	9	36	20
1993	413	14	6	122	58
1994	-	23	26	133	120
1995	-	23	36	89	105
1996	-	5	9	29	77
1997	-	9	19	2	22
Total	2758	165	190	441	421

TABLE A2. Mean and standard error of body mass (g), size at metamorphosis (mm) and date of metamorphosis (number of days since 1st January) of spadefoot toads in relation to year and sex. Note that only individuals that survived to maturity are included here (otherwise they were not sexed).

Year	Body mass		Size		Date	
	Male	**Female**	**Male**	**Female**	**Male**	**Female**
1989	4.28 (0.75)	4.32 (0.51)	30.17 (1.50)	30.40 (1.50)	221.4 (8.6)	216.1 (8.5)
1990	3.92 (0.64)	3.55 (0.57)	31.88 (1.38)	31.17 (1.30)	228.8 (13.9)	229.9 (9.2)
1991	5.12 (0.61)	5.07 (0.59)	33.77 (1.49)	33.66 (1.53)	230.7 (9.9)	231.7 (12.0)
1992	4.11 (0.52)	4.03 (0.55)	31.05 (1.41)	30.99 (1.61)	231.8 (21.0)	228.9 (15.6)
1993	3.69 (0.65)	3.46 (0.48)	30.61 (1.85)	29.82 (1.41)	222.3 (16.9)	215.4 (12.3)

[Back to E093-057]

Ecological Archives **E093-057-A2**

Benedikt R. Schmidt, Walter Hödl, and Michael Schaub. 2012. From metamorphosis to maturity in complex life cycles: equal performance of different juvenile life history pathways. *Ecology* **93:657–667.**

Appendix B. Tables showing model selection results for intermediate steps of the mark-recapture analysis.

TABLE B1. Results of model selection analysis for the relationship between body condition at and date of metamorphosis and body condition at maturity. Linear regression models of body condition (score of first principal component axis of size and body mass) at maturity (PC_{mat}) of spadefoot toads as functions of body condition (score of the first principal component axis of size and body mass; PC_{meta}) and date at metamorphosis. Males and females were analysed separately. Given are the coefficient of determination (R^2), the number of estimated parameters, the difference of the Akaike information criterion of the current and the best model (ΔAIC) and the Akaike weight (AIC weight).

Regression model	Model R^2	No. parameters[†]	ΔAIC	AIC weight
Males				
Intercept only	0.000	2	20.73	0.00
Body condition	0.027	3	14.94	0.00
Body condition + body condition²	0.022	4	16.91	0.00
Date	0.000	3	22.41	0.00
Date + date²	0.083	4	0.00	1.00
Body condition + date	0.028	4	15.36	0.00
Body condition + date + body condition × date	0.049	5	10.61	0.00
Females				
Intercept only	0.000	2	9.61	0.01
Body condition	0.010	3	8.49	0.01
Body condition + body condition²	0.009	4	9.77	0.00
Date	0.004	3	9.69	0.00
Date + date²	0.016	4	8.25	0.01
Body condition + date	0.055	4	0.00	0.69
Body condition + date + body condition × date	0.051	5	1.81	0.28

[†] Parameter count includes intercept and σ^2.

TABLE B2. Modelling recapture probabilities of spadefoot toads in relation to sex and time effects. In all models the age of full reproduction was fixed to 6 years, and the probability to reproduce for the first time was age, time and sex-specific ($\alpha_{a[6] \times t \times ex}$). Moreover survival was always time-, sex-, and age (2 age classes) dependent ($\varphi_{a2 \times sex \times t}$). In the model notification we omit these model parts and only show the recapture part. We also show the fit of the most general model, which considered for each capture cohort of the metamorphs and of the adults time- and sex-dependent survival and recapture probabilities. Subscript t refers to a time effect, subscript *sex* to a sex-effect, and subscript c to a cohort effect. Given

are the for overdispersion corrected deviance (Qdeviance), the number of estimated parameters, the difference of the small sample size and overdispersion adjusted Akaike information criterion of the current and the best model (ΔQAIC$_c$) and the Akaike weight (QAIC$_c$ weight). The overdispersion coefficient was ĉ = 1.385.

Model	QDeviance	No. parameters	ΔQAIC$_c$	QAIC$_c$ weight
$p_{t \times sex}$	157.8	76	8.20	0.01
$p_{t + sex}$	163.9	70	1.85	0.28
p_t	**164.1**	**69**	**0.00**	**0.71**
p_{sex}	183.6	65	11.17	0.00
$p_{.}$	185.2	64	10.72	0.00
$\varphi_{c \times t \times sex}, p_{c \times t \times sex}$	127.2	122	74.74	0.00

TABLE B3. Modelling age of full reproduction (i.e. the age at which as yet inexperienced breeders start to reproduce is 1) of spadefoot toads. In all models survival was kept at its most complex structure ($\varphi_{a2 \times t \times sex}$) and recapture probabilities at their most parsimonious structure (p_t). The structures for the ages of full reproduction were generally sex-, age- and time-dependent, but with different ages of full reproduction. All combination of the sex-specific age of full reproduction were considered. The figure in parentheses is the age at which full reproduction is reached (i.a. α [1]: age of full reproduction = 1 year). The superscript m refers to males, the superscript f to females. The table entries are the ΔQAIC$_c$ values and in parentheses the QAIC weights. The overdispersion coefficient was ĉ = 1.385.

	$\alpha^f[1]$	$\alpha^f[2]$	$\alpha^f[3]$	$\alpha^f[4]$	$\alpha^f[5]$	$\alpha^f[6]$
$\alpha^m[1]$	387.45 (0.00)	228.33 (0.00)	196.55 (0.00)	198.06 (0.00)	223.62 (0.00)	225.67 (0.00)
$\alpha^m[2]$	274.36 (0.00)	67.16 (0.00)	5.78 (0.04)	**0.00 (0.75)**	3.32 (0.14)	7.44 (0.02)
$\alpha^m[3]$	275.79 (0.00)	76.79 (0.00)	14.09 (0.00)	7.60 (0.02)	10.11 (0.00)	12.17 (0.00)
$\alpha^m[4]$	277.78 (0.00)	80.58 (0.00)	17.33 (0.00)	9.48 (0.01)	13.89 (0.00)	15.95 (0.00)
$\alpha^m[5]$	279.82 (0.00)	85.97 (0.00)	16.85 (0.00)	9.03 (0.01)	10.99 (0.00)	17.20 (0.00)
$\alpha^m[6]$	277.78 (0.00)	92.15 (0.00)	23.03 (0.00)	11.10 (0.00)	15.13 (0.00)	17.20 (0.00)

TABLE B4. Testing for time-dependence of the age-specific probabilities of first time breeding (α) in spadefoot toads. In all models survival ($\varphi_{a2 \times t \times sex}$) and recapture probabilities (p_t) were kept at their most parsimonious structures. Because only one α is estimated in males, the parameter could only be time-dependent or constant. In the females, 3 different α were estimated for each cohort, and

consequently different combinations of time (t) and age (a) combinations are possible. See Table B2 for the significance of the column headings. The overdispersion coefficient was ĉ = 1.385.

Model	QDeviance	No. parameters	ΔQAIC$_c$	QAIC$_c$ weight
$\alpha^m[2]_t$, $\alpha^f[4]_{a*t}$	179.9	53	10.66	0.00
$\alpha^m[2]_t$, $\alpha^f[4]_{a+t}$	187.4	46	3.77	0.13
$\alpha^m[2]_t$, $\alpha^f[4]_a$	**193.9**	**41**	**0.00**	**0.85**
$\alpha^m[2]$, $\alpha^f[4]_{a*t}$	199.5	49	22.04	0.00
$\alpha^m[2]$, $\alpha^f[4]_{a+t}$	201.6	42	9.80	0.01
$\alpha^m[2]$, $\alpha^f[4]_a$	211.7	37	9.70	0.01

TABLE B5. Modelling the general shape of first-year juvenile and adult (i.e. after first-year) survival of spadefoot toads. In all models the recapture probability (p_t) and the age-specific probabilities of first time breeding ($\alpha^m[2]_t$, $\alpha^f[4]_a$) were kept at their most parsimonious structures. Note that the model notation $\varphi_{a2 \times t \times sex}$ refers to the same model as notation $\varphi_{1y:\ t \times sex;\ ad:\ t \times sex}$. See Table B2 for the significance of the column headings. The overdispersion coefficient was ĉ = 1.385.

Model	QDeviance	No. parameters	ΔQAIC$_c$	QAIC$_c$ weight
$\varphi_{1y:\ t \times sex;\ ad:\ t + sex}$	**201.76**	**34**	**0.00**	**0.49**
$\varphi_{1y:\ t;\ ad:\ t + sex}$	213.14	29	1.21	0.26
$\varphi_{1y:\ t + sex;\ ad:\ t + sex}$	213.10	30	3.21	0.10
$\varphi_{1y:\ .;\ ad:\ t + sex}$	225.41	25	5.37	0.03
$\varphi_{1y\ =\ ad:\ t + sex}$	228.05	24	5.99	0.02
$\varphi_{1y:\ t \times sex;\ ad:\ t \times sex}$	193.85	41	6.37	0.02
$\varphi_{1y:\ t + sex;\ ad:\ sex}$	230.91	23	6.82	0.02
$\varphi_{1y:\ t \times sex;\ ad:\ sex}$	221.25	28	7.30	0.01
$\varphi_{1y:\ sex;\ ad:\ t + sex}$	225.39	26	7.38	0.01
$\varphi_{1y:\ t + sex;\ ad:\ t}$	220.28	29	8.36	0.01
$\varphi_{1y:\ t;\ ad:\ t \times sex}$	206.13	36	8.44	0.01
$\varphi_{1y:\ t + sex;\ ad:\ t \times sex}$	204.57	37	8.92	0.01
$\varphi_{1y:\ t;\ ad:\ sex}$	233.13	23	9.04	0.01
$\varphi_{1y:\ t \times sex;\ ad:\ t}$	214.23	33	10.44	0.00
$\varphi_{1y:\ t + sex;\ ad:\ .}$	236.83	22	10.72	0.00
$\varphi_{1y\ =\ ad:\ t \times sex}$	219.40	31	11.53	0.00
$\varphi_{1y:\ .;\ ad:\ t \times sex}$	219.42	31	11.56	0.00
$\varphi_{1y:\ sex;\ ad:\ t \times sex}$	218.72	32	12.89	0.00
$\varphi_{1y:\ t \times sex;\ ad:\ .}$	231.59	27	15.60	0.00
$\varphi_{1y:\ sex;\ ad:\ t}$	236.95	25	16.92	0.00

$\varphi_{1y\,=\,ad:\ t}$	248.89	23	24.80	0.00
$\varphi_{1y:\ .;\ ad:\ t}$	249.14	24	27.08	0.00
$\varphi_{1y:\ t;\ ad:\ .}$	253.96	22	27.85	0.00
$\varphi_{1y:\ .;\ ad:\ sex}$	265.59	19	33.42	0.00
$\varphi_{1y\,=\,ad:\ sex}$	269.30	18	35.10	0.00
$\varphi_{1y:\ sex;\ ad:\ sex}$	265.26	20	35.11	0.00
$\varphi_{1y:\ sex;\ ad:\ .}$	272.81	19	40.63	0.00
$\varphi_{1y\,=\,ad:\ .}$	287.80	17	51.59	0.00
$\varphi_{1y:\ .;\ ad:\ .}$	287.07	18	52.87	0.00

TABLE B6. A posteriori modelling of survival of spadefoot toads directed to test whether there were age-dependent effects. In these models the juvenile first-year survival probability of the females of cohort 1989 is separately estimated from all other survival probabilities (indicated by subscript f89). We tested whether the survival probabilities were age-, sex-, and time dependent. Moreover we tested whether the age of full reproduction in male for the cohorts 1990 to 1993 is the same and only that of cohort 1989 is different (indicated by $\alpha^m[2]_{89,\ 90-93}$, $\alpha^f[4]_a$). In all models the recapture probability (p_t) was always kept at its best structure. For comparison we included the best model from the a priori modelling ($\varphi_{1y:\ t\ \times\ sex,\ ad:\ t\ +\ sex,\ f89}$, $\alpha^m[2]_t$, $\alpha^f[4]_a$). See Table B2 for the significance of the column headings. The overdispersion coefficient was ĉ = 1.385.

Model	QDeviance	No. parameters	ΔQAIC$_c$	QAIC$_c$ weight
$\varphi_{1y\,=\,ad:\ t\ +\ sex,\ f89}$, $\alpha^m[2]_{89,\ 90-93}$, $\alpha^f[4]_a$	**219.28**	**22**	**0.00**	**0.70**
$\varphi_{1y\,=\,ad:\ t\ +\ sex,\ f89}$, $\alpha^m[2]_t$, $\alpha^f[4]_a$	215.73	25	2.52	0.20
$\varphi_{1y\,=\,ad:\ t\ \times\ sex,\ f89}$, $\alpha^m[2]_{89,\ 90-93}$, $\alpha^f[4]_a$	210.14	29	5.05	0.06
$\varphi_{1y:\ t\ \times\ sex,\ ad:\ t\ +\ sex,\ f89}$, $\alpha^m[2]_t$, $\alpha^f[4]_a$	201.76	34	6.83	0.02
$\varphi_{1y\,=\,ad:\ t\ \times\ sex,\ f89}$, $\alpha^m[2]_t$, $\alpha^f[4]_a$	206.49	32	7.49	0.02
$\varphi_{1y\,=\,ad:\ t,\ f89}$, $\alpha^m[2]_{89,\ 90-93}$, $\alpha^f[4]_a$	235.98	21	14.68	0.00
$\varphi_{1y\,=\,ad:\ t,\ f89}$, $\alpha^m[2]_t$, $\alpha^f[4]_a$	232.45	24	17.22	0.00
$\varphi_{1y\,=\,ad:\ sex,\ f89}$, $\alpha^m[2]_{89,\ 90-93}$, $\alpha^f[4]_a$	267.99	16	36.59	0.00
$\varphi_{1y\,=\,ad:\ sex,\ f89}$, $\alpha^m[2]_t$, $\alpha^f[4]_a$	265.26	19	39.92	0.00
$\varphi_{1y\,=\,ad:\ .,\ f89}$, $\alpha^m[2]_{89,\ 90-93}$, $\alpha^f[4]_a$	283.82	15	50.40	0.00
$\varphi_{1y\,=\,ad:\ .,\ f89}$, $\alpha^m[2]_t$, $\alpha^f[4]_a$	281.09	18	53.72	0.00

TABLE B7. Modelling the probabilities of first reproduction at an age of 1 year as function of individual covariates at metamorphosis in male spadefoot toads (α^m). These covariates were the scores of the first principal component axes of body mass and size (reflecting body condition, PC_{meta}) and date at metamorphosis. While modelling α, the other parts of the model were kept at their best structure ($\varphi_{1y\,=\,ad:\ t\ +\ sex,\ f89}$, $\alpha^m[2]_{89,\ 90-93}$, $\alpha^f[4]_a$, p_t). See Table B2 for the significance of the column headings. The overdispersion coefficient was ĉ = 1.385.

Model	QDeviance	No. parameters	ΔQAIC$_c$	QAIC$_c$ weight
Cohorts 90 to 93				
$\alpha^m[1]$ (.)	3530.59	21	4.59	0.06
$\alpha^m[1]$ (PC$_{meta}$)	3530.39	22	6.42	0.03
$\alpha^m[1]$ (PC$_{meta}$ + PC$_{meta}^2$)	3530.06	23	8.10	0.01
$\alpha^m[1]$ (date)	3527.94	22	3.97	0.09
$\alpha^m[1]$ (date + date²)	**3521.94**	**23**	**0.00**	**0.64**
$\alpha^m[1]$ (PC$_{meta}$ + date)	3526.21	23	4.26	0.08
$\alpha^m[1]$ (PC$_{meta}$ × date)	3523.72	24	3.80	0.10

TABLE B8. Modelling age-specific probabilities of first reproduction in female spadefoot toads (α^f) as function of individual covariates at metamorphosis. These covariates were the scores of the first principal component axes of body mass and size (reflecting body condition, PC$_{meta}$) and date at metamorphosis.. While modelling *a*, the other parts of the model were kept at their best structure ($\varphi_{1y\,=\,ad:\,t\,+\,sex,\,f89}$, $\alpha^m[2]_{89}$, $_{90\text{-}93}$, $\alpha^f[4]_a$, p_t). See Table B2 for the significance of the column headings. The overdispersion coefficient was ĉ = 1.385.

Model	QDeviance	No. parameters	ΔQAIC$_c$	QAIC$_c$ weight
First-time reproducer at age 1y				
$\alpha^f[4]$ (.)	**3530.59**	**21**	**0.00**	**0.25**
$\alpha^f[4]$ (PC$_{meta}$)	3528.80	22	0.23	0.22
$\alpha^f[4]$ (PC$_{meta}$ + PC$_{meta}^2$)	3527.43	23	0.89	0.16
$\alpha^f[4]$ (date)	3530.04	22	1.47	0.12
$\alpha^f[4]$ (date + date²)	3529.77	23	1.21	0.14
$\alpha^f[4]$ (PC$_{meta}$+date)	3528.63	23	2.09	0.09
$\alpha^f[4]$ (PC$_{meta}$ × date)	3528.59	24	4.07	0.03
First-time reproducer at age 2y				
$\alpha^f[4]$ (.)	3530.59	21	1.24	0.14
$\alpha^f[4]$ (PC$_{meta}$)	3527.39	22	0.06	0.26
$\alpha^f[4]$ (PC$_{meta}$ + PC$_{meta}^2$)	3527.39	23	2.08	0.09
$\alpha^f[4]$ (date)	3529.77	22	2.44	0.08
$\alpha^f[4]$ (date + date²)	3528.25	23	2.94	0.06
$\alpha^f[4]$ (PC$_{meta}$ + date)	3527.34	23	2.03	0.10
$\alpha^f[4]$ (PC$_{meta}$ × date)	**3523.28**	**24**	**0.00**	**0.27**
First-time reproducer at age 3y				
$\alpha^f[4]$ (.)	**3530.59**	**21**	**0.00**	**0.36**

$\alpha^f[4]$ (PC$_{meta}$)	3529.92	22	1.35	0.18
$\alpha^f[4]$ (PC$_{meta}$ + PC$_{meta}^2$)	3529.36	23	2.81	0.09
$\alpha^f[4]$ (date)	3530.59	22	2.02	0.13
$\alpha^f[4]$ (date + date^2)	3530.58	23	2.00	0.13
$\alpha^f[4]$ (PC$_{meta}$ + date)	3529.91	23	3.37	0.07
$\alpha^f[4]$ (PC$_{meta}$ × date)	3529.46	24	4.94	0.03

TABLE B9. Modelling age-specific probabilities of first reproduction (α^f) in female spadefoot toads as a function of individual covariates at metamorphosis. These covariates were the scores of the first principal component axes of body mass and size (reflecting body condition, PC$_{meta}$) and date at metamorphosis. While modelling a, the other parts of the model were kept at their best structure ($\varphi_{1y\,=\,ad:\,t\,+\,sex,\,f89}$, $\alpha^m[2]_{89,\,90\text{-}93}$, $\alpha^f[4]_a$, p_t). See Table B2 for the significance of the column headings. The overdispersion coefficient was ĉ = 1.385. Table B8 shows an analysis done separately for ages 1 through 4.

Model	QDeviance	No. parameters	ΔQAIC$_c$	QAIC$_c$ weight
Additive over all ages				
$\alpha^f[1, 2, 3]$ (.)	3530.59	21	3.04	0.08
$\alpha^f[1, 2, 3]$ (PC$_{meta}$)	**3525.52**	**22**	**0.00**	**0.37**
$\alpha^f[1, 2, 3]$ (PC$_{meta}$ + PC$_{meta}^2$)	3525.52	23	2.02	0.13
$\alpha^f[1, 2, 3]$ (date)	3529.68	22	4.16	0.05
$\alpha^f[1, 2, 3]$ (date + date^2)	3527.79	23	4.30	0.04
$\alpha^f[1, 2, 3]$ (PC$_{meta}$ + date)	3525.45	23	1.96	0.14
$\alpha^f[1, 2, 3]$ (PC$_{meta}$ × date)	3522.80	24	1.33	0.19

TABLE B10. Modelling the effects of body condition (PC$_{meta}$) and date of metamorphosis (date) on first-year juvenile survival probabilities of male and female spadefoot toads. In all models the recapture probability (p_t) and the age-specific probabilities of first time breeding ($\alpha^m[2]_t$, $\alpha^f[4]_a$) were kept at their most parsimonious structures. See Table B2 for the significance of the column headings. The overdispersion coefficient was ĉ = 1.385.

Model	QDeviance	No. parameters	ΔQAIC$_c$	QAIC$_c$ weight
Males				
$\varphi_{1y:\,t}$	3530.59	21	1.97	0.10
$\varphi_{1y:\,t\,+\,PC_{meta}}$	3528.67	22	2.08	0.09
$\varphi_{1y:\,t\,+\,PC_{meta}\,+\,PC_{meta}^2}$	3528.53	23	3.96	0.04
$\varphi_{1y:\,t\,+\,date}$	3527.74	22	1.15	0.15
$\varphi_{1y:\,t\,+\,date\,+\,date^2}$	3525.68	23	1.11	0.15
$\varphi_{1y:\,t\,+\,PC_{meta}\,+\,date}$	**3524.57**	**23**	**0.00**	**0.26**

$\varphi_{1y:\ t} + PC_{meta} \times date$	3523.00	24	0.45	0.21
Females				
$\varphi_{1y:\ t}$	**3530.59**	**21**	**0.00**	**0.35**
$\varphi_{1y:\ t} + PC_{meta}$	3530.27	22	1.71	0.15
$\varphi_{1y:\ t} + PC_{meta} + PC_{meta}^2$	3529.89	23	3.35	0.07
$\varphi_{1y:\ t} + date$	3529.47	22	0.90	0.23
$\varphi_{1y:\ t} + date + date^2$	3529.18	23	2.64	0.09
$\varphi_{1y:\ t} + PC_{meta} + date$	3529.47	23	2.29	0.08
$\varphi_{1y:\ t} + PC_{meta} \times date$	3529.42	24	4.90	0.03

[Back to E093-057]

Ecological Archives **E093-057-A3**

Benedikt R. Schmidt, Walter Hödl, and Michael Schaub. 2012. From metamorphosis to maturity in complex life cycles: equal performance of different juvenile life history pathways. *Ecology* **93:657–667.**

Appendix C. Description of the multi-state mark-recapture model in matrix notation.

To estimate age-specific survival probabilities, age-specific probabilities to start reproduction and recapture probabilities a multi-state model with the two states "metamorph" and "breeder" was used. From one occasion to the next, individuals may move between these two states, they may survive and the may be recaptured. These events can be described by a matrix of state transition probabilities, by a vector of state-specific survival probabilities and a vector of state-specific recapture probabilities, respectively. In the following, the states at time t are in rows and the states at time $t + 1$ in columns. Because the parameters change with age, we show the model for each age class:

$$\text{From age 0 to 1 year:} \quad \begin{bmatrix} 1 - \alpha_1 & \alpha_1 \\ 0 & 1 \end{bmatrix} \begin{bmatrix} \varphi_{1y} \\ \varphi_{ad} \end{bmatrix} \begin{bmatrix} 0 \\ p \end{bmatrix}$$

$$\text{From age 1 to } x \text{ - 1 years:} \quad \begin{bmatrix} 1 - \alpha_z & \alpha_z \\ 0 & 1 \end{bmatrix} \begin{bmatrix} \varphi_{ad} \\ \varphi_{ad} \end{bmatrix} \begin{bmatrix} 0 \\ p \end{bmatrix}$$

where α_z is the probability to start to reproduce at age z, and where z $\{2, \ldots, x$ - $1\}$

$$\text{From age } x \text{ - 1 to } x \text{ years (full reproduction is assumed at age } x \text{ [in fact } a_x = 1\text{]):} \quad \begin{bmatrix} 0 & 1 \\ 0 & 1 \end{bmatrix} \begin{bmatrix} \varphi_{ad} \\ \varphi_{ad} \end{bmatrix} \begin{bmatrix} 0 \\ p \end{bmatrix}$$

$$\text{From age } x \text{ onwards:} \quad \begin{bmatrix} 1 & 0 \\ 0 & 1 \end{bmatrix} \begin{bmatrix} \varphi_{ad} \\ \varphi_{ad} \end{bmatrix} \begin{bmatrix} 0 \\ p \end{bmatrix}$$

The parameters in this model are:

α_z: probability to start to reproduce at age z
φ_{1y}: survival probability in the first year
φ_{ad}: survival probability after the first year
p: recapture probability

[Back to E093-057]

Ecological Archives **E093-057-A4**

Benedikt R. Schmidt, Walter Hödl, and Michael Schaub. 2012. From metamorphosis to maturity in complex life cycles: equal performance of different juvenile life history pathways. *Ecology* **93:657–667.**

Appendix D. Description of the projection matrix model.

To estimate the asymptotic population growth rate we formulated a female based matrix projection model with 5 age classes (toadlet, 1 year old, 2, years old, 3 years old, more than 3 years old) using a post-breeding census and a projection interval of one year (Caswell 2001). The dominant eigenvalue of the projection matrix is an estimate of the asymptotic population growth rate, and thus of fitness. The projection matrix for the spadefoot toads is:

$$
A = \begin{bmatrix}
\varphi_{1y}A_1F_1\varphi_{tadpole}0.5 & \varphi_{ad}A_2F_2\varphi_{tadpole}0.5 & \varphi_{ad}A_3F_3\varphi_{tadpole}0.5 & \varphi_{ad}A_4F_4\varphi_{tadpole}0.5 & \varphi_{ad}A_5F_5\varphi_{tadpole}0.5 \\
\varphi_{1y} & 0 & 0 & 0 & 0 \\
0 & \varphi_{ad} & 0 & 0 & 0 \\
0 & 0 & \varphi_{ad} & 0 & 0 \\
0 & 0 & 0 & \varphi_{ad} & \varphi_{ad}
\end{bmatrix}
$$

where:

$A_1 = \alpha_1$
$A_2 = \alpha_1 + (1 - \alpha_1)\alpha_2$
$A_3 = \alpha_1 + (1 - \alpha_1)\alpha_2 + (1 - \alpha_1)(1 - \alpha_2)\alpha_3$
$A_4 = \alpha_1 + (1 - \alpha_1)\alpha_2 + (1 - \alpha_1)(1 - \alpha_2)\alpha_3 + (1 - \alpha_1)(1 - \alpha_2)(1 - \alpha_3)$

The parameters in the model are:

$\varphi_{tadpole}$: tadpole survival using the relationship logit($\varphi_{tadpole}$) = -5.24 + 8.09 × 10^{-5} x - 8.49 × 10^{-10} x^2, where x is the number of eggs in the pond (we used x = 90'000; regression model from Hels and Nachman 2002).
φ_{1y}: first year survival (own model averaged estimates)
φ_{ad}: adult year survival (based on our own data, we used an estimate of 0.43)
α_1: probability to start to reproduce when 1 year old (own model averaged estimates)
α_2: probability to start to reproduce when 2 year old (own model averaged estimates)
α_3: probability to start to reproduce when 3 year old (own model averaged estimates)
F_1: number of eggs a female of age 1 is producing, using the relationship $F_1 = 80.4BM_1$ (Hels 2002), where BM_1 is body mass of 1 year old toads (12.8g)
F_2: number of eggs a female of age 1 is producing, using the relationship $F_2 = 80.4BM_2$ (Hels 2002), where BM_2 is body mass of 1 year old toads (15.6g)
F_3: number of eggs a female of age 1 is producing, using the relationship $F_3 = 80.4BM_3$ (Hels 2002), where BM_3 is body mass of 1 year old toads (21.2g)
F_4: number of eggs a female of age 1 is producing, using the relationship $F_4 = 80.4BM_4$ (Hels 2002), where BM_4 is body mass of 1 year old toads (25.1g)
F_5: number of eggs a female of age 1 is producing, using the relationship $F_5 = 80.4BM_5$ (Hels 2002), where BM_5 is body mass of 1 year old toads (30.2g)

First year survival and the age-specific probabilities to reproduce depended on body condition (PC1) and timing of metamorphosis, and we therefore calculated the population growth rate for different conditions.

This population model assumes that females which have reproduced once, reproduce every year and that the males are an unlimited resource. To account for uncertainty in parameter estimates, we estimated confidence intervals for the population growth rate using simulation (see Schaub et al. 2009 for details). In each of the 1000 iterations we sampled φ_{1y}, φ_{ad}, α_1, α_2, and α_3 from beta distributions that were given by the estimated means and sampling variances of the corresponding parameters. For the other parameters of the matrix model no measures of uncertainty were available.

[Back to E093-057]

Ecological Archives **E093-057-A5**

Benedikt R. Schmidt, Walter Hödl, and Michael Schaub. 2012. From metamorphosis to maturity in complex life cycles: equal performance of different juvenile life history pathways. *Ecology* **93:657–667.**

Appendix E. Results of a simulation study exploring the effects (i.e., absolute and relative bias) of an uneven sex ratio at metamorphosis on juvenile survival, adult survival, recapture probability and probability to reproduce at an age of 1 year.

Since spadefoot toads can only be sexed when captured as breeders (they cannot be sexed at metamorphosis), we assigned a sex to the metamorphs that were not recaptured as adults. We assigned a sex in such a way that the sex ratio was even at metamorphosis. This approach works well if the assumption of the even sex ratio is fulfilled (Nichols et al. 2004). In order to check the consequences of the violation of the assumption of a 1:1 sex ratio at metamorphosis, we performed a simulation study. We were interested in computing the bias of age-specific survival, probability to start to reproduce and recapture probability when the sex ratio is uneven. A possibility to study bias is the analytical-numerical approach (Burnham et al. 1987). The principle is to create a data set using predefined parameter estimates and to analyse this data set. If the number of released individuals is very large, resulting maximum likelihood estimates and standard errors represent approximate expected values of the estimators and their standard errors, respectively (Burnham et al. 1987). This approach was used here. We only report mean and relative bias but not standard errors or coverage probabilities.

Simulating model

We considered a structurally identical model as the one presented in Appendix B. We assumed that most males and half of the females started to reproduce at an age of 1 year (i.e., $\alpha_{1,M} = 0.9$; $\alpha_{1,F} = 0.5$). In both sexes we assumed that so far inexperienced breeders start to reproduce at an age of 2 years (i.e., $a_{2,M} = \alpha_{2,F} = 1$). Further, we assumed juvenile and adult survival as well as recapture probability to be sex-specific (values see table D1). We further assumed that at each of the 7 occasions a number of metamorphic males (N_m) and females (N_f) are released. By varying the ratio of N_m / N_f we vary the true underlying sex ratio. At each occasion 48000 individuals were released, and we considered 7 scenarios regarding the true underlying sex ratio. In the first scenario we considered an even sex ratio. This scenario was included to evaluate whether all parameters were unbiased. Following Nichols et al. (2004), we expected a priori that survival and recapture should be unbiased, but this was not clear for the age-specific probability to start to reproduce. The next six scenarios considered uneven sex ratios (extreme: 2:1; strong: 7:5; moderate: 13:11) each either in favour of males or of females. Capture histories with these properties were constructed in R.

The sex of the individuals that have never been recaptured is known in the constructed capture histories. Yet, in reality we do not know the sex of unsexed metamorphs that are never recaptured and therefore we have to recalculate the number of released males and females that were never recaptured. Let n_i be the total number of individuals that are released at occasion i, and rf_i (rm_i) denote the number of these recaptured at least once and determined to be females (males), then - under the assumption of an even sex ratio - the number of females (males) released and never recaptured is [$0.5 \times n_i - rf_i$; $0.5 \times n_i - rm_i$]. For each constructed capture history file we recalculated these numbers and changed the input file accordingly. Finally, we analysed the data with program MARK (White & Burnham 1999).

Results

We computed absolute and relative bias of all the estimated parameters (Table D1). For the interpretation of the results it is important to note that some bias is always expected with the method that we used. This is because the computed values refer to one particular simulated data set. The random variation (i.e. "small sample size bias") is smoothed largely by the consideration of a large number of released individuals, but it is still persistent to some degree. We consider relative bias smaller than 3% as due to random variation.

If the sex ratio was even, then bias in the estimates of all parameters was negligible (relative bias < 3% for all parameters; Table E1). If the true underlying sex ratio is uneven and the data are analysed as if the sex ratio was even, then adult survival, recapture and the probability to start to reproduce still had negligible bias (relative bias < 3% for all these parameters and all scenarios). However, juvenile survival was biased. If the true sex ratio is in favour of males, juvenile survival of males is underestimated and that of females overestimated. If the true sex ratio is in favour of females, juvenile survival of males is overestimated and that of females is underestimated. The relative bias was more or less symmetrical for the two sexes, i.e. males survival was overestimated to the same degree as was females survival underestimated. The bias declined the closer the true sex ratio was to an even one. The relative bias was relatively small (< 8%) when the sex ratio was 13:11 (54% males vs 46% females).

The simulation study deals with the case where a sex is assigned with a probability of 50% to a metamorph. In our mark-recapture analysis, we used information on size at metamorphosis (male and female metamorphs differ in mean size at metamorphosis) to assign sex with a probability that depended on the size at metamorphosis. That is, our assignment of sex is not random but based on information in the data. Therefore, we assume that bias in our case study is smaller than in these simulations.

TABLE E1. Absolute (B) and relative bias (rB, in %) of male juvenile survival ($\varphi_{juv,\,M}$), female juvenile survival ($\varphi_{juv,\,F}$), male adult survival ($\varphi_{ad,\,M}$), female adult survival ($\varphi_{ad,\,F}$), male recapture (p_M), female recapture (p_F), probability of males to start to reproduce at an age of 1 year ($\alpha_{1,M}$), and probability of males to start to reproduce at an age of 1 year ($\alpha_{1,F}$) under variable true sex ratios, when the data are analysed as if the sex ratio were even. For each scenario a data set was computed where at each of 7 capture occasions 48000 individuals were released.

Parameter	True value	Even sex ratio (1:1)	Uneven sex ratio (1:2)	Uneven sex ratio (2:1)	Uneven sex ratio (5:7)	Uneven sex ratio (7:5)	Uneven sex ratio (11:13)	Uneven sex ratio (13:11)

		B	rB	B	rB	B	rB	B	rB	B	rB	B	rB	B	rB
$\varphi_{juv, M}$	0.2	-0.0001	-0.05	0.0670	33.49	-0.0653	-32.65	-0.0319	-15.95	0.0341	17.04	-0.0144	-7.20	0.0171	8.53
$\varphi_{juv, F}$	0.15	0.0044	2.96	-0.0484	-32.26	0.0501	33.41	0.0224	14.94	-0.0256	-17.09	0.0133	8.86	-0.0100	-6.64
$\varphi_{ad, M}$	0.4	-0.0047	-1.18	0.0020	0.50	-0.0012	-0.30	0.0053	1.33	-0.0036	-0.91	-0.0031	-0.78	0.0025	0.63
$\varphi_{ad, F}$	0.45	-0.0055	-1.23	-0.0034	-0.75	0.0024	0.54	0.0056	1.24	-0.0034	-0.75	-0.0099	-2.20	-0.0001	-0.03
p_M	0.6	0.0121	1.72	0.0050	0.72	0.0045	0.64	-0.0108	-1.54	0.0005	0.07	0.0107	1.53	0.0072	1.03
p_F	0.7	0.0048	0.80	0.0043	0.72	-0.0009	-0.15	0.0034	0.56	0.0016	0.26	0.0037	0.61	-0.0133	-2.21
$\alpha_{1,M}$	0.9	-0.0171	-1.91	-0.0067	-0.75	-0.0088	-0.98	0.0187	2.08	-0.0116	-1.29	-0.0216	-2.40	-0.0046	-0.51
$\alpha_{1,F}$	0.5	-0.0125	-2.49	-0.0049	-0.98	-0.0066	1.33	0.0127	2.53	-0.0025	-0.49	-0.0066	-1.31	0.0033	0.65
Proportion males		0.5		0.33		0.67		0.42		0.58		0.46		0.54	

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[Back to E093-057]