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Demographic dynamics of the afro-tropical pig-nosed frog, *Hemisus marmoratus*: effects of climate and predation on survival and recruitment

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Abstract We studied the population ecology of the West African pig-nosed frog, *Hemisus marmoratus*, to understand the relative contributions of adult survival and recruitment to population growth rate in savannah frogs using mark-recapture modelling. We marked a total of 821 adult frogs over 6 years and recaptured 74 at least once between years. Between-year adult survival was sex-specific and varied between 0.06 and 0.53 for males and 0.07–0.41 for females. Adult survival was significantly associated with annual rainfall and is cause for concern if rainfall declines further in the study region as predicted by changes in the global climate. There was a significant interaction between rainfall and sex with dry weather having a stronger negative effect on males than females. Pig-nosed frogs experienced boom and bust years with a single decline more dramatic than increases. Recruitment (in situ and immigration; 0.67–0.88) was substantially more important than adult survival (0.12–0.33) in determining realised population growth. In situ recruitment was highly variable between years with 1–36% of eggs and tadpoles released by females into the pond surviving to metamorphosis. Years of low tadpole survival were associated with high numbers of predatory tortoises. Thus, like other pond-breeding anurans, pig-nosed frogs showed highly variable juvenile recruitment, low adult survival and density-independent effects on population growth by predators and weather.

Keywords Population ecology · Mark-recapture · Amphibians · Tortoises · Tadpoles

Introduction

Understanding the factors that influence patterns of change in populations is of critical importance to many areas of fundamental and applied biology. In general, very little is known about within and between seasonal survival, the effects of predation on local recruitment, and other factors that influence population dynamics and life histories in anurans. This lack of information is especially apparent in tropical species in which even the most basic data are missing. Gaining insight into the factors affecting population fluctuations is especially urgent because of the worldwide decline in amphibian populations (Wake 1991; Alford and Richards 1999; Houlahan et al. 2000; Green 2003) and the difficulty of separating human impacts from natural fluctuations (Pechmann et al. 1991).

With their complex life cycles, population regulation in amphibians can occur at multiple stages, i.e. egg, tadpole, juvenile and/or adult stage (e.g. Hellriegel 2000; Vonesh and De la Cruz 2002). Although there are numerous reports on the magnitude of declines at different life stages in amphibians the effects on overall population growth rate (λ) are poorly understood. Since equivalent changes in different vital rates can have different effects on λ , demographic parameters need to be quantified at all life stages (Biek et al. 2002).

Adult survival and recruitment both determine population dynamics. In the past, long-term mark-recapture studies on anurans have often confused re-sighting rates with survival leading to considerable bias in estimates of survival (Schmidt et al. 2002). Recent advances in mark-recapture methodology allow rigorous data analyses that provide robust estimates of demographic parameters and an assessment of the relative importance of adult survival and recruitment (Lebreton et al. 1992; Kendall et al. 1995; White and Burnham 1999). Reliable estimates are necessary to parameterise demographic models and for predictions about the viability of populations.

The objective of this study was to estimate population parameters and evaluate the ecological factors that influence population dynamics in a tropical savannah anuran.

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The pig-nosed frog, *Hemissus marmoratus*, offers an excellent opportunity to investigate natural causes of population fluctuations as an example of pond-breeding savannah anurans because: (1) individuals are easily captured at drift fences since they cannot climb or jump, (2) toe-clipping is permanent allowing mark-recapture data to be collected over several years, (3) it is possible to obtain good estimates of both larval and adult survival under field conditions and thus examine the importance of different life history stages on population growth. In this study we provide quantitative links between variation in survival and recruitment and their relative effects on population growth and show that adult survival is closely associated with annual rainfall.

Materials and methods

Study site and species

We conducted field work in the Comoé National Park, in north-eastern Ivory Coast over 6 years from March 1997 until April 2002. Frogs were captured by hand along a 160-m drift fence that completely encircled a temporary pond (Lola Pond; 8°45'N, 3°49'W) of approximately 60 m² and a depth between 30–60 cm when completely filled (Kaminsky et al. 1999). Capture was aided by installing plastic bucket pitfall traps on both sides of the fence every 8 m (Kaminsky et al. 2004). The fence was checked several times daily: between 0600 and 0800 and 2200–2400 hours when it was dry and throughout the night from 1900 to 0600 hours when it rained.

The rainy season in the study area typically lasts from March till November. Annual precipitation, measured 2 km from the study site, averaged 980±177 mm/year during the 10-year period 1992–2001. Over the past five decades, there has been a decrease in annual rainfall in north-eastern Ivory Coast from 1,000 to 1,400 mm (1950–1970) to 800–1,000 mm (1970–2000) (J. Szarynski, personal communication).

Reproductive activity of the pig-nosed frog is highly synchronised with rains. Peak activity is at the beginning of the rainy season in March and April (Kaminsky et al. 1999, 2004). Females construct underground nests where they oviposit and attend eggs and tadpoles until subsequent rains completely fill the ephemeral ponds. Females release tadpoles from their nests during rains and leave the study pond. Early breeding, developmental plasticity as well as egg and tadpole attendance give tadpoles a head-start against competitors and predators that develop within the same water body (Rödel et al. 1995; Linsenmair 1997; Grafe et al., *in press*). Ovaries are easily viewed through the translucent skin allowing us to assess whether or not females had deposited eggs when attempting to leave the fenced area.

We determined how many females laid eggs during the first and second rain of the season (primary reproductive period) by counting the number of females leaving the fenced area with empty ovaries. We calculated the number of eggs laid by multiplying the number of females that deposited clutches by the average number of eggs/clutch (181±18, $n=5$, determined from nests constructed in large plastic tubs in the field). Our estimates of the number of females that laid eggs during the primary reproductive period are minimum estimates. They are confounded by an unknown number of females that were placed inside the fence but were not captured on their way out because they may have died after releasing their tadpoles or, more unlikely, circumvented the fence. Thus, more tadpoles were probably released into the pond than we estimated by capturing females with empty ovaries leaving the fenced area. In 1997, 26 out of 61 females (43%) were unaccounted for during the primary reproductive period.

To estimate survival rates of tadpoles during the primary reproductive period we calculated the proportion of tadpoles released that survived to metamorphosis. Knowing that tadpole development lasts approximately 3–4 weeks (Rödel et al. 1995) and since reproduction, induced by intermittent rains, took place in discrete bouts, we were able to accurately match egg cohorts to bursts of emerging metamorphic froglets. However, a close match was possible in only three out of 6 years (1997, 1999 and 2002) when rains were sufficiently widely spaced to separate cohorts. Estimates of tadpole survival are maximum estimates because the number of tadpoles released into the pond are minimum estimates.

Demographic analysis

The 6-year single-site capture-recapture dataset was used to estimate annual survival (ϕ) and recapture probabilities (p) of adult males and females. Sampling intensity varied somewhat between years (48 ±15 nights, range 29–69) with three to five sampling sessions each year (3.8±0.8 samples) depending on rains. Sampling took place in the months March–June. Reproductive activity is very low later in the rainy season. Variation in sampling effort was controlled for in estimates of demographic parameters. Frogs were captured at the drift fence, sexed, given unique toe clips if unmarked and immediately released on the other side of the fence. Frogs that entered and exited the breeding pond were monitored with equal intensity.

We used the standard Cormack–Jolly–Seber (CJS) open population model to estimate population parameters using methods described in (Lebreton et al. 1992). The fully time-dependent CJS model makes some fundamental assumptions (Pollack et al. 1990): (1) marks are not lost or overlooked, (2) samples are instantaneous compared to sample intervals with individuals released immediately after handling, (3) individuals of the i th sample have the same p , and (4) individuals of the i th sample have the same probability of surviving to $i+1$.

Toe-clipping in pig-nosed frogs is permanent since toes do not regenerate. In addition, mark identification was practised in pilot studies in 1995 and 1996 and cross checked by several observers throughout the study. This showed that mark overlook or misidentification was negligible suggesting that assumption 1 was not violated. Assumption 2 was also met for annual sampling periods since marking episodes lasted only several weeks each year and frogs were immediately released after marking.

We used the program U-Care to detect any departures of the data from assumptions 3 and 4 by calculating goodness-of-fit tests (GOF) that led to global model selection (Choquet et al. 2003). U-Care provides directional tests for transience and trap-dependence (trap-happiness or trap-shyness). We also examined the data for overdispersion in variance estimation and model selection by estimating the variance inflation factor \hat{c} that was obtained by dividing the GOF statistic (χ^2) of the highest dimension acceptable model by its df (Anderson and Burnham 1999a).

Having identified an acceptable general model (the standard CJS), we fitted progressively simpler models by minimising the small-sample version of Akaike's information criterion (AIC_c ; Anderson and Burnham 1999b) using the program MARK (version 3.0) (White and Burnham 1999). We modelled the effects of sex and annual rainfall on survival and sex and time on recapture probabilities. Annual rainfall was entered into models as an external covariate of survival by forcing the time-dependent survival rates to be estimated as linear functions of annual rainfall. Such a model is nested within the general CJS model in which survival varies with time. Transience and trap-dependence were not detected and thus not included in the models. Since there was no evidence for overdispersion ($\hat{c}=0.568$), i.e. fates of all individuals were independent, we did not adjust \hat{c} (Burnham and Anderson 1998).

Model selection was employed using the methodology outlined in (White and Burnham 1999; Cooch and White 2003) to identify the best model. Candidate models included the effects of time, sex and annual rainfall on survival and recapture. Because of model

uncertainty, parameter estimates and SEs were weighted by the AIC_c weights of the candidate models. This model selection criterion is gaining support in large areas of ecology and evolution (Johnson and Omland 2004).

We used the program Jolly (Pollock et al. 1990) to estimate population size (N) for each year of the study. Model A, the standard Jolly–Seber model with time-dependent capture and survival probabilities, was used after goodness-of-fit tests implemented in Jolly suggested a good fit ($\chi^2=5.7079$; $df=2$; $P=0.0576$). Rates of annual population change (λ) were estimated as N_{t+1}/N_t .

Recruitment rate ($1-\gamma$) was estimated by the method developed by Pradel (1996) using the program MARK (White and Burnham 1999). Capture histories were read backwards providing estimates of the probability that an individual caught at time $t+1$ was present in the population at time t . These probabilities are called seniority probabilities (γ) and represent the probability that a member of the population at $t+1$ is a survivor from the previous period. Thus, recruitment rates ($1-\gamma$) represent the fraction of new individuals in the population resulting from either in situ reproduction and/or immigration. Only the best model [$\gamma(t) p(t)$] was used to estimate γ (AIC_c weight=0.971), as it was overwhelmingly better supported than the next best model [$\gamma(g \times t) p(t)$, AIC_c weight=0.022; g stands for sex-specific variation and t for full time-specific variation].

Results

We captured and individually marked an average of 137 ± 64 pig-nosed frogs each year (range 79–255), a total of 821 over 6 years (497 males and 324 females). Within and between years, 322 frogs were recaptured at least once, a 39.2% recapture rate. A total of 74 adult frogs were recaptured between years throughout the study.

Tadpole survival showed large variation between years (Table 1). In 1999, a large proportion of the estimated number of eggs deposited in the pond during the first two rains of the season metamorphosed into froglets and left the fenced area of the pond. In contrast, the recruitment rate was much lower in 1997 and 2002. Tadpole survival was highest in the year with few tortoises and lowest when most tortoises entered the pond (Table 2).

Survival and capture probabilities

Goodness-of-fit tests indicated that there was no trap dependence between years [$N(0,1)$ statistic for trap-dependence = -1.171, $P=0.241$]. Likewise, tests of survival homogeneity or transience showed that newly marked and previously marked frogs were equally likely to survive [$N(0,1)$ statistic for transients = 0.457, $P=0.648$].

Our general model had separate survival parameters and capture probabilities for both sexes for each year [$\phi(g \times t)$, $p(g \times t)$] and fit the data (GOF: $\chi^2_{13}=7.385$; $P=0.881$). We

Table 2 Number of predatory tortoises encountered migrating into the pond

	1997	1999	2002
<i>Cyclanorbis senegalensis</i>	18	1	11
<i>Pelomedusa subrufa</i>	7	1	2
<i>Pelusios castaneus</i>	8	3	1
Tortoises total	33	5	14

used this model as a starting point to investigate the effects of sex and annual rainfall on survival and sex and time on recapture probabilities.

The most parsimonious model had rainfall and sex-specific survival and constant capture probabilities (model 1; Table 3) suggesting that both rainfall and sex explain a large part of the between-year variation in adult survival. Next best was a model with rain-specific survival and constant capture probabilities (model 2; Table 3). The five best supported models all had rain-specific survival probabilities. The most parsimonious model was 2.6 times and 3 times better supported than the second and third best model, respectively.

The rainfall and sex-specific survival estimates weighted by the AIC_c weights over all 12 models are shown in Fig. 1. Survival was higher in males than females in the first 4 years of the study. Survival estimates were lower for males for the last period (2001–2002) that was also the driest year of the study (Fig. 1). Average male survival was 0.261 ± 0.196 , whereas female survival averaged 0.216 ± 0.132 across all years. The model constraining survival by annual rainfall (model 2, $AIC_c=546.59$) was 14 times better supported than the time-specific model (model 6, $AIC_c=553.80$), suggesting that rainfall was highly significantly associated with survival.

We also modelled the effect of removing the interaction between rainfall and sex on survival. The model containing the interaction, $\phi(g \times \text{rain}) p(\cdot)$ (model 1, $AIC_c=546.59$) was 3 times better supported than the model $\phi(g + \text{rain}) p(\cdot)$ (model 3, $AIC_c=548.80$) suggesting that there was a significant interaction between rainfall and sex on survival. Table 4 shows the capture probabilities weighted by the 12 candidate models. Recapture probabilities varied according to sex and between years (range 0.35–0.50).

Table 1 Larval survival at the breeding pond in 3 years

Year	No. of clutches deposited ^a	No. of eggs deposited ^a	No. of froglets leaving pond	Survival to metamorphosis (%)
1997	35	6,335	67	1.06
1999	6	1,086	390	35.91
2002	14	2,534	69	2.72

^aNumber deposited in the first and second rain of the season

Table 3 The 12 candidate models of survival (ϕ) and recapture (p). AIC_c Estimated Akaike's information criterion (lower values indicate more parsimonious models), ΔAIC_c difference in AIC_c between the current model and the best model (model 1), t full time-specific variation, g sex-specific variation, $rain$ variation in annual rainfall, $.$ no time-specific variation

Model	AIC_c	ΔAIC_c	Weight	No. of estimated parameters	Deviance
1 $\phi(g \times rain) p(.)$	546.59	0	0.448	4	68.28
2 $\phi(rain) p(.)$	548.52	1.93	0.171	3	72.23
3 $\phi(g+rain) p(.)$	548.80	2.21	0.148	4	70.49
4 $\phi(rain) p(g+t)$	549.36	2.77	0.112	7	64.94
5 $\phi(rain) p(t)$	549.95	3.37	0.083	6	67.58
6 $\phi(t) p(.)$	553.80	7.21	0.012	6	71.42
7 $\phi(g) p(t)$	554.37	7.78	0.009	7	69.95
8 $\phi(.) p(t)$	554.80	8.22	0.007	6	72.43
9 $\phi(t) p(t)$	555.33	8.74	0.006	9	66.81
10 $\phi(g \times t) p(g \times t)$	556.16	9.57	0.004	15	55.18
11 $\phi(.) p(.)$	566.31	19.72	0.000	2	92.04
12 $\phi(g) p(.)$	566.71	20.12	0.000	3	90.42

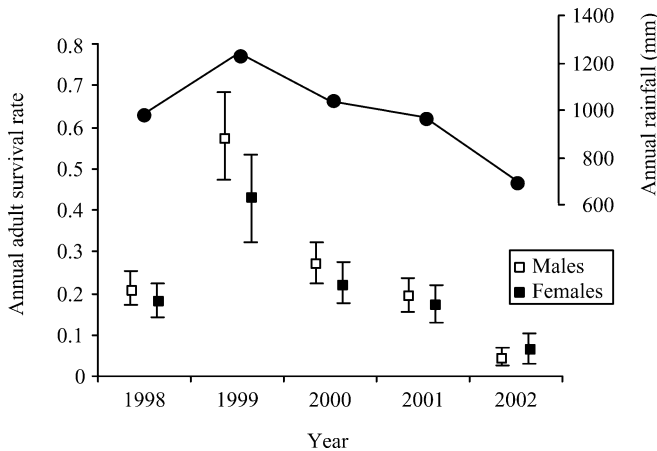


Fig. 1 Estimates of survival probabilities for males and females (squares) based on weighted averages of models in Table 1 and annual rainfall (circles) 2 km from the study pond in the preceding year. Error bars show SEs

Table 4 Estimated recapture probabilities (p) based on the weighted average of models in Table 1

Year	p_{males}	SE (p_{males})	p_{females}	SE (p_{females})
1997–1998	0.4152	0.0787	0.3970	0.0799
1998–1999	0.3626	0.0769	0.3504	0.0759
1999–2000	0.3619	0.0807	0.3524	0.0607
2000–2001	0.3865	0.0843	0.3670	0.0832
2001–2002	0.5031	0.0597	0.5021	0.0587

Population size, rates of change, and recruitment

The Jolly–Seber open-model estimates of population size showed considerable variation between years (Table 5). Robust estimates were possible only for the 2nd–5th year of the study. The time-specific rates of population increase λ ranged between 0.50–1.26, suggesting that the population showed substantial increases and a steep decline over the 6-year study period (Table 5). Years in which the population increased substantially (2000, 2001) were preceded by a year of very high in situ juvenile recruitment (1999).

Table 5 Estimates of population size (N), population growth rate (λ), and relative contributions to population growth of adult survival (γ) and recruitment ($1-\gamma$) for breeding adult pig-nosed frogs

Year	N (SE)	λ	γ (SE)	$1-\gamma$ (SE)
1998	736 (270)	–	–	–
1999	371 (171)	0.50	0.12 (0.04)	0.88 (0.04)
2000	438 (226)	1.18	0.33 (0.17)	0.67 (0.17)
2001	551 (525)	1.26	0.16 (0.07)	0.84 (0.07)
2002	–	–	0.14 (0.12)	0.86 (0.12)

The relative contributions of adult survival (γ) and recruitment ($1-\gamma$) to population growth also showed large variation between years (Table 5). Recruitment (both in situ and immigration) was more important than adult survival to population growth over all years of the study. The study population decreased by 50% between 1998 and 1999. A 113% increase in recruitment would have been necessary to stabilise λ at 0.997 in the time period 1998–1999. The decline in 1999 was more dramatic than the following increases in population size, suggesting that several years are needed to build up populations after single years of decline. In our case, it would take 3 years, under prevailing conditions, to build up population size to the level preceding the decline.

Discussion

We found considerable variation in estimates of λ that can be related to temporal variability in demographic variables. Recruitment had a stronger effect on population growth than adult survival. Recruitment into the population can occur from local recruitment of metamorphosed froglets from the study pond or from immigrants. Since we did not mark juvenile frogs we are unable to assess the relative importance of in situ recruitment versus immigration. However, it is interesting to note that population size increased in 2 years (2000 and 2001) after high local recruitment in 1999 when at least 390 juveniles entered the population in the first, and probably crucial weeks, of the breeding season. Recruitment later in the season is less likely because of higher larval mortality due to increases in

predator densities (Linsenmair 1997). Although we have no estimates of juvenile survival, it seems likely, given their large body size and life history, that a substantial proportion of individuals will survive to become adults. Size at metamorphosis has been shown to positively correlate with survival in amphibians (e.g. Altwegg and Reyher 2003).

We suggest that the population increase of reproductive individuals shown in 2000 and 2001 is due in large part to in situ juvenile recruitment in 1999. In many tropical and sub-tropical anurans, sexual maturity is often reached within a year especially in males (e.g. Kluge 1981; Lampert and Linsenmair 2002; Richter and Seigel 2002). Body size of pig-nosed frog males is on average only 71% that of females [$X \pm SD$; 31.7 ± 1.2 mm ($n=27$) and 44.6 ± 1.9 mm ($n=28$), respectively; T. U. Grafe, unpublished data]. Thus, males are likely to reach sexual maturity and enter the breeding population before females. The population increase may be due to adult males entering the breeding population in 2000, whereas females entered in 2001. Alternatively, the population increase in 2001 could also have been, in part, the result of juvenile recruitment in 2000 for which, however, we have no estimates.

Estimates of juvenile survival in other frogs and toads range between 0.26 and 0.36 (Biek et al. 2002). A juvenile survival rate of 0.46 would be necessary to fully explain population increases of pig-nosed frogs in 2000 and 2001 in the absence of immigration assuming that only 390 juveniles entered the population in 1999, and assuming zero recruitment in 2000. Immigration seems less likely than in situ recruitment to affect population size substantially because other large breeding sites were several kilometres away and the direction of those sites from the study pond cannot be predicted by frogs. Adult females that were followed telemetrically are not known to travel over such large distances at least during the breeding season (Kaminsky et al. 2004).

Local recruitment rates of juveniles is likely to be a function of predator densities in the pond that can cause high tadpole mortality (e.g. Semlitsch 1993; Murphy 2003). We found high recruitment in 1999 when very few predatory tortoises entered the study site whereas in situ recruitment was very low and probably often absent in years of high tortoise densities suggesting that tortoise predation has a considerable impact on recruitment and population growth of pig-nosed frogs. The severe impact of tortoise predation on larval pig-nosed frogs has been shown experimentally by Rödel (1999) and can cause significant mortality in other tadpoles as well (e.g. Gomez-Mestre and Keller 2003). Tortoises are not gape-limited when feeding on tadpoles and can consume up to 31% of their own body mass within one bout of feeding (Rödel 1999). Survival of pig-nosed frog tadpoles is also likely to be affected by pond drying and other predators (invertebrates, carnivorous tadpoles and fish). However, tadpoles are less vulnerable to these risks because they receive a head start when compared to other tadpoles found syntopically in the same pond. They are relatively large on hatching (11.5–25 mm snout-vent length) and are often

the first tadpoles found in savannah ponds (Rödel et al. 1995). Tadpoles develop well in advance of invertebrates and carnivorous *Hoplobatrachus* tadpoles and early cohorts also metamorphose before migratory fish reach savannah ponds early in the rainy season.

Large variation in juvenile recruitment has also been found in other pond-breeding anurans and salamanders (Caldwell 1987; Pechmann et al. 1991) depending on egg and tadpole survival (e.g. Blaustein et al. 1998; Kiesecker and Blaustein 1998). Tadpole survival is thought to be the most critical vital rate determining population dynamics in amphibians (Semlitsch 2002). However, recent studies that have also looked at juvenile and adult survival and thus postmetamorphic vital rates, have found that these can be important factors as well. Biek et al. (2002), for example, show that population growth in pond-breeding frogs and toads is most sensitive to juvenile and adult survival suggesting that research and management efforts should be directed to prevent reduction of these vital rates. Likewise, Conroy and Brook (2003) found that the population dynamics are most sensitive to juvenile survival in two species of myobatrachid frogs. Since we did not mark metamorphs, our study cannot evaluate the importance of juvenile survival. However, given the relatively large size of metamorphs, juvenile survival is likely to be relatively high and less variable than in those species with relatively small metamorphs. We therefore suggest that in pig-nosed frogs, tadpole survival is likely to be more important than juvenile recruitment in determining population dynamics.

Using a contiguous drift-fence we were not only able to measure juvenile recruitment but also to estimate survival to metamorphosis. This was possible by estimating the number of eggs or tadpoles released in the pond and counting the number of emerging postmetamorphic juvenile froglets. Our results show that there is high variation in survival to metamorphosis with estimates ranging between 1–36%. Furthermore, the number of juvenile recruits was similarly low in 1997 and 2002 although the percent that survived to metamorphosis was 2.5 times higher in 2002 than in 1997, because different amounts of eggs were deposited. In other pond-breeding anurans, estimates of survival to metamorphosis range between 0–5.4% in *Rana sevosia* (Richter et al. 2003) and 0–15.5% in *R. temporaria* (Ryszkowski and Truszkowski 1975; Riis 1991). Our estimate of 36% in 1997 shows the enormous growth potential of pig-nosed frog populations under field conditions. Larval survival is likely to be facilitated strongly by maternal care, i.e. low to absent egg mortality and release of competitively superior tadpoles early in the season from underground nests.

Estimates of the relative contribution of adult survival to population growth varied between years and ranged from 0.12 to 0.33 suggesting that adult survival contributed substantially less to population growth than recruitment throughout the study. Adult survival showed a close association with annual rainfall. During the dry year of 2001–2002, adult survival was only 5 and 24% of that in the wet year of 1998–1999 in males and females, respectively. There was a significant interaction between

rainfall and sex with dry weather having a much stronger negative effect on males than females. This is probably related to males being much smaller than females. Males may be more susceptible to physiological stress, i.e. evaporative water loss and/or more stressed energetically due to smaller stores of body fat than females and thus less likely to survive in dry years when soils dry out faster and when termites and ants, their food source, may be low in abundance (Eggleton et al. 1996).

Adult survival rates have been estimated in only a few amphibian species using rigorous capture-recapture methodology (e.g. Nichols et al. 1987; Wood et al. 1998; Richter and Seigel 2002; Schmidt et al. 2002; Anholt et al. 2003). Estimates of annual survival of common toads, for example, ranged between 21.4 and 48.7% in a 3-year study (Kuhn 1994; Schmidt et al. 2002). Annual survival varied much more in water frogs depending on winter severity (6–98%; Anholt et al. 2003).

It should be noted, however, that estimates of annual survival are confounded by emigration because mark-recapture analysis treats permanent emigration from the population as death. Thus, survival rates are generally higher than reported. We suggest that permanent adult emigration from our study pond was probably not very large because other suitable breeding sites were several kilometres away, but this needs to be addressed in future studies.

Our study has shown that recruitment is more important than adult survival in determining population growth using a reverse-time capture-recapture model. This approach is similar to elasticity analyses; however, it is retrospective instead of prospective (Nichols et al. 2000; Cooch and White 2003). It should be noted that, in contrast to elasticity analyses, the relative contributions of survival and recruitment are time-specific (Table 5) and can vary considerably such that a population cannot be easily characterised by single values (Nichols et al. 2000). Furthermore, the approach used here is thought to be more useful for parameter estimation for populations in highly variable environments as in our case, because elasticity analyses are sensitive to transient dynamics (Nichols et al. 2000).

What are the implications of this study for conservation and research programs on amphibian declines? Although the pig-nosed frog is currently not known to be threatened in any part of its extensive range, the results of this study can serve as baseline data to evaluate the relative importance of different vital rates to population viability in savannah habitats with strong seasonal variation. Biek et al. (2002) recommended that long-term demographic information should be collected for individual anuran species in a diversity of geographical regions and habitats that can serve as models for other species with similar life histories and population dynamics. Such data are useful not only in reversing population declines but also in efforts to proactively prevent declines from occurring in the first place. The pig-nosed frog is likely to be a model anuran since it shares many life history traits with other pond-breeding savannah denizens: highly variable juvenile

recruitment, influence of density-independent factors (predators and weather) on population growth, short generation time, and low adult survival that depends on highly variable weather conditions. The most notable exception to other afro-tropical anurans is that female pig-nosed frogs provide parental care suggesting that egg and possibly tadpole survival will be higher than in other syntopic pond-breeding anurans. In addition, the specialised mode of subterranean feeding on ants and termites may make them less susceptible to extrinsic factors.

Our study suggests that pig-nosed frog populations experience boom and bust years with declines more dramatic than increases. In our study population, it would take 3 years to offset the decline that occurred in 1999. This highlights the danger of reproductive failure over several consecutive years (Richter and Seigel 2002). The pattern of population dynamics further underscores the need for long-term studies to assess population dynamics because short-term studies may miss single years of decline (Meyer et al. 1998). The close association between adult survival and annual rainfall is cause for concern because long-term trends suggest that the climate changes which have taken place in West Africa within the last few decades have led to reduced rainfall (J. Szarzynski, personal communication). If this trend is to continue it is likely that this will significantly impact anuran populations throughout the region.

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