SURVIVAL OF ADULT SMOOTH FROGLETS (*GEOCRINIA LAEVIS* COMPLEX, ANURA, MYOBATRACHIDAE) IN AND AROUND A HYBRID ZONE

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Abstract.—I obtained skeletochronological data from phalanges of adult frogs of the *Geocrinia laevis* species complex collected at breeding aggregations in and around a hybrid zone in southwestern Victoria, Australia. I estimated rates of survival among adults by fitting the geometric probability distribution to these data using maximum likelihood methods. Information-theoretic comparison of alternative models for survival rates revealed a strong effect of sex on survival rates, but little evidence of differences between populations, or between hybrid and parental populations. I found adult males to have a mean annual rate of survival of 0.29, compared with a rate of 0.41 for adult females. The absence of a gross deficit in rates of survival within hybrid populations suggests that differences between hybrid and parental populations in this component of individual fitness are relatively unimportant in determining the structure and dynamics of the hybrid zone.

Key Words.—age structure; catch curve; *Geocrinia laevis* complex; hybrid zone; mortality; skeletochronology; survival

INTRODUCTION

In seeking to gain a thorough understanding of the dynamics of hybrid zones, consideration of many components of the fitness of parental and hybrid individuals is desirable (Arnold and Hodges 1995). Inter-specific variation in life-history traits is an important determinant of hybrid zone dynamics (Arntzen and Hedlund 1990; Scribner 1993). The life-history traits of individuals determine fitness; however, few studies have provided detailed descriptions of inter-populational variation in these traits in the context of inter-specific hybridization. Those studies of reptile and amphibian populations that have addressed variation in life-history traits of hybridizing populations have generally considered life-history components related to reproductive output, including clutch size, offspring size, and the viability of offspring (Arntzen and Hedlund 1990; Scribner 1993; Reed and Sites 1995; Kruuk et al. 1999). In contrast, relatively few studies have compared demographic parameters such as rates of survival, ages at maturity, and age-specific schedules of fecundity in hybrid and parental populations (e.g., Francillon-Vieillot et al. 1990; Holenweg Peter 2001).

Theoretical (Stearns 1992) and empirical (Sinervo and DeNardo 1996) evidence suggest the presence of trade-offs between life-history traits such as offspring size and number, and allocation of resources to growth, survival, and reproduction. Given the existence of such trade-offs, it is likely that consideration of one or a few traits in isolation will not allow complete assessment of the overall fitness consequences of particular life-history strategies. Hence, those studies that attempt to analyze

the dynamics of evolutionary scenarios where life-history traits are of potential significance should, as far as is possible, fully describe the life-history parameters of the taxa under consideration.

In southeastern Australia, several sibling taxa of anurans are known to form narrow, persistent hybrid zones where their geographic ranges abut (Littlejohn 1976; Woodruff 1979; Littlejohn and Watson 1985; Watson et al. 1985; Roberts 1993), including the myobatrachid smooth froglets *Geocrinia laevis* and *G. victoriana* (Littlejohn et al. 1971). These two species are very similar morphologically, and in most aspects of their biology. Both are autumn breeders, and exhibit terrestrial oviposition, followed by aquatic development of larvae (Littlejohn and Martin 1964). They differ chiefly in their advertisement calls, which are strikingly divergent for two such closely related species (Littlejohn et al. 1971; Littlejohn and Watson 1973). Differences in the territorial behavior and associated vocalizations of males have also been documented (Harrison and Littlejohn 1985; Littlejohn and Harrison 1985; Scroggie and Littlejohn 2005). The geographic ranges of the two species are parapatric, and abut in two distinct areas of western Victoria, where they form narrow hybrid zones (Littlejohn et al. 1971). Hybrids between the two species are highly viable, with no evidence of genetic incompatibility in either artificially produced F1 hybrids or natural hybrids (Littlejohn et al. 1971; Watson 1974). Natural hybrids exhibit a wide variety of calling behavior, with a range of intermediate and mosaic patterns of advertisement call structure having been reported (Littlejohn et al. 1971; Littlejohn and Watson 1973, 1976; Scroggie and Littlejohn 2005).

Mating and egg laying in the vicinity of the southwestern Victorian hybrid zone occurs from late March to early May (Littlejohn and Martin 1964; Littlejohn et al. 1971). There is evidence of differentiation in sizes of eggs of the two species in the vicinity of the hybrid zone with *G. victoriana* producing eggs that are larger than of *G. laevis* (Gollmann and Gollmann 1994b; Scroggie 2001). Eggs are laid in terrestrial situations, where the embryos develop within their capsules to development stage 26 of Gosner (1960) prior to hatching, which occurs in response to flooding of the nest site by rain, typically during June. Following an aquatic larval period of five to six months, metamorphosis occurs in late October and early November (Littlejohn and Martin 1964; Michael Scroggie, unpubl. data). Limited information currently exists regarding longevity or age at maturity of either species in the wild. Murray Littlejohn and Graeme Watson (unpubl. data) liberated larvae of *G. victoriana* into a site within the range of *G. laevis* during 1973 and then revisited the site during the breeding seasons of the two following years. During April 1975, two mature males of *G. victoriana* were heard calling at the site, when they would have been approximately 18 months post-metamorphosis, or two years post-zygote. These observations suggest that under natural conditions, males of the *G. laevis* complex may be expected to mature at a minimum age of not more than 18 months post-metamorphosis. These data are reinforced by observations on ages at maturity among captive specimens of *G. laevis.* Males and females of *G. laevis* reared from egg-masses collected in southeastern South Australia have successively reproduced at 18 months post-metamorphosis, and have survived in captivity to ages of more than eight years post-metamorphosis (Gerry Marantelli, pers. comm.).

Data concerning the rates of survival of larvae or adults of the *G. laevis* complex under natural conditions are entirely lacking. This represents a significant gap in our understanding of the demography of these taxa. Obtaining quantitative survival rate data for small, cryptic reptiles and amphibians is extremely difficult using most available methods for inferring rates of survival, such as mark-recapture analysis. Analysis of skeletochronological data, based on the predictable, annual formation of ring-like growth marks in the bones, provides a useful and convenient alternative means of obtaining demographic information from wild populations of reptiles and amphibians (Castanet and Smirina 1990; Tinsely and Tocque 1995; Reaser 2000; Matthews and Miaud 2007; Gillespie 2010).

In a population of animals where age-specific vital rates (mortality and fecundity) are constant, and where beyond a certain age, all age classes experience equal rates of survival, the expected population age-structure for the age classes subject to constant rates of survival is a decreasing geometric series (Seber 1982). Statistical analysis of age-structure samples from such a population allows inference regarding the survival rate, a method that is widely used by fisheries scientists, who use the term "catch-curve analysis" to describe this methodology (Chapman and Robson 1960; Seber 1982; Jensen 1985). Catch-curve methods are equally applicable to age-structure data collected from populations of other organisms (Skalski et al. 2006; McGowan et al. 2009), and have occasionally been applied to reptile and amphibian populations (Miaud et al. 1999, 2000; Lee et al. 2010). In this paper, I apply skeletochronological methods to determine the age structure of four populations of the *G. laevis* complex within, and adjacent to, the southwestern Victorian hybrid zone. The resulting age-composition data are then used to test hypotheses concerning the effects of sex, species, and hybrid status on rates of survival among adults from these populations.

MATERIALS AND METHODS

Age determination.—Both published accounts (Littlejohn and Martin 1964; Littlejohn et al. 1971; Littlejohn and Watson 1973; Littlejohn and Watson 1976) and observations during the course of this study have shown that in the vicinity of the southwestern Victorian hybrid zone, frogs of the *G. laevis* complex breed only during the southern autumn (March to May), with most breeding occurring during late April and early May. I sampled adult males and adult females from breeding aggregations at four study sites during the 1994, 1995, 1996, 1997, and 1998 breeding seasons. The study sites were: Garvoc (*G. laevis*), Barwon Downs (*G. victoriana*), Jancourt (intermediate hybrids), and Rankin Road (*G. laevis*-like hybrids; Table 1). I collected frogs using a combination of pitfall trapping (using 5 L metal pails with insect-mesh drift fences embedded in the ground), acoustic triangulation of calling males, and by active searching of chorus sites and surrounding areas at night.

At the Garvoc and Jancourt study sites, I sampled breeding males during all five years of the study. Sampling at the Rankin Road study site (a cleared firebreak separating farmland from adjacent forest) commenced in 1994. After the 1996 breeding season, the firebreak was bulldozed to eliminate regenerating shrubs and trees. Unfortunately, this action also eliminated most of the population of hybrid *Geocrinia* at the site. As a consequence, I abandoned further studies of the Rankin Road population, meaning sampling at this site was limited to only two breeding seasons. At the Barwon Downs site, I commenced sampling of frogs for

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TABLE 1. Locations of the four study sites to determine the age structure of the *Geocrinia laevis* complex in southwestern Victoria, Australia.

Site name	Taxon	Latitude	Longitude	Elevation (m)	Description
Garvoc	*Geocrinia laevis*	38° 20' S	142° 49' E	100	Roadside depression on the eastern side of the Garvoc-Laang Road, Garvoc.
Barwon Downs	*G. victoriana*	38° 29' S	143° 44' E	160	Forest track, immediately south of Seven Bridges Road, Barwon Downs.
Jancourt	hybrid	38° 23' S	143° 06' E	60	Series of depressions on the eastern side of Port Campbell Road, Jancourt.
Rankin Road	hybrid	38° 26' S	143° 25' E	200	Roadside drains and depressions near the intersection of Rankin Road and East-West Firebreak Road, Irrewillipe.

skeletochronology in 1995, and obtained samples of males in every season from that year until 1998. Females of *G. victoriana* proved difficult to locate at Barwon Downs, and I only obtained samples during the1998 breeding season.

Upon capture, I uniquely marked most individuals by toe-clipping (Hero 1989) and released them at their points of capture immediately after processing. Clipped toes were preserved and stored in 90% ethanol in individually labeled vials. I sacrificed subsamples of gravid females from each site, and preserved them in Tyler's fixative (Tyler 1962) for analysis of relationships between body-size, maternal age, and clutch attributes (Scroggie 2001).

I determined the age of each adult frog using the skeletochronological method (Castanet et al. 1993). I decalcified whole toes for 4–6 h in RDO® rapid decalcifying solution (Phoenix Scientific, Melbourne, Victoria, Australia), and then rinsed them for 2 h in running tap-water. The toes were dehydrated in a series of aqueous ethanol solutions of increasing concentration, and finally in two changes of histological solvent (Histolene, Phoenix Scientific, Melbourne, Victoria, Australia). I then vertically embedded the whole toes in blocks of Paraplast® embedding medium (Oxford Labware, St Louis, Missouri, USA) with the aid of a programmable, automated tissue processor. I cut serial, transverse sections from the diaphyseal region of the most proximal available phalanx of each toe at a thickness of 5 μm on a rotary microtome. I floated the sections onto gelatin-coated glass microscope slides in a heated water bath at approximately 55 °C. I then dried the slides overnight in an oven at 60 °C. I deparaffinized the slides in two changes of Histolene, rehydrated them in an aqueous ethanol series of decreasing concentrations, and finally rinsed them in two changes of deionized water. I stained batches of slides with Ehrlich's haematoxylin (Humason 1979) for 30 min. After rinsing in running tap-water for 5 min to remove excess stain, I dehydrated the slides in an aqueous ethanol series and two changes of Histolene and permanently mounted them in DPX mounting medium (BDH Laboratory Supplies, Poole, England) with glass coverslips.

I examined stained sections from the diaphyseal region of the most proximal available phalanx of each toe under a binocular, compound microscope at a magnification of 400x. I counted lines of arrested growth (LAG). I examined each set of sections on two occasions without reference to information concerning the animals from which they came, or in the case of the second examination, to the results of the first examination. I compared the resulting counts for consistency, and where they differed, I made a third examination in an attempt to resolve the inconsistency. In ambiguous cases, or where inconsistencies could not be satisfactorily resolved, I excluded their age data from subsequent analysis.

Validation of age estimates.—Skeletochronological age determination rests critically on the assumption that LAG are laid down in the bones in a reliable, annual pattern, and that LAG are not lost from the bones over time. To have confidence in the reliability of skeletochronological estimates of individual age, there is a need to test and validate these assumptions (Eden et al. 2007; Wagner et al. 2011). Validations of the annual periodicity of LAG formation in reptiles and amphibians are uncommon (Tucker 1997; Driscoll 1999; Coles et al. 2001; Matsuki and Matsui 2009). I attempted to validate the annual periodicity of LAG formation of frogs from my study populations by comparing LAG counts of successive bone samples taken from the same individuals, recaptured one or two years after initial sampling. If formation of LAG is an annual occurrence, then it would be expected that the number of LAG added by an individual between successive samplings would be equal to the number of years elapsed between the times the two bone samples were taken.

Estimation of survival rates.—Under the assumption of constant population vital rates and a single constant survival rate among adults, the ages of individual adults randomly sampled from a population will conform to a geometric probability distribution (Chapman and Robson

1960; Seber 1982). In this context, the geometric probability distribution has the density function:

$$\Pr(y) = (1-S)S^y$$

where S is the rate of survival, and y is age in years, such that the youngest age class subject to constant survivorship is coded as zero.

The likelihood of observing a particular set of ages in a sample of k individuals, drawn from a population subject to constant recruitment, and with a constant yearly probability of survival S is thus:

$$L = \prod_{i=1}^{i=k} (1-S)S^{y_i}$$

This simple statistical model can be readily extended to situations where heterogeneity in survival rates is expected among different subsets of the total sample, due to factors associated with the individual animals in the sample, such as sex, species, or other site or individual-specific covariates by relating survival rates in each subset to one or more covariates. This is accomplished by specifying a linear model, with a logistic link function, to describe the relationship between the covariates and the expected survival rates of each individual in the sample:

$$\log\left(\frac{S_i}{1-S_i}\right) = \mathbf{X_i}\beta$$

where S_i is the expected survival rate of the ith individual with the associated vector of covariate values $\mathbf{X}_i$, and β is a vector of regression parameters. Given a sample of age data for k individuals, and their covariate values, the values of the regression parameters (β) can be estimated by finding the values that maximize the likelihood expression:

$$L = \prod_{i=1}^{i=k} (1-S_i)S_i^{y_i}$$

Approximate standard errors for the regression coefficients can be found by taking the inverse of the matrix of partial derivatives of the likelihood with respect to the parameters, and taking square roots of the diagonal elements (Bolker 2008).

A priori, I considered it likely that rates of survival of adult smooth froglets might differ between the sexes, between populations, or on the basis of hybrid status (i.e., frogs from hybrid populations might have different rates of survival to those from either pure population). Accordingly, I devised a set of eight candidate statistical models allowing for the influence of each of these variables on survival, either separately, as additive combinations, or as interactive combinations. The set of candidate models also included a null model where the rate of survival was equal in all subgroups.

I assessed the parsimony of these alternative candidate models using information-theoretic methods (Burnham and Anderson 2002), based on Akaike's Information Criterion (AIC). The correction for small sample sizes (denoted AIC_c) proposed by Hurvich and Tsai (1989) and recommended by Burnham and Anderson (2002) was included in the calculations. I evaluated the relative support for alternative models using normalized Akaike weights (w), an elaboration of the AIC_c statistic that provides a measure of the relative support for each of a set of candidate statistical models fitted to the same set of data (Burnham and Anderson 2002).

Model-averaging, on the basis of the normalize Akaike weights of the eight candidate models, was undertaken to create predictions of the rates of survival of male and female frogs in each of the four study populations. This procedure allows prediction of the likely rates of survival that accounts for the predictions of all of the candidate models, with the influence of each model on the predictions determined by the strength of support for the model in the data (Burnham and Anderson 2002). I calculated approximate 95% confidence intervals of the model-averaged predictions by taking a weighted average (with the normalized Akaike weights providing the basis for the weighting) of the confidence limits of the predictions from each of the candidate models.

RESULTS

An inner layer of endosteal bone surrounding the medullary cavity was present in sections from the diaphyseal region of proximal phalanges. In most individuals, the inner portion of the periosteal bone and the outer portion of the endosteal bone were resorbed to some extent. This resorption often left a gap between the endosteal and periosteal layers of bone. Clearly defined LAG were present in the outer part of the periosteal bone, with a maximum of four LAG observed. Resorption of the periosteal bone was never extensive enough to lead to the loss of these outer LAG.

I sectioned toes from 484 adult frogs. Of these, 10 samples produced sections that were either inconsistent, of poor quality, or could not be interpreted. I successfully obtained counts of LAG from the remaining 474 toes (97.9%) and most counts for males (n = 297) and females (n = 177) were generally either one or two (Table 2). Examination of five pairs of successive samples of bone taken from the same individuals at intervals of either one (two individuals) or two (three individuals) years showed that lines of arrested growth are consistently added to phalanges at the rate of one LAG per year. With the exception of the sample of females of *G. victoriana* from the Barwon Downs site, I obtained age-structure samples in more than one year and then pooled the samples. Pooling of samples from

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TABLE 2. Observed frequencies of counts of lines of arrested growth (LAG) among males and females captured at breeding aggregations of four populations of the *Geocrinia laevis* complex. For catch-curve analyses, the LAG-count classes are recoded such that the first adult age class = 0. The true age of individuals of with one LAG was 1.5 years post-metamorphosis, or 2 years post-zygote.

Site name	Taxon	Sex	n	LAG count			
				1	2	3	4
Garvoc	*G. laevis*	Male	95	61	24	10	-
Garvoc	*G. laevis*	Female	83	45	25	10	3
Barwon Downs	*G. victoriana*	Male	54	40	13	-	1
Barwon Downs	*G. victoriana*	Female	17	8	3	5	1
Jancourt	hybrid	Male	120	85	27	4	4
Jancourt	hybrid	Female	39	21	13	3	2
Rankin Road	hybrid	Male	28	17	9	1	1
Rankin Road	hybrid	Female	38	15	20	2	1
Total			474	292	134	35	13

information-theoretic comparison of several years would tend to reduce the effects of inter- annual variation in rates of survival and recruitment on the calculated survival rates.alternative candidate models for survival rates, conditional upon various combinations of population identity, hybridity, sex and their interactions (Table 3) revealed very strong support for only one of the eight candidate models: themodel in which survival rates were dependent solely upon sex. On the basis of the normalized Akaike weights, the model conditional only on sex was 2.7 times better supported than the next most parsimonious model (sex + hybridity). All other candidate models had model selection weights < 0.1, indicating only very limited support in the data. Model-averaged inferences of survival rates for male and female frogs at each of the four study sites showed that across all sites, survival probabilities of male frogs were approximately 0.29, while survival probabilities for females were approximately 0.41 (Fig. 1). The model-averaged inferences show no meaningful difference between populations in probabilities of survival, consistent with the very weak support for models allowing for effects of population or hybridity on survival rates (Table 3).

DISCUSSION

Analysis of age-frequency data obtained by skeletochronology indicated similar rates of survival among adults from the study populations of *G. laevis* and *G. victoriana,* and from the two hybrid populations. Models of survival rate allowing for inter-populational differences in survival were poorly supported. The lack of observed differences between populations leads to the conclusion that inter-populational differences in adult rates of survival must be very small, and can have little direct impact on the dynamics of the southwestern Victorian hybrid zone.

This result accords with previous studies of the southwestern Victorian *Geocrinia* hybrid zone, which have noted no apparent evidence of increased levels of developmental abnormality or reduced rates of survival among hybrids in naturally occurring and artificially produced embryos and larvae of the *G. laevis* complex (Littlejohn et al. 1971; Watson 1974). Nevertheless, caution is needed when interpreting these results, even when no fitness deficit has been detected among hybrid individuals relative to parentals. It could be argued that not all components of the fitness of the various genotypes within the hybrid zone have been adequately assessed. In this and previous studies of the same hybrid zone, components of the fitness of hybrids have been measured on the basis of composite samples of individuals comprising a wide variety of genotypes, broadly defined as "hybrids." Previous genetic analyses have shown that populations within the southwestern Victorian hybrid zone contain few, if any individuals of either parental species (Gollmann 1991; Gartside et al. 1979). Rather, the populations consist of complex, multigenerational recombinations of genotypes derived from both parental species. Different genotypic classes of hybrid individuals within naturally-occurring hybrid zones can differ significantly in components of their fitness (Reed and Sites 1995). Hence, a simple comparison of components of fitness between a combined sample of various hybrid genotypes and samples of parental individuals may result in an overly simplistic and rather insensitive test of the relative fitness of hybrid and parental individuals in and around hybrid zones. Such criticisms can be directed at most studies that have claimed a lack of evidence for selection against hybrids; the possibility of selection against hybrids being very difficult to rule out completely in any particular case (Arnold and Hodges 1995).

Previous studies of offspring size (Gollmann and Gollmann 1994b, Scroggie 2001), rates of larval and

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TABLE 3. Information-theoretic comparison of fitted models for rates of survival ($\hat{S}$) conditional upon combinations of sex, population (pop), hybridity (hyb), and their interactions. AIC_c – Akaike's information criterion corrected for small samples, ΔAIC_c – difference between the AIC_c value of each model and the model with the smallest AIC_c value, w – normalized Akaike weights of the candidate models. Normalized Akaike weights for the set of candidate models sum to unity, and can be interpreted as a measure of the proportional support for each of the set of candidate models (Burnham and Anderson, 2002). Statistics for the most parsimonious model ($\hat{S} \sim sex$) are in boldface for emphasis.

Model	Log-likelihood	Number of parameters	AIC_c	ΔAIC_c	w
$\hat{S} \sim sex$	**453.67**	**2**	**911.36**	**0**	**0.629**
$\hat{S} \sim hyb + sex$	453.67	3	913.38	2.03	0.229
$\hat{S} \sim hyb + sex + sexhyb$	453.65	4	915.38	4.02	0.084
$\hat{S} \sim sex + pop$	453.38	5	916.89	5.54	0.039
$\hat{S} \sim constant$	459.10	1	920.21	8.86	0.008
$\hat{S} \sim sex + pop + sex.pop$	452.04	8	920.40	9.04	0.007
$\hat{S} \sim hyb$	459.07	2	922.17	10.81	0.003
$\hat{S} \sim pop$	457.91	4	923.91	12.55	0.001

embryonic development, and sizes at metamorphosis (Gollmann and Gollmann 1994a) have provided some evidence of differentiation between *G. laevis* and *G. victoriana* in these aspects of life history. These studies found clinal variation in offspring (egg) and metamorph sizes across the hybrid zone, with larger egg-sizes but smaller metamorphs observed in populations of *G. victoriana* (Gollmann and Gollmann 1994b, Scroggie 2001). In contrast, rates of growth of larvae in the laboratory were highest among hybrids (Gollmann and Gollmann 1994a). This differentiation in offspring size does not seem, on the basis of the results presented here, to be associated by any concomitant differences in rates of adult survival, underlying the importance of assessing multiple traits when assessing differences between the life histories of interacting hybrid and parental populations.

Few researchers have compared rates of survival among hybrid and parental populations of reptiles or amphibians. For example, Holenweg Peter (2001) used mark-recapture methods to estimate annual rates of survival among adults of the water frog *Rana lessonae* and its hybridogenetic sexual parasite, *R. esculenta*, in a region of broad sympatry in Switzerland. She found that adults of *R. lessonae* had consistently higher rates of survival compared to adults of *R. esculenta*. This finding stood in contrast to previous studies of the hybridogenic water frog complex, which had demonstrated higher rates of tadpole survivorship (Semlitsch 1993) and fecundity (Berger and Uzzell 1980) among *R. esculenta*. Francillon-Vieillot et al. (1990) used skeletochronology to determine age-frequency distributions, growth trajectories, and longevities of the newts *Triturus cristatus, T.*

marmoratus, and their hybrids in a sympatric population in western France. The two species of newts and their hybrids exhibited similar growth trajectories, and their age-frequency distributions were similar. It was concluded that inter-specific differences in age at maturity, growth, and longevity of the two taxa would be unlikely to influence the outcome of their interactions in parapatry. The above studies illustrate the range of patterns in survival of hybrid animals in nature, ranging from clear evidence of hybrid inferiority, through to equivalent or greater survival among hybrids, compared to individuals of either parental taxon.

The catch-curve analyses presented here rely on the assumption that the schedules of age-specific survival and recruitment of the sampled populations are constant. This assumption will certainly be violated to some extent. While the data collected during this study did not provide any insight into the extent of temporal variation in vital rates for the sampled populations, Driscoll (1999) and Conroy and Brook (2003) have reported significant levels of temporal variation in rates of mortality among adults of the related Western Australian species *G. alba* and *G. vitellina,* based on analyses of skeletochronological data and mark-recapture analysis respectively. Accordingly, it seems reasonable to conclude that rates of age-specific survival and recruitment for the populations sampled during the present study will be subject to some appreciable level of temporal variation, potentially violating the assumption of constant survival and recruitment inherent in the catch-curve analyses. In populations where survival and recruitment rates are subject to temporal variation, simulation studies have shown that catch-curve
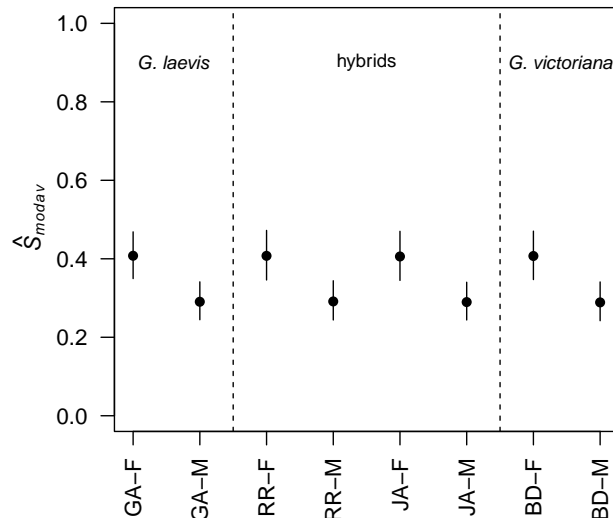
FIGURE 1. Model-averaged estimates of annual survival rates ($\hat{S}_{modav}$) for female (F) and male (M) smooth froglets, at the four study sites: GA = Garvoc (*G. laevis*), RR = Rankin Road (*G. laevis*-like hybrids), JA = Jancourt (intermediate hybrids) and BD = Barwon Downs (*G. victoriana*). Error bars delimit the 95% confidence limits of the model-averaged estimates.

of calling males, and pitfall trapping); however, the existence of some degree of age-related sampling biases, and subsequent bias in estimation of rates of survival cannot be ruled out entirely.

A wealth of data has been collected concerning age composition of reptile and amphibian populations, largely derived using skeletochronology (e.g., Castanet and Smirina 1990; Bastien and Leclair 1992; Castanet et al. 1993; Driscoll 1999; Gillespie 2010). However, catch-curve methods, as employed in this study, have rarely been applied to reptile or amphibian populations (but see Gibbons and McCarthy 1984; Schabetsberger and Goldschmid 1994; Miaud et al. 1999, 2000; Lee et al. 2010). Catch-curve analysis of skeletochronological data has considerable potential for inferring survival rates among populations of reptiles and amphibians in a variety of contexts, particularly in cases where other methods such as mark-recapture analysis are infeasible. Coupled with information-theoretic assessment of support for alternative hypotheses concerning differences in survival amongst population groups, catch-curve analysis is a powerful and underused tool for amphibian and reptile population ecologists.

estimates of survival rates may be both positively biased and over-precise (Allen 1997; Murphy 1997; Dunn et al. 2002). Therefore, depending on the extent of temporal variation in survival and recruitment in the sampled populations, the catch-curve analyses reported here may have somewhat overestimated the true survival rates, and underestimated the uncertainty (expressed as a 95% confidence interval, Fig. 1) with which the survival rates were estimated.

The catch-curve methods used in this study assume that individuals of all age-classes under consideration are equally likely to be sampled. If younger age-classes are under-represented in the sample, then survival rate will be over-estimated (Chapman and Robson 1960; Skalski et al. 2006). The estimates of survival rates for the *G. laevis* complex reported here were derived from samples of reproductively mature adults, collected in and around known breeding aggregations. It is possible that this approach to sampling may have led to some degree of under-sampling of particular age classes, resulting in biases in the estimates of survival probability. For example, if not all individuals of the youngest adult age class are reproductively mature, and therefore a proportion of them do not move into the areas from which frogs were sampled (i.e., breeding aggregations), then younger individuals will be under-represented in the samples, and survival rates over-estimated. The extent of any such sampling biases is unknown, but will have been mitigated to some extent by the use of multiple techniques for capturing frogs (active searching, capture

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