

# Six-year demographic study reveals threat of stochastic extinction for remnant populations of a threatened amphibian

EVAN JOHN PICKETT,<sup>1,2\*</sup> MICHELLE PIRRIE STOCKWELL,<sup>1</sup>  
DEBORAH SHEENA BOWER,<sup>1</sup> CARLA JEAN POLLARD,<sup>1</sup> JAMES IAN GARNHAM,<sup>1</sup>  
JOHN CLULOW<sup>1</sup> AND MICHAEL JOSEPH MAHONY<sup>1</sup>

<sup>1</sup>*School of Environmental and Life Sciences, University of Newcastle, Newcastle, New South Wales, Australia; and* <sup>2</sup>*School of Biological Sciences, University of Hong Kong, Kadoorie Biological Sciences Building, Pok Fu Lam Road, Hong Kong (Email: epickett@hku.hk)*

**Abstract** Sustained demographic studies are essential for early detection of species decline in time for effective management response. A paucity of such background data hindered the potential for successful conservation during the global amphibian decline and remains problematic today. The current study analysed 6 years of mark-recapture data to determine the vital demographic rates in three habitat precincts of the threatened frog, *Litoria aurea* (Hylidae) and to understand the underlying causes of variability in population size. Variability in population size of *L. aurea* was similar to many pond-breeding species; however this level of fluctuation is rare among threatened amphibians. Highly variable populations are at greater risk of local extinction and the low level of connectivity between *L. aurea* populations means they are at a greater risk of further decline due to stochastic extinction events and incapacity to recolonize distant habitat. We recommend that management of this species should encourage recolonization through creation of habitat corridors and reintroduction of *L. aurea* to areas where stochastic extinction events are suspected.

**Key words:** Anuran, conservation, growth, *Litoria aurea*, mark-recapture, variability.

## INTRODUCTION

An understanding of the demographic processes driving the persistence of populations is vital for the conservation of threatened species. Population declines can easily go unnoticed but baseline demographic data allow detection of population decline even when it is obscure (Wooler *et al.* 1992; Blaustein *et al.* 1994). Information on the four vital rates that drive variability in a population (mortality, recruitment, emigration and immigration) can inform management to specifically target the life-history trait that contributes most to conservation, with the least cost (Beissinger & McCullough 2002).

Over the past four decades, populations of amphibians have declined on a global scale (Wake 1991; Alford *et al.* 2001; Stuart *et al.* 2004). Early detection of this decline was hampered because it was long assumed that amphibian populations experience high levels of temporal variability and a decline could be confused with a trough in a fluctuating population (Alford & Richards 1999). This assumption was fuelled by a lack of long-term demographic data, as at

the time of recognizing global decline there was no published, long-term demographic study focused on amphibians and the natural variability of amphibian populations was largely unknown. As a result, one of the earliest recommendations to manage the global amphibian decline was to conduct long-term studies on populations of amphibians (Barinaga 1990). Some long-term population studies of amphibians have since been published (e.g. Semlitsch *et al.* 1996; Bell & Pledger 2010), but the lack of population data on a range of species, which is available for other taxa such as birds, still hinders conservation of amphibians.

Population data have been successfully used in the past to detect decline, determine cause for decline, and inform management agencies of effective options to reverse decline. Polar bears of the Hudson Bay region were monitored from 1987 to 1998 during a period of long-term warming in the Arctic region. Warm years and early break-up of ice resulted in a loss of condition in adult bears and lower recruitment (Saunders 1982). A 35-year study of prairie chickens observed a substantial decline in numbers (from 2000 to 50 individuals), genetic diversity, and hatching success of eggs. These data led to the recommendation of outbreeding through the introduction of individuals from a larger population, and saw a reverse of the decline (Westemeier *et al.* 1998).

\*Corresponding author.

Accepted for publication July 2013.

The focus of this study is the green and golden bell frog (*Litoria aurea*, Hylidae) which was a once common species of frog in eastern Australia that has experienced a substantial decline in populations and now has a vulnerable listing on the IUCN Red List of Threatened Species (Mahony 1999; Hero *et al.* 2004; White & Pyke 2008). The amphibian chytrid fungus (*Batrachochytrium dendrobatidis*) has been implicated as a contributing factor in the decline of *L. aurea* (Penman *et al.* 2008; Stockwell *et al.* 2008) along with habitat alteration and an introduced predatory fish (*Gambusia holbrooki*) (White & Pyke 2008).

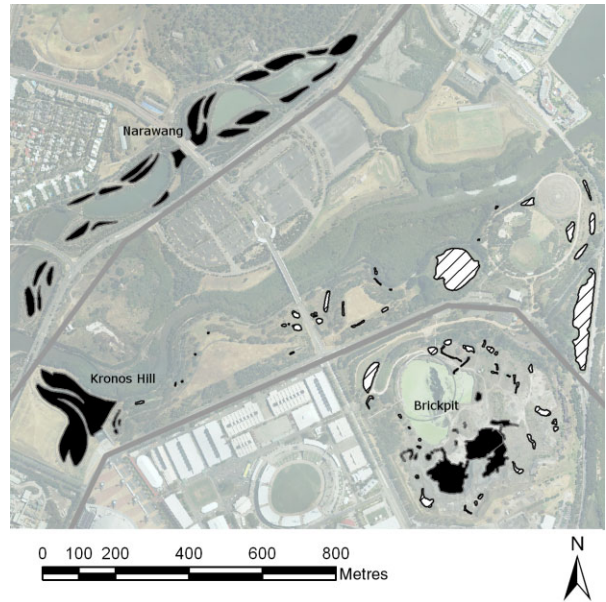
*Litoria aurea* has been described as having a 'fast' life-history strategy characterized by its high fecundity, with an average of 3773 eggs laid in one clutch, short tadpole development time, fast time to maturity, habitat generalization and a wide dispersal ability (Pyke & White 2001; Hamer & Mahony 2007). This life-history is well represented among invasive species (Sakai *et al.* 2001), as in the case of *L. aurea* which has successfully invaded many Pacific islands (Pyke & White 2001). However, few threatened species have such a life-history strategy (Purvis *et al.* 2000), and fast life-history species may experience different population pressures compared with these typical threatened species. Previous demographic studies of *L. aurea*, and the closely related *L. raniformis*, have focused on counts of animals or breeding events (Van de Mortel & Goldingay 1998), population size estimates (Goldingay & Newell 2005a,b) and short-term survival and growth rate estimation (Hamer & Mahony 2007; Heard *et al.* 2011).

Here we present the results of a longer-term demographic study of a remnant population of *L. aurea*. We aimed to determine the variation in demographic rates of the *L. aurea* population including population size, survival rate, recruitment rate and individual growth rates. We conclude by reviewing the implications of these results for the persistence and conservation of this species across its current, much reduced native range.

## METHODS

### Study site and species

This study focused on three habitat precincts where *L. aurea* occur within Sydney Olympic Park, NSW Australia (33°51'S, 151°4'E; Fig. 1). One of these precincts known as the Brickpit was conserved largely intact during (and beyond) construction of the surrounding 2000 Sydney Olympic Games venues as it was inhabited by a remnant population of *L. aurea* that was discovered during the initial environmental surveys prior to the creation of the park. The two other precincts known as Kronos Hill and Narawang Wetland are each a series of constructed ponds designed specifically as



**Fig. 1.** Distribution of ponds within the three precincts at Sydney Olympic Park: Brickpit, Narawang and Kronos Hill. Black ponds represent higher relative abundance ponds surveyed during mark-recapture study and striped ponds represent ponds omitted from survey. Separation of precincts is represented by the grey lines.

*L. aurea* habitat (Darcovich & O'Meara 2008). The three precincts are separated by substantial barriers to dispersal including major roads, a large tidal estuarine creek system, and frog fencing intended to reduce road mortalities, the latter being connected by a series of underpasses to increase connectivity (Muir 2008). Long-term monitoring of the population has been supported by the Sydney Olympic Park authority since 1996 (Darcovich & O'Meara 2008).

### Surveys

Each pond within the three precincts was surveyed once for post-metamorphic frogs in November, December and February of each year from November 2008 to February 2012 employing visual encounter (VE) survey techniques. VE surveys consisted of searching the vegetation and water within the pond as well as the surrounding terrestrial environment and its ground cover. *Litoria aurea* were captured by hand with the hand covered in a thin, disposable plastic bag; the bag was inverted and tied to contain the frog. All frogs were handled in accordance with the New South Wales hygiene protocol for the control of disease in frogs (Department of Environment and Climate Change (NSW) 2008). Other frog species were recorded when they were seen and a relative abundance index was determined following the methods of Bower *et al.* (2012).

After each survey, *L. aurea* were weighed, measured to the nearest millimetre (snout-to-vent length and right tibia length) and scanned using a Trovan LID-560ISO pocket reader to detect implanted passive integrated transponder (PIT) tags. The size of the PIT tag limited size at which

animals could be injected. In surveys prior to 2010, frogs that were greater than 45 mm snout–vent length that did not have a PIT tag were implanted subcutaneously in the dorsal or dorso-lateral regions (Christy 1996; Gibbons & Andrews 2004). From September 2010, smaller PIT tags were available and frogs between 35 mm and 45 mm were also tagged. After frogs were processed, they were released at the site of capture which was marked with flagging tape at the time of capture.

A subset of ponds in the Brickpit that contained the highest relative abundance of *L. aurea* in previous surveys was chosen as the site of a mark-recapture study from January 2007 to January 2012 (see Fig. 1). Prior to the commencement of the study by the authors of the current paper, 2 years of survey (2007–2008) were conducted by an environmental consultancy as part of a monitoring regime to gather data for the estimation of population size using a Lincoln-Petersen index method that requires one marking and one recapture session (Ecology Partners Pty Ltd 2008). The authors of the current paper continued mark-recapture surveys within the same sampling area; however the number of marking sessions per survey was increased. Annual mark-recapture surveys occurred in January of each year from 2007 until 2012 and additional surveys were undertaken in September 2010 and 2011. Occasionally, all ponds within the sampling area could not be sampled in one night and additional nights were required. Consequently, single sample events ranged from 1 to 3 nights depending on the number and experience of surveyors. The number of secondary samples ranged from 2 to 5 sampling periods per primary sampling period.

Mark-recapture sampling was also completed in four ponds within the Kronos Hill precinct in January of each year from 2010 to 2012. Sampling periods lasted one night and were repeated 3–6 times over consecutive nights.

Secondary sampling periods were conducted within at least one week of the previous sample for both the Brickpit and Kronos Hill surveys. Processing of frogs was consistent with VE surveys. As well as during the planned surveys, frogs were captured opportunistically and processed by the authors whenever they were found within Sydney Olympic Park; these data were included in analyses to determine individual growth rates for *L. aurea*.

## Analysis

### Mark-recapture

Estimates of population size were performed for populations from the Brickpit and Kronos Hill precincts using mark-recapture data based on Pollock's robust design and for Narawang from 2008 to 2012 using data from VE surveys and based on Cormack-Jolly-Seber (CJS) models.

Consistent closed-population mark-recapture surveys conducted in the Brickpit and at Kronos Hill conform to Pollock's robust design models which incorporate sampling at two temporal scales, known as primary and secondary sampling events (Pollock 1982; Kendall 2001). Primary sampling events were separated by long intervals at which migration, death and recruitment could occur (open population).

Model assumptions are typical of open population models with the additional restriction that secondary sampling periods are closed (Pollock 1982). Within each primary sampling event, more than one secondary sampling occasion occurred over a short period at which the population can be assumed to be closed. By incorporating closed population estimates for abundance and open estimators for survival within the one model, the overall analysis is more robust than if these were estimated separately (Kendall 2001). To remain consistent throughout the study, only individuals greater than 45 mm in length were included in mark-recapture analysis. Pollock's robust design estimates are:

- Apparent survival ( $\phi$ ) – probability an animal stays within the study area between primary surveys. Removal of an animal can occur through mortality or permanent emigration.
- Temporary emigration ( $\gamma$ ) – probability an animal migrates from the survey area for at least one sampling occasion and subsequently migrates back.
- Capture probability ( $p$ ) – probability an individual is captured during a survey period.
- Recapture probability ( $c$ ) – probability a marked animal is captured during a survey period.
- Population size ( $N$ ) – size of the target population.

Annual recruitment rate of adults was determined based on the apparent survival and population size:

$$R = \frac{N_t - \phi N_{t-1}}{N_t \times F} \quad (1)$$

Where  $N_t$  is the population size at time  $t$ ,  $\phi$  is the annual survival between  $N_t$  and  $N_{t-1}$  and  $F$  is the proportion of females greater than 65 mm in length captured during the breeding season at  $N_t$ , which is the size at which females are thought to reach sexual maturity in *L. aurea* (Pyke & White 2001). Variability in population size was determined using the methods of Green (2003) so comparisons of temporal variability could be made to populations in that study. The difference in population size between years was determined using the following equation:

$$\Delta N = \log(N + 1)_t - \log(N + 1)_{t-1} \quad (2)$$

Where  $N$  is the population size at time  $t$ , and the variance of  $\Delta N$  was used to illustrate variability in the population size.

Models were chosen *a priori* and fitted to the data which included no variation in the above parameters (constant); time variation where parameters varied between samples, and variation by sex. Capture and recapture rates were tested on two levels of time (primary and secondary samples) and were also tested for a behavioural response to capture whereby recapture and capture rate were independent or equal ( $p = c$ ). Covariates for the monthly Southern Oscillation Index (SOI) and monthly average rainfall between primary sampling periods from the Sydney Olympic Park Bureau of Meteorology weather station were fitted to the survival parameter. Covariates were not fitted to survival or population size for the Kronos Hill models as only two survival rates and three sizes could be estimated. Capture and recapture probability was fitted to the number of surveyors during a sample. Where the sample period spanned more than one day, two separate models were fitted with the average number of surveyors and the total number of surveyor days:



$$D = \sum_1^n S_i \quad (3)$$

Where  $D$  is 'surveyor days',  $n$  is the number of days in the sample and  $S$  is the number of surveyors on day  $i$ . Capture and recapture probability was also fitted to the maximum daily temperature and month (September or January). Rainfall was not used as the number of rainy days was too low over survey periods.

Population size was fitted to the SOI for the current and previous season, relative abundance of *L. aurea*, *Litoria peronii*, and *Limnodynastes peronii* during the breeding season within the mark-recapture ponds. Relative abundance ( $A$ ) of adult frogs was determined from the VE survey data:

$$A = \frac{n}{t \times s} \quad (4)$$

Where  $n$  was the number of frogs seen during the VE surveys,  $t$  was the time spent searching by  $s$  number of surveyors.

Mark-recapture data from the VE surveys in the Narawang precinct were analysed using CJS models. Sampling periods for CJS models are separated by intervals at which migration, death and recruitment occur under the assumptions listed by Pollock *et al.* (1990).

Constant, time varying, and sex varying models were fitted for both parameters. Daily maximum temperature, number of surveyors (as above) and month (November, December, January or February) covariates were fitted to capture probability and the monthly average SOI and rainfall were fitted to the survival probability. These values were obtained from the Sydney Olympic Park Bureau of Meteorology weather station.

All analysis of mark-recapture data was performed using Program MARK version 6.1 (White & Burnham 1999). Model selection was based on Akaike's Information Criterion with correction for small samples (AICc). The most parsimonious models were determined as those with the smallest AICc values. The  $\Delta$ AIC value is the difference between a model and the most parsimonious model, and  $\Delta$ AIC values of less than two could not be considered different enough to reject (Burnham & Anderson 2002). To remedy this, each model was weighted according to the  $\Delta$ AIC value and the parameter outputs were averaged according to the methods of Burnham and Anderson (2002). Models that failed to converge were removed from the candidate model set to prevent influence on the model averaging results. To determine the effect of covariates on a parameter, beta estimates were obtained from Program MARK for the most parsimonious models. Positive beta estimates suggested a positive correlation, and vice versa, with 95% confidence intervals that do not enclose zero indicating significance at the 5% level.

### Growth

Growth in post-metamorphic amphibians is best described by the von Bertalanffy growth model (Hota 1994). The von Bertalanffy model is characterized by an initial period of rapid growth and marked slowing at later stages (Fabens 1965). It is parameterized according to the following:

$$SVL = \alpha(1 - \beta(e^{-\gamma t})) \quad (5)$$

Where  $SVL$  is snout-to-vent length (size),  $\alpha$  is the asymptotic size,  $\beta$  is the fraction of the asymptotic size at metamorphosis,  $\gamma$  is a parameter to describe growth rate and  $t$  is the age of the animal. As age was not known for frogs in this study,  $\alpha$  and  $\gamma$  were estimated using the growth-interval model of Fabens (1965):

$$SVL_r = \infty - ((\infty - SVL_c)e^{-\gamma t}) \quad (6)$$

Where  $SVL_r$  is the size at recapture and  $SVL_c$  is the size at initial capture and  $t$  is the number of days between captures. The asymptotic size from Eqn 3 and the minimum size of a metamorphosed frog ( $SVL_0$ ) were used to determine  $\beta$ :

$$\beta = 1 - \frac{SVL_0}{\alpha} \quad (7)$$

Only growth intervals from one breeding season (September to February) were included to remove the effect of winter on growth rate and intervals of less than 30 days were excluded as the limited growth in this period and level of error in measurement resulted in multiple instances of negative growth. Fewer recaptures in Narawang produced fewer data and Narawang was therefore omitted from analysis.

An unstratified model was created using data from all recaptured frogs included in the analysis to compare with models stratified by sex or precinct. Models were compared using the likelihood ratio test to determine whether introducing these parameters to the model significantly improved model fit. Models were then fitted separately for each combination of sex and precinct. All the above models were fitted using the nonlinear least square function in the statistical program R version 2.14.2 (R Development Core Team 2011).

### Goodness of fit

To test goodness of fit for robust design models, for which there are no standard tests, we collapsed the encounter histories to only include whether an individual was captured during a primary sampling period to conform to the CJS format. We then tested goodness of fit for the Brickpit and Narawang data, which were already in CJS format, using Test 2 + 3 in Program RELEASE version 3.0 (Burnham *et al.* 1987). Goodness of fit could not be tested for the Kronos Hill data with just three primary sampling periods.

## RESULTS

A total of 1288 individual *L. aurea* were captured 2250 times (see Table 1 for breakdown over precincts). The pooled results from tests 2 and 3 in program RELEASE indicated a good fit for the Brickpit CJS model ( $\chi^2 = 23.578$ ,  $P = 0.3697$ ) and a reasonable fit for Narawang ( $\chi^2 = 38.723$ ,  $P = 0.0855$ ). A summary of the mark-recapture model candidate sets is in Table 2.

The best predictor for population size within the Brickpit was month (September or January) with an additive covariate of the relative abundance of *Litoria*

**Table 1.** Summary of mark-recapture studies conducted at Sydney Olympic Park

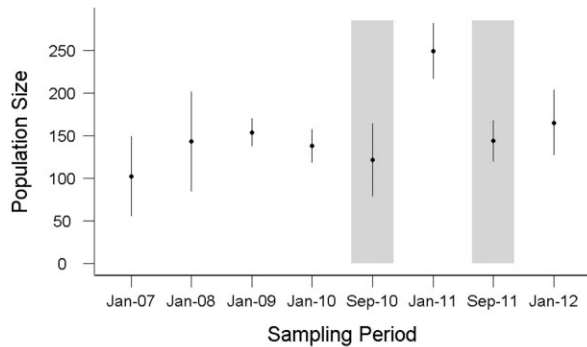
Precinct	Period	Surveys 1st (2nd)	Captures	Individuals
Brickpit	2007–2012	8 (25)	1309	647
Kronos Hill	2010–2012	3 (14)	421	299
Narawang	2008–2012	14	420	342

The number of surveys is split into primary (1st) and secondary (2nd) sampling occasions for robust design studies.

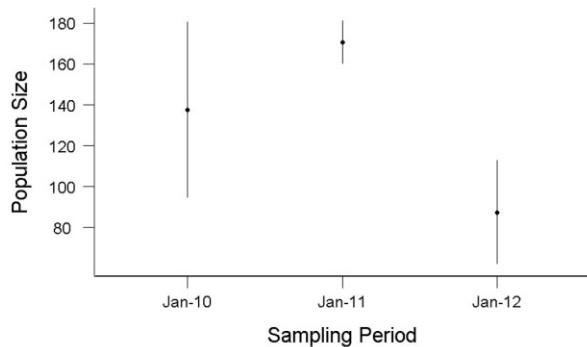
**Table 2.** Subset of candidate models with AICc weights greater than zero for the three mark-recapture studies conducted at Sydney Olympic Park

Model	AICc	$\Delta$ AICc	AICc weights	Likelihood	Num. Par	Deviance
<b>Brickpit</b>						
S(sex*rain) $G''=G'=0$ p(sex+time)=c N(season+RelLitP)	-723.469	0	0.29876	1	58	0
S(sex*rain) $G''=G'=0$ p(sex+time)=c N(time)	-723.192	0.2762	0.26022	0.87	63	0
S(sex) $G''=G'=0$ p(sex+time)=c N(time)	-722.783	0.6857	0.21204	0.71	61	0
S(sex*rain) $G''=G'=0$ p(sex+time)=c N(season*RelLitP)	-721.205	2.264	0.09632	0.32	59	0
S(sex*SOI) $G''=G'=0$ p(sex+time)=c N(time)	-720.557	2.9112	0.06969	0.23	63	0
S(sex+time) $G''=G'=0$ p(sex+time)=c N(time)	-718.677	4.7913	0.02722	0.09	73	0
S(sex+time) $G''=G'=0$ p(sex+time)=c N(SOI+season)	-717.042	6.427	0.01201	0.04	68	0
S(sex*rain) $G''=G'=0$ p(sex+time)=c N(season+RelLimP)	-716.135	7.334	0.00763	0.03	57	0
S(sex*rain) $G''=G'=0$ p(sex+time)=c N(season+RelLA)	-715.819	7.6498	0.00652	0.02	57	0
S(sex+time) $G''=G'=0$ p(sex+time)=c N(SOI*season)	-714.891	8.5774	0.00410	0.01	69	0
S(sex*rain) $G''=G'=0$ p(sex+time)=c N(season*RelLA)	-714.311	9.158	0.00307	0.01	58	0
S(sex*rain) $G''=G'=0$ p(sex+time)=c N(season*RelLimP)	-712.645	10.8239	0.00133	0.01	59	0
S(sex+time) $G''=G'=0$ p(time)=c N(time)	-710.907	12.5612	0.00056	0	48	0
S(sex+time) $G''=G'=0$ p(sex+time)=c N(.)	-707.699	15.7701	0.00011	0	66	0
S(sex+time) $G''=G'=0$ p(sex+time)=c N(preSOI+season)	-707.625	15.8432	0.00011	0	68	0
S(sex+time) $G''=G'=0$ p(sex+time)=c N(sex+time)	-707.363	16.1061	0.00010	0	81	0
S(sex+time) $G''=G'=0$ p(sex+time)=c N(sex+time)	-707.363	16.1061	0.00010	0	81	0
S(sex+time) $G''=G'=0$ p(sex+time)=c N(rain+season)	-707.042	16.427	0.00008	0	68	0
<b>Kronos Hill</b>						
S(time) $G''=G'=0$ p(time)=c N(time)	142.3716	0	0.99954	1	20	0
S(time) $G''=G'=0$ p(primary)=c N(time)	159.3646	16.993	0.00020	0	9	0
S(.) $G''=G'=0$ p(primary)=c N(time)	159.8507	17.4791	0.00016	0	8	0
S(time+sex) $G''=G'=0$ p(primary)=c N(time)	162.151	19.7794	0.00005	0	11	0
S(time) $G''=G'=0$ p(primary+sex)=c N(time)	164.8186	22.447	0.00001	0	12	0
S(time) $G''=G'=0$ p(time+sex)=c N(time)	165.2287	22.8571	0.00001	0	34	0
S(time+sex) $G''(time+sex)=G'$ p(primary)=c N(.)	166.2578	23.8862	0.00001	0	9	0
<b>Narawang</b>						
S(SOI) p(time)	514.1084	0	0.90806	1	14	170.729
S(.) p(time)	518.9247	4.8163	0.08171	0.09	14	175.545
S(rain) p(time)	523.0949	8.9865	0.01016	0.01	16	175.387
S(time) p(time)	533.9203	19.8119	0.00005	0	26	163.875
S(time) p(.)	536.1097	22.0013	0.00002	0	14	192.730
S(.) p(maxTemp)	537.5355	23.4271	0.00001	0	3	217.184

Kronos Hill and the Brickpit populations were analysed using the robust design method with the parameters of: survival probability (S), emigration ( $G'$ ) and immigration ( $G''$ ) probability, capture probability (p), recapture probability (c) and populations size (N), tested for the effects of time (t), primary sampling occasion (primary), sex, monthly average Southern Oscillation Index (SOI), relative abundance of *Litoria peronii* (RelLitP), average monthly rainfall (rain) and maximum temperature during the day before a sample (maxTemp). Narawang was modelled using the Cormack Jolly Seber method testing survival (S) and recapture (p) probability using the applicable constraints described above. Additive (+) and interaction (\*) models were tested for appropriate covariates. AIC, Akaike's Information Criterion.



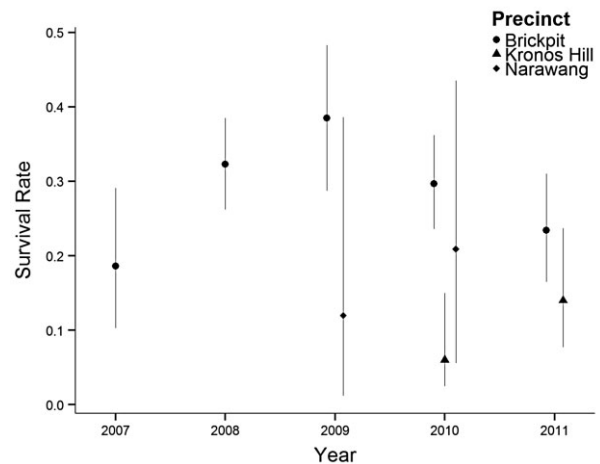
**Fig. 2.** Annual adult population size estimates in January and September with 95% confidence intervals for the mark-recapture surveys conducted in the Brickpit precinct from 2007 to 2012. September surveys are highlighted in grey.



**Fig. 3.** Annual adult population size estimates in January with 95% confidence intervals for the mark-recapture surveys conducted in the Kronos Hill precinct from 2010 to 2012.

*peronii* during November, December and February of the same season. Models with time varied population size were most parsimonious for Kronos Hill and could not be disregarded from the Brickpit models as the difference in AICc from the most parsimonious was less than 2. The population size estimates for January ranged from 102 to 249 in the Brickpit and 87 to 171 at Kronos Hill (Figs 2,3). The variance in  $\Delta N$  was 0.15 and 0.39 for the Brickpit and Kronos Hill precincts respectively ( $\mu = 0.27$ ,  $\sigma = 0.17$ ). Population size estimates for the Brickpit in September months were smaller than the subsequent January estimates in both 2010/2011 and 2011/2012 which suggests that September to January is a major period of adult recruitment, as expected for a spring/summer breeding species.

Annual survival ranged from 0.06 to 0.44 throughout the three precincts; however the higher estimates had large confidence intervals (e.g. 95% confidence intervals of 0.07 to 0.72). No significant difference was apparent between habitat precincts (Fig. 4). Average



**Fig. 4.** Annual survival rate estimates with 95% confidence intervals of adult *Litorea aurea* for three habitat precincts at Sydney Olympic Park.

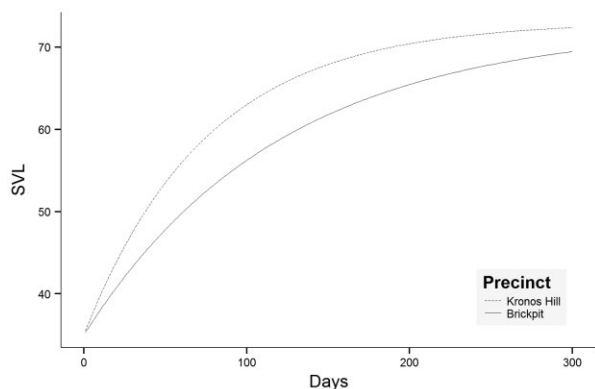
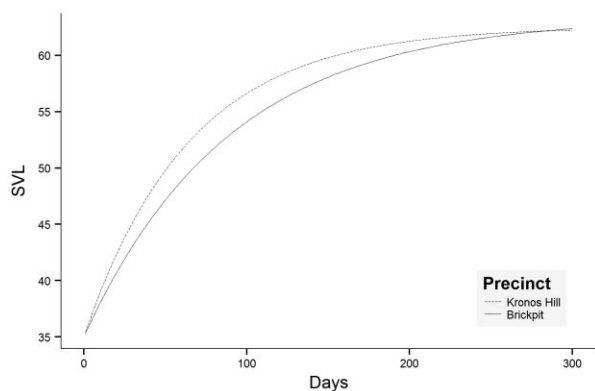
monthly rainfall interacting with sex was the best predictor of survival for the Brickpit population. However, AICc scoring for this model was close to the model without an effect of average monthly rainfall and this model could therefore not be discounted (Table 2). Average monthly Southern Oscillation Index was the best predictor of survival for Narawang Wetland. A time varying model was the best predictor of survival for the Kronos Hill populations. Beta estimates were positive for both average monthly rainfall (0.294–3.417 95% CI) and SOI (0.012–0.145 95% CI) against survival rate, suggesting dry periods correlate with higher mortality in both instances. Beta estimates of the sex covariate for the Brickpit population were positive suggesting males had higher apparent survival (0.2939150–3.4168749 95% CI). Recruitment rate ranged from 2.2 to 11.1 adults produced per mature female for the Brickpit ( $\mu = 5.65$ ,  $\sigma = 3.45$ ) and 2.4 to 5.2 adults per mature female for Kronos Hill ( $\mu = 3.77$ ,  $\sigma = 1.98$ ).

The temporary emigration parameter was not estimable for any model. This was likely due to the low survival rate; few individuals would survive the minimum of three sampling periods required to emigrate for one sampling period and immigrate at a subsequent sampling period. Subsequent models were set to 'no emigration' where both emigration parameters were set to zero, thus apparent survival would likely include instances of emigration and survival.

The addition of precinct ( $\chi^2 = 66.36$ , d.f. = 2,  $P < 0.001$ ) and sex ( $\chi^2 = 74.93$ , d.f. = 2,  $P < 0.001$ ) to the unstratified von Bertalanffy growth rate model both had a significant impact on model fit. Parameter estimates for the models (Table 3) suggest a slower growth rate in the Brickpit and a smaller maximum length for males (Figs 5,6).

**Table 3.** Parameter estimates for the von Bertalanffy growth model of *L. aurea* within the Brickpit and Kronos Hill precincts of Sydney Olympic Park

Precinct	Sex	$\alpha$ (95% CI)	$\lambda$ (95% CI)
Brickpit	Male	63.36 (62.46–64.41)	0.0112 (0.0092–0.0135)
Brickpit	Female	72.54 (70.37–75.32)	0.0083 (0.0056–0.0112)
Kronos Hill	Male	62.52 (61.17–64.21)	0.0154 (0.0054–0.026)
Kronos Hill	Female	73.08 (71.41–74.88)	0.0133 (0.0089–0.0192)

**Fig. 5.** Post-metamorphic growth curves for female *Litoria aurea* based on the von Bertalanffy growth model. Growth curves are separated by habitat precinct. SVL, snout-vent length .**Fig. 6.** Post-metamorphic growth curves for male *Litoria aurea* based on the von Bertalanffy growth model. Growth curves are separated by habitat precinct. SVL, snout-vent length .

## DISCUSSION

The Sydney Olympic Park population in this study experienced a high level of turnover with low survival and high recruitment, a result that was in accord with other studies of *L. aurea* and the related *L. raniformis* (Hamer & Mahony 2007; Heard *et al.* 2011). Despite this low survival, all populations persisted throughout

the study period. The population in the Brickpit precinct, which was subject to the longest period of study, experienced a short period of rapid change and high variability in population size from 2010 to 2011. Estimates of individual growth rate suggested differences between precincts for both sexes and this may have an effect on the time taken to reach maturity.

This study suggested that individual growth rate may vary between precincts. Growth rate of amphibians has been shown to differ along altitudinal gradients and has an appreciable impact on the time to sexual maturity (Marunouchi *et al.* 2000). An effect over a small geographic scale has not been observed previously, though many factors, such as larval growth rate, disease and density have been shown to impact growth in a laboratory system (Goater 1994; Hilken *et al.* 1995; Browne *et al.* 2003). Delayed maturity due to slow growth rate could have a drastic effect in populations that experience low survival as an individual is much less likely to survive to maturity when it takes extra time to mature. For example, extending the age of first breeding from 2 to 3 years for a species that experiences an annual survival rate of 0.3 would reduce the probability of reaching maturity from 0.09 to 0.027. Therefore, the impact of growth rate on the viability of a population requires further study and further data are required to determine whether this difference is real and the possible cause of such a difference.

The population size for both precincts where it was estimated was relatively small compared with most estimated minimum viable population sizes (Reed *et al.* 2003; Traill *et al.* 2007), but normal for populations of pond-breeding frogs where 78.3% of surveyed populations numbered fewer than 500 individuals (Green 2003). The role of migration at Sydney Olympic Park on population regulation is unknown, with just a single movement of a marked individual recorded between precincts (Smith & Saunders 1986). However, movements within precincts are common (Garnham, unpubl. data, 2013) and increased connectivity between precincts may have a positive effect on the long-term persistence of these precincts.

Small populations have an increased risk of extinction through the loss of fitness from genetic



bottlenecking (Madsen *et al.* 1996) and increased risk of extinction through stochastic processes. Demographic stochasticity is the variability experienced by a population that is caused by individual differences in survival and recruitment, and is independent of the fate of other individuals in the population. Risk of extinction from demographic stochasticity is directly related to population size and is greatest for small populations and mostly absent from large populations (Lande 1993). The small population size of *L. aurea* within precincts at Sydney Olympic Park therefore likely increases the risk of extinction or rapid and dangerous decline.

Pond-breeding frogs exhibit greater temporal variability in population size than species which occupy other types of breeding habitat, and this was confirmed for *L. aurea* which has a population variance typical of other pond-breeding species (Green 2003). The risk of local extinction from environmental stochasticity and catastrophes increases with the level of variability and is independent of population size (Lande 1993). Environmental stochasticity is where external factors similarly affect the mortality or recruitment of all individuals within an age-class or population and can affect populations of all sizes. Catastrophes are similar except they cause a more severe decline through an environmental change causing mass mortality. More frequent local extinction occurs for pond breeding species as is expected from their higher variability (Green 2003). However, it is often reversed by high dispersal and the ability to recolonize habitat after a local extinction event (Brown & Kodric-Brown 1977; Funk *et al.* 2005).

The level of population variability experienced during this study was likely due to the low survival rate and high level of adult recruitment. Survival was found to be most affected by the Southern Oscillation Index in Narawang and average monthly rainfall in the Brickpit whereby dry years were associated with lower survival. This suggests that environmental stochasticity affects *L. aurea* and drought may contribute to local extinction for this species. The added threat of climate change may further imperil *L. aurea* as the frequency of extended droughts may increase over the current distribution of *L. aurea* (Hughes 2003). The role of amphibian chytrid fungus in depressing the population size through increased mortality is unknown for this population; however, mortality events attributed to chytrid have been recorded at Sydney Olympic Park (Penman *et al.* 2008) and chytrid infection has been found to decrease over-wintering survival in a more northern population (Stockwell 2011).

While disjunct populations can be protected from the threatening process that caused extinction in the surrounding populations, they may be predisposed

to extinction due to their isolation (Mills & Smouse 1994; Frankham 1995; Young *et al.* 1996). The high variability experienced by *L. aurea* in combination with its range contraction to disjunct populations along the east coast of Australia means it is likely that this species is at further risk of decline from stochastic local extinction and an inability to recolonize over large distances.

## Conclusions

The global amphibian decline was more likely to affect stream-dwelling species (Stuart *et al.* 2004), which generally had stable populations prior to decline (Green 2003). The ecology of *L. aurea* does not fit this model. The level of variability experienced in *L. aurea* populations as demonstrated by this study may be of concern for their viability due to an increased risk of local extinction and low connectivity between populations along the east coast of Australia. Further studies are required to determine the persistence of *L. aurea* throughout Australia in the current context of habitat fragmentation and variability in demographic rates. This study has demonstrated the importance of demographic study, as it has identified a further threat to the sustainability of this highly disjunct species. We recommend that management strategies for *L. aurea* consider connectivity between populations and artificial reintroductions where stochastic extinction is suspected in the context of decreased survival from chytridiomycosis, habitat alteration and invasive species.

## ACKNOWLEDGEMENTS

We would like to thank the many volunteers who helped with field-work, particularly Daniel O'Brien and Rodney Wattus who assisted on multiple occasions. Dr Geoff Heard provided some statistical advice. We would like to thank Katie Oxenham, Jenny O'Meara and Kerry Darcovich of the Sydney Olympic Park Authority for operational and logistic assistance. The 2007–2008 mark-recapture data were collected by Ecology Partners Pty Ltd for the Sydney Olympic Park Authority. This study was funded as part of the ARC linkage project (LP0989459). We were supported by the following industry partners: Sydney Olympic Park Authority, NSW Roads and Traffic Authority, Strathfield Council, the Office of Environment and Heritage and the South Australia Museum. The project was conducted under NPWS Scientific Licence (SL100092) and approved by the University of Newcastle Animal Care and Ethics Committee (ACEC number A-2008-165).



## REFERENCES

- Alford R. A., Dixon P. M. & Pechmann J. H. K. (2001) Global amphibian population declines. *Nature* **414**, 449–500.
- Alford R. A. & Richards S. J. (1999) Global amphibian declines: a problem in applied ecology. *Annu. Rev. Ecol. Syst.* **30**, 113–65.
- Barinaga M. (1990) Where have all the froggies gone? *Science* **247**, 1033–4.
- Beissinger S. R. & McCullough D. R. (2002) *Population Viability Analysis*. The University of Chicago Press, London.
- Bell B. D. & Pledger S. A. (2010) How has the remnant population of the threatened frog, *Leiopelma pakeka* (Anura: Leiopelmatidae) fared on Maud Island, New Zealand, over the past 25 years? *Austral Ecol.* **35**, 241–56.
- Blaustein A. R., Wake D. B. & Sousa W. P. (1994) Amphibian declines: judging stability, persistence, and susceptibility of populations to local and global extinctions. *Conserv. Biol.* **8**, 60–71.
- Bower D. S., Stockwell M. P., Pollard C. J. *et al.* (2012) Life stage specific variation in the occupancy of ponds by *Litoria aurea*, a threatened amphibian. *Austral Ecol.* **38**, 543–7. DOI: 10.1111/j.1442-9993.2012.02452.x.
- Brown J. H. & Kodric-Brown A. (1977) Turnover rates in insular biogeography: effect of immigration on extinction. *Ecology* **58**, 445–9.
- Browne R. K., Pomeroy M. & Hamer A. J. (2003) High density effects on the growth, development and survival of *Litoria aurea* tadpoles. *Aquaculture* **215**, 109–21.
- Burnham K. P. & Anderson D. R. (2002) *Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach*. Springer-Verlag, Heidelberg.
- Burnham K. P., Anderson D. R., White G. C., Brownie C. & Pollock K. H. (1987) Design and analysis methods for fish survival experiments based on release-recapture. *American Fisheries Society, Monograph* **5**, Bethesda, Maryland.
- Christy M. T. (1996) The efficacy of using Passive Integrated Transponder (PIT) tags without anaesthetic in free-living frogs. *Aust. Zool.* **30**, 139–42.
- Darcovich K. & O'Meara J. (2008) An Olympic legacy: Green and Golden Bell Frog conservation at Sydney Olympic Park 1993–2006. *Aust. Zool.* **34**, 236–48.
- Department of Environment and Climate Change (NSW) (2008) *Hygiene Protocol for the Control of Disease in Frogs. Information Circular Number 6*. DECC, Sydney South.
- Ecology Partners Pty Ltd (2008) Green and Golden Bell Frog *Litoria aurea* monitoring at Sydney Olympic Park, New South Wales, 2007/08. *Report prepared for the Sydney Olympic Park Authority July 2008*.
- Fabens A. J. (1965) Properties and fitting of the von Bertalanffy growth curve. *Growth* **29**, 265–89.
- Frankham R. (1995) Inbreeding and extinction: a threshold effect. *Conserv. Biol.* **9**, 792–9.
- Funk W. C., Greene A. E., Corn P. S. & Allendorf F. W. (2005) High dispersal in a frog species suggests that it is vulnerable to habitat fragmentation. *Biol. Lett.* **1**, 13–16.
- Gibbons J. W. & Andrews K. M. (2004) PIT tagging: simple technology at its best. *Bioscience* **54**, 447–54.
- Goater C. P. (1994) Growth and survival of postmetamorphic toads: interactions among larval history, density and parasitism. *Ecology* **75**, 2264–74.
- Goldingay R. L. & Newell D. A. (2005a) Aspects of the population ecology of the green and golden bell frog *Litoria aurea* at the northern end of its range. *Aust. Zool.* **33**, 49–59.
- Goldingay R. L. & Newell D. A. (2005b) Population estimation of the green and golden bell frog *Litoria aurea* at Port Kembla. *Aust. Zool.* **33**, 210–6.
- Green D. M. (2003) The ecology of extinction: population fluctuation and decline in amphibians. *Biol. Conserv.* **111**, 331–43.
- Hamer A. J. & Mahony M. J. (2007) Life history of an endangered amphibian challenges the declining species paradigm. *Aust. J. Zool.* **55**, 79–88.
- Heard G. W., Scroggie M. P. & Malone B. S. (2011) The life history and decline of the threatened Australian frog, *Litoria raniformis*. *Austral Ecol.* **37**, 276–84.
- Hero J.-M., Gillespie G. R., Cogger H., Lemckert F. L. & Robertson P. (2004) *Litoria aurea* In IUCN 2011. IUCN Red List of Threatened Species. Version 2011.2. Available from URL: <http://www.iucnredlist.org>
- Hilken G., Dimigen J. & Iglauer F. (1995) Growth of *Xenopus laevis* under different laboratory rearing conditions. *Lab. Anim.* **29**, 152–62.
- Hota A. K. (1994) Growth in amphibians. *Gerontology* **40**, 147–60.
- Hughes L. (2003) Climate change and Australia: trends, projections and impacts. *Austral Ecol.* **28**, 423–43.
- Kendall W. L. (2001) *The Robust Design for Capture-Recapture Analysis Studies: Analysis Using Program MARK*. The Wildlife Society, Bethesda.
- Lande R. (1993) Risks of population extinction from demographic and environmental stochasticity and random catastrophes. *Am. Nat.* **142**, 911–27.
- Madsen T., Stille B. & Shine R. (1996) Inbreeding depression in an isolated population of Adders *Vipera berus*. *Biol. Conserv.* **75**, 113–8.
- Mahony M. J. (1999) Review of the declines and disappearances within the bell frog species group (*Litoria aurea* species group) in Australia. In: *Declines and Disappearances of Australian Frogs* (ed. A. Campbell) pp. 81–93. Environment Australia, Canberra.
- Marunouchi J., Ueda H. & Ochi O. (2000) Variation in age and size among breeding populations at different altitudes in the Japanese newts, *Cynops pyrrhogaster*. *Amphib-reptil.* **21**, 381–96.
- Mills L. S. & Smouse P. E. (1994) Demographic consequences of inbreeding in remnant populations. *Am. Nat.* **144**, 412–31.
- Muir G. W. (2008) Design of a movement corridor for the Green and Golden Bell Frog *Litoria aurea* at Sydney Olympic Park. *Aust. Zool.* **34**, 297–302.
- Penman T. D., Muir G. W., Magarey E. R. & Burns E. L. (2008) Impact of a Chytrid-related mortality event on a population of the Green and Golden Bell Frog *Litoria aurea*. *Aust. Zool.* **34**, 314–8.
- Pollock K. H. (1982) A capture-recapture design robust to unequal probability of capture. *J. Wildl. Manage.* **46**, 752–7.
- Pollock K. H., Nichols J. D., Brownie C. & Hines J. E. (1990) Statistical inference for capture-recapture experiments. *Wildl. Monogr.* **107**, 1–97.
- Purvis A., Gittleman J. L., Cowlshaw G. & Mace G. M. (2000) Predicting extinction risk in declining species. *Proc. R. Soc. Lond. B Biol. Sci.* **157**, 1947–52.
- Pyke G. H. & White A. W. (2001) A review of the biology of the Green and Golden Bell Frog *Litoria aurea*. *Aust. Zool.* **31**, 563–98.
- R Development Core Team (2011) *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria.

- Reed D. H., O'Grady J. J., Brook B. W., Ballou J. D. & Frankham R. (2003) Estimates of minimum viable population sizes for vertebrates and factors influencing those estimates. *Biol. Conserv.* **113**, 23–34.
- Sakai A. K., Allendorf F. W., Holt J. S. *et al.* (2001) The population biology of invasive species. *Annu. Rev. Ecol. Syst.* **32**, 305–32.
- Saunders D. A. (1982) The breeding behaviour and biology of the short-billed form of the White-tailed Black Cockatoo *Calyptorhynchus funereus*. *Ibis* **124**, 422–55.
- Semlitsch R. D., Scott D. E. & Pechmann J. H. K. (1996) Structure and dynamics of an amphibian community: evidence from a 16-year study of a natural pond. In: *Long-Term Studies of Vertebrate Communities* (eds M. L. Cody & J. D. Smallwood) pp. 217–48. Academic Press, New York.
- Smith G. T. & Saunders D. A. (1986) Clutch size and productivity in three sympatric species of Cockatoo (Psittaciformes) in the south-west of Western Australia. *Aust. Wildl. Res.* **13**, 275–85.
- Stockwell M. P. (2011) Impact and mitigation of the emerging infectious disease chytridiomycosis on the endangered green and golden bell frog. In: *School of Environmental and Life Sciences*. University of Newcastle, Newcastle.
- Stockwell M. P., Clulow S., Clulow J. & Mahony M. J. (2008) The impact of the Amphibian Chytrid Fungus *Batrachochytrium dendrobatidis* on a Green and Golden Bell Frog *Litoria aurea* reintroduction program at the Hunter Wetlands Centre Australia in the Hunter Region of NSW. *Aust. Zool.* **34**, 379–86.
- Stuart S. N., Chanson J. S., Cox N. A. *et al.* (2004) Status and trends of amphibian declines and extinctions worldwide. *Science* **306**, 1783–6.
- Traill L. W., Bradshaw C. J. A. & Brook B. W. (2007) Minimum viable population size: a meta-analysis of 30 years of published estimates. *Biol. Conserv.* **139**, 159–66.
- Van de Mortel T. F. & Goldingay R. L. (1998) Population assessment of the endangered green and golden bell frog *Litoria aurea* at Port Kembla, NSW. *Aust. Zool.* **30**, 398–404.
- Wake D. B. (1991) Declining amphibian populations. *Science* **253**, 860.
- Westemeier R. L., Brawn J. D., Simpson S. A. *et al.* (1998) Tracking the long-term decline and recovery of an isolated population. *Science* **282**, 1695–8.
- White A. W. & Pyke G. H. (2008) Green and Golden Bell Frogs in New South Wales: current status and future prospects. *Aust. Zool.* **34**, 319–33.
- White G. C. & Burnham K. P. (1999) Program MARK: survival estimation from populations of marked animals. *Bird Study* **46**, 120–39.
- Wooler R. D., Bradley J. S. & Croxall J. P. (1992) Long-term population studies of seabirds. *Trends Ecol. Evol.* **7**, 111–4.
- Young A., Boyle T. & Brown T. (1996) The population genetic consequences of habitat fragmentation for plants. *Trends Ecol. Evol.* **11**, 413–8.