Australian Journal of Zoology, 2015, **63**, 214–219 http://dx.doi.org/10.1071/ZO14106

Population stability in the endangered Fleay's barred frog (Mixophyes fleayi) and a program for long-term monitoring

Gemma Quick^A, Ross L. Goldingay^{A,B}, Jonathan Parkyn^A and David A. Newell^A

Abstract. In the wake of the global decline in amphibians there is a need for long-term population monitoring. Previous research suggested that the endangered Fleay's barred frog (Mixophyesfleayi) had recovered after a severe decline. We aimed to determine whether this recovery has been sustained and to test an example of a monitoring program that could be employed at intervals of five or more years to assess long-term population stability. We conducted capture—mark—recapture five years after the last detailed census at Brindle Creek in Border Ranges National Park, New South Wales. Frogs were captured along a 200 m creek transect between September 2013 and February 2014. We used program MARK to estimate demographic parameters of adult male frogs using two modelling approaches: robust design (RD) and the POPAN formulation of the Jolly—Seber model. Abundance was estimated at 38.2 ± 0.5 (s.e.) (RD) and 46.0 ± 2.7 (POPAN). Abundance in 2008 was estimated at 53.2 ± 10.0 (POPAN) male frogs. Estimates of apparent monthly survival over our five-month-long study were very high (RD: 1.0 ± 0.0 ; POPAN: 1.0 ± 0.02). Recapture estimates were also high (RD: 0.40 ± 0.07 to 0.72 ± 0.05 per session; POPAN: 0.84 ± 0.05 per month). These data suggest that the Brindle Creek population has remained relatively stable over a period of ~10 years.

Received 18 December 2014, accepted 22 July 2015, published online 20 August 2015

Introduction

Amphibians are recognised as more extinction-prone than any other class of vertebrate (Stuart *et al.* 2004; Beebee and Griffiths 2005). Australia typifies this pattern, with many species of frog suffering severe declines and at least four species becoming extinct since 1980 (Schloegel *et al.* 2006). For many species there is a lack of historical abundance data, which creates difficulties in identifying whether populations are stable, in decline, or recovering from a decline. Accurate estimates of population demography are necessary to understand population dynamics and to determine priority areas for management (McCaffery and Lips 2013). A long-term approach to monitoring is essential for recognising population trends (Alford and Richards 1999; Richards and Alford 2005; Pickett *et al.* 2014).

In the montane rainforests of eastern Australia, at least 14 frog species have severely declined since the 1970s, with some of the earliest declines occurring in north-eastern New South Wales and south-east Queensland (Laurance *et al.* 1996; Hero *et al.* 2006). Subtropical and tropical eastern Australia has subsequently become an important area for understanding the frog decline phenomenon. The highly pathogenic amphibian chytrid fungus (*Batrachochytridium dendrobatides*) (hereafter *Bd*) has been shown to be widespread in this region (Berger *et al.* 1998; Kriger and Hero 2007, 2008; Murray *et al.* 2009; Phillott *et al.* 2013). Chytridiomycosis, the amphibian disease caused by *Bd*, has been

described as one of the largest threats to wildlife (Venesky *et al.* 2014), and has been implicated in the decline of amphibians on a global scale (e.g. Berger *et al.* 1998; Bosch *et al.* 2001; Bell *et al.* 2004; Ouellet *et al.* 2005; Skerratt *et al.* 2007). There are now several reports of population return in north-eastern Australia (Retallick *et al.* 2004; Phillott *et al.* 2013; Scheele *et al.* 2014).

Fleay's barred frog (*Mixophyes fleayi*) (Fig. 1), a streambreeding frog endemic to the subtropical montane rainforests of north-eastern New South Wales and south-eastern Queensland, is among the species documented in the early Australian frog declines (Laurance *et al.* 1996; Goldingay *et al.* 1999). Chytridiomycosis has been implicated as a causal factor (Newell *et al.* 2013) because it was identified as the cause of death of *M. fleayi* at two locations (Berger *et al.* 1998), and it has been recorded in *M. fleayi* where declines have occurred (Berger *et al.* 1998; Symonds *et al.* 2007; Murray *et al.* 2010; Newell *et al.* 2013). Furthermore, it has been implicated in the decline and extinction of other species within the region where *M. fleayi* occurs (Skerratt *et al.* 2007).

In response to the apparent decline of *M. fleayi*, detailed research was undertaken at two locations in north-east New South Wales during the period 2001–08 (Newell *et al.* 2013). This revealed that a recovery in abundance had occurred. Initial population estimates were very low, but increased by up to 10-fold before reaching a plateau in the final four years of study.

^ASchool of Environment, Science and Engineering, Southern Cross University, PO Box 157, Lismore, NSW 2480, Australia.

^BCorresponding author. Email: ross.goldingay@scu.edu.au

This is one of the very few cases of an Australian frog showing recovery following a severe decline in the presence of *Bd*. However, species that have suffered declines from chytridiomycosis may be affected by continuing bouts of infection, and therefore, may be at risk of recurrent declines (Murray *et al.* 2009; Phillott *et al.* 2013). Thus, there is considerable biological interest in determining whether *M. fleayi* has maintained population stability since 2008 or suffered another decline.

Mixophyes fleavi is a Federal and State (New South Wales and Queensland) listed endangered species for which there is a need for periodic monitoring to determine population status, population trends and response to management actions (if any occur) (Hines et al. 2002). The New South Wales government has recently introduced a new approach to managing its threatened species that includes population monitoring (OEH 2013). The monitoring framework requires actions that are measureable and cost-effective (OEH 2014). At present, there is no agreed approach to monitoring the endangered M. fleavi. Our study addresses this information gap by testing a program of population monitoring that could be employed across a single season to provide a snapshot of local population abundance. When combined with earlier data, this will reveal how a population of M. fleavi is tracking, which is the main point of interest. We confront a challenge that others will also confront in that the data from different approaches may not be directly comparable. The earlier study of Newell et al. (2013) employed variable survey effort across variable periods, which led to the pooling of survey occasions for analysis. In the present study we had the opportunity to employ what is referred to as a 'robust design' in which sampling consists of secondary sampling events nested within primary sampling events, to allow for a population being closed over short intervals but open over long intervals (Pollock 1982). However, different approaches may not produce equal estimates of population size. To address this issue we used two population models to estimate local abundance. Thus, the aims of our study were to estimate population size based on a 'robust' sampling design and to determine whether the study population has remained at an equivalent level to that estimated five years earlier.

Methods

Study species

Mixophyes fleayi is known to exist at ~30 disjunct locations in a narrow range from the Conondale Range in south-eastern Queensland to the Yabbra Scrub in north-eastern New South Wales (Hines et al. 1999; Newell et al. 2013). It is a large, nocturnal, stream-breeding frog (Fig. 1) that is intermittently active from August to March. Male frogs form aggregations near suitable oviposition sites along streams (Stratford et al. 2010; Knowles et al. 2015), and call to defend territories and 'advertise' to female frogs. When inactive, M. fleayi seeks shelter beneath leaf litter and debris on the rainforest floor.

Study site

The study was conducted at one site where an increase in abundance of *M. fleayi* was documented between 2001 and 2008 (Newell *et al.* 2013) after a period of decline. Brindle Creek (28°22′S, 153°04′E) (Fig. 2) is situated within Border Ranges



Fig. 1. A male Fleay's barred frog (photo: R. Goldingay).



Fig. 2. Brindle Creek in Border Ranges National Park, New South Wales (photo: D. Newell).

National Park, north-eastern New South Wales, which forms part of the World Heritage—listed Gondwana Rainforest Reserves of Australia. It is a first-order stream at an elevation of 740 m. The original 200 m transect was utilised to enable comparison of population parameters between studies. The Brindle Creek local population represents one of few local populations of *M. fleayi* within Border Ranges National Park.

Survey design

Capture–mark–recapture (CMR) data were collected using the 'Robust Design' of Pollock (1982). The sampling scheme was structured into four primary samples (sessions) between 16 September 2013 and 19 February 2014. The site was surveyed for three consecutive nights (secondary samples) within each session. The sessions were selected on the basis of recent or forecast rainfall. At least 20 mm of rain fell during the five days preceding our sampling. Sessions were separated by sufficient intervals (32–54 days) so that gains and losses to the population could occur. We assumed that the population was closed during the secondary sampling occasions (Kendall and Nichols 1995; Kendall *et al.* 1997; Kendall 1999).

We collected CMR data using the methods of Newell *et al.* (2013). The creek and adjacent banks were traversed slowly just after nightfall, alternating the transect start and finish on consecutive nights in case individuals initiated activity at different times of the night. Prerecorded calls of *M. fleayi* and

216 Australian Journal of Zoology G. Quick et al.

mimicry were used to elicit responses from sheltering males, and frogs were subsequently located by eye-shine from spotlights and head torches. The calls of concealed frogs in cryptic habitats were triangulated by three searchers to assist capture. Frogs were captured by hand in separate plastic bags and scanned with a portable tag reader (Trovan Ltd, Douglas, UK) and visually examined to determine whether they had been tagged in previous surveys. Untagged individuals were implanted dorsally and subcutaneously with a passive integrated transponder (PIT) tag and the entry site sealed with medical grade cyanoacrylate (Vetbond) adhesive. The PIT tag number, sex, weight, snout-vent length and capture location for all individuals were recorded before release at their initial capture location. Sex was determined on the basis of the weight and size of the frog, the presence or absence of nuptial pads and calling activity. The ambient temperature, humidity and rainfall intensity were recorded at the start and finish of each survey. Surveys took between 2.5 and 5.5 h per night depending on the number of personnel and the number of captured frogs.

Data analysis

Capture histories were constructed for each frog. Program MARK was used to estimate demographic parameters and to test models of variables that influence these parameters (White and Burnham 1999). Program MARK uses maximum-likelihood methods to estimate parameters. We used two different model designs that have been used to estimate demographic parameters of Australian frogs previously: robust design (Pickett et al. 2014), and the POPAN formulation of the Jolly-Seber model (Newell et al. 2013). For the POPAN design, the capture histories were reduced to indicate whether a frog was captured on at least one night in the four primary sample sessions. Candidate models were run in which parameter values varied over time and/or were constant over time. The influence of rainfall, temperature and humidity were assessed as covariates on the probability of capture and recapture on the expectation that weather would influence frog activity.

Models were compared using the Akaike Information Criterion (AICc) corrected for small sample size (Burnham and

Anderson 2002). Models were ranked from smallest to largest AICc value with the top ranked model showing the best fit to the data. The difference in AICc (\triangle AICc) between the top model and any other model was used to determine the plausibility of each model. Models with $\triangle AICc < 2$ are equally plausible; models with $\triangle AICc = 2-7$ are different but if $\triangle AICc > 7$ it suggests that models are very different (Burnham and Anderson 2002). A goodness-of-fit test was conducted on the fully time-dependent model for each design. This essentially examines whether there has been violation of two key assumptions, that individuals have equal probability of capture and equal probability of survival. Goodness-of-fit was tested within MARK using the program RELEASE for the POPAN design. This indicated that there was no significant lack of fit ($\chi^2 = 3.50$, d.f. = 4, P = 0.48). There is no comprehensive test of goodness-of-fit for the robust design in program Mark (White and Burnham 1999); however, this was assessed using program U-Care ver. 2.3.2 (Choquet et al. 2009). This indicated that there was no significant lack of fit ($\chi^2 = 19.67$, d.f. = 16, P = 0.24).

In the robust design, models were developed with temporary emigration as random or Markovian and constant or varying by primary session. For Markovian temporary emigration models in which apparent survival varied by the interval between primary samples, the emigration (γ'') and immigration parameters (γ') for the last interval were set equal to those for the second-last interval (Kendall *et al.* 1997).

Results

Overall, a total of 54 frogs (45 males, 6 females, 3 juveniles) were captured on 230 occasions. Three amplecting pairs were encountered. Across the study, 17 frogs were captured in September, 21 (15 recaptures) in November, 32 (19 recaptures) in January and 38 (29 recaptures) in February.

Robust design

The model with the lowest AICc value was 4.4 times better fitting than the next model based on AICc weight (Table 1). In the best model, apparent survival $(1.0 \pm 0.0, \text{ s.e.})$ and both temporary

Table 1. Comparison of candidate models for Mixophyes fleayi mark-recapture data at Brindle Creek, New South Wales

 ϕ , apparent survival; γ'' , the probability of being off the study area, given that the animal was off the study area at the previous capture session; γ' , the probability of being off the study area, given that the animal was in the study area at the previous capture session; p, probability of capture; pent, probability of entry; c, probability of recapture; (.), constant; t, time varying; R (rain), ≥ 20 mm of rainfall in the three days prior to, or during, the three days of survey as measured at the closest rainfall station; T (temperature), ambient temperature measured at the start of each survey occasion; T (the start of each survey occasion)

Model	AICc	ΔΑΙСc	AICc weight	Model likelihood	No. of parameters	Deviance
Robust design						
$\phi(.) \gamma''(.) \gamma'(=\gamma'') p(R+T) c(R+T)$	463.46	0.00	0.74	1.00	8	466.77
$\phi(.) \gamma''(.) \gamma'(=\gamma'') p(R) c(R)$	466.46	3.00	0.17	0.22	6	454.06
$\phi(.) \gamma''(.) \gamma'(t) p(R) c(R)$	468.20	4.74	0.07	0.10	9	449.34
$\phi(.) \gamma''(.) \gamma'(t) p(R) c(R)$	469.95	6.49	0.03	0.04	8	453.26
POPAN						
$\phi(.) p(.) \text{ pent}(.)$	94.89	0	0.49	1.0	4	0
$\phi(.) p(.) \text{ pent(t)}$	95.87	0.98	0.30	0.61	6	0
$\phi(t) p(.) \text{ pent}(t)$	97.55	2.66	0.13	0.26	7	0
$\phi(t) p(.) \text{ pent}(.)$	98.57	3.68	0.08	0.16	6	0

emigration parameters were constant ($\gamma''=\gamma'$) over time (0.15 ± 0.05) with the probability of capture $(0.47\pm0.13$ to 0.95 ± 0.04 per session) and recapture $(0.40\pm0.07$ to 0.72 ± 0.05 per session) varying with weather. Models with detection probability fitted as a function of rainfall and temperature during each survey period were found to fit better that the model fitted with detection as constant over sampling occasions. Rain and temperature had a positive influence on initial capture (β =1.95, 0.39, respectively) but a negative influence on recapture (β =-1.14, -0.07, respectively). Models with humidity as a covariate were not among the top models. Abundance was estimated at 38.2 ± 0.5 in the February session when the population was at its highest.

POPAN design

Analysis with the POPAN design showed that the best-fitting model was that in which survival, recapture and the probability of entry were constant over time (Table 1). This model had 1.6 times as much support as the next model. A constant model with the inclusion of rain was within 2 Δ AICc of the top model. In this case rain represents an uninformative parameter (see Arnold 2010) that provides no better fit but is supported because it is added to a top model. This model has not been included in the top models (Table 1). Model averaging was applied to estimate parameters. Survival was estimated at 1.00 ± 0.02 per month, recapture as 0.84 ± 0.05 per month, and the probability of entry varied from 0.15 ± 0.04 to 0.24 ± 0.05 across occasions. Abundance was estimated for the fourth survey occasion with model averaging at 46.0 ± 2.7 individuals.

Discussion

Population stability

Population monitoring is fundamental to threatened species conservation in order to determine population stability over time (Lindenmayer et al. 2003; Lewis and Goldingay 2005; Wayne et al. 2013; OEH 2014; Willacy et al. 2015). We aimed to determine whether M. fleayi exhibited population stability within our study area at Brindle Creek and, in doing so, provide the basis for a long-term monitoring program. Our study follows on from another at the same location (Newell et al. 2013) in which the number of male frogs was estimated at 53.2 ± 10.0 (95% CI = 33.6–72.8) in 2008 based on a POPAN model. In the current study we estimated the population size of male frogs at 46.0 (95% CI = 40.7-51.4) (POPAN) and 38.2 (95% CI = 38.0-41.0) (RD). This represents a lower population size than five years earlier. We do not know how the population behaved in the intervening five years but our data do not suggest a decline has occurred given the overlap in the new and previous POPAN estimates.

The lower estimate from the RD model suggests that caution is required when comparing estimates from different models and consistency in model comparison is required. The POPAN model may consistently give higher estimates than the RD model (see Tezanos-Pinto *et al.* 2013). The monthly estimates of apparent survival across our five-month study period were 1.0 ± 0.0 for both model types, suggesting very high survival during the active season. Our recapture estimates were also high, at 0.83 ± 0.06 per month (POPAN) and ranging from 0.40 ± 0.07 to 0.72 ± 0.05 per session (RD). These values are consistent with previous

estimates of survival and recapture at this location (Newell et al. 2013). It is to be expected that annual population size will vary in response to environmental variation in Australian frogs (e.g. Bull and Williamson1996; Lewis and Goldingay 2005; Pickett et al. 2014). This suggests that some caution is needed in describing population trajectory when surveys are conducted at greater than annual intervals. Furthermore, frogs exhibit seasonal variation in abundance (Richards and Alford 2005; Pickett et al. 2014) so comparison of population estimates must be for equivalent times of the year. We observed a doubling in abundance of M. fleavi between September and February, so abundance for late summer should be used to characterise population size. The top RD model included rain and temperature whereas the top POPAN model did not. This difference is most likely because the capture data were pooled across occasions for the POPAN model so there was less variation in these parameters. We timed our survey occasions to coincide with periods of rain so one would expect this parameter to have limited influence. Rain was not included in the top POPAN model of Newell et al. (2013) at this location.

Our population estimates are for adult male frogs only. Adult female frogs were rarely encountered, which is consistent with population studies on the stream-breeding frogs *Litoria genimaculata* (Richards and Alford 2005), *L. pearsoniana* (Murray *et al.* 2009), *L. rheocola* (Phillott *et al.* 2013), and *Espadarana* (*Centrolene*) *prosoblepon* (McCaffery and Lips 2013). Our previous population estimates for Brindle Creek were also based only on male captures (Newell *et al.* 2013). We assume that the trajectory of the female segment of the population follows a similar path to that of the males. If a decline occurred among females this would be reflected in low recruitment rates and a decline in the abundance of adult males over subsequent years. Further studies are needed to understand the behaviour and habitat use of females.

Recent research in the Queensland wet tropics has demonstrated that two lowland populations of L. rheocola have persisted for 15 years after Bd infection (Phillott et al. 2013). Intensive CMR surveys revealed that annual adult survival was low (12-15%) due to high Bd prevalence but that high recruitment (71-91%) appeared to compensate. Phillott et al. (2013) concluded that L. rheocola and other species similarly infected with Bd were still vulnerable to decline if other threatening factors disrupted recruitment. Murray et al. (2009) found that Bd substantially reduced monthly survival probabilities of L. pearsoniana in south-east Queensland even after a 30-year period of coexistence. In these cases, a high level of recruitment or juvenile survival is required to balance mortality (see also Muths et al. 2011; Lampo et al. 2012; McCaffery and Lips 2013). This scenario does not seem to apply to M. fleavi, which has high annual survival and is long-lived (Newell et al. 2013). High levels of survival have been observed in other streambreeding species infected with Bd (e.g. Retallick et al. 2004).

Implications for management

The Brindle Creek local population of *M. fleayi* appears to have remained relatively stable over 10 years. We recommend continued monitoring because the population may still be at risk of future decline. However, monitoring could now occur at 5-year intervals. We have demonstrated a program of sampling that

should be adopted by future monitoring, involving four primary sample periods of three nights, spread across the active period of *M. fleayi* and timed to coincide with wet periods as in this study. Due to the high capture probability associated with males of this species, transect counts without capture during wet periods could be employed to cover a much broader spatial area to enable an estimate of the size of the broader population.

Abundance monitoring should also be extended to *M. fleayi* at other locations because knowledge of the stability of other populations is required to understand whether this species is adequately conserved. Species subject to previous *Bd*-related declines and range contractions may re-expand their distributions to new areas or areas of past occupancy (Scheele *et al.* 2014). Thus, monitoring should continue at remnant sites but expand to determine whether the recovery at Brindle Creek is indicative of range-wide recovery.

Lastly, understanding the dynamics of *Bd* infections is central to the conservation of species such as *M. fleayi* that are postulated to have previously undergone *Bd*-induced declines. *Mixophyes fleayi* provides an ideal opportunity to investigate the interaction between infection and individual survival because the capture probability of individuals is very high (frequently >0.6) and individuals may be long-lived (>6 years: Newell *et al.* 2013). These attributes are unusual among stream-breeding frogs (see Richards and Alford 2005; Phillott *et al.* 2013) so *M. fleayi* may provide opportunities for investigation not available with other species. *Litoria pearsoniana*, which is still susceptible to *Bd* infection (Murray *et al.* 2009), is also present at Brindle Creek so a comparison with *M. fleayi* would be invaluable.

Acknowledgements

We thank Sophy Millard, Josh McKenna, Caroline Murray, Sophie Lancaster-Pembroke and Dusty Thomas for assistance in field surveys.

References

- Alford, R. A., and Richards, S. J. (1999). Global amphibian declines: a problem in applied ecology. *Annual Review of Ecology and Systematics* 30, 133–165. doi:10.1146/annurev.ecolsys.30.1.133
- Arnold, T. W. (2010). Uninformative parameters and model selection using Akaike's information criterion. *Journal of Wildlife Management* **74**, 1175–1178. doi:10.1111/j.1937-2817.2010.tb01236.x
- Beebee, T. J. C., and Griffiths, R. A. (2005). The amphibian decline crisis: a watershed for conservation biology? *Biological Conservation* 125, 271–285. doi:10.1016/j.biocon.2005.04.009
- Bell, B. D., Carver, S., Mitchell, N. J., and Pledger, S. (2004). The recent decline of a New Zealand endemic: how and why did populations of Archey's frog *Leiopelma archeyi* crash over 1996–2001? *Biological Conservation* 120, 189–199. doi:10.1016/j.biocon.2004.02.011
- Berger, L., Speare, R., Daszak, P., Green, D. E., Cunningham, A. A., Goggin, C. L., Slocombe, R., Ragan, M. A., Hyatt, A. D., McDonald, K. R., Hines, H. B., Lips, K. R., Marantelli, G., and Parkes, H. (1998). Chytridiomycosis causes amphibian mortality associated with population declines in the rain forests of Australia and Central America. *Proceedings of the National Academy of Sciences of the United States of America* 95, 9031–9036. doi:10.1073/pnas.95.15.9031
- Bosch, J., Martínez-Solano, I., and García-París, M. (2001). Evidence of a chytrid fungus infection involved in the decline of the common midwife toad (*Alytes obstetricans*) in protected areas of central Spain. *Biological Conservation* 97, 331–337. doi:10.1016/S0006-3207(00)00132-4

- Bull, C. M., and Williamson, I. (1996). Population ecology of the Australian frog *Crinia signifera*: adults and juveniles. *Wildlife Research* 23, 249–266. doi:10.1071/WR9960249
- Burnham, K. P., and Anderson, D. R. (2002). 'Model Selection and Multimodel Inference: a Practical Information-Theoretic Approach.' (Springer-Verlag: New York.)
- Choquet, R., Lebreton, J. D., Gimenez, O., Reboulet, A. M., and Pradel, R. (2009). U-CARE: utilities for performing goodness of fit tests and manipulating CApture–REcapture data. *Ecography* 32, 1071–1074. doi:10.1111/j.1600-0587.2009.05968.x
- Goldingay, R. L., Newell, D. A., and Graham, M. (1999). Status of rainforest stream frogs in north-eastern New South Wales: decline or recovery? In 'Declines and Disappearances of Australian Frogs'. (Ed. A. Campbell.) pp. 64–71. (Environment Australia: Canberra.)
- Hero, J.-M., Morrison, C., Gillespie, G., Roberts, J. D., Newell, D., Meyer, E., McDonald, K., Lemckert, F., Mahony, M., Osborne, W., Hines, H., Richards, S., Hoskin, C., Clarke, J., Doak, N., and Shoo, L. (2006). Overview of the conservation status of Australian frogs. *Pacific Conservation Biology* 12, 313–320.
- Hines, H. B. and the South-east Queensland Threatened Frogs Recovery Team (2002). Recovery plan for stream frogs of south-east Queensland 2001–2005. Report to Environment Australia, Canberra. Queensland Parks and Wildlife Service. Brisbane.
- Hines, H., Mahony, M., and McDonald, K. (1999). An assessment of frog declines in wet subtropical Australia. In 'Declines and Disappearances of Australian Frogs'. (Ed. A. Campbell.) pp. 44–63. (Environment Australia: Canberra.)
- Kendall, W. L. (1999). Robustness of closed capture–recapture methods to violations of the closure assumption. *Ecology* 80, 2517–2525. doi:10.1890/0012-9658(1999)080[2517:ROCCRM]2.0.CO;2
- Kendall, W. L., and Nichols, J. D. (1995). On the use of secondary capture– recapture samples to estimate temporary emigration and breeding proportions. *Journal of Applied Statistics* 22, 751–762. doi:10.1080/ 02664769524595
- Kendall, W. L., Nichols, J. D., and Hines, J. E. (1997). Estimating temporary emigration using capture–recapture data with Pollock's robust design. *Ecology* 78, 563–578. doi:10.1890/0012-9658(1997)078[0563:ETEUCR] 2.0.CO:2
- Knowles, R., Thumm, K., Mahony, M., Hines, H., Newell, D., and Cunningham, M. (2015). Oviposition and egg mass morphology in barred frogs (Anura: Myobatrachidae: Mixophyes Günther, 1864), its phylogenetic significance and implications for conservation management. Australian Zoologist 37, 381–402. doi:10.7882/AZ.2014.040
- Kriger, K. M., and Hero, J. M. (2007). Large-scale seasonal variation in the prevalence and severity of chytridiomycosis. *Journal of Zoology* 271, 352–359.
- Kriger, K. M., and Hero, J. M. (2008). Altitudinal distribution of chytrid (Batrachochytrium dendrobatidis) infection in subtropical Australian frogs. Austral Ecology 33, 1022–1032. doi:10.1111/j.1442-9993.2008. 01872.x
- Lampo, M., Celsa, S. J., Rodríguez-Contreras, A., Rojas-Runjaic, F., and García, C. Z. (2012). High turnover rates in remnant populations of the harlequin frog *Atelopus cruciger* (Bufonidae): low risk of extinction? *Biotropica* 44, 420–426. doi:10.1111/j.1744-7429.2011.00830.x
- Laurance, W. F., McDonald, K. R., and Speare, R. (1996). Epidemic disease and the catastrophic decline of Australian rain forest frogs. *Conservation Biology* 10, 406–413. doi:10.1046/j.1523-1739.1996.10020406.x
- Lewis, B. D., and Goldingay, R. L. (2005). Population monitoring of the vulnerable wallum sedge frog (*Litoria olongburensis*) in north-eastern New South Wales. *Australian Journal of Zoology* 53, 185–194. doi:10.1071/ZO03063
- Lindenmayer, D. B., Cunningham, R. B., MacGregor, C., Incoll, R. D., and Michael, D. (2003). A survey design for monitoring the abundance of arboreal marsupials in the Central Highlands of Victoria. *Biological Conservation* 110, 161–167. doi:10.1016/S0006-3207(02)00171-4

- McCaffery, R., and Lips, K. (2013). Survival and abundance in males of the glass frog *Espadarana* (*Centrolene*) prosoblepon in central Panama. *Journal of Herpetology* 47, 162–168. doi:10.1670/11-327
- Murray, K. A., Skerratt, L. F., Speare, R., and McCallum, H. (2009). Impact and dynamics of disease in species threatened by the amphibian chytrid fungus, *Batrachochytrium dendrobatidis*. *Conservation Biology* 23, 1242–1252. doi:10.1111/j.1523-1739.2009.01211.x
- Murray, K., Retallick, R., McDonald, K. R., Mendez, D., Aplin, K., Kirkpatrick, P., Berger, L., Hunter, D., Hines, H. B., Campbell, R., Pauza, M., Driessen, M., Speare, R., Richards, S. J., Mahony, M., Freeman, A., Phillott, A. D., Hero, J.-M., Kriger, K., Driscoll, D., Felton, A., Puschendorf, R., and Skerratt, L. F. (2010). The distribution and host range of the pandemic disease chytridiomycosis in Australia, spanning surveys from 1956–2007. *Ecology* 91, 1557–1558. doi:10.1890/09-1608.1
- Muths, E., Scherer, R. D., and Pilliod, D. S. (2011). Compensatory effects of recruitment and survival when amphibian populations are perturbed by disease. *Journal of Applied Ecology* 48, 873–879. doi:10.1111/j.1365-2664.2011.02005.x
- Newell, D. A., Goldingay, R. L., and Brooks, L. O. (2013). Population recovery following decline in an endangered stream-breeding frog (*Mixophyes fleayi*) from subtropical Australia. *PLoS One* 8, e58559. doi:10.1371/journal.pone.0058559
- OEH (2013). Saving our species technical report. Office of Environment & Heritage, Sydney.
- OEH (2014). Monitoring, evaluation and reporting framework: approach to conservation projects for site-managed species. Office of Environment & Heritage, Sydney.
- Ouellet, M., Mikaelian, I., Pauli, B. D., Rodrigue, J., and Green, D. M. (2005). Historical evidence of widespread chytrid infection in North American amphibian populations. *Conservation Biology* 19, 1431–1440. doi:10.1111/ j.1523-1739.2005.00108.x
- Phillott, A. D., Grogan, L. F., Cashins, S. D., McDonald, K. R., Berger, L., and Skerratt, L. F. (2013). Chytridiomycosis and seasonal mortality of tropical stream-associated frogs 15 years after introduction of *Batrachochytrium* dendrobatidis. Conservation Biology 27, 1058–1068. doi:10.1111/cobi. 12073
- Pickett, E. J., Stockwell, M. P., Bower, D. S., Pollard, C. J., Garnham, J. I., Clulow, J., and Mahony, M. J. (2014). Six-year demographic study reveals threat of stochastic extinction for remnant populations of a threatened amphibian. *Austral Ecology* 39, 244–253. doi:10.1111/aec.12080
- Pollock, K. H. (1982). A capture–recapture design robust to unequal probability of capture. *Journal of Wildlife Management* 46, 752–757.
- Retallick, R. W. R., McCallum, H., and Speare, R. (2004). Endemic infection of the amphibian chytrid fungus in a frog community post-decline. *PLoS Biology* 2, e351. doi:10.1371/journal.pbio.0020351
- Richards, S. J., and Alford, R. A. (2005). Structure and dynamics of a rainforest frog (*Litoria genimaculata*) population in northern Queensland. *Australian Journal of Zoology* 53, 229–236. doi:10.1071/ZO03036

- Scheele, B. C., Guarino, F., Osborne, W., Hunter, D. A., Skerratt, L. F., and Driscoll, D. A. (2014). Decline and re-expansion of an amphibian with high prevalence of chytrid fungus. *Biological Conservation* 170, 86–91. doi:10.1016/j.biocon.2013.12.034
- Schloegel, L. M., Hero, J.-M., Berger, L., Speare, R., McDonald, K., and Daszak, P. (2006). The decline of the sharp-snouted day frog (*Taudactylus acutirostris*): the first documented case of extinction by infection in a free-ranging wildlife species. *EcoHealth* 3, 35–40. doi:10.1007/s10393-005-0012-6
- Skerratt, L. F., Berger, L., Speare, R., Cashins, S., McDonald, K. R., Phillott, A. D., Hines, H. B., and Kenyon, N. (2007). Spread of chytridiomycosis has caused the rapid global decline and extinction of frogs. *EcoHealth* 4, 125–134. doi:10.1007/s10393-007-0093-5
- Stratford, D. S., Grigg, G. C., McCallum, H. I., and Hines, H. B. (2010). Breeding ecology and phenology of two stream breeding myobatrachid frogs (*Mixophyes fleayi* and *M. fasciolatus*) in south-east Queensland. *Australian Zoologist* 35, 189–197. doi:10.7882/AZ.2010.007
- Stuart, S. N., Chanson, J. S., Cox, N. A., Young, B. E., Rodrigues, A. S. L., Fischman, D. L., and Waller, R. W. (2004). Status and trends of amphibian declines and extinctions worldwide. *Science* 306, 1783–1786. doi:10.1126/science.1103538
- Symonds, E. P., Hines, H. B., Bird, P. S., Morton, J. M., and Mills, P. C. (2007). Surveillance for *Batrachochytrium dendrobatidis* using *Mixophyes* (Anura: Myobatrachidae) larvae. *Journal of Wildlife Diseases* 43, 48–60. doi:10.7589/0090-3558-43.1.48
- Tezanos-Pinto, G., Constantine, R., Brooks, L., Jackson, J. A., Mourão, F., Wells, S., and Baker, C. S. (2013). Decline in local abundance of bottlenose dolphins (*Tursiops truncatus*) in the Bay of Islands, New Zealand. *Marine Mammal Science* 29, E390–E410.
- Venesky, M. D., Raffel, T. R., McMahon, T. A., and Rohr, J. R. (2014). Confronting inconsistencies in the amphibian–chytridiomycosis system: implications for disease management. *Biological Reviews of the Cambridge Philosophical Society* 89, 477–483. doi:10.1111/brv.12064
- Wayne, A. F., Maxwell, M. A., Ward, C. G., Vellios, C. V., Wilson, I., Wayne, J. C., and Williams, M. R. (2013). Importance of getting the numbers right: quantifying the rapid and substantial decline of an abundant marsupial, *Bettongia penicillata*. *Wildlife Research* 40, 169–183. doi:10.1071/WR12115
- White, G. C., and Burnham, K. P. (1999). Program MARK: survival estimation from populations of marked animals. *Bird Study* **46**, S120–S139. doi:10.1080/00063659909477239
- Willacy, R. J., Mahony, M., and Newell, D. A. (2015). If a frog calls in the forest: bioacoustic monitoring reveals the breeding phenology of the endangered Richmond Range mountain frog (*Philoria richmondensis*). *Austral Ecology*, in press. doi:10.1111/aec.12228

Handling Editor: Phillip Cassey