Climate Change and Australia's frogs: how much do we need to worry?

Francis Lemckert[1,*] and Trent Penman[1,2]

[1]Forest Science Centre, NSW Department of Primary Industries

PO Box 100, Beecroft, NSW. 2119. Australia. Current address: Environmental Heritage, PO Box W36 Parramatta NSW, 2150

[2]Current location: Centre for Environmental Risk Management of Bushfires, School of Biological Sciences, University of Wollongong. NSW. 2522. Australia

*Corresponding Author: Francis Lemckert. Email flemckert@niche-eh.com,

Fax: +61 2 98716941

ABSTRACT

Three aspects of the biology of anurans indicate that climate change could have a significant impact on these vertebrates: a) they are ectotherms and ambient temperatures can strongly influence their activity, b) a permeable skin requires them to have regular access to sources of moisture, and c) most species require free water for larval development. Research from the northern hemisphere suggests climatic changes have already impacted amphibians through changes in breeding phenology, loss of breeding sites, changes in moisture regimes and a possible increased impact of disease. Such impacts have yet to be tested for or detected in Australia's species, which are adapted to different environments and have different ancestries. Species of most concern are narrow range, montane species with unique breeding strategies and that occupy consistently moist environments. Recent predictive modeling however, has suggested that species with much broader distributions could experience significant range reductions by 2070, mainly as a result of a reduction in seasonal rainfall patterns. Changes in the frequency and regularity of rainfall may result in detrimental shifts in pond hydroperiod and this could negatively impact many species. Further research is required to determine just which species are at significant risk from predicted climate changes and generate discussion on appropriate adaptive strategies.

Key words: anuran, climate change, temperature, rainfall

Introduction

Anurans are the most successful group of amphibians on the planet, with over 5000 species being currently recognized and with many more expected to be named. As a group they have been present on earth since the Jurassic Period, at least 150 million years ago (Duellman and Trueb 1986) and have colonised every continent at various periods of the earth's history, including Antarctica. Amphibians may be found in such extreme environments as sub-arctic tundra, tidal estuaries, mountain peaks and hot deserts (Duellman and Trueb 1986). Within Australia, frogs are the only naturally occurring amphibian group and form a very important part of the vertebrate fauna. Fossil frogs dating back to 50 million years ago are known within Australia (Roberts and Watson 1993), and frogs are likely to have been present for somewhat longer in view of their distinctive lineages.

Despite the ability of frogs to exist in a range of environments, anurans are currently under significant population stress, with major declines having occurred in many species in all parts of the world (Stuart *et al.* 2004; McCallum 2007). Australian has been as severely affected as parts of the world with at least three species being considered extinct, several more possibly so, and nearly 25% of 216 species considered to be under threat of extinction (Hero *et al.* 2006). Declines have been attributed to many factors, including land clearance and modification, fragmentation of habitats, pollution, and introduced predators and competitors (Keisecker *et al.* 2001; Collins and Storfer 2003). Of particular importance has been the amphibian chytrid fungus that appears to have caused a wave of rapid and often catastrophic declines in Australia (and the rest of the world) through the 1980s and 1990s (Berger *et al.*. 1998; James *et al.*. 2009). The reduced frog populations may be more susceptible to other threatening processes, and may be less able to respond to environmental changes either because they have a reduced genetic diversity or cannot share the available genetic diversity amongst increasingly isolated populations.

Climate change appears to be an emerging major threat to the world's anurans as it can strike at a global scale and is likely to affect many populations. Anurans are considered to be highly susceptible to climate change because they are ectothermic, have permeable skins and generally rely on the availability of free water for successful reproduction (Carey and Alexander 2003). Climate change models for Australian suggest a general trend towards higher temperatures and changed rainfall patterns across the continent (Suppiah *et al.* 2007). Hence, there can be expected to be impacts on Australian amphibian populations over the next 100 years.

Pp 92 - 98 in *Wildlife and Climate Change: towards robust conservation strategies for Australian fauna*, edited by Daniel Lunney and Pat Hutchings, 2012. Royal Zoological Society of NSW, Mosman, NSW, Australia.

Predicted Climate Changes in Australia

Expectations as to how the climate in Australia will change vary depending on the model and greenhouse gas emission scenario used. For the purposes of this paper, only broad climatic assessments will be considered. Fortunately, all models forecast similar general climatic changes for Australia. The technical report prepared for the Australian Government (see http://climatechangeinaustralia.com.au/technical_report.php) indicates that the most likely climatic changes to occur over the next 60 years include:

a. Temperatures will increase across the continent. Southern and north-eastern Australia will see the smallest rises and the inland areas of the continent the greatest. Overall, temperatures are expected to rise at least an average of 1.8ºC and up to an average of 3.4ºC (in the highest warming scenarios). The north-west of Australia is the area expected to have the greatest rises.

b. The estimates for rainfall change are much less consistent and/or certain with models having greater variations in predicted outcomes, often providing an almost equal chance of annual increases in rainfall as decreases. However, the general trend is for slight declines to occur. The lower estimates for changes in rainfall by 2070 indicate that annual rainfall will tend to remain the same in northern Australia, but grade to around a 7.5% decrease in southern Australia. Under the more extreme models, annual rainfall in the far north still remains the same, but grades down to around a 10% decrease in annual rainfall in southern Australia. Note that the predicted change in southern areas ranges from -30% to +5% in the model, so there is a reasonable degree of uncertainty as to just what change will occur.

c. Of added importance is the predicted change in the seasonality of rainfall. In the south-west of Australia, rainfall will shift away from the current winter and spring rainy season (declining by up to 40%) to a pattern of greater summer rainfall. A similar but less pronounced pattern is evident for most of southern Australia, providing a significant change in the timing of larger rainfall events.

d. Models also show an increase in daily precipitation intensity and an associated increase in the number of dry days annually. This means that rainfall events will be less frequent, but will be heavier when they do occur, leading to the overall minor or no reductions in annual rainfall levels throughout Australia. Notably, daily precipitation intensity is not expected to increase in southern parts of Australia and so will not compensate for the expected reduction in the number of rainy days. This is the reason for the predicted stronger decreases in mean rainfall in parts of southern Australia.

Climate Change and Frogs

Changes in rainfall patterns are of obvious importance as anurans in Australia are dependent on water for successful reproduction. The majority (> 90%) of Australian species follow the typical anuran pattern of laying eggs into, on or immediately adjacent to water, with tadpoles hatching from the eggs after 1-7 days and then developing as free living aquatic individuals until metamorphosing into frogs (Cogger 2000). The tadpole stage usually lasts two to three months, but can be as little as two weeks or take over a year (Anstis 2002). The length of the tadpole stage is often strongly tied to the expected hydroperiod of the breeding site, hence changes in rainfall patterns that lead to reduced or altered periods of free water availability can lead directly to increased reproductive failure.

Notably, a number of Australian anuran species have evolved a significant terrestrial component to their larval stage (see Anstis 2002) and are likely to be even more susceptible to changes in rainfall patterns. There are species that lay eggs into moist "nest" areas that subsequently flood, with the tadpoles hatching and developing in free water (e.g., *Pseudophryne* spp. and *Heleioporus* spp.). Species of *Philoria* lay foamy egg masses into soaked nest areas but, upon emergence, the tadpoles remain in the nest and develop into frogs without free water. *Assa darlingtoni* lays eggs into wet situations on forest floors and the hatched tadpoles are taken into pouches on the backs of the male to complete development. Finally, some species have development that occurs completely within the egg stage with fully formed froglets emerging (e.g., *Arenophryne* and *Myobatrachus*). Such unusual strategies have generally been developed in response to unusual environmental conditions (eg, consistently wet montane areas – *Philoria* spp., or areas with little available free water - *Arenoprhyne*). There is a strong reliance on microhabitats that retain relatively high levels of moisture that will prevent desiccation of the eggs and/or tadpoles. Natural declines in moisture levels have been demonstrated to cause hydrological stress and egg mortality in a species of *Philoria* (Seymour *et al.* 1995) and declines in rainfall are very likely to affect most or all species with these unusual reproductive habits.

Anurans also have a permeable skin and most species have a very limited ability to regulate water loss from their bodies into a dry surrounding environment (see Duellman and Trueb 1986) and this is the case for Australian frog species (e.g., Tracy *et al.* 2008). Anurans are dependent on the availability of surface and ground moisture to be able to forage and migrate between habitats and when entering periods of inactivity. This is of most importance in species adapted to constantly moist environments and changes in rainfall patterns will alter moisture availability and may impact upon species tied to existing moisture regimes.

Thirdly, anurans are ectotherms. They do not generate significant amounts of their own body heat and essentially conform to available environmental temperatures. Most species are inactive during the colder parts of the year when they enter periods of aestivation (Cogger 2000). As for all vertebrates, frogs have a preferred temperature range in which they operate most effectively (Brattstrom 1963, 1970). Reproductive activity in particular, is tied to temperature for most species, with calling and breeding migratory events activity being strongly influenced by ambient temperatures (Dankers 1977; Humphries 1979; Lemckert 2001; Penman *et al.* 2006; Lemckert and Grigg 2010). Changes in temperature patterns have the potential to significantly change frog activity patterns.

Current Evidence for Climate Change Impacts on Frogs

The evidence for climate change induced impacts on frogs remains limited, but a few studies have found impacts that would be predicted under observed increases in temperatures and/or changes in rainfall and moisture patterns. Declines in frog populations in Yellowstone National Park between 1992 and 2008 corresponded with the longest droughts and highest temperatures recorded for the spring/summer period in over 100 years, with the four-fold increase in permanently dry ponds leaving fewer successful breeding ponds (McMenamin *et al.* 2008). Similarly, reduced rainfall resulting in declines in recorded pond hydroperiods was linked to declines in frog populations by Daszak *et al.* (2005). In Central America, declines of a frog species in Puerto Rico correlated with an increase in the number of periods with less than 3 mm of rain (Stewart 1995). Winter droughts appeared to cause reproductive failure and loss of *Rana pipiens* populations (Corn and Fogleman 1984) and unusually dry winters have also been linked to declines of frogs in Brazil (Weygoldt 1989). Finally, changes in mist frequencies have been specifically related to declines of amphibians in the Costa Rican highlands (Pounds *et al.* 1999). None of these studies could conclude that these unusual conditions were the direct result of climate change, and the presence of the amphibian chytrid fungus provided a confounding factor in the declines in higher altitude populations. However, the results provide a strong indication of what climate change may do to populations.

A secondary effect of early pond drying has been the finding of an increased threat of disease to populations. Earlier pond drying and the associated lower water levels was found to lead to increased exposure of tadpoles to UV radiation and a resultant lowered immunity to the fungus *Saprolegnia ferax* (Keisecker *et al.* 2001). Laboratory research has also found that the more rapid metamorphosis required to escape earlier drying ponds can decrease immunocompetence in newly metamorphosed froglets (Gervasi *et al.* 2008). This may have significance with regards to the spread of a number of amphibian diseases, including the chytrid fungus (see below).

With regards to a changed phenology in frog activity, several studies have indicated an earlier onset of calling and breeding activity of some species of frogs from the northern hemisphere (Beebee 1995; Reading 1998; Gibbs and Breisch 2001), but other studies have found no such effect (Blaustein *et al.* 2001) and even some species within the study of Gibbs and Breisch (2001) did not show a change to earlier reproduction.

One area of particular concern has been the implication that the chytrid fungus has had an increased impact on populations of frogs as a result of climate change. Comparisons of chytrid fungus related declines and temperature changes in frogs in Costa Rica indicated that the fungus (*Batrachochytrium dendrobatidis*) was better able to grow under increased nightly temperatures and mistier daytime conditions, leading to increased spread of this disease (La Marca *et al.* 2005 ; Pounds *et al.* 2006). It should be noted however, that other researchers found no such relationship and dispute this finding (Lips *et al.* 2008; Rohr *et al.* 2008). The true effect that climate change may have on the impacts of chytridiomycosis remains unclear as there are both negatives and positives to changing climatic conditions. The optimal window for growth for *B. dendrobatidis* is 17–25°C (Piotrowski *et al.* 2004) and areas that are now too cold for the disease to exist may warm sufficiently to further aid in its spread (Pounds *et al.* 2006). However, *B. dendrobatidis* can be killed where temperatures exceed 30°C for any period of time (Berger 2001 in Woodhams *et al.* 2003) and so other areas may become too hot for the fungus to be effective, protecting frog populations from infection.

Increasing temperatures may lead to shorter and inadequate hibernating conditions for some species (Reading 2007). When hibernating, frogs have greatly depressed metabolic rates and so expend very little energy (e.g., Withers 1993) and the degree of depression is strongly dependent on temperature: the lower the temperature the lower the metabolic rate (see Wells 2007). Depressed metabolic activity during aestivation may be obligate in many frog species and if metabolic rates are raised because of greater ambient temperatures, the additional energy demand may ultimately lead to death before conditions are suitable for frogs to replenish their energy reserves are depleted when they enter the overwintering period and such a situation has been observed for female common toads, *Bufo bufo* (Reading 2007).

What is happening in Australia?

To date, very little direct evidence has been gathered for or against impacts of climate change on Australian frogs. Mac Nally *et al.* (2009) compared the presence of anuran species with vegetated and agricultural landscapes in Victoria, taking into consideration the potential for a changed climate to have influenced their current distributional patterns. The study found that serious declines had taken place in most species and concluded that these were probably the result of failed reproduction after more than 12 years of drought. They concluded that reproduction had failed because there had been too few winter rainfall events that normally act as the breeding cues for frogs in the region. As noted previously, climate modelling suggests that rainfall patterns will shift towards increased summer rainfall in the region over time and so winter-breeding cues may be further reduced or lost altogether, precipitating further declines in regional anuran populations.

The main area of study for climate change impacts in Australia has been bioclimatic modelling of current and predicted ranges of anurans under differing climate change scenarios. In these studies, the climatic envelope of target anuran species is determined by comparing a series of climatic variables with known "presence" and selected "absence" sites in order to select variables that strongly correlate with the presence of the species. These variables are assumed to be restricting the current range of a species and so, if they alter under predicted climate change models, may lead to changes in the ranges of species. Bioclimatic modelling has indicated a major loss of suitable range in a number of montane and/or narrow-range endemic frog species from northern Australia (Williams *et al.* 2003; Meynecke 2004; and see Hilbert *et* *al.* 2001). Such species are predicted to be under greatest threat from climate change in many areas of the world and are noted to be those most likely already in decline (Hero *et al.* 2005; Sodhi *et al.* 2008).

Studies in more temperate areas of Australia have also indicated possible impacts of climate change. A study of the climatic envelopes of three species from southeastern Australia indicated that all would likely suffer declines, with the alpine tree frog (*Litoria verreauxii alpina*) possibly becoming extinct (Brereton 1995). The identification of climatic envelopes of three species of threatened frogs from the Sydney Basin (*Litoria littlejohni, Heleioporus australiacus* and *Pseudophyrne australis*) indicated that, under more extreme climate change models, by 2070 all three species would no longer have any climatically suitable areas remaining in the study region (Penman and Lemckert 2010). All three frog species appeared most adversely affected by reductions in autumn and winter rainfall levels, periods when these species commonly reproduce. All breed on streams in sandstone areas where water is highly ephemeral and *P. australis* (Thumm and Mahony 1999) and *H. australiacus* (Lemckert Pers. Obs.) are often dependent on a few permanent pools on these creek-lines for successful reproduction. Any reduction in rainfall or a change to fewer but heavier rainfall events may lead to such sites failing to hold water for periods sufficient to allow successful metamorphosis of tadpoles.

If these species are currently constrained by climatic envelopes, the predicted climatic changes are likely to result in their extinction as there is no opportunity for them to migrate to new, suitable climatic areas. It needs to be established whether the physiological tolerances of these and other frogs is the limiting factor on their range. If physiology and climate is key to determining their current range, only drastic and somewhat novel approaches to conservation may enable their survival into the future, including artificial watering of breeding sites and movements of populations to newly suitable habitats (see Shoo *et al.* 2011).

The various impacts reported for frog species overseas may also apply to Australian frogs. Australian frogs are generally dependent on free water for reproduction and a number of species are specialised to breed in temporary water bodies, particularly in the more arid inland areas (Cogger 2000; Anstis 2002). Changes in rainfall patterns, in particular, could lead to water being unavailable for reproduction, or streams and ponds not holding water for long enough to allow successful metamorphosis.

The ability that Australian frogs have to cope with climatic changes is unclear, but Australian frogs may be able to withstand human-induced climate change better than frogs elsewhere. Australia's climate is already considered to be relatively variable (Nicholls *et al.* 1997), with regular periods of drought interspersed amongst much wetter years. Australian frogs are relatively opportunistic in terms of the timing of reproduction, being able to vary the onset of breeding activity from year to year depending on climatic and environmental conditions (e.g., Dankers 1977; Humphries 1979; Lemckert and Grigg 2010). They also tend to have relatively long breeding seasons, generally at least three months and often six or more months and even the so called "winter" breeders tend to be able to call anywhere between autumn and spring (Anstis 2002). By not having tightly defined breeding seasons, Australian frogs are able to wait for suitable breeding conditions to arise in any given year, maximising their chances of a successful reproduction. As a result, Australian frogs may be pre-adapted to some degree to cope with new weather patterns that may arise as a result of climate change.

The frogs most likely at risk in terms of their reproduction appear to be those that do not have an aquatic larval stage and are restricted to relatively small geographic ranges. This includes the mountain frogs (*Philoria spp.*) and hip-pocket frog (*Assa darlingtoni*) of eastern Australia and the microhylids of northern Australia. Mountainous areas maintain continuously moist microhabitats for nest sites through a combination of topographic position and regular cloud cover (Hilbert *et al.* 2001). Decreases in rainfall and cloud cover levels are likely to have severe effects as the eggs and larvae develop in constantly wet nest sites and, as noted before, at least *Philoria loveridgei* egg masses suffer significant mortality under drying conditions (Seymour *et al.* 1995). The corroboree frogs (*Pseudophyrne corroboree* and *P. pengilleyi*) of southeastern Australia also have a terrestrial egg stage followed by an aquatic phase that may rely on snow-melt to fill the natal pond and so they may also be at greater risk of reproductive failure due to climate change.

The potential for changes in the incidence of disease would appear to be similar for Australian species as for frogs elsewhere. Many frogs throughout the world have suffered significant chytrid related declines (Berger *et al.* 1988; Drew *et al.*. 2006) and other epidemic diseases are known to be present. The effect of reduced pond levels and hydroperiods on the immunocompetance of Australian frogs needs to be tested to determine the likely impact of these climatic changes on Australian species.

One factor that seems less likely to be of concern within Australia is the effect of warmer winter periods when hibernation may occur in frogs. Australia has a relatively brief and mild winter and, as such, species do not generally face extended very cold (near or below 0^{o}C) conditions that will lead to regularly and greatly reduced metabolic rates. This probably means that the internal energy requirements of Australian frogs are already relatively high and they are unlikely to be obligate in requiring a low metabolic hibernation phase for their survival. However, like many of the assumptions about Australian frogs, this suggestion also needs to be tested as it may be an important requirement for species that occur in the alpine areas in southeastern Australia.

Conclusion

Whilst it may appear likely that long-term changes in the climate of Australia will impact upon Australian frogs, the true impacts remain unclear as we do not understand how much climatic conditions currently constrain the ranges or activities of many species. Furthermore, the predictions in changes in rainfall and temperature remain variable and uncertain. Australian frogs have evolved in a highly variable climatic environment and they may be better able to cope with changing weather conditions than species found in more climatically stable areas of the world. More testing of the physiological limits of Australian frogs will provide a better understanding of their ability to cope with predicted changes in temperature and moisture levels and so better indicate the extent to which any future climate change may affect the frogs of Australia.

Acknowledgments

We would like to thank Brad Law for encouraging us to present this work at the Royal Zoological Society forum and the RZS for accepting us to do so. We also thank Industry and Investment NSW for allowing us to work on this subject and thank the anonymous reviewers of this paper.

References

Anstis, M. 2002. Tadpoles of South-eastern Australia: A Guide with Keys. Reed New Holland, Sydney.

Beebee. T. J. C. 1995. Amphibian breeding and climate. *Nature* **374:** 219-220.

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. & 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* **95:** 9031–9036.

Berger, L. 2001. Diseases in Australian Frogs. PhD thesis, James Cook University, Townsville.

Blaustein, A. R., Belden, L. K., Olson, D. H., Green, D. M., Root, T. L. and Kiesecker, J. M. 2001. Amphibian breeding and climate change. *Conservation Biology* **15:** 1804-1809.

Brattstrom, B. H. 1963. A preliminary review of the thermal requirements of amphibians. *Ecology* **44:** 238-255.

Brattstrom, B. H. 1970. Thermal acclimation in Australian amphibians. *Comparative Biochemistry and Physiology* **35:** 69-103.

Brereton, R., Bennett, S., Mansergh, I. 1995. Enhanced greenhouse climate change and its potential effect on selected fauna of South-Eastern Australia: a trend analysis. *Biological Conservation* **72:** 339–354.

Carey, C. and Alexander, M. A. 2003. Climate change and amphibian declines: is there a link? *Diversity and Distributions* **9:** 111-121.

Cogger, H. G. 2000. *Reptiles and Amphibians of Australia*. Reed Books, Sydney, NSW.

Collins, J. P. and Storfer, A. 2003. Global amphibian declines: sorting the hypotheses. *Diversity and Distributions* **9:** 89-98.

Corn, P. S. and Fogleman, J. C. 1984. Extinction of Montane Populations of the Northern Leopard Frog (*Rana pipiens*) in Colorado. *Journal of Herpetology* **18:** 147-152.

Dankers, N. M. J. A. 1977. The ecology of an anuran community. PhD Thesis, University of Sydney, Sydney.

Daszak, P., Scott, D. E., Kilpatrick, A. M., Faggioni, C., Gibbins, J. W. and Porter, D. 2005. Amphibian population declines at Savannah River site are linked to climate, not chytridiomycosis. *Ecology* **86:** 3232–3237.

Drew, A., Allen, E. J. and Allen, L. J. 2006. Analysis of climatic and geographic factors affecting the presence of chytridiomycosis in Australia. *Diseases of Aquatic Organisms* **68:** 245-250.

Duellman, W. E. and Trueb, L. 1986. *Biology of Amphibians*. McGraw-Hill, New York.

Gervasi, S. S. and Foufopoulos, J. 2008. Costs of plasticity: responses to desiccation decrease post-metamorphic immune function in a pond-breeding amphibian. *Functional Ecology* **22:** 100-108.

Gibbs, J. P., and Breisch, A. R. 2001. Climate warming and calling phenology of frogs near Ithaca, New York, 1900-1999. *Conservation Biology* **15:** 1175-1178.

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.

Hero, J-M., Williams, S. E. and Magnusson W. 2005. Ecological traits of declining amphibians in upland areas of eastern Australia. *Journal of Zoology, London* **267:** 221-232.

Hilbert, D. W., Ostendorf, B. and Hopkins, M. 2001. Sensitivity of tropical forests to climate change in the humid tropics of North Queensland. *Austral Ecology* **26:** 590–603.

Humphries, R. B. 1979. Dynamics of a Breeding Frog Community. PhD Thesis, Australian National University, Canberra.

James, T.Y., Litvintseva, A.P., Vilgalys, R., Morgan, J. A. T., Taylor, J. W., Fisher, M. C., Berger, L., Weldon, C., du Preez, L. and Longcore, J. E. 2009. Rapid global expansion of the fungal disease chytridiomycosis into declining and healthy amphibian populations. *PLOS Pathogens. 2009; 5. e1000458.*

Keisecker, J. M., Blaustein, A. R. and Belden, L. K. 2001. Complex causes of amphibian declines. *Nature* **410:** 681-683.

La Marca, E., Lips, K. R., Lotters, S., Puschendorf, R., Ibanez, R., Rueda-Almonacid, J. V., Schulte, R., Marty, C., Castro, F., Manzanilla-Puppo, J., Garcia-Perez, J. E., Bolanos, F., Chaves, G., Pounds, J. A., Toral, E. and Young, B. E. 2005. Catastrophic population declines and extinctions in neotropical Harlequin frogs (Bufonidae: *Atelopus*). *Biotropica* **37:** 190–201.

Lemckert, F. L. 2001. The influence of micrometeorological factors on the calling activity of the Australian frog *Crinia signifera* (Anura: Myobatrachidae). *Australian Zoologist* **31:** 625-631.

Lemckert, F. and Grigg, G. 2010. Living in the 80s – seasonality and phenology of frog calling activity at Darkes Forest from 1987-1989. *Australian Zoologist* **35**: 245-250.

Lips, K. R., Diffendorfer, J., Mendelson, J. R. III and Sears, M. W. 2008. Riding the wave: reconciling the roles of disease and climate change in amphibian declines. *PLoS Biol* **6:** 441-454.

Mac Nally, R., Horrocks, G., Lada, H., Lake, P. S., Thomson, J. R. and Taylor, A. C. 2009. Distribution of anuran amphibians in massively altered landscapes in south-eastern Australia: Effects of climate change in an aridifying region. *Global Ecology and Biogeography* **18:** 575-585.

McCallum, M. L. 2007. Amphibian decline or extinction? Current declines dwarf background extinction rate. *Journal of Herpetology* **41:** 483-491.

McMenamin, S. K., Hadly, E. A. and Wright, C. K. 2008. Climatic change and wetland desiccation cause amphibian decline in Yellowstone National Park. *Proceedings of the National Academy of Sciences of the United States of America* **105:** 16988-16993.

Meynecke, J.-O. 2004. Effects of global climate change on geographic distributions of vertebrates in North Queensland. *Ecological Modelling* **174:** 347-357.

Nicholls, N., Drosdowsky, W. and Lavery, G. 1997. Australian rainfall variability and change. *Weather* **52:** 66-71.

Penman, T. D., Lemckert, F. L. and Mahony, M. J. 2006. Meteorological effects on the activity of the giant burrowing frog, *Heleioporus australiacus*, in south-eastern Australia. *Wildlife Research* **33**: 35-40.

Penman, T. D. and Lemckert, F. L. 2010. Predicted impact of climate change on threatened amphibians. Unpublished report to the Department of the Environment, Climate Change and Water, Hurstville.

Piotrowski, J. S., Annis, S. L. and Longcore, J. E. 2004. Physiology of *Batrachochytrium dendrobatidis*, a chytrid pathogen of amphibians. *The Mycological Society of America* **96:** 9-15.

Pounds, J. A., Fogden, M. P. L. and Campbell, J. H. 1999. Biological response to climate change on a tropical mountain. *Nature* **398:** 611-615.

Pounds, J. A., Bustamante, M. R., Coloma, L. A., Consuegra, J. A., Fogden, M. P. L., Foster, P. N., La Marca, E., Masters, K. L., Merino-Viteri, A., Puschendorf, R., Ron, S. R., Sanches-Azofeifa, G. A., Still, C. J. and Young, B. E. 2006. Widespread amphibian extinctions from epidemic disease driven by global warming. *Nature* **439:** 161–167.

Reading, C. J. 1998. The effect of winter temperatures on the timing of breeding activity in the common toad, *Bufo bufo*. *Oecologia* **117:** 469-475.

Reading, C. J. 2007. Linking global warming to amphibian declines through its effects on female body condition and survivorship. *Oecologia* **151:** 125-131.

Roberts, J. D. and Watson, G. F. 1993. Biogeography and phylogeny of the anura. Pp 35-40 in Fauna of Australia. Vol 2a Amphibia and Reptilia, edited by C. J. Glasby, G. J. B., Ross, and P. L. Beesley. Australian Government Printing Service, Canberra.

Rohr, J. R., Raffel, T. R., Romansic, J., McCallum, H. and Hudson, P. J. 2008. Evaluating the links between climate, disease spread, and amphibian declines. *Proceedings of the National Academy of Sciences* **45:** 17436-17441.

Seymour, R. S., Mahony, M. J. and Knowles, R. 1995. Respiration of embryos and larvae of the terrestrially breeding frog *Kyarranus loveridgei*. *Herpetologica* **51:** 369-376.

Shoo, L. P., Olson, D. H., McMenamin, S. K., Murray, K. A., Van Sluys, M., Donnelly, M. A., Stratford, D., Terhivuo, J., Merino-Viteri, A., Herbert, S. M., Bishop, P. J., Corn, P. S., Dovey, L., Griffiths, R. A., Lowe, K., Mahony, M., McCallum, H., Shuker, J. D., Simpkins, C., Skerratt, L. F., Williams. S. E. and Hero, J-M. 2011. Engineering a future for amphibians under climate change. *Journal of Applied Ecology doi: 10.1111/j.1365-2664.2010.01942.*

Sodhi, N. S., Bickford, D., Diesmos, A. C., Lee, T. M., Koh, L. P., Brook, B. W., Sekercioglu, C. H. and Bradshow, C. J. A. 2008. Measuring the meltdown: drivers of global amphibian extinction and decline. *PLoS One* **3:** e1636.

Stewart, M. M. 1995. Climate Driven Population Fluctuations in Rain-Forest Frogs. *Journal of Herpetology* **29:** 437-446.

Stuart, S. N. Chanson, J. S., Cox, N. A., Young, B. E., Rodrigues, A. S. L., Fischman, D. L., Waller, R. W. 2004. Status and trends of amphibian declines and extinctions worldwide. *Science* **306:** 1783-1786.

Suppiah., Hennessy, K. J., Whetton, P. H., McInnes, K., Macadam, I., Bathols, J., Ricketts, J. and Page, C. M. 2007. Australian climate change projections derived from simulations performed for the IPCC 4th Assessment Report. *Australian Meteorological Magazine* **56:** 131-152.

Thumm, K. and Mahony, M., 1999. Loss and degradation of red-crowned toadlet habitat in the Sydney region, Pp 99-108 In Declines and Disappearances of Australian Frogs, edited by A. Campbell. Environment Australia, Canberra.

Tracy, C. R., Christian, K. A., Betts, G., Tracy, C. R. 2008. Body temperature and resistance to evaporative water loss in tropical Australian frogs. *Comparative Biochemistry and Physiology* A **150:** 102-108.

Wells, K. D. 2007. The Ecology and Behavior of Amphibians. The University of Chicago Press.

Weygoldt, P. 1989. Changes in the composition of mountain stream frog communities in the Atlantic mountains of Brazil: frogs as indicators of environmental deteriorations. *Studies on Neotropical Fauna and Environment* **24:** 249-256.

Williams, S. E., Bolitho, E. E. and Fox, S. 2003. Climate change in Australian tropical rainforests: an impending environmental catastrophe. *Proceedings of the Royal Society of London B.* **270:** 1887-1892.

Withers, P. C. 1993. Metabolic depression during aestivation in the Australian frogs, *Neobatrachus* and *Cyclorana*. *Australian Journal of Zoology* **41:** 467-473.

Woodhams, D. C., Alford, R. A. and Marantelli, G. 2003. Emerging disease of amphibians cured by elevated body temperature. *Diseases of Aquatic Organisms* **55:** 65–67.

APPENDIX I

Heath frogs *Litoria littlejohni.*
Photo, F. Lemckert.

Male *Helioperus australiacus*.
Photo, F. Lemckert.