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# Crossing the Tasman Sea: Inferring the introduction history of *Litoria aurea* and *Litoria raniformis* (Anura: Hylidae) from Australia into New Zealand

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**Abstract** The amphibian fauna of New Zealand consists of three native species (*Leiopelma* spp.), and three *Litoria* species introduced from Australia in the last 140 years. We conducted a molecular phylogeographical study that aimed to identify the Australian origins of two species, *Litoria aurea* and *Litoria raniformis*. We used partial sequences of the mitochondrial cytochrome oxidase I (*cox1*) gene from 59 specimens sampled from across the range of both species to identify the probable source populations for the New Zealand introductions, and to describe the current genetic diversity among New Zealand *Litoria* populations. Our genetic data suggest that *L. aurea* was introduced into the North Island of New Zealand from two regions in Australia, once from the northern part of coastal New South Wales and once from the southern part of coastal New South Wales. Our data indicate that *L. raniformis* introductions originated from the Melbourne region of southern Victoria and once established in the South Island of New Zealand, the species subsequently spread throughout both islands. In addition, we found a distinct haplotype in *L. raniformis* from Tasmania that strongly suggests, contrary to earlier reports, that this species was not introduced into New Zealand from Tasmania. Finally, we identified two very distinctive mitochondrial lineages of *L. raniformis* within the mainland Australia distribution, which may be previously unrecognized species.

**Key words:** Australia, *Litoria*, mitochondrial DNA, New Zealand, phylogeography.

## INTRODUCTION

Introduction of non-native species can cause major environmental damage in sensitive habitats. Introduction of exotic species, usually by humans, can have a detrimental influence on native biota and can be one of the most influential sources of biodiversity loss (Courchamp *et al.* 2003; Kats & Ferrer 2003). One phenomenon that has received increased attention in recent years is biotic homogenization, which is the increased similarity of biotas over time caused by the replacement of native species with non-indigenous species (Vitousek *et al.* 1997; McKinney & Lockwood 1999; Rahel 2002; Olden & Poff 2004; Didham *et al.* 2005). Homogenization is the outcome of three interacting processes: introductions of non-native species, extirpation of native species and habitat alterations that facilitate these two processes (Rahel 2002).

Non-native organisms can be introduced accidentally via human travel and global trade, or deliberately, such as for hunting, fishing, farming or biological control. Biological control via an upper-trophic-level organism that can utilize the exotic pest as a resource is a powerful methodology for the management of invasive species (Hoddle 2004). Amphibians were used as biological control species during the twentieth century (Crossland 2000; Lever 2003), but introduction of these alien species sometimes led to the decline or even extinction of native amphibian populations (Collins & Storfer 2003). The cane toad *Bufo marinus* is native to central and tropical South America and was introduced as a biological control agent against cane beetles to several countries throughout the tropics. Once established, *B. marinus* became a pest species in Hawaii (Kraus *et al.* 1999) and Australia (Mungomery 1935). In Australia, *B. marinus* has had negative effects on the native amphibian fauna (Crossland 2000), and it also may have had direct or indirect long-term effects on other vertebrate and invertebrate taxa (Covacevich & Archer 1975; Catling *et al.* 1999).

Two hylid frog species, *Litoria aurea* (Lesson, 1829) and *Litoria raniformis* (Keferstein, 1867), commonly described as bell frogs, were introduced from Australia into New Zealand (Thomson 1922) in the late 1800s supposedly to provide food for ducks and to control

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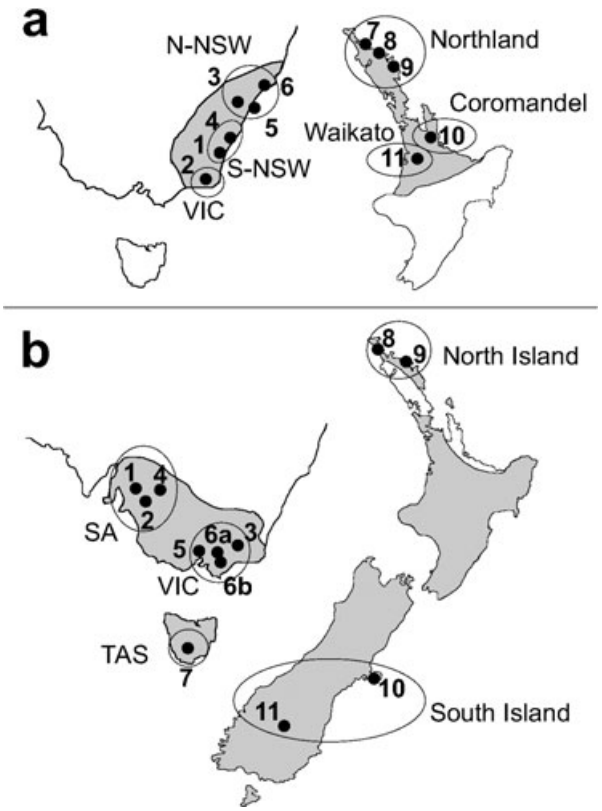


**Fig. 1.** Maps of Australia and New Zealand with the distribution (grey area) of *Litoria aurea* (a) and *Litoria raniformis* (b). Sampling sites of 10 *L. aurea* (a) and 11 *L. raniformis* (b) populations used in this study are indicated by black points and numbers. Sampling localities and corresponding geographical regions are listed in Table 1.

mosquito larvae (McCann 1961; Druett 1983). *Litoria aurea* is distributed throughout eastern and south-eastern New South Wales and far eastern Victoria (Fig. 1a), while *L. raniformis* occurs in the south-eastern slopes and plains of New South Wales through Victoria to south-eastern South Australia, and Tasmania (Cogger 1975) (Fig. 1b). In their native Australia, both species are threatened and they are considered to be nationally vulnerable (Pyke 2002; Pyke *et al.* 2002).

While *L. raniformis* and *L. aurea* are now endangered in their native habitats, they have successfully dispersed throughout New Zealand (Gill & Whitaker 1996), establishing large and widespread populations in areas of similar breeding habitat to those in their native Australia (Pyke 2002; Pyke *et al.* 2002). *Litoria aurea* is now present in New Zealand on the northern half of the North Island (Fig. 1a), while *L. raniformis* is distributed across the whole of the North Island and the South Island (Fig. 1b), with the species coexisting in Northland (Bell 1982).

Few accounts of the time and place of the introduction of *Litoria* spp. into New Zealand exist, and the precise source of the introduced species is unknown. Thomson (1922) states that '*Hyla aurea*' was introduced from Sydney, New South Wales to Auckland, New Zealand in 1867 by the Auckland Acclimatization Society. '*Hyla aurea*' was introduced from Hobart, Tasmania to Canterbury, New Zealand by the Canterbury Acclimatization Society (presumably *L. raniformis*, because it is the only species of the *L. aurea* group in Tasmania) in 1867, and again into Southland (Wallacetown) by the Southland Acclimatization Society in 1868. In addition, several regional translocations took place within New Zealand; for instance, 60 '*Hyla aurea*' reportedly were introduced to Southland from Napier in 1888 (Thomson 1922).

In this study, we identify the origins of the current New Zealand *L. aurea* and *L. raniformis* populations, examine the relationships among these populations, and propose their possible paths of migration within New Zealand. In addition, we discuss the ecological and evolutionary consequences of the introduction and dispersion of these alien species in New Zealand. We used partial mtDNA cytochrome oxidase I (*cox1*) gene sequences from 59 specimens, broadly sampled from across the range of both species, to describe current levels of genetic diversity among New Zealand bell frog populations and to identify their probable Australian source populations.

## METHODS

### Sampling

Frogs were captured from seven locations in New Zealand and 13 locations in Australia (Table 1, Fig. 1) during their breeding season between 2002 and 2005 by localizing calling males at night and looking for basking adults during the day. Toe clips (approximately 1 $mm^2$) were taken from each individual using a sterile scalpel and the tissue was stored in 98% ethanol. Handling of the animals was kept to a minimum and each frog was released at the place of capture immediately after sampling. Additional alcohol-preserved tissue samples of Australian specimens were obtained from the South Australian Museum, Geoffrey Heard (La Trobe University) and Emma Burns (University of New South Wales). Four alcohol-preserved specimens from New Zealand with unknown origin have been sampled and are also included in this study.

### Mitochondrial DNA amplification and sequencing

DNA was extracted using a modified Cetyltrimethylammonium Bromide (CTAB) protocol (Cullings 1992). Partial sequences of the *cox1* gene were ampli-

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**Table 1.** Localities and grouping design applied in the analyses for the samples used in this study, sample sizes and haplotypes found at each population for the mitochondrial gene cytochrome oxidase I

| Species, locality and group name | Locality ID | *n* | Haplotype | GenBank accession n° |
|---|---|---|---|---|
| *Litoria aurea* | | | | |
| Homebush (S-NSW, Aus) | 1 | 2 | La2, La6 | EU043182, EU043183 |
| Point Hicks (Vic, Aus) | 2 | 2 | La5 | EU043185, EU043186 |
| Sandgate, Newcastle (N-NSW, Aus) | 3 | 2 | La1 | EU043177, EU043184 |
| Lake Meroo (S-NSW, Aus) | 4 | 2 | La2, La4 | EU043178, EU043179 |
| Broughton Island (N-NSW, Aus) | 5 | 2 | La1 | EU043187, EU043188 |
| Crescent Head (N-NSW, Aus) | 6 | 2 | La1 | EU043180, EU043181 |
| Karikari peninsula (Northland, NZ) | 7 | 4 | La1 | EU043166–EU043169 |
| Kerikeri (Northland, NZ) | 8 | 2 | La1 | EU043162, EU043163 |
| Whangarei (Northland, NZ) | 9 | 2 | La1 | EU043164, EU043165 |
| Te Aroha (Coromandel, NZ) | 10 | 2 | La2, La3 | EU043171, EU043172 |
| Otorohanga (Waikato, NZ) | 11 | 1 | La2 | EU043174 |
| Unknown localities (Unknown, NZ) | | 4 | La1, La2, La3 | EU043170, EU043173, EU043175, EU043176 |
| *Litoria raniformis* | | | | |
| Waikerie (SA, Aus) | 1 | 1 | Lr10 | EU043219 |
| Murtho Park (SA, Aus) | 2 | 1 | Lr11 | EU043220 |
| Strathbogie (Vic, Aus) | 3 | 1 | Lr9 | EU043215 |
| Chowilla (SA, Aus) | 4 | 1 | Lr10 | EU043216 |
| Colac (Vic, Aus) | 5 | 1 | Lr6 | EU043218 |
| Donnybrook, Melbourne (Vic, Aus) | 6a | 1 | Lr3 | EU043201 |
| Campbellfield, Melbourne (Vic, Aus) | 6b | 3 | Lr1, Lr7 | EU043202–EU043204 |
| Gretna, Tasmania (Tas, Aus) | 7 | 1 | Lr8 | EU043217 |
| Karikari peninsula (North Island, NZ) | 8 | 2 | Lr3 | EU043197, EU043198 |
| Whangarei (North Island, NZ) | 9 | 2 | Lr3 | EU043199, EU043200 |
| Christchurch (South Island, NZ) | 10 | 8 | Lr1, Lr4, Lr5 | EU043189–EU043196 |
| Alexandra (South Island, NZ) | 11 | 10 | Lr1, Lr2 | EU043205–EU043214 |

Species assignment is based on mtDNA haplotypes. Locality ID refers to numbers in Fig. 1, haplotype numbers refer to haplotype codes shown in Fig. 2. GenBank accession numbers for each haplotype are shown.

fied by the polymerase chain reaction (PCR) using the primers Cox (5′-TGATTCTTTGGGCATCCTG AAG-3′) and Coy (5′-GGGGTAGTCAGAATAGC GTCG-3′) (Schneider *et al*. 1998) with thermal cycles of 93°C for 3 min followed by 93°C for 30 s, 50°C for 45 s and 72°C for 45 s, repeated 37 times, with a final cycle 70°C for 5 min. The PCR products were purified using Perfectprep PCR cleanup kits (Eppendorf) and sequenced for both the sense and anti-sense strands using standard cycle sequencing protocols. Sequencing reactions were purified using Sephadex G-50 (Amersham Biosciences) columns, and visualized using an ABI 3100 automated sequencer at the DNA sequencing facility, School of Biological Sciences, University of Canterbury, Christchurch.

## Sequence alignment and population analysis

Cytochrome oxidase I (*cox1*) sequences were aligned manually using Bioedit (Hall 1999) and all variable sites were confirmed by visual inspection of the chromatograms. Samples were then grouped according to geographical regions as follows: *L. aurea* – Northland, Coromandel Peninsula and Waikato region within New Zealand, and New South Wales and Victoria within Australia; *L. raniformis* – North Island and South Island within New Zealand, and Victoria, South Australia and Tasmania within Australia (Fig. 2).

Relationships among haplotypes were inferred by constructing statistical parsimony networks using TCS (version 1.21, Clement *et al*. 2000), in which haplotypes are joined in a network based on the number of mutational differences that separate them.

To investigate the nested genetic structure of populations and the relationship between haplotypes found in different regions of Australia and New Zealand, we used Bayesian model-based clustering to assign individuals into clusters based on genetic similarity, implemented in the software BAPS 3.2 (Corander *et al*. 2006). We applied trained clustering containing the Australian samples grouped by geographical regions (Victoria, Northern New South Wales and Southern New South Wales for *L. aurea* and Victoria and South Australia for *L. raniformis*) as reference groups for possible colonization origins, and individuals from New Zealand as sampling units with unknown origin to infer the Australian source of New Zealand


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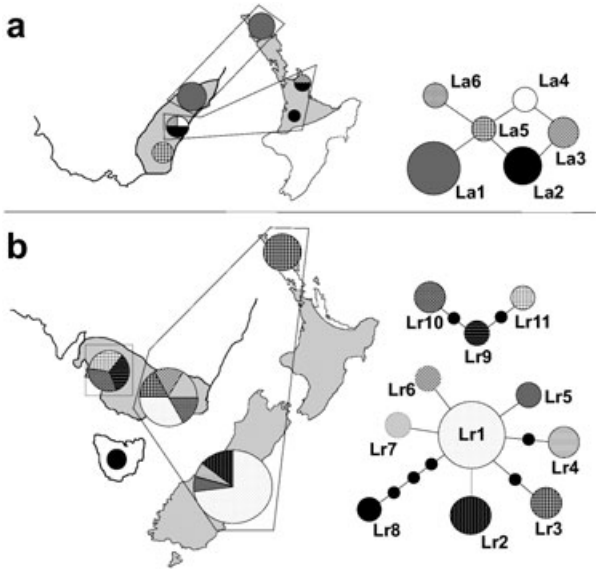


**Fig. 2.** Statistical parsimony network of cytochrome oxidase I haplotypes of *L. aurea* (a) and *L. raniformis* (b) sequences. Circles represent haplotypes connected by lines indicating single mutational events. The sizes of circles correspond to the number of individuals within the haplotype. Small filled circles (•) represent hypothetical missing haplotypes. Haplotypes are mapped to show regional distribution. Clusters are shown as revealed by BAPS and are indicated by groupings with respect to haplotype relationships on the network.

populations. Four *L. aurea* individuals from unknown North Island localities were included in the analysis to predict their population origin.

## RESULTS

The final alignment consisted of 594 bp of partial sequence for the mitochondrial *cox1* gene from 27 individuals of *L. aurea* and 32 individuals of *L. raniformis* (Table 1). There were six haplotypes observed for *L. aurea* and 11 for *L. raniformis*. *Litoria raniformis* was further subdivided into two lineages. Within *L. aurea* there were four variable positions (three parsimony informative), and within *L. raniformis* there were 50 variable positions (43 parsimony informative) defining haplotypes.

### Phylogeographical pattern

Weak geographical structure was observed for *L. aurea* (Fig. 2) with six different haplotypes occurring among the two main regions (Fig. 2a). Two of the haplotypes (La1 and La2) were shared among Australian and New Zealand populations. Frogs from Northland and New South Wales share the La1 haplotype, while individuals from the Coromandel Peninsula and Waikato share the La2 haplotype with New South Wales. Victorian frogs all have one haplotype (La5), New South Wales frogs have two haplotypes (La4 and La6) unique to that region, and Coromandel Peninsula frogs possess one unique haplotype (La3), differentiated from the other haplotypes by single mutational events.

In contrast, considerable genetic structure was observed for *L. raniformis* (Fig. 2b). There is one shared haplotype among Victorian and South Island samples (Lr1), and six unique haplotypes separated from the most common haplotype by at least one mutational step (Lr2–Lr7). Three mutational steps separate the Tasmanian haplotype Lr8 from the most common haplotype. Interestingly, one Victorian (Lr9) and two South Australian haplotypes (Lr10–Lr11) are separated from the rest of the haplotypes by at least 38 mutational steps so could not be joined to the statistical parsimony network with greater than 95% confidence.

### Bayesian population structure analysis

For the most likely partition within *L. aurea* population structure analysis clustered all the Northland individuals from New Zealand to the Northern New South Wales group from Australia, and individuals from the Coromandel and Waikato region, New Zealand, were assigned to the Southern New South Wales cluster from Australia (Fig. 2a) (marginal likelihood of optimal partition = −11.21). One of the samples with unknown origin was clustered to Northland region (La1 haplotype), and three individuals were grouped with the Coromandel – Waikato region (La2 and La3 haplotypes).

For *L. raniformis*, the partition assigned all New Zealand individuals to the Victorian group containing haplotypes Lr1–Lr7. The South Australia group remained a separate cluster with haplotye Lr9 and Lr11 unique to the region, and Lr10 shared with Victoria (Fig. 2b; marginal likelihood of optimal partition = −146.7). The haplotype Lr8 with one individual from Tasmania was not included in the analysis.

## DISCUSSION

### *Litoria aurea*

The mtDNA sequence data indicate that *L. aurea* was most likely introduced from New South Wales into the North Island of New Zealand. The statistical parsimony network (Fig. 2a) shows that populations from

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Northland (Kerikeri) shared the most common haplotype (La1) with populations sampled from the northern part of New South Wales (Sandgate, Crescent Head, Broughton Island).

Another haplotype (La2) was shared by samples from the Coromandel Peninsula and Waikato region and the southern part of New South Wales (Lake Meroo, Homebush). This result suggests that a second introduction event may have occurred in which frogs from a southern population of *L. aurea* were introduced into the Coromandel – Waikato region. This introduction supports the historical records which indicate *L. aurea* was introduced to New Zealand from Sydney (Thomson 1922).

Based on a mtDNA phylogenetic analysis (Burns *et al.* 2007), two different Pleistocene refuges for *L. aurea* may have existed in Australia, one in the South Coast of NSW and one within Victoria. According to these results, the isolated populations came into a secondary contact as they expanded from the southern and the central refugee. This would explain the central position of an ancestral La5 haplotype, which may be one of the founder haplotypes that expanded to the north and then declined.

The greatest haplotype diversity was apparent within the Coromandel Peninsula and New South Wales. Haplotype La3 from the Coromandel region represents a distinct third haplotype within New Zealand that we might have failed to sample in Australia, and there are three more independent haplotypes from Victoria (La5) and New South Wales (La4, La6). Our data are consistent with a detailed study on *L. aurea* population structure in Australia using microsatellites by Burns *et al.* (2004) which showed significant genetic structuring throughout the species range, but a lack of structure among some sites within areas of continuous habitats. Burns *et al.* (2004) suggested that recent population fragmentation, as little as 30–40 years ago, has led to pronounced genetic drift in *L. aurea* at sites experiencing habitat discontinuity. However, gene flow may still occur among frog populations occurring in regions of continuous habitat in mainland New South Wales and Victoria, leading to the lack of genetic structure observed among those populations.

### *Litoria raniformis*

This species shows more genetic structure in New Zealand than *L. aurea*. The statistical parsimony network suggests that *L. raniformis* was introduced from southern Victoria (around Melbourne) into the South Island of New Zealand. Within New Zealand the species dispersed, with human assistance (Pyke 2002), and became established on both islands. However, our data fail to support Tasmania as the potential source population for the introduction of *L. raniformis* into Canterbury (Thomson 1922). The Tasmanian haplotype (Lr8) was separated from the most common haplotype (Lr1) by three mutational steps, suggesting that Tasmania is a genetically distinct population, which may have been isolated from mainland populations since the island itself was isolated from Victoria about 14 000 years ago (Lambeck & Chappell 2001). The genetic distance between the Tasmanian haplotype and other haplotypes is so large that a Tasmanian origin for New Zealand *L. raniformis* seems unlikely. However, as we may have failed to identify haplotypes present in Tasmania because of the small sample size, it remains possible that the New Zealand *L. raniformis* do originate from Tasmania. More extensive sampling of Tasmanian *L. raniformis* is warranted to address this issue.

Each of the haplotypes Lr9–Lr11 was separated on the statistical parsimony network (Fig. 2) by at least 38 mutational steps from the most common haplotype (Lr1) found in eastern Australia and New Zealand. This extremely high difference suggests the existence of two different haplotype lineages within *L. raniformis*, and potentially a previously unrecognized cryptic species. Three of the four localities possessing haplotypes Lr9–Lr11 (Chowilla, Waikerie, Murtho Park) are located in the Murray River Valley which suggests a role for this western-flowing river in the possible allopatric fragmentation of the two lineages. However, the fourth population possessing the Lr9–Lr11 haplotypes, Strathbogie, is from the Western Plains of Victoria and is geographically separated from the Murray River Basin. The dramatic difference in this population as compared with those sampled from elsewhere in Victoria, Colac and Melbourne, suggests that considerable geographical structure exists within the Victorian Plains. A similarly complex pattern of genetic diversity was recognized within populations of water skinks (*Eulamprus tympanum*) in Western Victoria (Scott & Keogh 2003).

Our sampling in the present study is insufficient to draw strong phylogeographical interpretations for *L. raniformis* in Australia, but further studies to investigate this east–west split seem warranted.

## Biotic homogenization

Fossil records indicate that endemic *Leiopelma* species were widely distributed in New Zealand, but arrival of humans about 1000–1200 years ago significantly modified the native biota by introduction of exotic predators or through environmental changes, leading to severe range contraction in some species and the extinction of others (Bell 1994). The arrival of Europeans further increased extirpation of native fauna by the introduction of pests (rats, cats, mustelids) as well as exotic invertebrates and weeds (Veitch & Clout 2002).


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*Litoria aurea* and *L. raniformis* were introduced into New Zealand about 140 years ago and subsequently both species spread within New Zealand. Levels of genetic variation in species colonizing new ranges often are reduced because of founder effects. However, subsequent movements of frogs within New Zealand may have homogenized haplotype polymorphism, because both species are unprotected in New Zealand and local introductions are very common. The pet trade, in particular, plays a significant role in moving frogs between the two islands, and most of these frogs are liberated far from their original source populations (Waldman *et al.* 2001).

The phylogeographical framework developed here, while far from definitive, provides an important first step in understanding patterns of historical and contemporary movements of frogs among localities. Here we have been able to delineate the probable sources of the New Zealand *Litoria* and also have developed a preliminary framework that should enable us to determine the source of further translocations or population expansions of *Litoria*. These frogs are not yet ubiquitous throughout New Zealand and being able to track or even predict their spread may be an important tool for the conservation management of New Zealand endemics, particularly native leiopelmid frogs but also other species that *Litoria* either competes with or predates.

Introduced *Litoria* species and endemic New Zealand *Leiopelma* species rarely interact in natural conditions, because these species normally live in different microhabitats (Bell 1982). However, Thurley and Bell (1994) found evidence of predation of *Leiopelma archeyi* by *L. aurea* in the Whareorino Forest in the Waikato region, where *L. archeyi, L. hochstetteri* and *L. aurea* have sympatric distributions. Although the introduced *Litoria* species may have little direct ecological impact on the native New Zealand frogs, they potentially might spread chytrid fungus to them (Waldman *et al.* 2001; Bell *et al.* 2004). The effects of chytrid fungus on the native New Zealand frogs are as yet not completely understood, but initial work suggests that this may be a factor in their current decline (Waldman *et al.* 2001; Bell *et al.* 2004).

Urbanization is one of the leading causes of biotic homogenization. As settlements expand, they not only extirpate native species, but create habitat for species that are able to adapt to urban conditions. In Australia, *L. aurea* and *L. raniformis* inhabit still water bodies with high level of disturbance but mainly away from urban areas, while in New Zealand the frogs are located mostly in garden or farmland areas (Pyke *et al.* 2002). The non-native *Litoria* species translocated from Australia into New Zealand in the last 140 years may have evolved to adapt to their new environment, and their populations presently are more numerous and exist at higher densities than the native (*Leiopelma*) species. The two bell frogs are an integral part of the New Zealand amphibian fauna. Although their populations appear to be more robust in New Zealand than Australia, recent surveys suggest that the New Zealand populations too are declining because of chytridiomycosis (Waldman *et al.* 2001).

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