ASSESSING THE IMPACTS OF URBANISATION ON GROWLING GRASS FROG METAPOPULATIONS

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Cover Illustration: Growling Grass Frog (*Litoria raniformis*) floating amongst Water Ribbon (*Triglochin procerum*), Merri Creek, Donnybrook. The cover of aquatic plants with foliage that floats on the water's surface (such as Water Ribbon) is an important determinant of habitat quality for *L. raniformis* in this region. Note also the Water Spider (*Dolomedes* sp.) in the foreground – a potentially important prey species for the frog.
                          Photograph: G. Heard, February 2007.

ACKNOWLEDGMENTS

PROJECT BACKGROUND

The Growling Grass Frog (*Litoria raniformis*) is a large hylid frog which is listed as vulnerable to extinction under the Commonwealth *Environmental Protection and Biodiversity Conservation Act 1999*, and considered endangered in Victoria. A major issue for the conservation of *L. raniformis* in southern Victoria is the species' apparent sensitivity to habitat alterations caused by urban development. In greater Melbourne for example, the frog was historically widespread, but is today restricted to the urban-fringe and beyond. Further expansion of urban development around the city will exacerbate the decline of the frog unless its impact is understood and mitigated. This report details an assessment of the impacts of urbanisation on a metapopulation of *L. raniformis* situated within the Merri Creek corridor (MCC) on Melbourne's northern outskirts.

The project entailed completion of four specific actions considered crucial to our understanding of the impacts of urbanisation on *L. raniformis* in the MCC. These actions were:
  i.   Develop an improved understanding of the metapopulation structure of *L. raniformis* in the MCC;
  ii. Refine predictive models of habitat occupancy for *L. raniformis* in the MCC;
  iii. Develop models of the processes of patch-level extinction and recolonisation for *L. raniformis* in the MCC, and;
  iv. Produce an updated assessment of the status of the nationally-significant metapopulation of *L. raniformis* in the MCC, and describe the impacts of urbanisation on metapopulation viability.

The work was funded by the Commonwealth Department of Environment, Water and Heritage, via the Biodiversity and Ecosystem Services division of the Victorian Department of Sustainability and Environment (Project No. 20081119). The total value of this project is $45,000, of which $37,785 was expended on the completion of the four actions reported on in this document (breakdown provided below). The final action of this project ('Collate knowledge allowing for the development of strategic plans for conservation of the GGF in the Merri Creek corridor and other urbanising landscapes') entails the development of guidelines for the management of *L. raniformis* metapopulations in urbanising landscapes. This action is to be completed as of the 31st September 2009, as per the Memorandum of Understanding for this project.

Project Budget

Action	Tasks	Time	Cost*
Action 1	Collate and compile existing data Analyse data Prepare progress reports Prepare relevant section of final report	Heard: 25 days Scroggie: 2 days	$13390
Action 2	Measure additional variables Analyse data Prepare relevant section of final report	Heard: 20 days Scroggie: 2 days	$11430
Action 3	Analyse data Prepare relevant section of final report	Heard: 15 days Scroggie: 2 days	$8930
Action 4	Analyse data Prepare relevant section of final report	Heard: 7 days	$3495
Action 5	*Analyse data* *Prepare guidelines*	*Heard: 13 days* *Scroggie: 1 day*	*$7215*
		Total	**$45000**

*GST inclusive

KEY FINDINGS

Action 1: Develop an improved understanding of the metapopulation structure of *L. raniformis* in the MCC

- Given congruence between predictions derived from classical metapopulation theory and a substantial occupancy and mark-recapture data-set for *L. raniformis* in the MCC, it is inferred that the species forms classical metapopulations in this region.
- The application of classical metapopulation theory to the species' regional conservation is therefore justified by this study.

Action 2: Refine predictive models of habitat occupancy for *L. raniformis* in the MCC

- Patch occupancy data supported a model in which the probability of occupancy was:
    i. Positively influenced by patch area, hydroperiod, aquatic vegetation cover and connectivity, and;
    ii. Negatively influenced by urban cover in and adjacent to the terrestrial zone.
- Variables not supported by the data included predatory fish occurrence, salinity, length of streams within 1000 m and urban cover within 1000 m.
- The resulting model provides a tool for predicting the distribution of *L. raniformis* at unsurveyed wetlands in the MCC, or in other urbanising landscapes (given adequate survey data).

Action 3: Develop models of the processes of patch-level extinction and recolonisation for *L. raniformis* in the MCC

- Patch occupancy turnover data supported a model in which:
    i. The annual probability of extinction was negatively influenced by hydroperiod, aquatic vegetation cover and connectivity, and;
    ii. The annual probability of colonisation was positively influenced by connectivity.
- Patch area and surrounding urban cover did not influence the probability of extinction (as suggested by the occupancy data), and no patch level variables influenced the probability of colonisation.
- The resulting model has various practical applications, but perhaps most importantly, will allow development of a stochastic metapopulation model which could be used to predict viability of *L. raniformis* in the MCC and elsewhere under varying habitat management scenarios.

Action 4: Produce an updated assessment of the status of the nationally-significant metapopulation of *L. raniformis* in the MCC, and describe the impacts of urbanisation on metapopulation viability

- Survey data suggest that *L. raniformis* is rapidly declining in the MCC.
- Fifty-four percent of historical populations were observed to be extinct as of the 2006-2007 breeding season, and the estimated annual probability of extinction between 2001 and 2007 was estimated to be over twice that of the probability of colonisation.
- Urbanisation is concluded to be an important agent of decline for *L. raniformis*, because of the habitat loss and fragmentation it entails, and because it will exacerbate declines caused by climate-change.

RECOMMENDATIONS

- Significant conservation initiatives are urgently required to conserve *L. raniformis* in the MCC (and elsewhere around Melbourne), given the ongoing urban expansion and the looming threat posed by climate-change.

- Initiatives should be pursued to secure all remnant populations of *L. raniformis* at high risk of extinction in the MCC, and to attempt to re-establish those that have been recently lost (via habitat enhancement). Priorities for habitat acquisition, protection and/or enhancement are provided to facilitate this (Appendices I & II).

- Guidelines to be developed as the final action of this project will be of great benefit for the preservation of *L. raniformis* across Melbourne's urban-fringe. These guidelines should be published and disseminated to land managers across the region.

- In the medium-term, it is imperative that explicit strategies are developed for the conservation of *L. raniformis* in the MCC and other urban-fringe landscapes around Melbourne. Opportunities to develop these strategies should be explored during a forthcoming project, which will use the extinction and colonisation models developed here as the basis of a stochastic metapopulation model for the species.

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1.1.   The Growling Grass Frog

1.1.1.   An ecological overview

The Growling Grass Frog (*Litoria raniformis*) Keferstein is a member of the 'bell frog' species complex (Anura: Hylidae), a group of morphologically and ecologically similar frogs found across the temperate regions of southern Australia (Courtice and Grigg 1975; Barker *et al.* 1995; Thomson *et al.* 1996; Mahony 1999). The complex was historically thought to consist of seven species, but only five of those are currently included: the Green and Golden Bell Frog (*L. aurea*), Yellow-spotted Bell Frog (*L. castenea*), *L. raniformis*, Spotted-thighed Frog (*L. cyclorhyncha*) and Moore's Frog (*L. moorei*) (Burns and Crayn 2006). *Litoria raniformis* is the most widely distributed member of the complex, inhabiting (or formerly inhabiting) the Australian Capital Territory, New South Wales, Victoria, South Australia and Tasmania (Courtice and Grigg 1975; Barker *et al.* 1995; Thomson *et al.* 1996; Mahony 1999).

Litoria raniformis generally inhabits mesic, lowland environments. In Victoria, the frog inhabits most regions but is largely absent from the semi-arid mallee environments of the north-west, and the alps in the north-east (Brook 1982). Nonetheless, the species displays some intrusions into both environments: in semi-arid regions via the Murray–Darling River system, and in the alps via river valleys and associated lake systems (Osborne *et al.* 1996; Pyke 2002; Wassens 2005; Smith *et al.* 2008). *Litoria raniformis* is a largely aquatic species, and has been reported to occupy a variety of permanent and ephemeral wetlands including slow-flowing sections of rivers and streams, lakes, swamps, billabongs, and ponds (Ashworth 1998; Robertson *et al.* 2002; Heard *et al.* 2004; Wassens 2005; Hamer and Organ 2006; Heard *et al.* 2008a; Smith *et al.* 2008). The species will also readily utilise artificial wetlands such as irrigation canals, rice growing bays, quarries, farm dams, and water treatment ponds.

As with other members of the bell frog complex, *L. raniformis* is primarily active during the spring and summer (Pyke 2002). Activity is limited during the cooler winter months, and frogs may be located in torpor beneath cover close to wetlands at this time (Pyke 2002; G. Heard, M. Scroggie pers. obs.). Temporal patterns of mate-calling by males indicate that reproductive activity begins in early September, and continues until January or February (Ashworth 1998; G. Heard unpubl. data). However, calling frequency and intensity peaks between November and December (G. Heard unpubl. data), and this coincides with observations of amplexus (A. Organ, Ecology Partners, pers. comm.; G. Heard pers. obs.). Activity during the remainder of summer and early autumn appears focussed on obtaining sufficient fat reserves for the winter months: frogs are often located in apparent 'ambush' positions at the waterline, or in the nearby terrestrial zone (< 100 m from the waterline) during this time of year (Heard *et al.* 2008a). Activity wanes as temperatures decrease during autumn.

The diurnal habitats of *L. raniformis* are well known, particularly its propensity to bask in the sun (Pyke 2002). Males also frequently call during daylight hours, generally during mild, sunny conditions (Ashworth 1998; G. Heard unpubl. data). Nonetheless, most activity occurs at night (Pyke 2002). Whilst nocturnal activity can occur over a wide range of weather conditions, it appears heightened by mild temperatures, with little wind.

Knowledge of the diet of *L. raniformis* is restricted to anecdotal information, and inferences from dietary studies of *L. aurea*. As alluded to above, *L. raniformis* displays an 'ambush' or 'sit-and-wait' foraging strategy to capture prey, both in the water when amongst floating and submerged vegetation, and when on land (Heard *et al.* 2008a). Dietary studies on *L. aurea* indicate that the species is a generalist carnivore, and will consume a variety of invertebrates and small vertebrates (Christy 2000; Miehs 2000; Pyke and White 2001). Anecdotal data suggest the diet of *L. raniformis* is very similar (Pyke 2002). Both species are also known to devour tadpoles and metamorphs of their own species (Miehs 2000; Pyke and White 2001; Pyke 2002). Indeed, cannibalism may represent an important means of fuelling the rapid growth rates and great fecundity that both species display: such prey is likely to be rich in fat and protein, and can make up over 20% of the stomach contents of these frogs (Miehs 2000). Other small vertebrates are also likely to be valuable in this regard, and are eaten opportunistically (e.g. Romijn 2007).

1.1.2. Conservation status

Formerly considered both widespread and abundant, *L. raniformis* is currently recognised as endangered. The species is listed as such on the IUCN Red List 2004, and listed as vulnerable to extinction under the Commonwealth *Environmental Protection and Biodiversity Conservation Act* 1999. It is also listed as threatened in each state within which it occurs (Clemann and Gillespie 2007).

The conservation status of *L. raniformis* became of concern only relatively recently, following a marked contraction in its distribution during the latter half of last century (Osborne *et al.* 1996; Ashworth 1998; Mahony 1999; Pyke 2002). These declines appear to have been ubiquitous across the frogs' range, and are likely to have been caused by a synergy of threatening processes (Pyke 2002). Habitat destruction, fragmentation and alteration appear ultimate causes of most disappearances, with stochastic events being likely proximate causes. For example, populations of *L. raniformis*, *L. aurea* and *L. castanea* on the Southern Tablelands of New South Wales and the Australian Capital Territory disappeared almost completely sometime between 1978 and 1981 (Osborne *et al.* 1996). These populations were likely subject to habitat destruction, fragmentation and alteration throughout the preceding century as agricultural practices expanded in the region, but were probably exterminated by the combination of a severe drought and the introduction of the exotic disease chytridiomycosis caused by the pathogen *Batrachochytrium dendrobatidis*, which spread across eastern Australia at roughly this time, and caused rapid declines or extinctions of numerous Australian frog species (Osborne *et al.* 1996; Berger *et al.* 1998).

1.1.3. Urbanisation as a key threatening process

In southern Victoria, a major issue for the conservation of *L. raniformis* is the species' apparent sensitivity to habitat alterations caused by urban development. In greater Melbourne, this frog was historically widespread, but is today restricted to urban-fringe environments (Figure 1) where wetland habitats and open space remain prominent landscape features. The planned expansion of urban development in these areas may cause further population declines of this species unless sound conservation strategies are devised and implemented.

To this end, research on the conservation requirements of *L. raniformis* in Melbourne's urbanising landscapes has been conducted in recent years (Robertson *et al.* 2002; Heard *et al.* 2004; Poole 2004; Hamer and Organ 2006; Heard *et al.* 2006, 2008a). This work has

produced two important findings: (i) that the frog appears to form metapopulations in urbanising landscapes (demographically independent populations connected by dispersal; Hanski and Simberloff 1997), and therefore, that habitat management should allow metapopulation processes to continue, and; (ii) that the probability of wetland occupancy declines with increasing urbanisation of the surrounding landscape. These findings have provided important interim guidance to conservation initiatives for *L. raniformis* around Melbourne. However, given the rapid and extensive expansion of urban development in areas supporting remnant populations of *L. raniformis* around Melbourne, land managers urgently require a more detailed understanding of the impacts of urbanisation on this species, and identification of means by which those impacts can be mitigated.
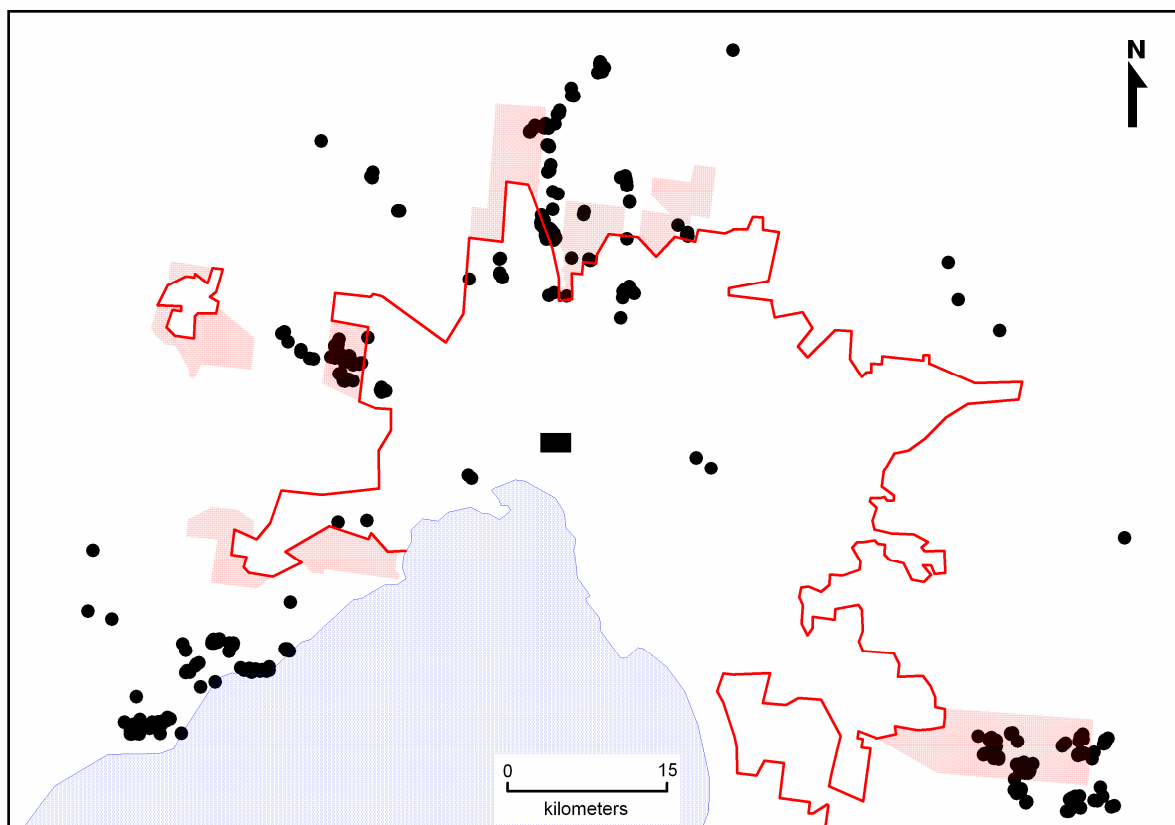
Figure 1. The known contemporary distribution of *Litoria raniformis* in the vicinity of Melbourne, Victoria. The blue hatched area is Port Phillip Bay, and the black rectangle is the Central Business District. Dots are individual records of the frog, the red-line is the current extent of urban development, and the red-hatched areas are designated urban growth zones. Only records from 2000 onwards are displayed. Source: Atlas of Victorian Wildlife, 2008.

1.2.   Project background and actions

This project sought to examine the structure and dynamics of a metapopulation of *L. raniformis* situated within the Merri Creek corridor (herein, MCC) on Melbourne's northern outskirts, and, in doing so, assess the regional impacts of urbanisation on this species. It was broadly motivated and guided by two recovery actions listed in the draft National Recovery Plan for *L. raniformis* (Clemann and Gillespie 2007): (i) To improve understanding of the biology and ecology of *L. raniformis* so effective management and sustainable use of natural resources within its habitat can be achieved, and (ii) To identify causes for the observed decline of *L. raniformis* across its geographic range. The project was funded by the Commonwealth Department of Environment, Water, Heritage and the Arts

(DEWHA), via the Biodiversity and Ecosystem Services division (BES) of the Victorian Department of Sustainability and Environment (DSE).

The project draws together an extensive data-set on the metapopulation dynamics of *L. raniformis* in the MCC acquired between the 2001 and 2007 (Organ 2002; Robertson *et al.* 2002; Williams 2002; Wilson 2003; Heard *et al.* 2004; Moysey *et al.* 2004; Poole 2004; Renowden 2005; Wilson *et al.* 2005; Heard *et al.* 2006; Renowden *et al.* 2006; Heard *et al.* 2008a; Heard *et al.* 2008b; G. Heard unpubl. data). It sought to address five specific actions considered crucial to our understanding of the potential impacts of urbanisation on the species in the MCC (and elsewhere), and ways by which those impacts may be mitigated. This report details completion of four of these actions. Each action and its justification are outlined below.

1.2.1.   Actions

Develop an improved understanding of the metapopulation structure of* L. raniformis *in the MCC

As outlined above, previous research on *L. raniformis* in Melbourne's urbanising landscapes indicated that the species displays metapopulation dynamics within this region. Evidence includes spatially clustered patterns of wetland occupancy (Robertson *et al.* 2002; Heard *et al.* 2004), infrequent, distance-limited dispersal (Hamer and Organ 2008), and apparent extinctions and recolonisations (Heard *et al.* 2004; Wilson *et al.* 2005). These findings have provided important qualitative guidance to conservation strategies, but the metapopulation dynamics of the species, and their implications for its conservation, have never been assessed in any detail. Specifically, whilst observations of population turnover (above) have been indicative of a classical metapopulation structure for *L. raniformis* ('classical metapopulations' being those in which habitat occupancy is dynamic, given frequent extinction and colonisation), it is also possible that the species dynamics are better described by a 'mainland-island' structure in which populations are generally stable and maintained by the export of individuals from large, high quality sites. Distinguishing between the two is important because it determines which type of models should be applied to forecasting population viability under different management scenarios (Sjögren-Gulve and Hanski 2000).

This action sought to rectify this ambiguity for *L. raniformis* within the MCC. Four predictions were derived from the notion that the frog forms classical metapopulations, and tested against a multi-season occupancy and mark-recapture dataset. Firstly, if habitat patches support demographically independent populations connected by distance-limited dispersal, it was predicted that: (i) the probability of patch (= wetland) occupancy would be positively influenced by connectivity, and; (ii) only a minority of individuals would disperse from their patch of origin. Secondly, if populations are extinction prone, given demographic or environmental stochasticity, but may be re-established via immigration from neighbouring populations, it was predicted that: (iii) patch occupancy would be temporally dynamic, and; (iv) the probability of extinction would be negatively influenced by patch area (the traditional surrogate for population size in classical metapopulation models; Hanski 1994, 1998), whilst the probability of colonisation would be positively influenced by connectivity.

Refine predictive models of habitat occupancy for **L. raniformis** *in the MCC*

Heard *et al.* (2004) developed predictive models of habitat occupancy for *L. raniformis* in the MCC. This work was a useful step in our understanding of the habitat requirements of the species in urbanising landscapes; however, the modelling had four deficiencies. Firstly, it did not include all sites that were surveyed in the 2001-2002 season. Secondly, it did not incorporate three patch-level variables that may be important: patch area, salinity and urban cover in the terrestrial zone (i.e., the buffer zone). All have been found to have important effects on wetland occupancy by amphibians (e.g. Semlitsch and Bodie 2003; Parris 2006; Smith *et al.* 2007). Thirdly, building cover was ignored when measuring the extent of urban development in the dispersal neighbourhood, which was approximated by road density. Buildings are also likely to influence 'landscape-permeability' for *L. raniformis*, and hence, a combined measure is desirable. Finally, it did not account for imperfect detection in the assignment of habitat occupancy. Exclusion of detection uncertainty has the potential to undermine conclusions drawn from habitat models, or at least, to bias estimates of their parameters (MacKenzie *et al.* 2006).

Refinement of these models is also an important step towards the development of models of population extinction and recolonisation (Action 3), because variables related to a pattern of habitat occupancy should, in theory, be those that influence the underlying dynamics.

Develop models of the processes of patch-level extinction and recolonisation for **L. raniformis** *in the MCC.*

Monitoring of habitat occupancy by *L. raniformis* within the MCC between 2001-2002 and 2006-2007 provides a unique opportunity to develop models of the processes of population extinction and recolonisation for the species. Development of these models will identify the variables relevant to the viability of individual populations in the MCC. In turn, this will enable: (i) development of qualitative description of the conditions required for persistence of remnant populations, prescriptions of the conditions required for recolonisation of currently vacant habitat, and prescriptions for the creation of additional habitat, and; (ii) development of a 'stochastic patch occupancy model' (SPOM) for the species that could be used to assess future metapopulation viability under different management scenarios or environmental conditions (Sjögren-Gulve and Hanski 2000).

Produce an updated assessment of the status of the nationally-significant metapopulation of **L. raniformis** *in the MCC, and describe the impacts of urbanisation on metapopulation viability in this species.*

The extensive habitat occupancy data-set available for *L. raniformis* in the MCC (above) enables population trends within the region to be assessed. This is of substantial importance in its own right, because the metapopulation of *L. raniformis* occurring within the MCC is of national significance (Clemann and Gillespie 2007). However, the trends apparent within this region, when combined with the information acquired under the proceeding actions, also allow general conclusions about the impacts of urbanisation on *L. raniformis* and how they can be mitigated.

2.   METHODS

2.1.   Study area, patch definition and selection

This study was conducted in the middle and upper catchments of the Darebin, Merri and Yuroke Creeks on the northern outskirts of Melbourne. These catchments together encompass an area of over 350 square kilometres, and make up a significant proportion of Melbourne's northern volcanic plain. The climate is temperate, with cool winters (July mean maximum temperature, 13.4^0C), warm summers (January mean maximum temperature, 25.9^0C) and an average annual rainfall of 649 mm (Beardsell 1997). The landscape is undulating (rising to a maximum elevation of only ~200 m asl), and historically was characterised by a mosaic of grassland, scrub, woodland and wetland ecosystems (Beardsell 1997). Remnants of these ecosystems remain today, but the contemporary landscape is dominated by livestock-based agriculture in the north (upper catchments), and urban and industrial development in the south (middle and lower catchments). The Darebin, Merri and Yuroke Creeks subsequently traverse an urban-rural gradient. Urban development of these catchments will continue into the foreseeable future.

Litoria raniformis inhabits a wide variety of lentic wetlands, but also breeds within still or slowly-flowing sections of streams (Pyke 2002). A habitat patch for the species' was subsequently defined as 'any lentic wetland, or any still or slowly-flowing pool along a stream'. In accord with the frog's use of the terrestrial surrounds of wetlands in the study area (Heard *et al.* 2008a), patches are further defined here as both the aquatic zone and surrounding land to a distance of 100 m perpendicular to the water-line.

One hundred and sixty seven patches were included in this study. All were originally surveyed in 2001-2002, and have been monitored haphazardly thereafter (see below). The majority of patches (157) were identified between December 2001 and May 2002 (Robertson *et al.* 2002). Three approaches were used. In the first instance, pools along each of the named streams in the study area were located at random using a 'kilometre on, kilometre off' scheme. Square kilometre grid cells of the Australian Map Grid (1966) were used to delineate ~1 km long segments of each stream on topographical maps, and every second kilometre (beginning from the southern-most point reached by each stream in the study area) selected for inspection. One pool was located within each of these sections, along the 500 m of stream with the best road access. The position of these patches was determined by pacing a random number of steps (between 0–500) upstream from the downstream end of the pre-selected 500 m section of stream (located using pre-calculated coordinates and a Garmin® 12XL GPS unit), and locating the nearest pool. Where the random position fell on a dry stretch of stream, the nearest pool containing water was selected. The second approach entailed including any pool that was found to be occupied by *L. raniformis* during either diurnal or nocturnal searches along each stream (conducted in conjunction with occupancy surveys; see below). These searches generally entailed listening for and locating calling males, and occurred both within and beyond the kilometre sections of stream in which the random pools were located. Thirdly, lentic wetlands were identified using topographical maps, satellite imagery of the study area (courtesy of the Victorian Department of Sustainability and Environment Corporate Geospatial Data Library), or by ground reconnaissance (December 2001–May 2002). Their selection was based on the cooperation of the relevant landholders. The remaining 10 patches included in this study were surveyed during the 2001-2002 season as part of several environmental impact assessments. These patches are herein referred to as 'EIA wetlands'.

2.2. Field surveys

2.2.1. Original occupancy surveys (2001-2002)

Each patch was surveyed for *L. raniformis* on between one and four occasions during the 2001-2002 active season of the frog (288 surveys in total). Standardised surveys were undertaken at all but the 10 EIA wetlands (Robertson *et al.* 2002), which were surveyed by private consultants. Survey data for the latter were extracted from the relevant reports (Organ 2002; Williams 2002), or acquired through personal communication. In the interests of brevity, survey protocols employed by consultants are not separately described here; they were largely consistent with those outlined below.

To minimise variability in detection probabilities, surveys were only undertaken during weather conditions considered suitable for activity by *L. raniformis*: during the day, air temperature greater than 15°C, with moderate to no wind; during the night, air temperature greater than 12°C, with moderate to no wind. The chronology of surveys was also randomised for this purpose. Wetlands were grouped into spatially proximate clusters (between four and eight patches per group), and both clusters, and patches within clusters, selected at random for survey on any given day or night. Surveys commenced with a standard period of ten minutes spent listening for frog calls from the water's edge at the beginning of each survey. Vocal imitation of *L. raniformis* advertisement calls was conducted during the last five minutes of this period in an attempt to stimulate production of calls by males. Each wetland was then systematically searched for frogs. Binoculars (during the day) and spotlights (during the night) were used to scan all surfaces of the water body whilst traversing its length. Frogs active within the terrestrial zone, or sheltering under surface cover, were pursued, but these searches were generally limited to within 15 m of the waterline given the largely aquatic nature of *L. raniformis* (Pyke 2002; Heard *et al.* 2008a). Frogs were detected either by direct observation or (at night) by identification of their eye-shine. Survey date and time, weather conditions, personnel and survey duration were recorded (Heard *et al.* 2006). Survey duration varied with patch area and habitat complexity, but typically lasted between 30 and 60 minutes. Measures to reduce the possible spread of infectious pathogens between wetlands were implemented (NPWS 2001). Survey protocols are described in greater detail by Heard *et al.* (2006).

2.2.2. Mark-recapture

A mark-recapture study was implemented at 31 wetlands to examine the rate of dispersal of *L. raniformis* in the study area. Patch selection proceeded with the aim of maximising the chance of observing both short- and long-distance dispersal. Patches selected encompassed the majority available within three spatially discrete patch-clusters in the middle reaches of the Merri Creek catchment (Campbellfield, Somerton and Donnybrook). Inter-patch distance ranged from 30 to 16,380 m.

Wetlands were monitored between October and April in 2004-2005 and 2005-2006. However, logistical and access constraints did not allow all patches to be censused in each season, and resulted in some variation in survey intensity within seasons. Eight surveys were conducted at 23 patches in 2004-2005, and 10 surveys conducted at 13 in 2005-2006. Surveys were conducted on a rotational basis (i.e., all patches were surveyed before proceeding to the next survey round). Rotation length was three-weeks in 2004-2005 and two-weeks in 2005-2006. The chronology of surveys within each rotation was randomised, as above.

Wetlands were surveyed at night (using techniques identical to those described above), and capture by hand or net attempted for all *L. raniformis* located. Co-ordinates of the point of capture were recorded for each frog using the Universal Transverse Mercator system (AGD 1966). Frogs were retained overnight and marked in the laboratory the following day by either subcutaneous injection of a Passive Integrated Transponder (PIT) tag (11.5×2.12 mm, Trovan Ltd, East Yorkshire, United Kingdom), or a Visible Implant Alphanumeric (VIA) tag (Northwest Marine Technology, Shaw Island, USA). Tagging procedures are described in detail by Heard *et al.* (2008b). To enable identification of frogs that lost tags, the toe-pad on the right middle finger of the left-hand was also clipped following standard procedures (Donnelly *et al.* 1994).

Frogs were released at their point of capture within 24 hrs. Subsequent to the initial survey at each patch, all captured frogs were scanned for the presence of a PIT tag (using a Trovan® 'LID570 Pocket Reader'), inspected for the presence of a VIA tag (using an LED torch and viewing glasses), or inspected for the presence of toe-clips in the absence of either tag. Unmarked individuals were retained and marked as described above. Recaptured frogs were released immediately following data collection, which replicated that undertaken following initial capture. A total of 807 frogs were marked and released.

2.2.3.   Monitoring occupancy dynamics (2001-2002 to 2006-2007)

Rates and correlates of temporal changes in patch occupancy were inferred from survey data collected between 2001-2002 and 2006-2007. Surveys were conducted at a subset of patches in each year between 2002-2003 and 2005-2006, and all 167 patches resurveyed in 2006-2007 (total number of surveys, 1380). Annual survey data were acquired during specific research projects (Wilson 2003; Heard *et al.* 2004; Poole 2004; Heard *et al.* 2006, 2008a), the mark-recapture study (above), or as part of several environmental impact assessments. Survey data from the latter were again extracted from the relevant literature (Moysey *et al.* 2004; Renowden 2005; Wilson *et al.* 2005; Renowden *et al.* 2006), or acquired through personal communications. Annual survey data were available for 54 patches, but those surveyed in any given year varied according to the objectives of the relevant research. Nonetheless, in all years the sub-set of patches selected was distributed widely across the study area, displayed variable attributes, and included wetlands found to be occupied and unoccupied in 2001-2002. Surveys were conducted between October and April in each season, with most occurring between December and March. Surveys were conducted both diurnally and nocturnally following the techniques described above, with repeat surveys conducted at the majority of patches (range, 1–10 surveys/patch/season).

2.3.   Data analysis

2.3.1.   Metapopulation structure

The probability of patch occupancy would be positively influenced by connectivity

The influence of connectivity on the probability of patch occupancy (ψ) was investigated using single-season zero-inflated binomial occupancy models (MacKenzie *et al.* 2002; MacKenzie *et al.* 2006). These models treat sites as being either occupied, at which the species in question will be detected with a probability <1, or unoccupied, at which the probability of detection is zero. They use detection histories from multiple surveys to jointly estimate ψ and the probability of detection (p) (MacKenzie *et al.* 2002; MacKenzie *et al.* 2006). The influence of connectivity on ψ was investigated by developing models in which

this parameter was constrained to be a linear function of an autocovariate term (Besag 1972; Augustin *et al.* 1996), and comparing the fit of these models to those that lacked such terms. The autocovariate term was defined as the distance-weighted number of neighbouring patches that were occupied, as follows:

$$acov_i = \sum_{j \in N_i} w_{ij} y_j \qquad \qquad \text{(Eq 1)}$$

where N_i defines a neighbourhood region surrounding patch i, w_{ij} is the inverse of the Euclidean distance (m) between i and each of its j neighbouring patches (i.e., $1/d_{ij}$), and y_j are the occupancy statuses of each neighbour j (one if the patch is occupied, zero if not). To enable assessment of the spatial scale over which connectivity effects extended (and hence, assessment of the average maximum dispersal distance), models were developed in which the neighbourhood radius for the autocovariate term varied from 500 m to 3000 m, at 500 m increments. The lower limit was based on the dispersal distances observed during the mark-recapture component of this study (see below), and the upper limit was based on maximum dispersal distance known for the closely-related *L. aurea* (Patmore 2001). Calculation of autocovariate terms was undertaken using package *spdep* (Bivand 2008) in *R* version 2.8.1 (R Development Core Team 2008). To avoid potential convergence problems during model fitting, the autocovariate function was multiplied by a large constant (1000) prior to the analysis.

The use of an autocovariate term as an explicit measure of connectivity is somewhat atypical. These terms are typically applied to account for spatial dependence of patch occupancy (spatial autocorrelation), with little reference to whether this dependence arises from extrinsic (e.g., autocorrelation of patch quality) or intrinsic (distance-limited dispersal) processes (Augustin *et al.* 1996; Klute *et al.* 2002; Moore and Swihart 2005). Use of an autocovariate term as a measure of connectivity may be misleading if there is strong spatial dependence in the extrinsic factors that influence patch occupancy. However, this problem is common to all connectivity measures that are applied in metapopulation models (Morris and Doak 2002). The likelihood that such 'environmental noise' could produce spurious connectivity effects in the 2001-2002 occupancy data is explored below (see 'Discussion').

The candidate model set was extended to include models in which p was constant, or constrained to be linear functions of survey effort (person minutes), time of day (diurnal or nocturnal), date (days since September 1, which is the approximate commencement of the reproductive season for *L. raniformis* in the study area), or additive combinations of these covariates. Models in which p was constrained to be a quadratic function of 'date' (to account for a possible mid-season peak in detectability; see below) were not considered, as the vast majority of surveys were completed in the latter half of the season. Meteorological covariates were also not considered, given that they have relatively little influence on the probability of detection of *L. raniformis* in the study area when using weather-standardised survey protocols (Heard *et al.* 2006).

Goodness-of-fit of the most parameterised models was assessed using the technique of MacKenzie and Bailey (2004), implemented in PRESENCE version 2.0 (Hines 2006). These tests indicated only slight over-dispersion (minimum $\hat{c}$ estimate, 1.213). The candidate model set was subsequently fit to the data using MARK version 5.1 (White and Burnham 1999). Relative support for alternative models was determined on the basis of the corrected Akaike's Information Criterion (AIC$_c$) and normalised model selection weights

(Burnham and Anderson 2002). These weights were also used to derive model-averaged estimates of the regression coefficients for the autocovariate term that displayed the highest level of support (Burnham and Anderson 2002).

Only a minority of individuals would disperse from their patch of origin

Recaptures proved too infrequent for estimation of dispersal rates whilst accounting for the uncertainties of the recapture process (Schwarz 2005). Analysis of these data was therefore restricted to description of observed dispersal, and calculation of a naïve estimate of the dispersal rate. The latter was calculated following exclusion of the four individuals that were observed to lose their tags during this study.

Patch occupancy would be temporally dynamic

Temporal flux in patch occupancy by *L. raniformis* was assessed using multi-season zero-inflated binomial occupancy models (MacKenzie *et al.* 2003; MacKenzie *et al.* 2006). These models extend the single-season approach discussed above, and enable modelling of annual probabilities of extinction (ε) and colonisation (γ) whilst accounting for imperfect detection. Assessment of the presence of temporally dynamic patch occupancy was achieved by comparing models in which the probability of occupancy (ψ) does not change from year to year (i.e., ε and γ are fixed at zero), to models in which annual changes in ψ are incorporated by allowing ε and γ to be separately estimated (MacKenzie *et al.* 2006).

Results of the single-season analysis were used to guide model structure. The probability of occupancy (ψ) was constrained in each case to be a linear function of the autocovariate term that displayed the greatest support in the single-season analysis. The probability of detection (*p*) was modelled as per the single-season analysis, except that models that included a quadratic effect of survey date were added to account for a possible mid-season peak in detectability. For simplicity, ε and γ were modelled as spatially and temporally constant in the situations where they were separately estimated.

Owing to the lack of an appropriate test, goodness-of-fit of these models was not assessed. However, to meet the assumption of closure within seasons (MacKenzie *et al.* 2003; MacKenzie *et al.* 2006), six surveys at three patches completed in 2004-2005 were excluded from the analysis. These wetlands were inundated by heavy rain after the fifth survey (following several years of being dry), and were colonised by *L. raniformis* at this time (see 'Results'). The candidate model set was fit to the abridged data-set using MARK, and relative support for alternate models determined on the basis of AIC$_c$ and model selection weights.

Probability of extinction would be negatively influenced by patch area and the probability of colonisation positively influenced by connectivity

Determinants of extinction and colonisation were also investigated using the multi-season zero-inflated approach outlined above (MacKenzie *et al.* 2003; MacKenzie *et al.* 2006). The probability of occupancy (ψ) was again constrained to be a linear function of the autocovariate term which displayed the greatest support in the single-season analysis. The probability of detection (*p*) was modelled only as a linear function of survey effort, date and time of day, given the apparent inferiority of models incorporating the quadratic 'date' effect (see 'Results'). The influence of patch area (measured using satellite imagery) and connectivity on ε and γ was investigated by developing models in which these parameters

were constrained to be linear functions of these factors, and comparing the support for these models to those that lacked such terms. Patch area was log(x+1) transformed for the purposes of this analysis. Again, only the autocovariate term that displayed substantial support in the single-season analysis was applied. The candidate model set was fit to the data-set using MARK, and relative support for alternate models determined on the basis of AIC_c and model selection weights. Model-averaged estimates of the regression coefficients for the effects of patch area and the autocovariate on ε and γ (respectively) were derived as above.

2.3.2.   Refining predictive models of habitat occupancy

Relationships between the probability of occupancy (ψ) by *L. raniformis* and nine patch- and landscape-scale variables (Table 1) were determined using the single-season zero-inflated binomial approach described above (MacKenzie *et al.* 2002; MacKenzie *et al.* 2006). The nine variables selected incorporated all those originally assessed by Heard *et al.* (2004), and have plausible ecological mechanisms linking them to the likelihood of extinction and colonisation for *L. raniformis* in the study area, via their influence on population size and immigration rate (Table 1).

Candidate model set

A candidate model set was first developed on the basis that the mechanisms identified here that link patch- and landscape-level variables to extinction and colonisation dynamics for *L. raniformis* (and hence, occupancy) were likely to interact in an additive fashion. An initial model set was developed in which all additive combinations of the nine selected variables were represented, and then pruned to avoid 'overfitting' (Burnham and Anderson 2002). Firstly, all models that did not include the autocovariate and aquatic vegetation cover were excluded. Connectivity→colonisation relationships are fundamental to metapopulations (see above), and aquatic vegetation has been repeatedly suggested to be an important determinant of habitat quality for *L. raniformis* (see Table 1). Secondly, no models that included additive combinations of the two 'landscape permeability' variables were considered. As parkland corridors are maintained along most streams in the urbanised zone of the study area, both landscape permeability variables represented measures of the extent of open space in the neighbourhood, and were therefore functionally inter-related. Finally, models with additive combinations of more than six variables were not considered given sample size constraints. Model structure for *p* was based on the preceding analysis of these data (see 'Prediction 1' above). The final model set was composed of 70 models.

Model fitting

Missing covariate data is problematic when fitting zero-inflated binomial models to occupancy data. The mean aquatic vegetation cover and salinity over all patches was substituted for those patches at which estimates of these covariates were unavailable. Missing survey covariate data was also accounted for in this way (with the value used being the mean over all surveys). To avoid potential convergence problems, patch area, salinity and the length of streams in the neighbourhood were log(x+1) transformed prior to the analysis. As above, the autocovariate was also multiplied by a large constant (1000) for this purpose.

Table 1. Patch- and landscape-level variables considered as potential determinants of extinction and colonisation for *Litoria raniformis* in the Merri Creek corridor. Variable selection and expected relationships with occupancy are based on mechanisms linking them to population size and immigration rate for the frog. Mechanisms were identified using existing information on the biology of *L. raniformis*, *L. aurea* and *L. castanea*. 'Source' details the relevant literature.

Variable	Title	Measure of	Relationship with occupancy	Mechanism/s	Source[†]
Area (square meters)	Area	Population size	Positive linear	Territoriality in adults, cannibalism, interference competition in larvae (= density-dependence)	1, 10, 11, 13, 15, 18, 19
Hydroperiod (score, 0-3)	Hydro	Population size	Positive linear	Physiological needs of adults and larvae	1, 2, 10, 11, 13, 14, 15, 18, 19, 22, 24, 25
Aquatic vegetation cover (%)	Aqveg	Population size	Positive linear	Microhabitat requirements of adults and larvae, substrate requirements for egg incubation, food requirements of larvae	1, 2, 5, 6, 8, 10, 13, 14, 15, 17 19, 22, 24, 25, 26, 27, 29, 30, 31
Predatory fish (presence or absence)	Fish	Population size	Negative linear	Predation of eggs and larvae	6, 7, 10, 12, 15, 20, 23, 33
Salinity (μS cm^{-1})	Sal	Population size	Negative linear	Physiological requirements of larvae	9, 10, 15, 16, 27
Urban cover in and adjoining terrestrial zone (%)	T-urban	Population size	Negative linear	Microhabitat and foraging requirements of adults, traffic mortality	1, 3, 4, 10, 21, 22, 24, 27, 28, 30
Distance-weighted number of occupied patches in neighbourhood (connectivity)	Acov	Immigration rate	Positive linear	Distance-limited dispersal	1, 10, 17, 22, 27, 29, 32
Length of stream in neighbourhood (m)	N-stream	Immigration rate	Positive linear	Physiological and microhabitat requirements of migrants, lack of physical barriers	10, 14, 27, 30
Urban cover in neighbourhood (%)	N-urban	Immigration rate	Negative linear	Physical barriers, traffic mortality	3, 4, 10, 14, 27, 22, 24, 28

† 1, Humphries (1979); 2, Cree (1984); 3, Daly (1995); 4, Pergolotti (1995); 5, Gillespie (1996); 6, Morgan and Buttemer (1996); 7, Pyke and White (1996); 8, Ashworth(1998); 9, Penman (1998); 10, Christy (2000); 11, Miehs (2000); 12, Pyke and White (2000); 13, Miehs and Pyke (2001); 14, Patmore (2001); 15, Pyke and White (2001); 16, Christy and Dickman (2002); 17, Hamer *et al.* (2002a); 18, Hamer *et al.* (2002b); 19, Pyke (2002); 20, Pyke *et al.* (2002); 21, Wilson (2003); 22, Heard *et al.* (2004); 23, Howard (2004); 24, Poole (2004); 25, Goldingay and Newell (2005a); 26, Goldingay and Newell (2005b); 27, Wassens (2005); 28, Romjin(2007); 29, Hamer and Organ (2008); 30, Heard *et al.* (2008a); 31, Smith *et al.* (2008); 32, Wassens *et al.* (2008); 33, Reynolds (2009).

Goodness-of-fit of the most parameterised models was first assessed. Fit was good (minimum $\hat{c}$ estimate, 1.084), and the candidate model set was subsequently fit to the data using MARK. Relative support for alternate models was determined on the basis of AIC_c and model selection weights. Model-averaged estimates of the regression coefficients for each of the patch- and landscape-scale covariates were derived, and used to produce a final model of patch occupancy for *L. raniformis* in the study area.

2.3.3.   Developing models of extinction and recolonisation

The development of models of population extinction and colonisation for *L. raniformis* in the MCC focused on the identification of relationships between these processes and the patch- and landscape-level variables considered in the preceding section (recalling that variables that influence the probability of occupancy (ψ) should, in theory, be those that influence extinction and colonisation dynamics). Identification of these relationships proceeded with the aid of the multi-season zero-inflated binomial approach of MacKenzie *et al.* (2003), as outlined above. It represents an extension of the modelling of extinction and colonisation conducted as part of Action 1.

Candidate model set

A candidate model set was developed that incorporated the five variables found to have support as determinants of patch occupancy by *L. raniformis*. Eight models were initially developed in which the probability of extinction (ε) was constrained to be an additive linear function of the four 'population size' variables supported above (but note that all models included aquatic vegetation cover automatically, given the previous evidence of its importance and its clear relationship with occupancy), and the probability of colonisation (γ) was constrained to be a linear function of connectivity. The possibility of 'rescue' and 'immigration' effects was subsequently considered and incorporated. A rescue effect represents the situation in which small populations can be bolstered by immigration from nearby larger ones, which in turn reduces their likelihood of extinction (Brown and Kodric-Brown 1977). An immigration effect (as termed here) refers to the possibility that immigration rates vary amongst patches not only due to landscape-level variables, but due to patch-level variables as well (i.e., immigrants are more likely to find larger patches, or are more likely to settle in those of higher quality; Hanski 1999). Rescue effects were considered plausible for *L. raniformis* in the study area, given the very strong relationship between ψ and connectivity (see 'Results'). A rescue effect was included in all models simply by adding connectivity as a linear covariate of ε. The possibility of immigration effects was included by developing another eight models, identical to those described above, but with the relevant patch-level variables also added as linear covariate of γ. The candidate model set therefore consisted of 16 models.

Model fitting

Results of previous analyses were used to guide model structure for both ψ and *p*: the former was set to be an additive linear function of the five patch- and landscape-level variables supported in Action 2; the latter was set to be an additive linear function of person minutes, date since commencement of the breeding season and time of day. Patch area was again log(x+1) transformed prior to the analysis, and the autocovariate multiplied by a large constant (1000). Missing values were accounted for as above.

Fitting of the candidate model set to the data was conducted using MARK, and relative support for alternate models determined on the basis of AIC_c and model selection weights. Model-averaged estimates of the regression coefficients for each variable for both ε and γ (respectively) were derived. These estimates were used, as above, to produce final models of extinction and colonisation for *L. raniformis* in the MCC.

2.3.4. Status assessment

Two approaches were used to asses the status of the MCC metapopulation of *L. raniformis*. The first entailed re-survey during the 2006-2007 season of all wetlands at which the species had been previously observed, and estimation of the likelihood of persistence for these populations. The second approach entailed using models developed under Action 3 to estimate annual probabilities of extinction and colonisation within the MCC between 2001-2002 and 2006-2007, and therefore evaluation of the trajectory of the metapopulation during that period.

Prior to the 2006-2007 season, all records of *L. raniformis* that were available from within the MCC were compiled. This included those acquired during the monitoring detailed above, as well as those available from other sources. The latter included historical records (i.e., pre-2001) at the 167 monitored wetlands, and both historical and contemporary records at additional locations. Sources of these records included the Atlas of Victorian Wildlife (AVW), Robertson *et al.* (2002) (whom compiled additional historical records available within the MCC), consultancy reports (Beardsell 1997; George *et al.* 2001; Williams 2001; Organ 2002; Wilson *et al.* 2005), Melbourne Water frog census data, and personal communications with local naturalists, consultants and land managers. A canvass of 143 previously known populations of *L. raniformis* within the MCC was compiled. All but 14 of these populations were re-surveyed during that season. The probability of occupancy during 2006-2007 under average conditions was subsequently estimated using the single-season zero-inflated binomial approach described above. This probability may be interpreted as the average chance of a previously known population having persisted to that season. Model structure was guided by that identified in Action 2.

Annual probabilities of extinction (ε) and colonisation (γ) for *L. raniformis* in the MCC during the monitoring period were estimated in a similar fashion. Both probabilities were calculated with all covariates held at their mean, and hence, they represent annual probabilities of extinction and colonisation for an average population/patch. Estimates were model-averaged according to the procedures explained above.

2.3.5. Limitations

The above analyses entail two shortcomings. The first is obvious: the calculation of the autocovariate term ignores detection uncertainty, and may subsequently be biased by low and/or heterogeneous detection probabilities. It is considered unlikely that the autocovariate terms used here were badly biased, given a reasonable overall probability of detection in most cases (~0.855 when based on one diurnal and one nocturnal survey). The second problem arises from the use of maximum likelihood procedures to estimate the parameters of models incorporating an autocovariate term. The between-site dependency inherent in autologistic models (or any occupancy model that includes a measure of connectivity) renders their full likelihood intractable, and necessitates an approximation known as the 'maximum pseudo-likelihood' (Besag 1972). This scheme has been shown to produce useful models of occupancy (Augustin *et al.* 1996; Klute *et al.* 2002; Moore and Swihart 2005) and

occupancy turnover (Sjögren-Gulve and Ray 1996; Kindvall 2000; Harrison and Ray 2002), but it evidently loses accuracy when the degree of spatial dependence is high (Wintle and Bardos 2006). As such, the parameter estimates and their 95% confidence intervals presented here should be treated with some caution. Whilst it is unlikely that the conclusions drawn from this study would change with the application of techniques that account for these short-comings, a future test of this would be worthwhile.

3.   RESULTS

3.1.   Metapopulation structure

3.1.1.   The probability of patch occupancy would be positively influenced by connectivity

Analysis of patch occupancy data acquired during the 2001-2002 season strongly supports the prediction that the probability of occupancy would be positively influenced by connectivity. *Litoria raniformis* was detected at 62 patches across the study area (naïve probability of occupancy, 0.371), including both lotic and lentic wetlands in each of the major catchments surveyed. However, observed patch occupancy was far from spatially uniform, instead displaying the strong spatial clustering that would be expected to result from a strong positive influence of connectivity on patch occupancy (Figure 2).

Model selection statistics for the alternative occupancy models clearly demonstrate that connectivity influenced the probability of patch occupancy by *L. raniformis*: models in which this parameter was not constrained to be a function of an autocovariate displayed model selection weights of zero (Table 2). These weights are also unambiguous with regard to the spatial scale over which this relationship extends. Models in which the probability of occupancy was constrained to be a function of an autocovariate with a neighbourhood of 1000 m accounted for >99% of the model selection weights (Table 2). The model-averaged regression coefficient for the autocovariate measured over this neighbourhood was 0.811 (95% CI, 0.424–1.198).

Table 2. Relative support for models relating patch occupancy by *Litoria raniformis* in the Merri Creek corridor to connectivity. Occupancy-connectivity relationships were modelled by constraining the probability of occupancy (ψ) to be a linear function of autocovariate functions calculated with radii between 500 and 3000 m ('Acov…'). The strength of these relationships was assessed by comparing models that included them ($\psi \sim \alpha + \beta_i(\text{Acov}…)$) to models in which ψ was spatially constant ($\psi \sim \alpha$). The probability of detection (p) was either modelled as a constant, or constrained to be a linear function of combinations of person minutes ('Effort'), date of survey ('Date', defined as days since September 1), and time of day ('Night', a binary covariate denoting whether the survey was conducted during the day or night). The number of parameters (K), model deviance, distance from the most parsimonious model (ΔAIC_c) and model selection weights (w) are provided. Only the top ten models are shown for clarity.

Model structure		K	Deviance	ΔAIC_c	w
ψ	p				
$\sim \alpha + \beta_1(\text{Acov1000})$	$\sim \alpha + \beta_1(\text{Effort}) + \beta_2(\text{Date}) + \beta_3(\text{Night})$	6	230.864	0.000	0.444
$\sim \alpha + \beta_1(\text{Acov1000})$	$\sim \alpha + \beta_1(\text{Date}) + \beta_2(\text{Night})$	5	233.764	0.748	0.306
$\sim \alpha + \beta_1(\text{Acov1000})$	$\sim \alpha + \beta_1(\text{Effort}) + \beta_2(\text{Date})$	5	234.701	1.685	0.191
$\sim \alpha + \beta_1(\text{Acov1000})$	$\sim \alpha + \beta_1(\text{Date})$	4	240.132	4.991	0.037
$\sim \alpha + \beta_1(\text{Acov1000})$	$\sim \alpha + \beta_1(\text{Effort}) + \beta_2(\text{Night})$	5	240.426	7.410	0.011
$\sim \alpha + \beta_1(\text{Acov1000})$	$\sim \alpha + \beta_1(\text{Effort})$	4	245.241	10.099	0.003
$\sim \alpha + \beta_1(\text{Acov1000})$	$\sim \alpha + \beta_1(\text{Night})$	4	245.318	10.176	0.003
$\sim \alpha + \beta_1(\text{Acov2000})$	$\sim \alpha + \beta_1(\text{Effort}) + \beta_2(\text{Date}) + \beta_3(\text{Night})$	6	242.968	12.104	0.001
$\sim \alpha + \beta_1(\text{Acov2000})$	$\sim \alpha + \beta_1(\text{Date}) + \beta_2(\text{Night})$	5	245.352	12.336	0.001
$\sim \alpha + \beta_1(\text{Acov1500})$	$\sim \alpha + \beta_1(\text{Effort}) + \beta_2(\text{Date}) + \beta_3(\text{Night})$	6	244.323	13.459	0.001
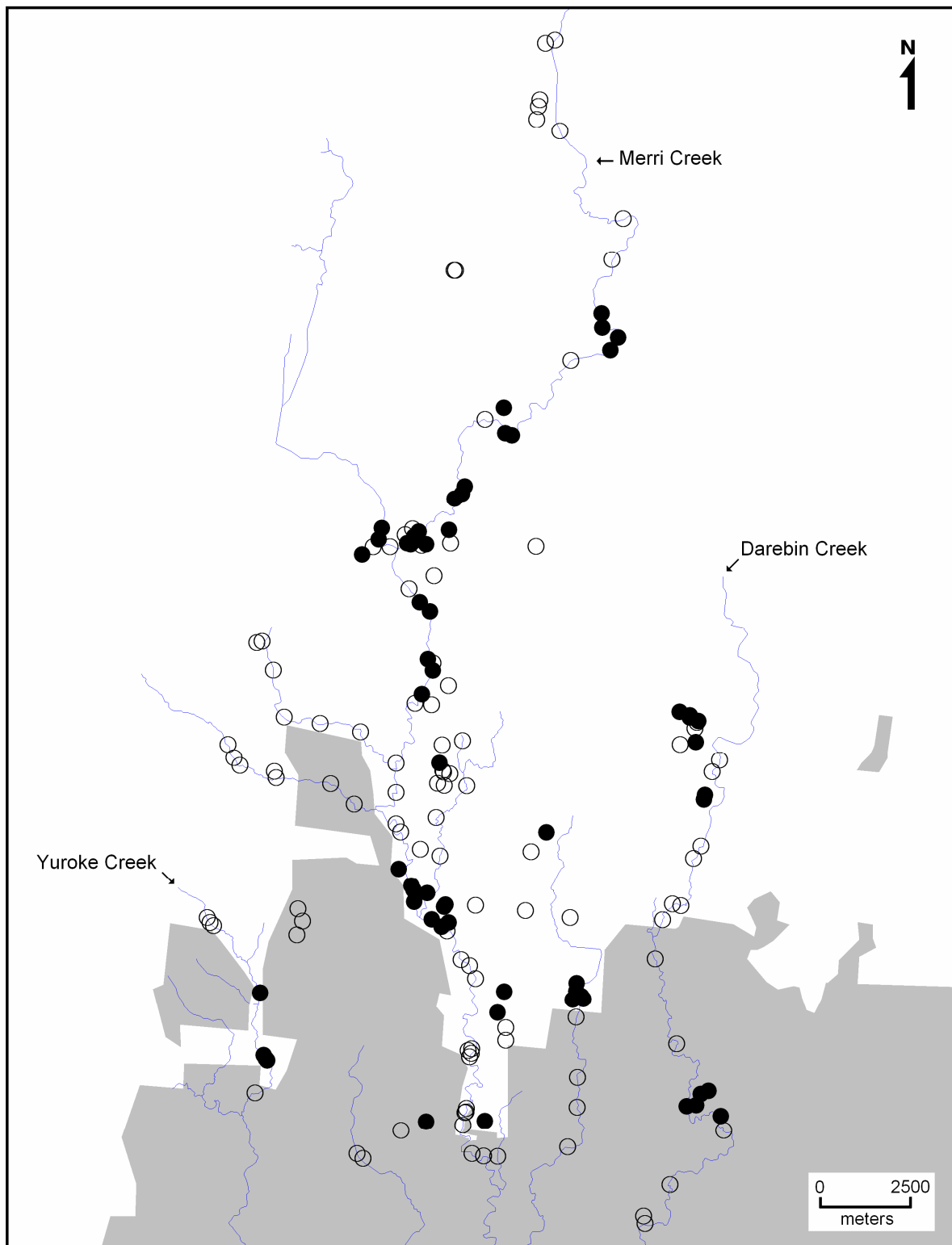
Figure 2. Observed patch occupancy by *Litoria raniformis* in the Merri Creek corridor during the 2001-2002 season. Symbols denote wetlands where the species was detected (●) or not detected (○). The hatched area represents the extent of urban development in that season.

3.1.2.   Only a minority of individuals would disperse from their patch of origin

One hundred and thirty one frogs were recaptured, on up to five occasions each. Only eighteen of these individuals were observed to disperse from their original wetland of capture to another (naïve dispersal rate, 14%), and only one observed to undertake a return movement. This individual was one of 17 frogs that dispersed between adjacent pools of the Merri and Kalkallo Creeks in Donnybrook (Figure 3).

The remaining recaptured individual was the only one known to undertake an extensive overland movement. This frog (an adult male) moved 427 m from a pool on the Merri Creek to a pool on the Curley Sedge Creek in Somerton, following its inundation by heavy rainfall in February 2005 (Figure 3). Nonetheless, additional overland movements were recorded. Four unmarked *L. raniformis* (three adults, one juvenile) were observed at Curley Sedge Creek following its inundation, and 12 frogs (seven adults, five juveniles) recorded at two nearby swamps that were also inundated at this time (Figure 3). All three wetlands had been dry during the preceding two years, and no *L. raniformis* had been detected there since 2001-2002 (despite being surveyed on up to 13 occasions in the intervening period). The nearest occupied patches from which these colonising individuals could have originated were between 260 m and 490 m away. No dispersal was observed in Campbellfield (Figure 3), or between the clusters. These data support the prediction that only a minority of *L. raniformis* disperse from their patch of origin, and suggest that overland dispersal occurs only during particularly wet conditions.

3.1.3.   Patch occupancy would be temporally dynamic

Apparent changes in occupancy status occurred at 39 patches between 2001-2002 and 2006-2007 (Figure 4). All but one of the 62 wetlands originally found to be occupied by *L. raniformis* remained intact throughout the monitoring period, but the species was not detected at 20 of these in 2006-2007. Sixty-two percent of these extinctions were apparently compensated for by colonisations; surveys during 2006-2007 detected *L. raniformis* at 13 patches where the species was not recorded in 2001-2002. Both extinction and colonisation were observed at six patches (Figure 4).

Fitting of multi-season occupancy models to these data provides unequivocal support for the prediction that patch occupancy by *L. raniformis* would be temporally dynamic. Models in which ε and γ were fixed at zero displayed essentially no support: ΔAIC_c for these models were > 80 and model selection weights trivial (Table 3).

3.1.4.   Probability of extinction would be negatively influenced by patch area and the probability of colonisation positively influenced by connectivity

Apparent extinctions occurred at patches that were highly variable in size, ranging from small pools along streams (minimum area, 150 m^2) to large lentic wetlands (maximum area, 8741 m^2). Nevertheless, those at which extinction was observed were smaller on average than those at which *L. raniformis* was observed to persist throughout the monitoring period (3293.433 m^2 vs. 4530.972 m^2 respectively). Wetlands at which colonisation or recolonisation was observed were consistently close to occupied patches. All 19 were located within 1220 m of a patch occupied in 2001-2002 (mean, 510.555 m).
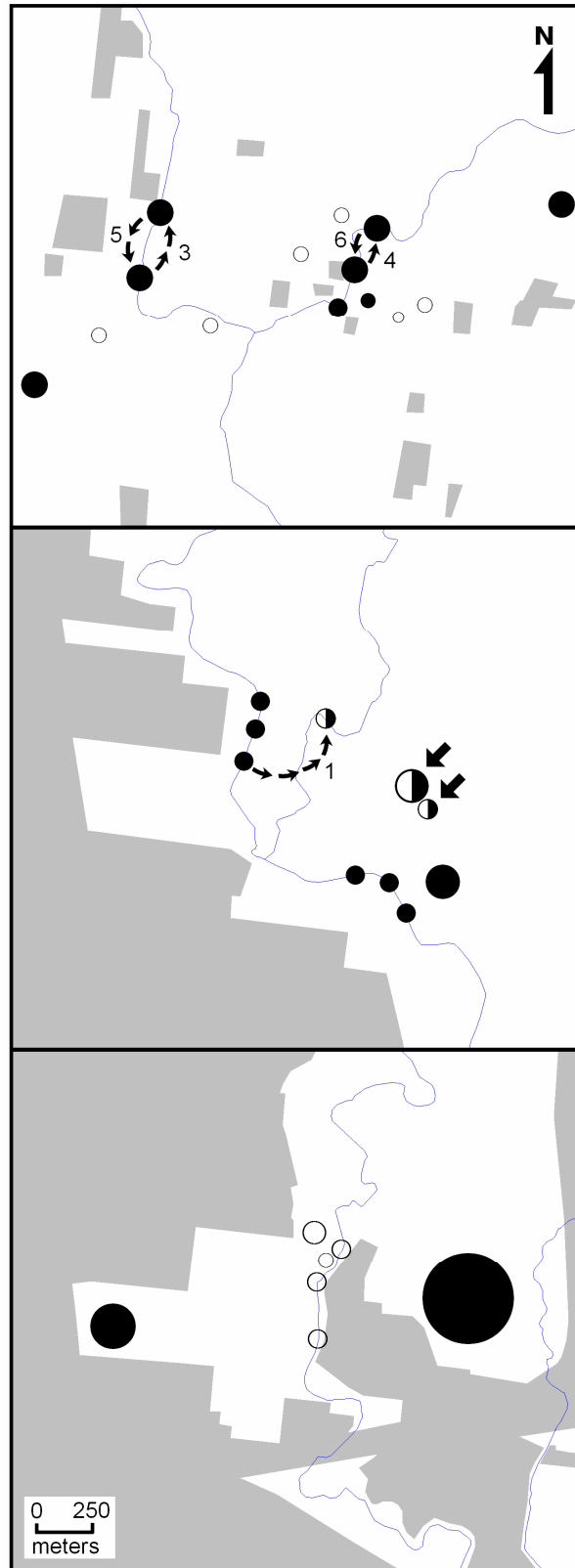
Figure 3. Observed dispersal by *Litoria raniformis* during the mark-recapture study at Donnybrook (top panel), Somerton (middle panel) and Campbellfield (bottom panel). Symbols denote wetlands that were occupied (●), unoccupied (○) or colonised during the study period (◑). Patch shapes are stylised, but their relative areas are represented accurately. Small arrows indicate the direction and number of observed dispersal events. The large arrows in the middle panel represent the wetlands that were colonised in February 2005, but at which no marked individuals were recaptured. The hatched area represents the extent of urban development in the relevant seasons.
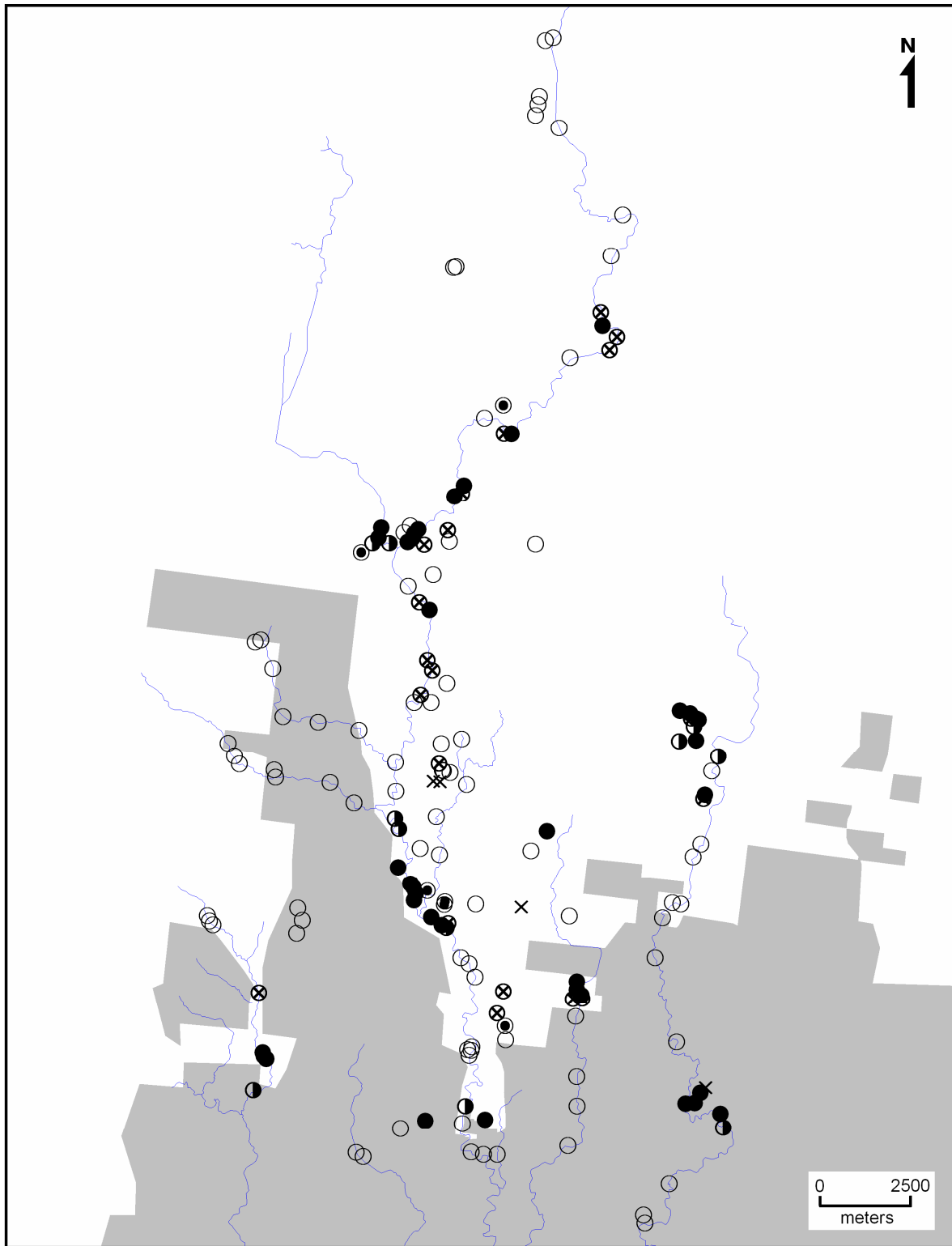
Figure 4. Observed patch occupancy dynamics of *Litoria raniformis* in the Merri Creek corridor between 2001 and 2007. Symbols denote wetlands at which the species was detected in each season that they were surveyed (●), those at which the species was never detected (○), those at which extinction was observed (⊗), those at which colonisation was observed (◐), those at which both extinction and recolonisation was observed (◉), and those that were destroyed during this period (×). The hatched area represents the extent of urban development in the final season (2006-2007).

Table 3. Relative support for models describing stable and dynamic patterns of patch occupancy by *Litoria raniformis* in the Merri Creek corridor. In all models, the probability of occupancy (ψ) was constrained to be a linear function of an autocovariate term calculated with a neighbourhood of 1000 m ('Acov1000'). Models differed in structures for ε (the probability of extinction), γ (the probability of colonisation) and p (the probability of detection). The first two of these parameters were either fixed at zero (the stable-occupancy scenario, signified by =0) or allowed to fluctuate between years at a constant rate (the dynamic-occupancy scenario, signified by $\sim\alpha$). Covariates on p were survey effort ('Effort', defined as person minutes), date of survey (days since September 1, either as a linear ['Date'] or quadratic [Date^2] effect), and time of day ('Night', a binary covariate denoting whether the survey was conducted during the day or night). The number of parameters (K), model deviance, distance from the most parsimonious model (ΔAIC_c) and model selection weights (w) are provided.

Model structure			K	Deviance	ΔAIC_c	w
ε	γ	p				
α	α	$\alpha+\beta_1(Effort)+\beta_2(Date)+\beta_3(Night)$	8	969.486	0.000	0.725
α	α	$\alpha+\beta_1(Effort)+\beta_2(Date)+\beta_3(Date^2)+\beta_4(Night)$	9	969.343	1.940	0.275
=0	=0	$\alpha+\beta_1(Effort)+\beta_2(Date)+\beta_3(Night)$	6	1058.447	84.824	0.000
=0	=0	$\alpha+\beta_1(Effort)+\beta_2(Date)+\beta_3(Date^2)+\beta_4(Night)$	7	1058.415	86.856	0.000

Models in which γ was constrained to be a function of an autocovariate term calculated over a neighbourhood of 1000 m accounted for > 99% of the model selection weight (Table 4), and the model averaged estimate of the regression coefficient for this effect was clearly positive as predicted (0.135; 95% CI, 0.070–0.199). However, the predicted negative relationship between patch area and ε was less well supported. The model averaged estimate of the regression coefficient for this effect was negative (-0.037; 95% CI, -0.131–0.057), but models in which ε was constrained to be a function of patch area were slightly inferior to those in which this parameter was modelled as a constant.

Table 4. Relative support for models relating extinction and colonisation probabilities of *Litoria raniformis* in the Merri Creek corridor to patch area and connectivity. In all models, the probability of occupancy (ψ) was constrained to be a linear function of an autocovariate term calculated with a neighbourhood of 1000 m ('Acov1000'), and the probability of detection (p) constrained to be a linear function of person minutes ('Effort'), date of survey (days since September 1), and time of day ('Night', a binary covariate denoting whether the survey was conducted during the day or night). Patch area→extinction relationships were modelled by constraining ε (the probability of extinction) to be a linear function of patch area ($\varepsilon\sim\alpha+\beta_1(Area)$). Connectivity→colonisation relationships were modelled by constraining γ (the probability of colonisation) to be a linear function of the above autocovariate ($\gamma\sim\alpha+\beta_1(Acov1000)$). These models were compared to those in which ε and γ were spatially constant ($\sim\alpha$). The number of parameters (K), model deviance, distance from the most parsimonious model (ΔAIC_c) and model selection weights (w) are provided.

Model structure		K	Deviance	ΔAIC_c	w
ε	γ				
$\sim\alpha$	$\sim\alpha+\beta_1(Acov1000)$	9	953.135	0.000	0.677
$\sim\alpha+\beta_1(Area)$	$\sim\alpha+\beta_1(Acov1000)$	10	952.528	1.486	0.322
$\sim\alpha$	$\sim\alpha$	8	969.486	14.268	0.001
$\sim\alpha+\beta_1(Area)$	$\sim\alpha$	9	969.099	15.964	0.000

3.2.   Refining predictive models of habitat occupancy

Model selection statistics are presented in Table 5, and model-averaged regression coefficients and cumulative weights for each patch- and landscape-level variable presented in Table 6. Model-averaged relationships between the probability of occupancy (ψ) by *L. raniformis* and the five variables with reasonable support in the data are depicted in Figure 5.

As expected *a priori*, wetlands at which *L. raniformis* was detected were larger in size than those at which it was not (+963.847 m^2 on average). Model selection statistics clearly support a relationship between ψ and patch area (cumulative weight for this variable being 0.999), and the model averaged regression coefficient confirms that it is strongly positive (Table 6, Figure 5). Patches at which the frog was detected also displayed longer hydroperiods (+0.344) and higher aquatic vegetation cover (+15.182%) as presumed *a priori*. Positive relationships between these variables and the probability of occupancy were well supported. Models that included hydroperiod ranked highly on the basis of AIC$_c$ and model selection weights (Table 5), its cumulative model selection weight was moderately high (Table 6), and the 95% CI of its model averaged regression coefficient only slightly overlapped zero (Table 6). Model selection statistics were uninformative for aquatic vegetation cover (it being included in all models automatically); however, the 95% CI of its regression coefficient did not overlap zero (Table 6).

Table 5. Relative support for models relating patch occupancy by *Litoria raniformis* in the Merri Creek corridor to the nine patch- and landscape-scale variables. Models vary only in the relationships between the probability of occupancy (ψ) and combinations of these variables (see text). The number of parameters (*K*), model deviance, distance from the most parsimonious model (ΔAIC$_c$) and model selection weights (*w*) are provided. Only the top 10 models are shown for clarity.

Model structure	K	Deviance	ΔAIC$_c$	w
α+β_1(Area)+β_2(Hydro)+β_3(Aqveg)+β_4(T-urban)+β_5(Acov)	10	196.778	0.000	0.119
α+β_1(Area)+β_2(Hydro)+β_3(Aqveg)+β_4(T-urban)+β_5(Acov) +β_6(N-stream)	11	195.340	0.855	0.077
α+β_1(Area)+β_2(Hydro)+β_3(Aqveg)+β_4(Acov)	9	199.915	0.874	0.077
α+β_1(Area)+β_2(Aqveg)+β_3(T-urban)+β_4(Acov)+β_5(N-stream)	10	197.822	1.044	0.070
α+β_1(Area)+β_2(Hydro)+β_3(Aqveg)+β_4(Acov)+β_5(N-stream)	10	197.899	1.121	0.068
α+β_1(Area)+β_2(Hydro)+β_3(Aqveg)+β_4(Acov)+β_5(N-urban)	10	198.357	1.579	0.054
α+β_1(Area)+β_2(Aqveg)+β_3(Acov)+β_4(N-stream)	9	200.925	1.884	0.046
α+β_1(Area)+β_2(Hydro)+β_3(Aqveg)+β_4(Fish)+β_5(Acov)	10	198.985	2.207	0.039
α+β_1(Area)+β_3(Aqveg)+β_4(Fish)+β_4(T-urban)+β_5(Acov) +β_6(N-stream)	11	196.704	2.219	0.039
α+β_1(Area)+β_2(Aqveg)+β_3(Sal)+β_4(Acov)+β_5(N-stream)	10	199.057	2.280	0.038

In contrast with the *a priori* reasoning, predatory fish were present at a higher proportion of wetlands at which *L. raniformis* was detected, and salinity was higher on average at these patches (+610.633 μS cm^{-1} on average). Fitting of occupancy models to these data did not support these relationships, nor those originally posed. These variables displayed the lowest cumulative model selection weights, and 95% CI's for their model-averaged regression coefficients substantially overlapped zero (Table 6). Nevertheless, the expectation of a negative relationship between patch occupancy and urban cover in and adjacent to the terrestrial zone (the final patch quality variable considered here) was reasonably well

supported. Models including this variable were highly ranked (Table 5), its cumulative model selection weight was moderate, and the 95% CI of its model-averaged regression coefficient only slightly overlapped zero (Table 6).

Table 6. Model-averaged regression coefficients (β_i) and cumulative weights (w_+) for relationships between patch occupancy by *Litoria raniformis* in the Merri Creek corridor and the nine patch- and landscape-scale variables. Confidence intervals (95%) for each regression coefficient are provided in parentheses. The cumulative weight for each variable is simply the sum of weights of models including that variable.

Variable	β_i	w_+
Area[†]	1.805 (0.366–3.245)	0.999
Hydro	1.119 (-0.237–2.474)	0.605
Aqveg[‡]	0.079 (0.016–0.142)	1
Fish	-0.155 (-0.682–0.373)	0.196
Sal	0.101 (-0.145–0.347)	0.196
T-urban	-0.034 (-0.075–0.006)	0.452
Acov[‡θ]	1.287 (0.421–2.154)	1
N-stream[†]	0.285 (-0.168–0.738)	0.448
N-urban	-0.002 (-0.012–0.007)	0.177

† Log(x+1) transformed
‡ Included in all models *a priori*
θ $\times 10^3$

As above, modelling confirmed a strong positive relationship between ψ and connectivity. Raw data suggested that both landscape permeability variables were related to patch occupancy as expected: length of stream within the neighbourhood was higher on average for patches at which *L. raniformis* was detected (+535.430 m), whilst the opposite was true for urban cover in the neighbourhood (-7.324%). However, neither of these relationships proved to be well supported. Several models that included length of stream in the neighbourhood ranked highly based on AIC_c and model selection weights (leading to a moderate cumulative weight for this variable), but the 95% CI of its regression coefficient overlapped zero substantially (Table 6). Urban cover in the neighbourhood performed worse-still, having a regression coefficient centred on zero, and cumulative weight of < 0.2 (Table 6).

The model-averaged relationship between ψ and the five patch- and landscape-level variables supported by the data was as follows:

$$\text{logit}(\psi) \sim -23.238 + 1.805(\text{Area}) + 1.119(\text{Hydro}) + 0.079(\text{Aqveg})$$
$$-0.034(\text{T-urban}) + 1.287(\text{Acov}) \qquad \text{(Eq 2)}$$
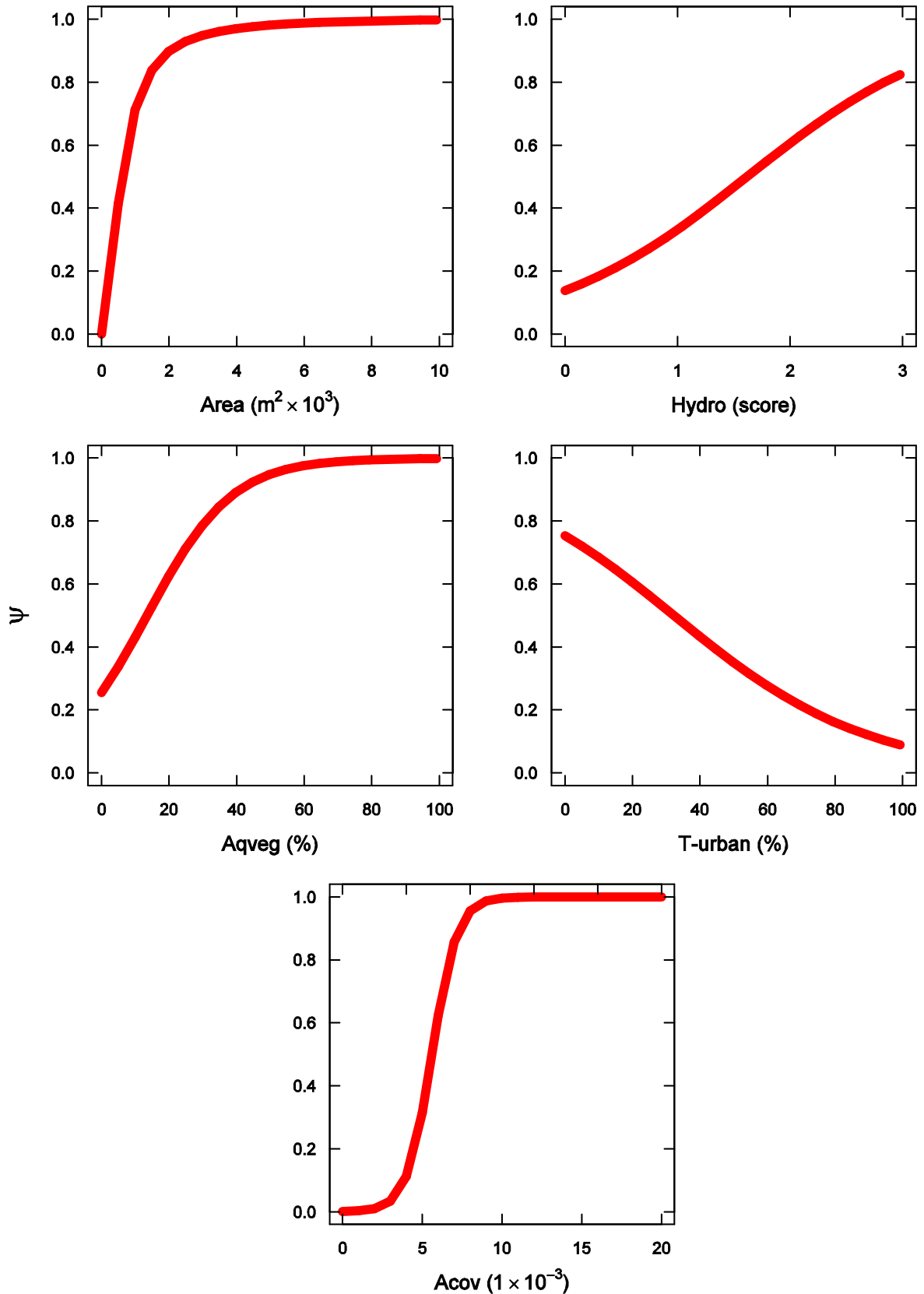
Figure 5. Model-averaged relationships between the probability of patch occupancy (ψ) of *Litoria raniformis* in the Merri Creek corridor and the five patch- and landscape-scale variables with reasonable support in the data. See Table 1 for variable definitions. Relationships are depicted with all other variables held at their mean.

3.3.   Developing models of extinction and recolonisation

Models 13–15 were clearly superior to all others on the basis of model selection statistics, encompassing 89% of the model selection weight (Table 7). Nevertheless, this apparent support was tempered by some incongruous results. Common to each model was the proposal that ε would be negatively related to hydroperiod, aquatic vegetation cover, and connectivity (the latter representing the rescue effect). Model averaged regression coefficients and cumulative weights support each of these relationships: their regression coefficients were negative and displayed 95% CIs that did not overlap zero, and their cumulative weights (where informative) were > 0.9 (Table 8). Model 15 also entailed a negative relationship between ε and patch area. Patches at which extinction was observed were smaller on average than those that remained occupied (as above), but in both cases patch sizes displayed considerable variability. The proposed negative relationship between ε and patch area had very little support (95% CI for the regression coefficient substantially overlapped zero, cumulative weight < 0.3; Table 8). However, the most striking discrepancy between the hypotheses represented by these models and the data is the fact that there was strong support for a negative, rather than positive, relationship between the likelihood of extinction and urban cover in and adjacent to the terrestrial zone. The 95% CI of the regression coefficient for this effect did not overlap zero, and it displayed a high cumulative weight (0.934; Table 8).

Fitting of the 16 models provides little support for any effect of patch area or quality on the likelihood of colonisation for *L. raniformis* in the MCC. Whilst model 14 (which included an immigration effect) was the second highest ranked on the basis of model selection statistics, the other three in the top-four supposed that γ was related only to connectivity (Table 7). Examination of model averaged regression coefficients and cumulative weights for each variable (Table 8) confirm the lack of any significant immigration effects. All variables except connectivity displayed regression coefficients whose 95% CI substantially overlapped zero, and had cumulative weights < 0.3.

Model-averaged relationships between ε and γ and the variables supported by the above analysis are depicted in Figure 6. Note that this does not include the negative relationship between ε and the surrounding urban cover. As argued below (see 'Discussion'), this relationship is considered spurious. For this reason, it is also excluded from the models of ε and γ presented below.

$$\text{logit}(\varepsilon) \sim 7.222 - 2.600(\text{Hydro}) - 0.044(\text{Aqveg}) - 0.125(\text{Acov}) \qquad \text{(Eq 3)}$$

$$\text{logit}(\gamma) \sim -3.855 + 0.111(\text{Acov}) \qquad \text{(Eq 4)}$$

Table 7. Relative support for models relating extinction and colonisation probabilities of *Litoria raniformis* in the Merri Creek corridor to the five patch- and landscape-scale variables with *a priori* support as determinants of these processes. Models vary only in their structure for the probability of extinction (ϵ) and colonisation (γ): in all models the probability of occupancy in the first season (ψ) was set to be an additive linear function of each of the five patch- and landscape-level variables, and the probability of detection (p) modeled as an additive linear function of survey effort, survey date and time of day (see text). The number of parameters (K), model deviance, distance from the most parsimonious model (ΔAIC_c) and model selection weights (w) are provided.

Hypothesis	Model structure		K	Deviance	ΔAIC_c	w
	ϵ	γ				
13	$\sim\alpha+\beta_1(Hydro)+\beta_2(Aqveg)+\beta_3(T\text{-}urban)+\beta_4(Acov)$	$\sim\alpha+\beta_5(Acov)$	17	868.276	0.000	0.499
14	$\sim\alpha+\beta_1(Hydro)+\beta_2(Aqveg)+\beta_3(T\text{-}urban)+\beta_4(Acov)$	$\sim\alpha+\beta_5(Acov)+\beta_6(Hydro)+\beta_7(Aqveg)+\beta_8(T\text{-}urban)$	20	863.559	1.826	0.200
15	$\sim\alpha+\beta_1(Area)+\beta_2(Hydro)+\beta_3(Aqveg)+\beta_4(T\text{-}urban)+\beta_5(Acov)$	$\sim\alpha+\beta_6(Acov)$	18	868.035	1.929	0.190
5	$\sim\alpha+\beta_1(Hydro)+\beta_2(Aqveg)+\beta_3(Acov)$	$\sim\alpha+\beta_4(Acov)$	16	875.056	4.619	0.050
16	$\sim\alpha+\beta_1(Area)+\beta_2(Hydro)+\beta_3(Aqveg)+\beta_4(T\text{-}urban)+\beta_5(Acov)$	$\sim\alpha+\beta_6(Acov)+\beta_7(Area)+\beta_8(Hydro)+\beta_9(Aqveg)+\beta_{10}(T\text{-}urban)$	22	862.112	4.791	0.046
6	$\sim\alpha+\beta_1(Hydro)+\beta_2(Aqveg)+\beta_3(Acov)$	$\sim\alpha+\beta_4(Acov)+\beta_5(Hydro)+\beta_6(Aqveg)$	18	873.647	7.541	0.012
10	$\sim\alpha+\beta_1(Area)+\beta_2(Hydro)+\beta_3(Aqveg)+\beta_4(Acov)$	$\sim\alpha+\beta_5(Acov)+\beta_6(Area)+\beta_7(Hydro)+\beta_8(Aqveg)$	20	872.682	10.948	0.002
9	$\sim\alpha+\beta_1(Area)+\beta_2(Hydro)+\beta_3(Aqveg)+\beta_4(Acov)$	$\sim\alpha+\beta_5(Acov)$	17	880.246	11.969	0.001
11	$\sim\alpha+\beta_1(Area)+\beta_2(Aqveg)+\beta_3(T\text{-}urban)+\beta_4(Acov)$	$\sim\alpha+\beta_5(Acov)$	17	904.924	36.648	0.000
12	$\sim\alpha+\beta_1(Area)+\beta_2(Aqveg)+\beta_3(T\text{-}urban)+\beta_4(Acov)$	$\sim\alpha+\beta_5(Acov)+\beta_6(Area)+\beta_7(Aqveg)+\beta_8(T\text{-}urban)$	20	902.220	40.486	0.000
7	$\sim\alpha+\beta_1(Aqveg)+\beta_2(T\text{-}urban)+\beta_3(Acov)$	$\sim\alpha+\beta_4(Acov)$	16	910.968	40.531	0.000
8	$\sim\alpha+\beta_1(Aqveg)+\beta_2(T\text{-}urban)+\beta_3(Acov)$	$\sim\alpha+\beta_4(Acov)+\beta_5(Aqveg)+\beta_6(T\text{-}urban)$	18	909.252	43.146	0.000
1	$\sim\alpha+\beta_1(Aqveg)+\beta_2(Acov)$	$\sim\alpha+\beta_3(Acov)$	15	916.276	43.688	0.000
2	$\sim\alpha+\beta_1(Aqveg)+\beta_2(Acov)$	$\sim\alpha+\beta_3(Acov)+\beta_4(Aqveg)$	16	915.316	44.879	0.000
3	$\sim\alpha+\beta_1(Area)+\beta_2(Aqveg)+\beta_3(Acov)$	$\sim\alpha+\beta_4(Acov)$	16	916.258	45.821	0.000
4	$\sim\alpha+\beta_1(Area)+\beta_2(Aqveg)+\beta_3(Acov)$	$\sim\alpha+\beta_4(Acov)+\beta_5(Area)+\beta_6(Aqveg)$	18	915.286	49.181	0.000

Table 8. Model-averaged regression coefficients (β_i) and cumulative weights (w_+) for each of the patch- and landscape-scale variables with *a priori* support as determinants of the annual probabilities of extinction (ε) and colonisation (γ) of *Litoria raniformis* in the Merri Creek corridor. Confidence intervals (95%) for each regression coefficient are provided in parentheses. The cumulative weight for each variable is simply the sum of weights of models including that variable.

Variable	β_i	w_+
ε		
Area[†]	0.020 (-0.080–0.121)	0.239
Hydro	-2.600 (-3.869 to -1.331)	0.999
Aqveg[‡]	-0.044 (-0.087 to -0.001)	1
T-urban	-0.146 (-0.283 to -0.001)	0.935
Acov[‡θ]	-0.125 (-0.227 to -0.023)	1
γ		
Area[†]	-0.014 (-0.040–0.011)	0.047
Hydro	0.143 (-0.126–0.412)	0.259
Aqveg	0.004 (-0.004–0.012)	0.259
T-urban	-0.007 (-0.018–0.004)	0.245
Acov[‡θ]	0.111 (0.042–0.180)	1

[†] Log(x+1) transformed
[‡] Included in all models *a priori*
[θ] $\times 10^3$

3.4.   Status assessment

Re-survey of the 123 previously known populations of *L. raniformis* in the MCC indicates that the metapopulation has declined markedly. Wetland destruction has eliminated six populations, whilst a further 70 were not detected during the 2006-2007 season (Figure 7). Observed extinctions were widespread, but clusters of extinctions were noted, including all populations previously known from the vicinity of La Trobe University, Bundoora; most populations south of Cooper Street, Campbellfield; all populations between Craigieburn Rd and Summerhill Road, Craigieburn (including all those previously known from Aitken and Malcolm Creeks), and; all but one population from Merriang or areas further to the north.

Extant populations (53) were located along the Yuroke and Moonee Ponds Creek, Westmeadows; in the vicinity of the McKimmies Road landfill sites, Bundoora; within the Edgars Road landfill site, Epping; in the vicinity of O'Herns Road, Somerton; in the vicinity of the Wollert landfill site, Wollert; and; around Donnybrook. The probability of occupancy (= persistence) under average conditions was estimated at 0.463 (95% CI, 0.334–0.596).

Within the 167 patches monitored between 2001-2002 and 2006-2007, patch occupancy was also observed to decline. Populations of *L. raniformis* were detected at 62 of the 167 wetlands visited in the original survey season (naive occupancy rate of 0.371), whereas only 51 were detected in the final monitoring season (naive occupancy rate of 0.305). Model averaged estimates of the annual probability of extinction (ε) and colonisation (γ) also suggest metapopulation contraction during the monitoring period; although, the uncertainty around these estimates renders them equivocal. Under average conditions, ε was estimated to be 0.115 (95% CI, 0.037–0.321) and γ to be 0.049 (95% CI, 0.025–0.095).
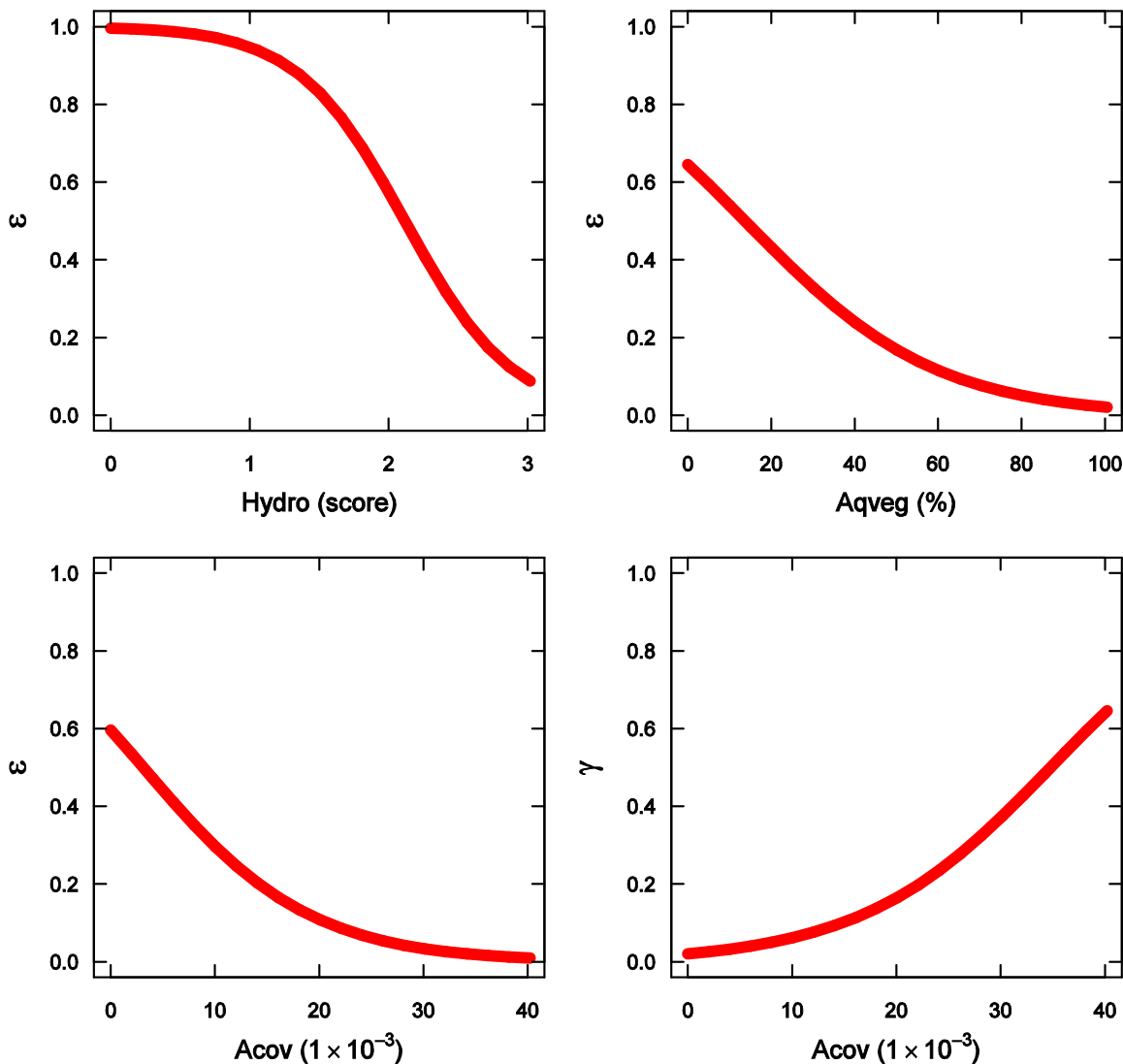
Figure 6. Model-averaged relationships between the annual probabilities of extinction (ε) and colonisation (γ) of *Litoria raniformis* in the Merri Creek corridor and the three patch- and landscape-level variables supported as determinants of these processes. For each variable, the 95% CI of their regression coefficient did not overlap zero, cumulative model selection weights were high and the relationship was congruent with that expected *a priori*.
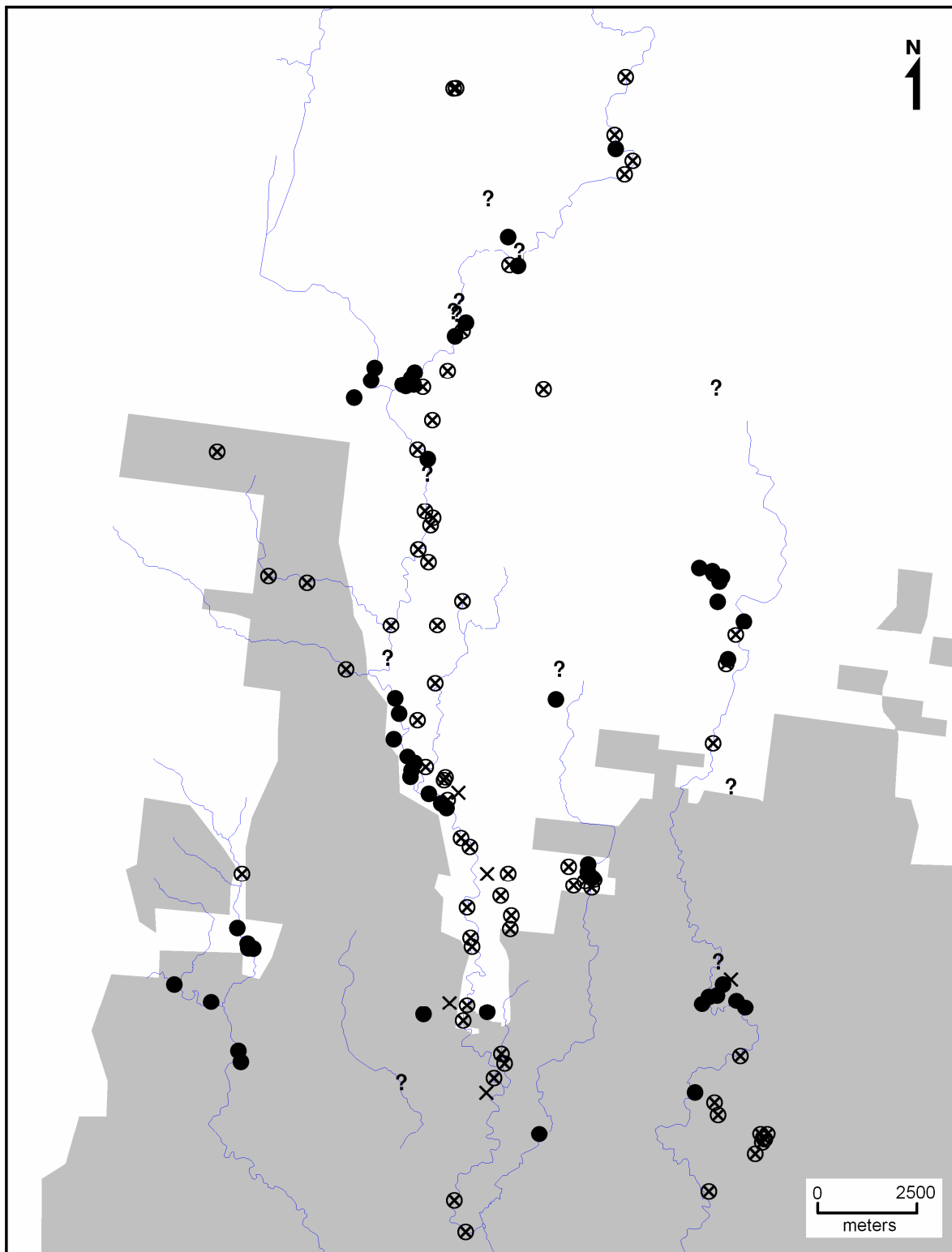
Figure 7. Status of previously known populations of *Litoria raniformis* in the Merri Creek corridor during the 2006-2007 season. Symbols denote populations observed to have persisted (●), populations observed to have gone extinct (⊗), populations known to be extinct given wetland destruction (×), and populations who's status could not be ascertained (?) given access or logistical constraints. The shaded area represents the extent of urban development in the 2006-2007 season.

4.   DISCUSSION

4.1.   Metapopulation structure

As an initial step, this study sought to rectify ambiguity from previous research regarding the metapopulation dynamics of *Litoria raniformis* within the MCC. Four predictions were derived from the notion that the frog forms classical metapopulations, and tested against a multi-season occupancy and mark-recapture dataset. The broad congruence observed between these predictions and the data suggest that this notion is plausible.

Take the first prediction: that the probability of wetland occupancy by *L. raniformis* would be positively influenced by connectivity. It was derived from the concept, in classical metapopulation theory, that populations are linked by distance-limited dispersal (Hanski and Gilpin 1991; Hanski and Simberloff 1997; Hanski 1999). Modelling of survey data acquired during 2001-2002 demonstrated that models in which the probability of occupancy was constrained to be a function of connectivity were vastly superior to those in which it was not, and that the effect of connectivity on patch occupancy was strongly positive. Nevertheless, as alluded to above (section 2.3.1), there are circumstances in which this relationship could result from mechanisms other than distance-limited dispersal. Theoretical and empirical evidence exists for spatially autocorrelated population extinctions in metapopulations (given spatially autocorrelated patch-quality or environmental stochasticity; Harrison and Quinn 1990; Hanski 1991; Sjögren-Gulve 1994; Smith and Gilpin 1997), which also produce the clustered patterns of patch occupancy expected from distant-limited dispersal (Clinchy *et al.* 2002). Three facts can be cited to reject this possibility for *L. raniformis* in the MCC: (i) the mark-recapture data strongly suggest that dispersal rates are distance-limited (Figure 8); (ii) observed extinctions were not spatially autocorrelated, and; (iii) the likelihood of colonisation was clearly linked to connectivity.
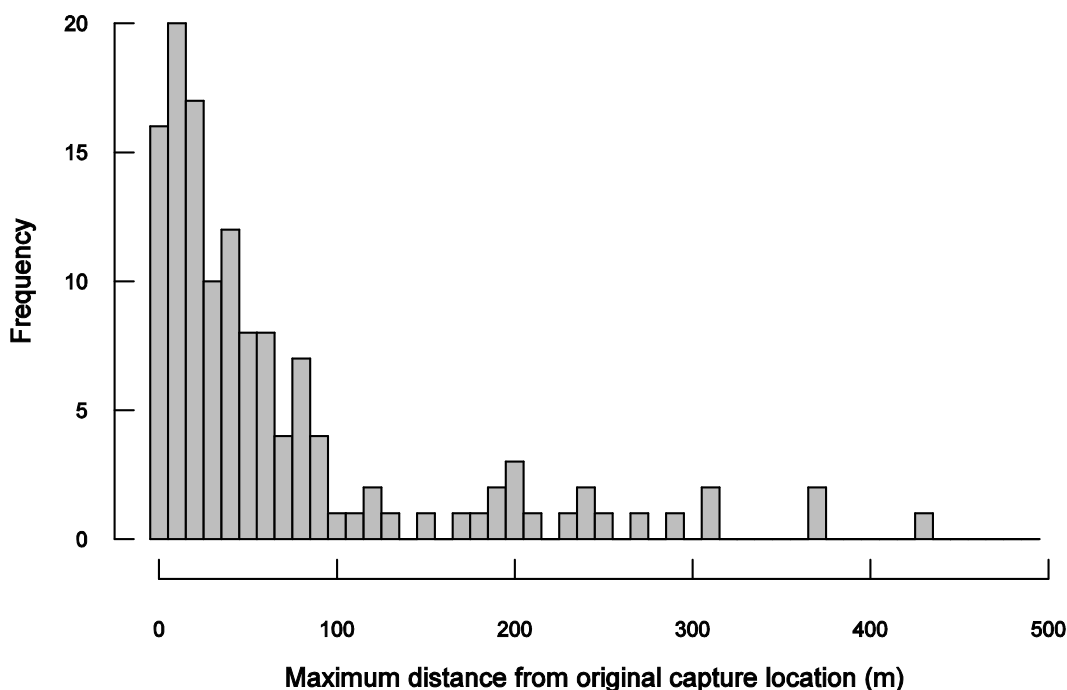
Figure 8. Histogram showing the distribution of maximum distances moved by individual *Litoria raniformis* from their original point of capture during the mark-recapture study. Movements include those observed both within and between patches.

Despite the importance of dispersal to classical metapopulation dynamics, the theory also requires that populations are demographically independent (Hanski and Gilpin 1991; Hanski and Simberloff 1997; Hanski 1999). For this to occur, dispersal must be relatively infrequent. The mark-recapture data obtained here support this expectation for *L. raniformis* in the study area, with only 14% of marked individuals being observed to disperse from one patch to another. The reliability of this finding hinges on uncertainties in the recapture process, which could not be accounted for here given sample size constraints. It may be that the dispersal between wetlands was frequent, but simply not observed as a result of the low rate of recapture (16%). This possibly cannot be discounted, but the apparently high patch fidelity recorded during this study is congruent with that observed for *L. raniformis* elsewhere on Melbourne's urban fringe, and for other members of the *L. aurea* complex (Humphries 1979; Christy 2000; Patmore 2001; Goldingay and Newell 2005a; Hamer *et al.* 2008; Hamer and Organ 2008).

The multi-season occupancy data compiled here also enabled scrutiny of the notion that populations are extinction prone given demographic or environmental stochasticity, but may be re-established via immigration from neighbouring populations. As predicted, wetland occupancy by *L. raniformis* was temporally dynamic, the probability of extinction was negatively influenced by wetland area, and the probability of colonisation positively influenced by connectivity. It is notable however, that the confidence interval for the effect of patch area on the likelihood of extinction was wide. Whilst this may appear problematic for the application of classical metapopulation theory, it is simply indicative of the greater importance of patch-quality and connectivity to population size for *L. raniformis* in the study area, as revealed by the subsequent analysis of the turnover data.

4.2.   Refining predictive models of habitat occupancy

The modelling of habitat occupancy completed here refines that previously undertaken for *L. raniformis* in the MCC by Robertson *et al.* (2002) and Heard *et al.* (2004). It incorporated data from a further 28 wetlands, assessed the importance of several additional patch-level variables, and accounted for imperfect detection in the assignment of habitat occupancy (with the exception of the calculation of the autocovariate term). It also served as an important component of the development of models of extinction and colonisation, because, as highlighted above, variables related to occupancy should in theory be those that drive the underlying dynamics.

Congruent with the earlier modelling, wetland hydroperiod and aquatic vegetation cover were both found to be important patch-level determinants of habitat occupancy for *L. raniformis* in the MCC. That hydroperiod should influence extinction likelihood for this highly aquatic frog (Pyke 2002; Heard *et al.* 2008a) is logical. The specific underlying mechanisms are discussed below. Since the original work of Robertson *et al.* (2002) and Heard *et al.* (2004), several additional studies conducted in Victoria have highlighted the positive relationship between aquatic vegetation cover and habitat occupancy by *L. raniformis*. Poole (2004) found a strong positive relationship between occupancy and aquatic vegetation cover in a study that spanned (primarily) Melbourne's western suburbs. Hamer and Organ (2008) found that wetlands occupied by the frog within the Pakenham area to Melbourne's south-east also displayed a higher cover and diversity of submerged and floating vegetation (particularly *Potamogeton* spp.). Smith *et al.* (2008), working within the riverine landscapes of north-western Victoria, demonstrated that this relationship is not peculiar to populations around Melbourne. Three mechanisms were proposed (Table 1) to link aquatic vegetation cover to population size and extinction likelihood for this frog, but it

is microhabitat availability that is perhaps most crucial. Adults of this species have been shown to display strong preferential use of submerged and floating vegetation during nocturnal activity (Heard *et al.* 2008a), and emergent vegetation provides sheltered perches for basking and ambushing prey during the day (Pyke 2002; G. Heard pers. obs.). These plants also appear to be important microhabitats for aquatic larvae, and likely serve as a refuge from predatory fish. Experimental work suggests tadpoles of this species, *L. aurea* and *L. moorei* are quite vulnerable to fish predation (Morgan and Buttemer 1996; Howard 2004; Reynolds 2009), and that aquatic vegetation cover reduces predator related mortality in anurans (Babbitt and Jordan 1996; Babbitt and Tanner 1997; Babbitt and Tanner 1998; Baber and Babbit 2004). It would not be surprising if the lack of a relationship between predatory fish occurrence and patch occupancy by *L. raniformis* in this study and others (Poole 2004; Hamer and Organ 2008) resulted from the mitigating force of aquatic vegetation cover.

Two of the three additional patch-level variables displayed relationships with wetland occupancy by *L. raniformis*: patch area and the cover of urban development in and adjacent to the terrestrial zone. Although others exist, the mechanism traditionally invoked to explain a positive relationship between patch area and extinction likelihood in classical metapopulations is density-dependent population growth (Hanski 1999). Individuals compete for space and other resources, and hence, only large patches can support large, resilient populations. Density-dependent population growth is considered plausible for *L. raniformis* for two reasons. Firstly, its sister-taxa are to display substantial intraspecific aggression during the reproductive season (Humphries 1979), and observational data suggest this is also the case for *L. raniformis* (G. Heard unpubl. data). Secondly, these frogs are highly cannibalistic (Pyke and White 2001; Pyke 2002). Dietary studies of *L. aurea* and *L. castanea* reveal that adults regularly consume conspecific juveniles, and indicate that conspecifics are an energetically important component of the adult diet (Humphries 1979; Christy 2000; Miehs 2000). Again, specific data are lacking for *L. raniformis*, but adults of this species have been observed to ambush and consume large numbers of juveniles as they metamorphose (G. Heard pers. obs).

The negative relationship between wetland occupancy by *L. raniformis* and urban cover in the terrestrial zone accords with many recent studies on amphibious herpetofauna (Burke and Gibbons 1995; Semlitsch 1998; Gibbons 2003; Semlitsch and Bodie 2003; Roe *et al.* 2006; Roe and Georges 2007). Of the various mechanisms thought to link conditions in the terrestrial zone to population size for these animals, microhabitat availability and traffic-related mortality are perhaps most relevant for *L. raniformis* in the MCC. This species is highly aquatic (above), but also known to be reliant on terrestrial microhabitats such as large boulders, logs and soil cracks for sheltering and overwintering (Pyke 2002; Wilson 2003; Wassens *et al.* 2008). No specific research has been undertaken on traffic-related mortality for *L. raniformis*, or other taxa within the *L. aurea* complex, but several authors have noted that these frogs are susceptible to collisions with vehicles when crossing roads (Daly 1995; Pergolotti 1995; Romjin 2007).

Contrary to expectations, neither of the 'landscape permeability' variables considered here (length of streams in the neighbourhood, urban cover in the neighbourhood) proved to be strongly related to patch occupancy. Urban cover, approximated by road density, was previously found to influence occupancy by *L. raniformis* in the MCC (Heard *et al.* 2004), an influence of both variables was suggested by dispersal events observed during the mark-recapture work (no dispersal being recorded in the most urbanised cluster monitored [Campbellfield], and dispersal being most frequent along the Merri and Kalkallo Creeks in

Donnybrook), and the literature is replete with examples of these variables influencing occupancy patterns of amphibians (Reh and Seitz 1990; Gibbs 1998; Hitchings and Beebee 1998; Vos and Chardon 1998; Knutson *et al.* 1999; Trenham *et al.* 2003; Mazerolle 2004; Pellet *et al.* 2004a; Pellet *et al.* 2004b; Parris 2006; Eigenbrod *et al.* 2007; Denoël and Ficetola 2008; Pillsbury and Miller 2008; Ficetola *et al.* 2009; Hartel *et al.* 2009; Simon *et al.* 2009). Rather than concluding that these two variables are unimportant for immigration and colonisation for *L. raniformis* in the MCC, we believe that the occupancy data used here were inadequate for quantifying their effect. Given that very few lentic wetlands are preserved outside of stream-corridors in urbanising land around Melbourne, patches far from streams or in areas completely surrounded by urban development were rare in the data-set. It is likely that these variables would have displayed a clearer relationship with patch occupancy if the data-set had been less effected by these constraints.

4.3. Developing models of extinction and recolonisation

To our knowledge, this is the first time that models of the processes of population extinction and colonisation have been developed for an Australian amphibian, and one of very few occasions where it has been achieved worldwide.

Modelling supported a strong negative relationship between the probability of extinction and wetland hydroperiod. As discussed above, the biology of *L. raniformis* renders its populations inherently susceptible to wetland desiccation. This is clear from a reproductive stand-point, because the species is an obligate aquatic breeder, and larvae require roughly 3 months to complete metamorphosis (G. Heard unpubl. data). However, there are also logical links between survival rates post-metamorphosis and wetland hydroperiod. Juvenile and adult *L. raniformis* are highly aquatic, being active primarily either at the water's edge or in or on aquatic vegetation within the water-body itself (Heard *et al.* 2008a). It is apparent that this proximity to water is central to their foraging strategy (e.g., ambushing aquatic arthropods as they emerge from the water), and allows rapid escape from terrestrial predators (Heard *et al.* 2008a). On a more fundamental level, long periods of wetland desiccation are likely to be physiologically stressful. These frogs do have some physiological and behavioural adaptions to deal with adverse hydroregulatory conditions (Cree 1984; Pyke 2002), but these adaptions are unlikely to be effective during sustained exposure to dry conditions.

The apparent relationship between aquatic vegetation cover and population size and extinction likelihood for *L. raniformis* suggested by the occupancy modelling was also strongly supported by the multi-season data. Populations inhabiting wetlands with a diverse and healthy cover of aquatic vegetation displayed a significantly lower chance of extinction than those inhabiting wetlands in which this attribute was deficient. As argued in the preceding section, microhabitat availability for adults and larvae is considered the primary mechanism through which this relationship is mediated. Whilst the occupancy turnover data collected here cannot be used to confirm this contention, they are supportive of the notion that the aquatic vegetation cover buffers larvae from predation by native and exotic fish. Within the sub-set of permanent wetlands in which *L. raniformis* was detected during the original season, and in which predatory fish were also observed, those in which the frog persisted throughout this study displayed higher aquatic vegetation cover on average than those at which it evidently disappeared (36% versus 25%).

'Mainland-island' or 'source-sink' dynamics have been distinguished from classical metapopulation dynamics on the basis of the presence of large, resilient populations that

sustain surrounding smaller ones via emigration (Harrison and Taylor 1997). This 'rescue effect' (Brown and Kodric-Brown 1977) is nevertheless well known amongst species that match the concept of a classical metapopulation (i.e., high likelihood of population turnover, producing dynamic patch occupancy). Examples include butterflies (Hanski 1994, 1999), small mammals (Ozgul *et al.* 2006) and amphibians (Sjögren-Gulve 1991). The strong negative relationship identified here between extinction likelihood and connectivity for *L. raniformis* in the MCC indicates a reasonably strong rescue effect. As outlined below, this finding has important ramifications for our understanding of the effect of urbanisation on this species.

The occupancy analysis suggested a negative relationship between patch area and extinction likelihood for *L. raniformis* in the MCC, and a positive relationship between this process and surrounding urban cover. The former was thought the result of density-dependant population growth, and the latter the result of resource limitations or road mortality (above). However, neither of these relationships was supported by the data. Patch area displayed essentially no relationship, whilst surrounding urban cover found to *negatively* influence extinction likelihood. These contradictory results are intriguing, but are not entirely unexpected for a study of this nature. Several authors have noted the potential for discrepancies between 'pattern' and 'process' based analyses (Tyre *et al.* 2001; Clinchy *et al.* 2002; MacKenzie *et al.* 2006), citing the ultimately stochastic nature of population dynamics (which are conducive to the creation of misleading relationships), and the limited temporal and spatial replication that they usually entail.

The data gathered here cannot be used to distinguish amongst these possibilities, but some thoughts are offered on their likely influence. For patch area, the inconsistency observed is potentially the result of rainfall variability producing a spurious relationship in the original survey data. High rainfall in the year preceding the 2001-2002 season had inundated several large, 'short-hydroperiod' wetlands (swamps, pools along small-catchment streams), which had evidently been recently colonised by *L. raniformis* and contributed to the positive area-occupancy relationship. However, the short hydroperiod of these wetlands ensured that they dried in subsequent seasons, and that the resident frog populations failed. For urban cover in the terrestrial zone, sample size constraints appear a likely cause. Amongst the 62 wetlands found to be occupied in 2001-2002, only a few displayed high surrounding urban cover, and all those that did were of otherwise high-quality or close to large populations of *L. raniformis*. The result was a low ratio of extinctions amongst patches with high surrounding urban cover, and a spurious negative relationship between extinction likelihood and this variable.

The extended modelling of occupancy turnover confirms that connectivity was the primary driver of the likelihood of colonisation for *L. raniformis* during the course of this study. The upshot is that the chance of vacant (or new) wetlands in the MCC being colonised by *L. raniformis* is determined overwhelmingly by the presence and proximity of other occupied wetlands within a 1000 m radius. Nevertheless, it must be remembered that the wetlands monitored during study were largely restricted to stream-based corridors of open-space (above); it is considered highly likely that urban development of the matrix between wetlands will be detrimental to their likelihood of colonisation (see also below).

4.4.   Status assessment and impacts of urbanisation of metapopulation viability

Concern about the conservation status of *L. raniformis* was provoked by a sharp contraction in its distribution and abundance during the 1970's and 1980's, which left only disjunct clusters of remnant populations (Mahony 1999; Pyke 2002). The MCC metapopulation of *L. raniformis* represents a component of one of these remnant clusters; that distributed around the fringes of Melbourne (Pyke 2002; Figure 1). For this reason, and because it has been the subject of extensive research (above), it is considered of national-significance (Clemann and Gillespie 2007).

Worryingly, this study indicates that the MCC metapopulation of *L. raniformis* is rapidly declining. Re-survey of the 143 patches from which populations were known prior to the 2006-2007 season paints a particularly concerning picture in this regard. Amongst those populations that were able to be re-visited, 5% are known to be extinct (the relevant wetland having been destroyed), and a further 54% failed to be detected. The estimated probability of persistence was, on average, just 0.463. Data obtained during the six-year monitoring period are less dire, but in-line with the longer-term trend suggested by the re-survey data. The observed occupancy rate dropped by 18% between the first and last seasons, and the estimated annual probability of extinction (under average conditions) was over twice that of the probability of colonisation.

Fluctuations in occupancy are an inherent part of the dynamics of species structured as classical metapopulations, and are not necessarily problematic in the long-term (Hanski 1999). It could be argued that the declines suggested by this study are therefore of little concern. Whilst it is true that some of the extinctions observed during this study will be reversed by recolonisation (and may already have been), the distribution of remnant populations in fact suggests that most past extinctions have a very low chance of reversal. Take the 70 populations observed to be extinct in 2006-2007, for which the colonisation model developed under Action 3, and the survey data from that season, can be used to estimate their annual probability of recolonisation. Sixty-percent have no remnant populations within their neighbourhood, meaning that their annual probability of recolonisation is only 0.021. A further 36% display an annual probability of recolonisation of < 0.1 based upon the occupancy statuses of their neighbours in 2006-2007. A scenario such as this, in which almost all previously occupied patches have a low chance of recolonisation, is what one would expect for a sharply declining metapopulation, not one fluctuating around some long-term equilibrium rate of occupancy.

This point brings us to the key impact of urbanisation on *L. raniformis*. Robertson *et al.* (2002), Heard *et al.* (2004) and Hamer and Organ (2008) have previously suggested that connectivity was likely to be important for *L. raniformis* in urbanising landscapes, based upon the spatially clustered pattern of habitat occupancy they documented. The modelling of occupancy turnover conducted in this study confirms that connectivity is vital for this species. Not only is recolonisation dependant on the persistence of multiple populations in the surrounding landscape, but populations in close proximity (< 1000 m) evidently exchange migrants and have a substantially lower chance of extinction as a result ('rescue effect' as above). It is now well documented that urban development typically entails significant wetland loss (e.g. Gibbs 2000). The result for amphibians is a significant reduction in population density, and therefore, connectivity (Cushman 2006; Hamer and McDonnell 2008). Typically, this situation is further exacerbated by the construction of buildings and roads, which act as physical barriers to migrants. Within the MCC, it is probable that the historical loss and fragmentation of wetlands in the downstream reaches of

the Merri and Darebin Creeks has led to the demise of remnant populations of *L. raniformis* in these areas (see Figure 7). However, it is also likely that the recent extinction of several populations in the vicinity of Cooper Street (Campbellfield and Epping) is linked to the filling of several quarries in this area, and fragmentation arising from construction of the Craigieburn Bypass and Edgars Road extension. The risk posed by continued wetland loss and fragmentation for *L. raniformis* in the MCC is discussed specifically below.

This study identified two attributes as key determinants of wetland quality for *L. raniformis*: hydroperiod and aquatic vegetation cover. Urbanisation can drastically alter these attributes for both streams and retained off-stream wetlands (Hamer and McDonnell 2008), meaning that reduced habitat quality is another important impact of urbanisation for *L. raniformis*. Of course, reductions in habitat quality increase the likelihood of extinction for individual populations of the frog. Less obvious however, is the fact that these extinctions further reduce population density (= connectivity), and therefore have the potential to drastically compound the effects of habitat loss and fragmentation.

Urbanisation can reduce wetland hydroperiod in a number of ways (Hamer and McDonnell 2008). The most obvious is the direct capture and diversion of surface runoff. However, streams may also be channeled and levees constructed to reduce the likelihood of floodplain inundation, and the extensive area of impervious surfaces constructed can reduce ground-water inflows. Changes in hydroperiod are also one of the mechanisms by which urbanisation can alter aquatic vegetation communities, given the sensitivity of these plants to the water depths, length of inundation etc. Urban infrastructure can also block solar radiation, which alters the photosynthetic capacity of aquatic plants, and the diversion of storm-water into wetlands can either cause dislodgement of aquatic plants (via storm-surges), smother them with sediment, or place them under physiological stress via over-nutrification and accumulation of pollutants (Hamer and McDonnell 2008).

This study also provides some evidence that *L. raniformis* is sensitive to reductions in the extent of terrestrial buffers. Whilst this effect was not demonstrated by the modelling of occupancy turnover, it is nonetheless congruent with knowledge of the ecology of this frog, and amphibious herpetofauna generally (Semlitsch and Bodie 2003). Given this fact, and that the Draft EPBC Act Policy Statement for *L. raniformis* identifies terrestrial buffers as a requirement for its conservation, it is concluded that buffer reduction should be viewed as another potentially important impact of urbanisation on this species.

Thus, it is clear that urbanisation has a variety of potentially highly detrimental impacts on *L. raniformis* metapopulations. Nevertheless, it is also true that urban development can provide opportunities to conserve the species' around Melbourne. It is apparent that this region is facing substantial reductions in rainfall given global climatic shifts, and that wetland hydroperiods will be altered as a result. For example, since the completion of the field-work described in this report, a series of extremely dry years has led to the desiccation of many of the wetlands monitored, including some of those deemed to be 'permanent' (score of 3 on the hydroperiod scale used here). Given the strong relationship between wetland hydroperiod and extinction likelihood for *L. raniformis*, these climate shifts will have dire consequences for the frog. One possible strategy to mitigate these impacts is to pursue conservation of the species' in extensive urban-parklands, within which wetland hydroperiods are maintained by urban-runoff. Urban-runoff has inherent problems for *L. raniformis* (above); however, these problems are not insurmountable with careful planning and implementation. Furthermore, urban-runoff could be used to create additional wetlands and preserve the extensive wetland systems that *L. raniformis* evidently requires.

4.5.   Recommendations and future directions

It is apparent that the persistence of *L. raniformis* in the MCC is dependant on the immediate implementation of significant conservation initiatives. The urgency of such initiatives comes in part from the climatic shifts described above. However, in the short-term a more pressing concern (or at least, the one that is most amendable to local action) is the ongoing loss, fragmentation and degradation of the species habitat.

Two processes, one general and one specific, have the potential to greatly exacerbate current levels of habitat change for *L. raniformis* in the MCC. Firstly, the MCC has been identified by the Victorian State Government as one of Melbourne's urban growth areas (DOI 2002). Current proposals (DPCD 2009) entail drastic expansion of the previously proposed urban growth boundary, and will allow urbanisation of much of the region. In doing so, they inadvertently propose further destruction, fragmentation and degradation of the frogs remaining habitat. Of specific concern is the fact that a third of the populations detected during the last full survey-season (2006-2007) inhabited wetlands either within quarries, or in close proximity to them. Quarry wetlands are invariably of high quality for *L. raniformis* (permanent, high aquatic vegetation cover), yet they are also attractive landfill sites for private industry. This study suggests that if the remaining quarries in the MCC are filled, not only will we lose their resident populations of *L. raniformis*, but the loss of connectivity is likely to drive all populations associated with them to extinction as well.

Preservation of *L. raniformis* in the MCC will require moves to secure all remnant populations which are under imminent threat, and to attempt to re-establish those that have been recently lost. To facilitate this, the models of extinction and recolonisation developed under Action 3, in conjunction with knowledge of the system gathered over the course of this study, have been used to identify priorities for acquisition, protection and/or enhancement (Appendix I, II). This includes populations with an inherently high risk of extinction (given wetland characteristics and location), those at risk from wetland filling, and patches that have potential to be recolonised and to maintain viable populations should some habitat enhancement be conducted.

An additional short-term initiative that will be of great benefit for the preservation of *L. raniformis* in the MCC (and elsewhere across Melbourne's urban fringe) is the production of guidelines for the management of its habitat and monitoring of its population trends. The final action of this project is to develop such guidelines, using the data and models outlined in this report. These guidelines are currently in preparation.

In the longer-term, it is clear that explicit strategies are required for the conservation of *L. raniformis* in the MCC and other urbanising landscapes around Melbourne. The extinction and colonisation models developed during this study allow sophisticated conservation-planning tools to be applied to this problem. Specifically, it is now possible to develop a stochastic metapopulation model for *L. raniformis*, with which predictions of metapopulation viability under differing habitat management scenarios can be made. These predictions can in turn be coupled with decision analyses (Maguire 1986; Possingham *et al.* 2002) to identify scenarios that minimise both extinction risk and cost. One of us (GH) will develop these tools over the next three years, as part of a post-doctoral fellowship at the University of Melbourne. Opportunities to develop the required strategies during this project should be explored.

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Appendix I. Populations of *Litoria raniformis* in the Merri Creek corridor known to be extant as of the 2006-2007 season, but which have a relatively high risk of extinction in the short-term. Extinction risk is based upon: (i) estimates of their annual probability of extinction (Pr(Ext)), derived using the extinction model developed under Action 3 and measures of habitat quality and connectivity ('inherent constraints to persistence'), or (ii) knowledge of external threats to these populations. With regard to the former, only populations with an annual probability of extinction >0.1 are shown. Co-ordinates are Australian Map Grid references, based upon the Australian Geodectic Datum 1966.

Location	Easting	Northing	Pr(Ext)	Inherent constraints on persistence	Imminent external threats
Broadmeadows					
Yuroke Creek, adjacent to Ripplebrook Drive	315308	5827736	0.151	Low aquatic vegetation cover, isolation	
Bundoora					
Wetland, Bundoora Park Golf Course	326830	5824980	0.339	Low aquatic vegetation cover, isolation	
Darebin Creek, below Western Ring Road	328170	5826699	0.132	Low aquatic vegetation cover, isolation	Isolation given filling of McKimmies Road Quarry
Wetland, opposite McKimmies Road Quarry	327030	5827220	0.114	Low aquatic vegetation cover	Isolation given filling of McKimmies Road Quarry
Wetland, McKimmies Road Quarry	327550	5827710	0.035		Being filled (landfill)
Darebin Creek, adjacent to Josef Street	328102	5827103	0.035		Isolation given filling of McKimmies Road Quarry
Darebin Creek, below Leslie Street	327181	5827385	0.028		Isolation given filling of McKimmies Road Quarry
Wetland, Botanica Park Estate	327880	5827270	0.025		Isolation given filling of McKimmies Road Quarry
Wetland, McKimmies Road Quarry	327413	5827411	0.023		Being filled (landfill)
Campbellfield					
Wetland, below Horne Street	321101	5827287	0.311	Low aquatic vegetation cover, isolation	Isolation given potential filling of Bolinda Road and Boral Quarries
Wetland, Boral Quarry	321632	5826970	0.160	Isolation	Potential to be filled
Wetland, Bolinda Road Quarry	320016	5826939	0.139	Isolation	Potential to be filled
Donnybrook					
Merri Creek, Mineral Springs Picnic Area	320827	5844061	0.843	Low aquatic vegetation cover, moderate hydroperiod, isolation	
Wetland, south of Shell Service Station	318256	5842504	0.663	Moderate aquatic vegetation cover, moderate hydroperiod	Construction of Hume Highway-Donnybrook Road Interchange
Merri Creek, south-east of Bald Hill	322370	5845795	0.615	Moderate hydroperiod, isolation	
Wetland, property south of Donnybrook Road	318567	5842705	0.613	Low aquatic vegetation cover, moderate hydroperiod	

Appendix I. (cont)

Location	Easting	Northing	Pr(Ext)	Inherent constraints on persistence	Imminent external threats
Donnybrook (cont)					
Merri Creek, Mineral Springs Picnic Area	321075	5844373	0.579	Moderate hydroperiod, isolation	
Kalkallo Creek, below Donnybrook Road	318717	5842940	0.278	Moderate hydroperiod	Construction of Hume Highway-Donnybrook Road Interchange
Wetland, just south of Donnybrook Road	319695	5842859	0.192	Low aquatic vegetation cover, moderate hydroperiod	
Merri Creek, above Donnybrook Road	319804	5843142	0.187	Moderate hydroperiod	
Dam, property south of Donnybrook Road	319027	5842710	0.179	Moderate hydroperiod	
Wetland, south-east of Bald Hill	322146	5846532	0.146	Isolation	
Kalkallo Creek, upstream of Donnybrook Road	318802	5843218	0.115	Moderate hydroperiod	
Epping					
Wetland, Epping Tip	324260	5830390	0.623	Low aquatic vegetation cover, moderate hydroperiod	Potential to be filled
Wetland, Epping Tip	324150	5830740	0.144	Low aquatic vegetation cover	Potential to be filled
Wetland, north of Harvest Home Lane	323328	5834883	0.115	Isolation	Being filled (for Aurora Estate)
Wetland, Epping Tip	324150	5830520	0.036		Potential to be filled
Glenroy					
Wetland, just south of Western Ring Road	315399	5825750	0.683	Low aquatic vegetation cover, moderate hydroperiod, isolation	
Wetland, just north of Western Ring Road	315346	5826025	0.100	Isolation	
Reservoir					
Wetland, Edwardes Lake Reserve	322940	5823924	0.158	Isolation	
Somerton					
Wetland, Rushwood Drive	319389	5834506	0.534	Moderate hydroperiod	
Merri Creek, below Freight Drive	320590	5832180	0.104	Low aquatic vegetation cover	
Wollert					
Darebin Creek, below Bridge Inn Road	328057	5836852	0.986	Low aquatic vegetation cover, short hydroperiod, isolation	Isolation given filling of Wollert Landfill
Wetland, east of Bindts Road	327660	5835873	0.225	Low aquatic vegetation cover, isolation	Isolation given filling of Wollert Landfill
Wetland, Wollert Landfill	327383	5837715	0.158	Moderate hydroperiod	Being filled (landfill)
Wetland, Wollert Landfill	326980	5837283	0.147	Low aquatic vegetation cover	Isolation given filling of Wollert Landfill

Appendix I. (cont)

Location	Easting	Northing	Pr(Ext)	Inherent constraints on persistence	Imminent external threats
Wollert (cont)					
Wetland, Wollert Quarry	326977	5838190	0.075		Isolation given filling of Wollert Landfill
Wetland, Wollert Landfill	327419	5837371	0.054		Isolation given filling of Wollert Landfill
Wetland, Wollert Landfill	327267	5838092	0.018		Being filled (landfill)
Wetland, Wollert Landfill	327472	5837950	0.013		Being filled (landfill)
Wetland, Wollert Landfill	327442	5837880	0.011		Being filled (landfill)
Westmeadows					
Moonee Ponds Creek, adjacent to Raleigh Street	313750	5827700	0.636	Moderate hydroperiod, isolation	
Moonee Ponds Creek, adjacent to Johnstone Street	314670	5827261	0.138	Moderate aquatic vegetation cover, isolation	

Appendix II. Habitat patches for *Litoria raniformis* in the Merri Creek corridor found to be vacant during the 2006-2007 season, but which have some potential to be colonised by the frog in the short-term. Colonisation likelihood was assessed by calculating the annual probability of colonisation (Pr(Col)) using the model developed under Action 3 and connectivity measurements derived from the 2006-2007 survey data. Only patches with annual probabilities of colonisation >0.025 are shown. Inherent constraints on persistence following colonisation are provided, as are known external threats to persistence (see Appendix I). Co-ordinates are Australian Map Grid references, based upon the Australian Geodectic Datum 1966.

Location	Easting	Northing	Pr(Col)	Inherent constraints on persistence (if colonised)	Imminent external threats (if colonised)
Bundoora					
Wetland, Bundoora Park	327328	5824756	0.025	Low aquatic vegetation cover, isolation	
Campbellfield					
Merri Creek, below Horne Street	321103	5827218	0.114	Low aquatic vegetation cover, isolation	
Wetland, Horne Street	321071	5827195	0.074	Low aquatic vegetation cover, isolation	
Merri Creek, below Horne Street	321020	5826832	0.031	Low aquatic vegetation cover, isolation	
Donnybrook					
Wetland, property north of Donnybrook Road	319443	5843038	0.219	Low aquatic vegetation cover, short hydroperiod	
Wetland, property north of Donnybrook Road	319627	5843200	0.190	Low aquatic vegetation cover, short hydroperiod	
Wetland, property south of Donnybrook Road	319890	5842743	0.124	Low aquatic vegetation cover, short hydroperiod	
Wetland, property south of Donnybrook Road	320005	5842780	0.089	Low aquatic vegetation cover, short hydroperiod	
Merri Creek, Mineral Springs Picnic Area	321016	5844183	0.057	Low aquatic vegetation cover, short hydroperiod	
Merri Creek, south-east of Bald Hill	322194	5845832	0.044	Low aquatic vegetation cover, short hydroperiod	
Wetland, Spring Street	320636	5843192	0.033	Low aquatic vegetation cover	
Wetland, property north of Donnybrook Road	320691	5842802	0.029	Low aquatic vegetation cover, short hydroperiod, isolation	
Merri Creek, south-east of Bald Hill	321624	5846216	0.028	Short hydroperiod, isolation	
Merri Creek, above train-line bridge	319849	5841208	0.028	Isolation	

Appendix II. (cont.)

Location	Easting	Northing	Pr(Col)	Inherent constraints on persistence (if colonised)	Imminent external threats (if colonised)
Epping					
Wetland, Epping Tip	324310	5830340	0.174	Low aquatic vegetation cover, short hydroperiod	
Wetland, Epping Tip	324070	5830320	0.074	Low aquatic vegetation cover, short hydroperiod	
Wetland, Epping Tip	324270	5830158	0.052	Short hydroperiod	
Wetland, Melbourne Wholesale Market site	323810	5830230	0.039	Low aquatic vegetation cover, short hydroperiod	Isolation given construction of the Market, potential filling of Epping Tip
Wetland, Melbourne Wholesale Market site	323690	5830670	0.039	Low aquatic vegetation cover, short hydroperiod	Being filled (for the Wholesale Market)
Merriang					
Merri Creek, property west of Epping Road	324830	5849130	0.027	Low aquatic vegetation cover, isolation	
Merri Creek, property west of Epping Road	325281	5848481	0.026	Short hydroperiod, isolation	
Reservoir					
Darebin Creek, above Gronn Street	326701	5825206	0.031	Low aquatic vegetation cover, isolation	
Somerton					
Curly Sedge Creek, Craigieburn Grasslands	320047	5833227	0.082	Short hydroperiod	
Wetland, City of Whittlesea property	320628	5832387	0.075	Short hydroperiod	
Wetland (O'Herns Swamp), propert east of O'Hern's Road	320514	5832862	0.054	Short hydroperiod	
Wetland, City of Whittlesea property	320539	5832897	0.052	Short hydroperiod	
Wetland, Craigieburn Grasslands	319852	5834419	0.039	Low aquatic vegetation cover, short hydroperiod	
Thomastown					
Edgars Creek, downstream of Epping Tip	324119	5829793	0.032	Short hydroperiod, isolation	Isolation given potential filling of Epping Tip
Wollert					
Wetland, Wollert Landfill	327305	5838031	0.447	Short hydroperiod	Being filled (landfill)
Wetland, property east of Bindts Road	327652	5835800	0.088	Short hydroperiod, isolation	Isolation given filling of Wollert Landfill
Darebin Creek, downstream of Bridge Inn Road	327853	5836528	0.036	Low aquatic vegetation cover, short hydroperiod, isolation	Isolation given filling of Wollert Landfill