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The presence and persistence of frog species in the New England Tablelands, eastern Australia

Submitted by

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Abstract

Introduction: Frogs are important vertebrate species in freshwater ecosystems. However, they are currently suffering declines worldwide. One way to monitor declines is to compare historical occupancy to present-day occupancy. The aim of the present study was to revisit historical sites on the New England Tablelands and to compare the current occupancy of frog species found to their historical occupancy. As part of this undertaking, some of the processes currently threatening frogs were also explored, including the difference in infection intensity and prevalence of the Amphibian chytrid fungus (*Batrachochytrium dendrobatidis*) between a still water and running water site, the influence of a known *B. dendrobatidis* reservoir host, the common eastern froglet (*Crinia signifera*), on the other frog species and the influence of an invasive fish species, the eastern mosquito fish (*Gambusia holbrooki*), on the occupancy of frog species still persisting in the New England Tablelands.

Methods: Two hundred of 898 historical sites in the New England Tablelands were revisited during the period extending from 2017 through to 2019. Occupancy estimation models were used to analyse the historical survey data from all sites and the results of the current visits to the selected sites. Initially, single-visit occupancy estimation models were created for each of the species in the historical records to determine historical occupancy. Secondly, single-species, single-season occupancy models with the inclusion of covariate information were generated to model the current occupancy of the species found in the present survey. Finally, two-species occupancy models were used to determine if the presence of *Cri. signifera* at a site influenced the occupancy probability of each of the other frog species found at that site, and to determine if the presence of *G. holbrooki* at a site also influenced the occupancy probability of each of the frog species found at the same site.

Two hundred and ninety-two individuals from three frog species at two different sites; Thomas Lagoon and Blue Hole, were swabbed for *B. dendrobatidis*. Of these species, the eastern dwarf sedge frog (*Litoria fallax*) was a habitat generalist which maintained its occupancy since the historical study and was found at both sites. The spotted marsh frog (*Limnodynastes tasmaniensis*) also maintained its occupancy since the historical study, but was found only at Thomas Lagoon. The eastern stony creek frog (*Litoria wilcoxii*) is a habitat specialist, had a lower present average occupancy than its historical average occupancy and was found only at Blue Hole. Swabs were analysed using qPCR at the Australian Museum. qPCR results were modelled for infection intensity and infection prevalence using generalised linear models.

Results: Eighteen of the original (historical) 39 frog species found in the New England Tablelands were found during the present study. Of these 18 species, only six had increased or maintained their historical average occupancy. Analysis of the results of the current surveys found that latitude, longitude, altitude and emergent vegetation were important covariates to consider when modelling occupancy for the frog species found in the New England Tablelands, while temperature and humidity were important covariates when modelling detection. From the occupancy models with *Cri. signifera* included as a covariate, the occupancy for two frog species was influenced by the presence of *Cri. signifera*. Of these two, only one was negatively influenced. From the occupancy models *G. holbrooki*, none of the frog species were negatively influenced by the presence of *G. holbrooki*.

Infection intensity was higher in *Lit. wilcoxii* and *Lim. tasmaninensis* than it was in *Lit. fallax*. Similarly, infection prevalence was higher in *Lit. wilcoxii* and *Lim. tasmaniensis* than *Lit. fallax*.

Discussion: In the New England Tablelands, fewer species were found in the present study than were found in the historical study. Frog species which were habitat generalists generally maintained or in some instances increased their occupancy in the current study when compared to the historical study. Species which were less likely to occupy sites with *Cri. signifera* and *G. holbrooki*, showed higher occupancy historically than they did currently. Infection intensity and infection prevalence of *B. dendrobatidis* was higher in species whose occupancy has decreased since the historical study.

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1. Introduction

Severe amphibian declines have been observed worldwide and have been well documented (Blaustein & Wake 1990; de Solla *et al.* 2005; Fellers & Drost 1993; Fellers *et al.* 2008; Fite *et al.* 1998; Kiesecker *et al*. 2001; Lampo *et al.* 2006; La Marca *et al.* 2005; Lane & Burgin 2008; Muths *et al.* 2003; Pearl *et al.* 2009; Stuart *et al.* 2004; Wente *et al.* 2005). More than 40% of frogs are threatened with extinction worldwide (International Union for the Conservation of Nature [IUCN] 2023)). In Australia, 22% of frog species are classified as threatened, while there are eight species that are equivocally classified as data deficient (IUCN 2023). With so many species facing decline, monitoring of remaining frog populations becomes crucial in relation to making conservation decisions.

1.1 Threats to frogs

Declines of frog species have been linked to a combination of factors (Barinaga 1990; Blaustein & Wake 1990; Davidson *et al.* 2002; Fellers & Drost 1993; Laurance 1996; Kiesecker *et al*. 2001; Pearl *et al*. 2009; Tyler 1991), the effects of which have been compounded by differences in each species' respective susceptibility to changes in its environment (Gillespie & Hines 1999; Hazell 2003). Implicated causes of frog species decline include changes in habitat such as habitat modification (Gillespie & Hines; Laurance 1996; Lehtinen *et al.*; 1999; MacNally *et al.* 2009) and fragmentation (Lehtinen *et al.* 1999; MacNally *et al.* 2009), pollution (Hero & Shoo, 2003) and changes to hydrology (Wassens *et al.* 2013; Wilson *et al.* 2013). Other implicated causes include disease and invasive predators such as the Amphibian chytrid fungus (*Batrachochytrium dendrobatidis*) (Berger *et al.* 1998; Blaustein *et al.* 2018; Daszak *et al.* 1999; Daszak *et al.* 2003; Fellers *et al.* 2004; Hyne *et al.* 2009), fish (Gillespie & Hero, 1999; Knapp & Mathews, 2000), cane toads (*Rhinella marina*), cats (*Felis catus*) and foxes (*Vulpes vulpes*). These causes can be further exacerbated by increased levels of ultraviolet radiation and ongoing climate change (Blaustein *et al.* 1994a, 1994b, 1998; Broomhall *et al.* 2000; Kiesecker *et al.*, 2001), which is causing unpredictable weather patterns, increased evaporation, higher temperatures and severe weather events such as flooding or extreme drought (Walls et al. 2013; Wassens *et al.* 2013). Those threats thought to be the predominant drivers of frog species decline in the New England Tablelands are discussed in more detail in the section.

1.1.1 The Amphibian Chytrid fungus (*Batrachochytrium dendrobatidis*)

Disease is a natural occurrence in any population. However, it becomes problematic if it is an introduced strain and one that is particularly virulent. One amphibian disease which has received much attention in Australia, is the Amphibian chytrid fungus (*B. dendrobatidis*); a pathogen that has been implicated in the decline of frog species worldwide (Bell *et al*. 2004; Berger *et al*. 1998; Bosch *et al*. 2001;Lips 1998; Lips *et al*. 2003, 2004; Muths *et al*. 2003; Puschendorf *et al.* 2006). *Batrachochytrium dendrobatidis* grows in the keratinised tissues of the epidermis of frogs and tadpoles (Beard & O'Neil 2005; Berger *et al*., 1998) and can cause mortality in adult frogs (Berger *et al*. 1999; Longcore *et al*. 1999). It occurs on almost all continents, including Australia (Berger *et al*. 1998; Bosch *et al.* 2001; Green & Sherman 2001; Guayasamin *et al*. 2004; Lips *et al*. 2004; Ron & Merino 2000; Weldon *et al*. 2004), and has been found in many frog species populations, both declining and non-declining (Berger *et al.* 2004; Cashins *et al*. 2013; Kriger & Hero 2006; Kriger *et al.* 2007; Mahony *et al.* 2013; Miaud *et al.* 2016; Portway *et al.* 2020; Pounds *et al.* 2006; Puschendorf et al. 2006; Rachowicz and Vrendenburg 2004; Retallick *et al.* 2004; Scheele *et al.* 2017; Stockwell *et al.* 2008; Woodhams *et al.* 2007; Young et al. 2012).

A major concern of frog species susceptible to *B. dendrobatidis* infection, are the presence of reservoir hosts for this fungus (Brannelly *et al.* 2018; Burns *et al.* 2021). Competent reservoir hosts for *B. dendrobatidis* share several characteristics. These include the prevalence of *B. dendrobatidis* infection is high in the population; hosts can maintain a high infection intensity over a long period of time; hosts suffer no fitness cost from infection; and, as a species, hosts have not seen a decline in numbers or changes in demographics from the disease (Brannelly *et al.* 2018; Scheele *et al.* 2017; Stockwell *et al.* 2016). Further, the continued presence of reservoir species at a site can maintain zoospore densities, even when other frog species which are present are declining (Brannelly *et al.* 2018; Scheele *et al.* 2017).

Two species which are present in the New England Tablelands and have been implicated as reservoir hosts include; *Crinia signifera* (Brannelly *et al.* 2018; Burns *et al.* 2021; Hunter et al. 2009; Scheele *et al.* 2016, 2017) and *Litoria wilcoxii* (Franklinos *et al.* 2020). Research has shown that *Cri. signifera* is a competent reservoir host of *B. dendrobatidis* (Burns *et al.* 2021; Brannelly *et al.* 2018). Burns *et al.* (2021) found that populations of *Philoria frosti* were only present at sites that *Cri. signifera* had yet to occupy, and in the laboratory mortality rate of *Phi. frosti* was found to increase with higher *B. dendrobatidis* infection loads in *Cri. signifera*. Brannelly *et al.* (2018) found that high densities of *Cri. signifera* were present at sites where three alpine frog species had previously been recorded and were declining or had extirpated locally. Further, the infection intensity of *B. dendrobatidis* in *Cri. signifera* was much higher than those of the declining species (Brannelly *et al.* 2018).

1.1.2 Habitat Modification

Historically, land use changes, especially those associated with urbanisation, have been found to have a negative impact on frog species; often leading to local extinctions (Gillespie & Hines 1999; Hazell 2003; Honeggar 1981; Howard *et al.* 2010). The loss of suitable habitat for breeding, in particular, has important consequences (Howard *et al.* 2010; White & Burgin 2004). A decline in suitable breeding habitat is especially detrimental to the prolonged persistence of species in an area (Howard *et al.* 2010; Pearl *et al*. 2009). Low-lying areas that could historically have filled with water under wet conditions have been infilled to provide more space for development, while paved surfaces cause rapid run-off of rainwater (White & Burgin 2004). On the other hand, some other, mainly agricultural practices (creation of dams, diversion of rivers for irrigation and the creation of drainage channels and reservoirs) have generated large numbers of similar habitats with greater water permanence (MacNally *et al.* 2009). Frog species which require semi-permanent water sources for breeding have become scarce because of these developments (White & Burgin 2004). Furthermore, contamination of storm water run-off from residential and industrial chemicals and sewage, can further reduce the quality of breeding sites (White 1998; White & Burgin 2004). Chemicals can also cause skewed sex ratios (Cary & Karasov 2013), and deformities or abnormalities during development (Blaustein & Johnson 2003). This is especially problematic with pond-breeding species (Rowe *et al*. 1996, 1998). Malformations negatively affect survival and increase exposure to predation through slowed development, late metamorphosis and small metamorph size (Rowe *et al*. 2001; Pahkala *et al.* 2002, 2003). Habitat degradation may also cause physiological stress, which can render frogs more susceptible to disease (Carey 1993; Hyne *et al.* 2009; Relyea 2004; Rohr & Raffel 2010; Wassens *et al.* 2013).

1.1.3 Invasive Predatory Fish

The presence of exotic fish is also an issue for breeding habitat suitability. The presence of frogs at a site has usually been found to be negatively affected by the presence of fish (Pearl *et al*. 2009; Pyke & White 1999; White & Burgin 2004). Invasive predatory fish, such as the eastern mosquito fish (*Gambusia holbrooki*), are known to consume tadpoles and eggs of many different frog species (Hamer 2021; Hamer & Parris 2013; Harris 1995; Hunter *et al*. 2011; Klop-Toker *et al.* 2018; Morgan & Buttemer 1996; Pyke & White 1996, 2000; Webb & Joss 1997) and is found in great numbers in the New England Tablelands (Gillespie & Hines 1999). Further, *G. holbrooki* can spread relatively rapidly between sites given sufficient water coverage (as little as 3 mm, Alemadi & Jenkins 2007). Such dispersal abilities mean that this species can rapidly occupy new sites from which they were previously absent.

Specifically for frog species in the New England Tablelands, Hunter *et al*. (2011) found that *G. holbrooki* will consume the tadpoles of *Litoria booroolongensis*, while Pyke and White (1996) found a similar predation of *G. holbrooki* on *Litoria aurea* tadpoles. There is some conjecture that the presence of *G. holbrooki* has contributed to the decline of *Adelotus brevis* (Gillespie & Hero 1999), although experimental studies have not yet been undertaken to verify predation of *A. brevis* tadpoles by *G. holbrooki*. *Litoria lesueuri* has also shown to be susceptible to predation by *G. holbrooki* (Harris 1995). Given that *Litoria lesueuri* is closely related to *Litoria wilcoxii* (Anstis 2017; Donnellan & Mahony 2004) and the study by Harris (1995) was conducted in the New England Tablelands before the taxonomic reclassification of the *Lit. lesueuri* complex occurred (See Section 3.1.2), it is likely that the tadpoles of *Lit. wilcoxii* would be heavily preyed upon by *G. holbrooki* if they were both present at a site. Other frog species with a negative association with *G. holbrooki* include; *Limnodynastes peronii* (Klop-Toker *et al.* 2018), *Crinia parinsignifera* (Komak & Crossland 2000; Littlefair *et al.* 2021), *Litoria verreauxii* (Hamer & Parris 2013; Harris 1995; Klop-Toker *et al.* 2018; Morgan & Buttemer 1996; Webb & Joss 1997), *Litoria fallax* (Hamer & Parris 2013; Harris 1995; Klop-Toker *et al.* 2018; Morgan & Buttemer 1996; Webb & Joss 1997) and *Litoria dentata* (Hamer & Parris 2013; Harris 1995; Klop-Toker *et al.* 2018; Morgan & Buttemer 1996; Webb & Joss 1997).

1.1.4 Climate Change

Unusual weather patterns are another common explanation for frog declines (Beebee 1995; Corn & Fogleman 1984; Crump *et al*. 1992; Czechura & Ingrain 1990; Fellers & Drost 1993; Heyer *et al*. 1988; Ingram 1990; Laurance 1996; Weygoldt 1989). Large-scale climatic degradation affects frogs in all parts of the world (Laurance 1996). Climate models in Australia predict a future increase in temperature, evaporation and extreme hydrological events such as drought (Murphy & Timbal, 2008; Smith & Chandler; 2010; Wassens *et al.* 2013). Associated with changes to climate are alterations to weather patterns. This can be of particular importance because frogs are sensitive to such changes (Laurance 1996). For most species, reproductive behaviour is especially dependent on temperature and rainfall, and any unusual weather changes could affect this (Beebee 1995). Warmer temperatures and rainfall variability can alter breeding cues such as calling (Blaustein *et al*. 2010; Neveu 2009), while unusual climate variability can increase mortality of both tadpoles and adults (Blaustein *et al*. 2010; Dahl *et al*. 2009; Gomez-Rodrıguez *et al*. 2009; Vignoli *et al*. 2007; Wassens *et al.* 2013). This ultimately reduces breeding success and lowers recruitment at affected sites, challenging a species' persistence at sites it occupies (Babbitt & Tanner 2000; MacNally *et al*. 2009; McMenamin *et al*. 2008; Piha *et al*. 2007; Rohr & Madison 2003; Rohr & Raffel 2010; Wassens *et al.* 2013). The species which suffer most from these issues are the ones with very specific meteorological requirements for breeding (Tyler 1989); species with longer and less flexible development times (Wassens *et al.* 2013) and species which breed in temporary pools which are sensitive to extreme changes in precipitation and temperature (Blaustein *et al.* 2010; Wassens *et al.* 2013).

1.2 Importance of Frogs

In freshwater ecosystems, frogs often occur in high densities and can comprise a major part of the vertebrate biomass in the system (Ficetola *et al*. 2008; Ranvestral *et al.* 2004; Stewart & Woolbright 1996). They play important roles in the functioning of these ecosystems, often as keystone species having both top-down and bottom-up effects in trophic webs (Flecker *et al.* 1999; Kupferberg 1997; Lamberti *et al.* 1992; Ranvestral *et al.* 2004) and also acting as indicators of the overall health of the system (Ficetola *et al*. 2008; Kotwal *et al*. 2008).

Frogs have physiological and ecological traits which make them particularly susceptible to environmental disturbance (Vitt *et al.* 1990). They have thin, semi-permeable skin and, as tadpoles, gill membranes, both of which easily absorb contaminants from water (Bishop & Gendron 1998; DeGarady & Halbrook 2006; Lambert 1997). Frogs also use multiple habitats in their life cycle, which, because of this, can expose them to a wider range of environmental stressors (Johnson *et al.* 2002; Noss 1990; Steven *et al.* 2007). Major changes in the health of an ecosystem can lead to an alteration in frog species abundance and distribution (Davis 2001; Kitching *et al.* 2000; Kotwal *et al*. 2008), with the response to environmental change often being species-specific (Steven *et al.* 2007). Some frog species, such as the eastern common toadlet (*Crinia signifera*), may be tolerant of many disturbances to which other frog species might be susceptible (Hopkins *et al.* 2020; Lane & Burgin 2008; Parris *et al.* 2009; Scheele *et al.* 2017). Frog species might also indicate a high presence of contaminants in the system, such as pesticides and herbicides, through the manifestation of morphological mutations (Knutson *et al.* 1999; Lehtinen *et al*. 1999; Price *et al.* 2005; Rubbo & Kiesecker 2005; Spolyarich *et al.* 2010).

As keystone species, frogs play an important role in trophic webs. Through their different life stages, frogs play a central role in food webs in both aquatic and terrestrial habitats (Cary & Karasov 2013). Adult frogs influence prey dynamics, plant performance and leaf-litter decomposition rates (Beard *et al.* 2003; Persson *et* *al.* 1996; Zheng *et al*. 1997), while tadpoles can control periphyton growth in waterways, reduce sedimentation, act as prey for vertebrate and invertebrate predators and act as decomposers of detritus (Flecker *et al.* 1999; Kupferberg 1997; Lamberti *et al.* 1992; Mallory *et al.* 2005; Ranvestral *et al.* 2004). Both adult frogs and tadpoles are food for a range of predators, including lizards and snakes, birds, mammals, and, in the case of tadpoles, large aquatic invertebrates (Flecker *et al.* 1999; Kupferberg 1997; Lamberti *et al.* 1992). As well as themselves being food for larger vertebrates, adult frogs, through their predation, control the abundance of invertebrates (Beard *et al.* 2003; Ficetola *et al.* 2008; Lambert 1997; Stewart & Woolbright 1996). Further, frogs enhance nutrient cycling and availability, as well as primary productivity as a result of elimination and excretion (Beard *et al.* 2002, 2003; Bloomfield *et al*. 1993; Ficetola *et al.* 2008; Mattson & Addy 1975; McNaughton *et al*. 1988; Sin *et al.* 2008). Foliage development is increased by the high nutrient content in the soil which improves plant performance (Beard *et al.* 2003). The increase in nutrients in the soil also increases the productivity of soil organisms and increases microbial communities, which then increases decomposition rate (Beard *et al*. 2002, 2003; Gallardo & Schlesinger 1994; Hanlon & Anderson 1980; Ineson *et al*. 1982; Wardle 1992).

1.3 Frogs in the New England Tablelands

There are approximately 50 frog species that have been recorded as being present in the New England Tablelands, (Anstis 2017; Heatwole *et al.* 1995; Hoskin *et al.* 2015). Of these 50 species, eight are threatened, two are near-threatened and another four are unlisted or are data-deficient (Department of Agriculture, Water and Environment [DAWE] 2020; IUCN 2023). The remaining 36 species are classified as least concern (IUCN2023).

The threats to the frog species of the New England Tablelands are mainly thought to be linked to habitat loss and fragmentation through land clearing, the presence of an invasive predatory fish, *G. holbrooki*, alteration to the hydrology of streams and reduction of available waterbodies (Gillespie & Hero 1999; Gillespie & Hines 1999; Hines *et al.* 1999; Howard *et al.* 2010; Mahony 1999; McDonald *et al.* 2012; Spark 2020).

Life history and breeding behaviours range from habitat generalists which will breed in any waterbody, to dedicated stream and terrestrial breeders with specific habitat requirements, as well as opportunistic species which utilise ephemeral pools and need specific meteorological conditions to breed (Anstis 2017; Hoskin *et al.* 2015). Frogs differ in their abundance within the region. Some species are found throughout the region and can be found at most waterbodies (Anstis 2017; Hoskin *et al.* 2015). While others have no or very few records in the present and are thought to be locally extinct (Anstis 2017). Still, other species have very small distributions and are only endemic to the New England Tablelands. Eight of the 50 frog species are thought to have only a tiny part of their distribution extending along one edge of the New England Tablelands.

In the last 60 years, there have been several frog studies focused in the New England Tablelands. Many have focused on threatened species (Clulow *et al.* 2009; Gillespie 2001; Gillespie & Hines; Gillespie & Hero 1999; Hunter *et al.* 2010, 2018) in the region, while Heatwole *et al.* (1995), conducted a species wide survey over a number of years in the 1960s, 1970s and 1980s. Such studies have implicated invasive fish such as trout (*Salmo sp.*) and *G. holbrooki* in the decline and disappearance of several stream breeding species in the region; *Litoria booroolongensis*, *Litoria piperata*, members of the *Litoria phyllochroa* complex and *Litoria subglandulosa* (Gillespie 2001; Gillespie & Hines 1999; Gillespie & Hero 1999). However, Clulow *et al.* (2009) investigated the effects of trout on threatened stream breeding species but found no difference in the presence of species related to trout. Hunter *et al.* (2010) and others (Gillespie & Hines 1999, Mahony 1999; Rowley & Cutajar 2018) have also linked the decline of many New England Tablelands frog species including *Lit. booroolonensis, Litoria piperata* and members of the bell frog complex (*Litoria aurea* and *Litoria castenea*) to the widespread Amphibian chytrid fungus. Hunter determined that *B. dendrobatidis* was not present in specimens collected before 1980 but were present after 1990, corresponding to when many of these frogs started to disappear.

1.4 Aims

The composition of the frog community of the New England Tablelands was established in relation to an extensive survey of frog species that was undertaken between 1966 and 1990, with material also being added from museum records from earlier collections (Heatwole *et al.* 1995). Although the records of frog species were obtained opportunistically and intermittently, the study, nevertheless, gave some idea of the distribution of frog species within the bioregion (Heatwole *et al.* 1995). Some frog surveys have been conducted in the region since then, although these focused predominantly on particular threatened species suspected of being in decline (Gillespie & Hero 1999; Gillespie & Hines 1999).

The primary aim of the study that forms the basis of this thesis was to revisit sites in the New England Tablelands that were historically known to support frog species, and to determine and compare the historical species composition at these sites with the current species composition. As part of this, historical occupancy was determined using single visit occupancy modelling (Lele *et al.* 2012; Solymos *et al.* 2012). Further, current occupancy for each frog species found will be determined using single-species, single-season occupancy models. Secondly, the study will explore some of the factors that may have impacted upon any of the observed changes in occupancy. This will include creating two-species models examining the co-occurrence of detected frog species with the common eastern froglet, *Cri. signifera*, a known carrier of the Amphibian chytrid fungus. Two-species models will also be created for co-occurrence of each detected frog species with the eastern mosquito fish (*G. holbrooki*), an invasive, potentially predatory fish found in the region (Gillespie & Hines 1999). Finally, a comparison of the infection intensity and prevalence of the Amphibian chytrid fungus (*Batrachochytrium dendrobatidis*) was made between two water body types; running and still waterbodies, to determine if there is a difference between these waterbody structures. As part of this process, three frog species were swabbed for *B. dendrobatidis*. These include one species which was a generalist, occurred at the two types of sites and has maintained or increased its average occupancy since the historical study, and two species which are exclusive to either the running waterbody or the still waterbody but have reduced their average occupancy since the historical study. It was hypothesised that generalist species will have maintained or increased their occupancy in the region, while habitat specialist species, those species susceptible to *B. dendrobatidis* infection, and predation by *G. holbrooki* will have reduced occupancy.

1.5 Occupancy Estimation

Occupancy estimation modelling has been developed as a method to assess patterns of species distribution and to account for variation in associated detection probabilities (Azuma *et al*. 1990; Bayley & Peterson 2001; Geissler & Fuller 1987; MacKenzie *et al*. 2002, 2018; Pearl *et al*. 2009). Occupancy is defined as the probability that a given species will occupy a particular site (Azuma *et al*. 1990; Bayley & Peterson 2001; Geissler & Fuller 1987; MacKenzie *et al.* 2002, 2018; Nichols & Karanth 2002). The simplest way to estimate this proportion is by generating a naïve occupancy value. However, naïve occupancy can be problematic in that it assumes that detection is without problems and therefore perfect (Guillera-Arroita *et al.* 2014). With this almost certainly not being the case, naïve occupancy is therefore confounded by issues associated with detection (MacKenzie *et al.* 2018).

Detection probability is the probability of detecting the species during a single sampling occasion (Bailey *et al.* 2004; Boulinier *et al*. 1998; MacKenzie *et al*. 2002, 2018). Species detection at sites is imperfect. That is, species which are present at sites may never be detected (MacKenzie *et al.* 2018). In relation to occupancy estimation there exist three states: the species is present and detected, the species is absent, and the species is present but not detected. Thus, occupancy estimation is a method which allows detection and site occupancy to be determined separately (MacKenzie *et al.* 2018). It is a robust method of dealing with presence-absence data which allows differences in detection probabilities to be placed into the final occupancy model (MacKenzie *et al.* 2018). This in turn helps reliably predict site characteristics which may influence detection. (Gu & Swihart 2004).

Species occurrence is affected by both suitable habitat distribution and population processes of a species; e.g., dispersal (Moore & Swihart 2005). Detectability can vary between sites and species, depending upon changes in environmental factors. For example, frogs during a breeding season are relatively easy to detect due to the male’s propensity to reveal their location through song (Lips *et al.* 2001; Zimmerman 1994), while females actively seek out males for breeding. On other occasions, they may be silent and therefore harder to detect (Brander *et al.* 2007; Cook *et al.* 2011; Gooch *et al.* 2006).

Occupancy estimation is based predominantly upon presence-absence data, which is readily collected from various sampling regimes such as biological surveys or ecological monitoring programs (Tyre *et al.* 2003). Surveys are conducted over a relatively short period of time at a selection of sites that are a representation of the environmental variability commonly found for the region under study (Guillera-Arroita *et al.* 2014; MacKenzie *et al.* 2002, 2012; Pollock *et al.* 2002; Royle & Nichols 2003; Tyre *et al.* 2003; Yoccoz *et al.* 2001). During a visit to a site, the presence (1) or absence (0) of the target species is recorded. From this, a unique binary detection history for a species can be developed from repeated visits to a site (MacKenzie *et al*. 2002, 2012, 2018; Royle & Nichols 2003). This can be modelled, with the habitat attributes to identify those features that are associated with species presence (MacKenzie *et al.* 2018; Tyre *et al.* 2003).

The final estimation model is used to assess species trends in occupancy with most surveys being focused on species declines or range reductions (Tyre *et al.* 2003). This is critically important for both species that are uncommon or scarce (rare) and those whose presence may be difficult to determine (elusive) (Mackenzie *et al.* 2018). It is important to note that the two are not mutually exclusive; a “rare” species can still be infrequently encountered and be “elusive” due to either small population density in a large region or a larger population occupying only a small fraction of the landscape (MacKenzie *et al.* 2005). Rarity is also associated with low detection probability, which provides a challenging prospect for biologists who face substantial sampling difficulties (MacKenzie *et al.* 2005).

1.5.1 Assumptions of Occupancy Estimation

Several assumptions are made when using occupancy estimation. These assumptions are critical with regard to designing an occupancy study. Violations of these assumptions can result in inaccurate occupancy estimation (MacKenzie *et al*. 2002, 2012, 2018; Miller *et al*. 2011a Tyre *et al.* 2003).

One important assumption of occupancy estimation is that of “closure” between sites, i.e. there was no change in occupancy over the course of the survey period (MacKenzie *et al.* 2012, 2018; Nichols *et al.* 2008; Rota *et al.* 2009) and that any changes within the habitat itself during this period will be inconsequential (Miller *et al.* 2011b). When a species is detected at a site during a visit then it is assumed to be present during subsequent visits, regardless of whether it is found again (MacKenzie *et al.* 2012; Rota *et al.* 2009). Therefore, under such circumstances, any previous or subsequent absences are assumed to be a “false negative” and the species targeted was simply not found because the observer could not detect it. This is often the case for amphibians due to differences in the species behaviour in relation to breeding time. The species will still be present at a site but less likely to be detected outside its normal breeding cycle (Brander *et al.* 2007; Cook *et al.* 2011; Gooch *et al.* 2006).

Non-detection only results in a complete absence if the detection probability is known to be certain; equal to one (MacKenzie *et al.* 2002, 2018; Moore & Swihart 2005; Tyre *et al.* 2003). However, this assumption is often violated in nature because there is no guarantee that a species will be present as the result of changes in daily movement patterns (Miller *et al.* 2011b; Rota *et al.* 2009; Tyre *et al.* 2003). When sampling anurans, detection probability may be very close to one at a site when sampling species with set breeding times during the sampling period. However, for species that breed opportunistically, detection probability may never be very high. This is especially true for burrowing species which may remain inactive until conditions are suitable to promote activity (breeding, foraging and dispersal) (Ocock *et al.* 2014; Paltridge & Southgate 2001; Penman *et al.* 2006; Wassens *et al.* 2013).

Studies have been undertaken that have explored the sensitivity of such methods to the violation of closure (Gu & Swihart 2004; Moore & Swihart 2005; Rota *et al.* 2009). Violation of this assumption leads to biased estimates and can have quite severe consequences when associated with specific covariates (Gu & Swihart 2004; Moore & Swihart 2005). This can have severe consequences for animal management, considering decisions are often based on what is found (Rota *et al.* 2009).

Another assumption of the occupancy model is that misclassification does not produce “false positives” (Miller *et al.* 2011a). In theory, species are never falsely detected at a site when absent and it is impossible to identify a species at a site if it is, in fact, not there at all (MacKenzie *et al.* 2002, 2012, 2018). However, in practice this may not be the case. Misclassification of an individual or indirect observation may result in the recording of a species’ presence when that species was never there (Miller *et al.* 2011a; Tyre *et al.* 2003). If false positives are not accounted for, overestimation of occupancy can occur (Miller *et al.* 2011a; Royle & Link 2006).

When sampling a large area, the site selection needs to be representative of the overall area of interest (Royle & Nichols 2003; Yoccoz *et al.* 2001). Detection of the species at a site is assumed to be independent of detecting the species at all other sites (MacKenzie *et al.* 2002, 2018; Moore & Swihart 2005). Again, this is rarely the case in nature, with sites that are closer together being more likely to exhibit similar characteristics than those that are farther apart (Moore & Swihart 2005). Sites which are closer together may provide easier means of colonisation for new populations, than those sites that are farther away.

Surveys conducted at a single site should be independent of each other, with no spatial or temporal correlations (MacKenzie *et al.* 2018). However, this is harder to achieve as an observer may put more effort into surveying a particular site for a particular species if that species had previously been found there (Tyre *et al.* 2003). Another possibility is that disturbance incurred at a site through sampling may impact on the detectability of species in the future, though this is not well documented (Heyer *et al.* 1994; Bailey *et al.* 2004).

1.5.2 Detection Probability Bias in Occupancy Estimation

Surveys do not always detect a species when it is present (MacKenzie & Kendall 2002; MacKenzie *et al.* 2004; Royle & Nichols 2003). This means that non-detection is ambiguous because species may still be present at a site and simply not found by the observer (MacKenzie *et al.* 2002, 2012, 2018; Royle & Nichols 2003). Estimation of population parameters can be problematic when a species is rare or difficult to detect (Miller *et al.* 2011b). According to Tyre *et al.* (2003) it is difficult to distinguish between two different situations when there is low detectability. For example, at one site, the species could be quite common but difficult to detect (elusive) and at another site, the species could be rare but easy to detect. Both situations can cause the surveyor to fail to observe the species at all during visits to such survey sites. This means that it is not always possible to detect the species of interest (MacKenzie *et al.* 2002, 2005). By being able to separate true absences from non-detections, the detection probability can be accounted for and occupancy can be estimated (MacKenzie *et al.* 2002, 2018; Royle & Nichols 2003).

Detection can vary with environmental variables (Bailey *et al.* 2004; MacKenzie & Kendall 2002), observer experience (Link & Sauer, 1998, 1999; MacKenzie & Kendall 2002; Sauer *et al.* 1994; Shirose *et al.* 1997; Tyre *et al.* 2003), survey methodology (MacKenzie & Kendall 2002; Tyre *et al.* 2003) and characteristics of the target species (Bailey *et al.* 2004). Not accounting for these influences in the model can cause disparity in occupancy estimation (Diefenbach *et al.* 2003; Miller *et al.* 2011b; Nichols *et al.* 2000; Robbins 1981; Sauer *et al.* 1994). In terms of surveying frogs, meteorological conditions (temperature and rainfall) often play a critical role in their detectability (Ocock *et al.* 2014; Paltridge & Southgate 2001; Penman *et al.* 2006; Wassens *et al.* 2013). It is possible to classify these differences and incorporate them into the final model of detection probability (Nichols *et al.* 2000), which makes these variations a critical consideration when modelling occupancy estimation for frogs (Royle & Nichols 2003).

Only relatively recently have studies begun to focus on identifying differences in detection probability (Barbraud *et al.* 2003; MacKenzie *et al.* 2003; Moilanen 2002; Nichols *et al.* 2000; Royle & Nichols 2003). Ignoring detection probability leads to bias in occupancy estimates (Gu & Swihart 2004; MacKenzie *et al.* 2002, 2018; Tyre *et al.* 2003). However, bias is not constant (Grant *et al.* 2005; Weir *et al.* 2005). False-negatives can lead to an inaccurate estimation of the effect of habitat, often underestimating occupancy values (MacKenzie *et al.* 2018). False-positives can lead to the overestimation of occupancy (Brown & Olsen 2013; Tanadini & Schmidt 2011). For example, consider a species that uses two different habitats; an open habitat and the other, a closed habitat. The species may be more likely to occupy a closed habitat in preference to the open habitat, but since it is easier to detect it in the open habitat, the differences observed between the two habitats may be overestimated. Miller *et al.* (2011a) found that even small misclassifications can lead to significant bias, so it is critical to account for detectability and how it varies with each variable (McClintock *et al.* 2010; Royle & Link 2006; Tyre *et al.* 2003).

When designing an occupancy study, methods can be incorporated to improve detection probability (MacKenzie *et al.* 2002, 2018; Nichols *et al.* 2000; Rota *et al.* 2009; Tyre *et al.* 2003). One simple method to improve detection probability is by adjusting for imperfect detection by adding multiple visits to the chosen sites (MacKenzie *et al.* 2002; Rota *et al.* 2009 Tyre *et al.* 2003). However, though this may account for false-negatives, it does little to reduce bias from false-positives (Miller *et al.* 2011a).

When detectability is not accounted for, inference drawn from occupancy estimation can be significantly impaired. Failure to account for imperfect detection in a model is now strongly criticised (Kéry & Schmidt 2008; Kroll 2009; MacKenzie *et al.* 2005; Otto & Roloff 2011; Yoccoz *et al.* 2001). It is now an important consideration in wildlife studies (Kéry & Schmidt 2008; Kroll 2009; Mazerolle *et al.* 2007; O'Connell *et al.* 2006). The development of methods to account for such bias, will improve the accuracy of detection probability and will greatly increase the precision in occupancy estimation (Miller *et al.* 2011a). Accurate occupancy estimation models are critical in monitoring programs as using limited data to detect long-term ecological trends, can result in misinformed wildlife management decisions (Field *et al.* 2005; Eaton *et al.* 2011).

1.5.3 Advantages of Using Occupancy Estimation

There have been massive changes in distribution of species across the world (Webb *et al.* 2007). Understanding historical changes and the changes species now face is of upmost importance for maintaining and managing biodiversity (MacKenzie *et al.* 2012). Occupancy estimation is a useful tool for investigating such ecological questions, especially when it is impractical or expensive to conduct more involved studies (MacKenzie *et al.* 2012). Other forms of sampling include capture-markrecapture (CMR) sampling, population counts and determining naïve presence-absence estimates. There are several advantages to using occupancy estimation rather than the more traditional methods of monitoring frog populations.

One advantage of the occupancy method is that you do not need to collect information on an individual or species during the survey; species absence or presence is simply recorded (MacKenzie *et al.* 2012). This is advantageous from a logistical and monetary perspective as occupancy surveys are relatively cheap and easy to conduct (Brown & Olsen 2013; Corn *et al.* 2005; Gould *et al.* 2012; MacKenzie *et al.* 2012, 2018; Rota *et al.* 2009; Royle & Nichols 2003; Zielinski & Stauffer 1996). These surveys generally require fewer resources and less effort to carry out than do species density estimation using methods such as CMR sampling (Gaston *et al.* 2000; Pollock *et al.* 1990) or even distance sampling (Royle & Nichols 2003). Bailey *et al.* (2004) corroborated this by suggesting that estimation methods like CMR are impractical and expensive to carry out for large, long-term amphibian monitoring programs.

Occupancy estimation is also good from a legal and ethical standpoint when compared to marking individuals for CMR studies which can face some ethical resistance if there is a possibility of a negative impact to the individual (MacKenzie *et al.* 2005, 2012). Anuran CMR studies often utilises invasive methods including PIT-tagging, radio tracking (external and internal), pressurised fluorescent marking, toe-clipping, spooling, pattern mapping and visible implant tags (Parris & McCarthy 2001; Phillott *et al.* 2010). Toe-clipping, the most common method utilised, has differing effects on frogs in the literature. Some studies have demonstrated that it can cause an increased stress response in frogs than simple capture and handling (Narayan *et al.* 2011). While others have found no or little difference in stress levels between manual handling and toe clipping (Fisher *et al.* 2013; Perry *et al.* 2011). Other implications that have arisen with this method of marking are its effects on foraging (Davis & Ovaska 2001), locomotion (Ott & Scott 1999), return rate of individuals to the site (Parris & McCarthy 2001), the potential for inflammation (Philott *et al.* 2011) and body condition (Davis & Ovaska 2001).

However, if occupancy surveying is undertaken in the frog species' breeding period, presence of a species can be determined by calling males with no need to disturb individuals. Further, when employing acoustical surveys, researchers can efficiently determine frog species presence without the need to disturb calling frogs (Lips *et al.* 2001; Zimmerman 1994)

Shifting interest from numbers of animals to sites occupied by animals, reduces effort in large scale monitoring programs (Royle & Nichols 2003). Occupancy estimation appears to be an appropriate method for use in management and monitoring programs. For example, methods used for assessing the marsh rabbit (*Sylvilagus palustris*) populations such as CMR sampling was logistically problematic and costly to use over a large area with large populations (Eaton *et al.* 2011). The use of presence-absence data was found to be more logistically appealing and consistent with the management guidelines (Eaton *et al.* 2011; Royle & Nichols 2003). Occupancy estimation is particularly advantageous when determining population factors for rare and elusive species. Their low detectability makes it inefficient to count individuals, so recording presence-absence data may be more effective (Tyre *et al*. 2003; MacKenzie *et al*. 2005).

1.5.4 Adaptations to the Methodology

Different studies have focused on improving the effectiveness of the standard methodology (Field *et al.* 2005; Guillera-Arroita *et al.* 2014; Hall 2000; MacKenzie & Royle 2005, MacKenzie *et al.* 2003, 2018; Rota *et al.* 2009; Tyre *et al.* 2003). MacKenzie *et al.* (2002) provided a more flexible model that allowed for the inclusion of covariate information. The detection history can be modelled with habitat attributes to identify those features that are associated with species presence and the probability of detection (Tyre *et al*. 2003). Since detectability of a species is often variable, this type of model provides a way of determining the effects of covariates on species occupancy. A later model developed by MacKenzie *et al.* (2003) modelled seasonal changes in the colonisation and extinction of species, not only presence or absence at the chosen site (Nichols *et al.* 2008; Miller *et al.* 2011), making it much more complex than the original model (Miller *et al.* 2011b).

Many studies are now using multiple detection methods as a way to target multiple species (Balas *et al.* 2012; Brown *et al.* 2007; Dahl *et al.* 2009; Farmer *et al.*

2009; Manley *et al.* 2004, 2005; Mattfeldt & Grant 2007; O'Connell *et al.* 2006; Sorensen *et al.* 2002), or different life stages of a single species (Mattfeldt & Grant 2007; Smith *et al.* 2006) which often provides a more comprehensive idea of community structure and changes in distribution (Nichols *et al.* 2008). There is some controversy with using multiple detection methods, although most researchers claim that it increases detectability (Garden *et al.* 2007; Ribeiro-Junior *et al.* 2008; Ryan *et al.* 2002). There is also an added cost to time and materials to implementing multiple detection methods, with no guarantee of suitable information being collected (Mattfeldt & Grant 2007; Nichols *et al.* 2008). Despite this issue, the multiple detection method has several advantages. Firstly, it deals with the lack of independence often found in conducting multiple surveys at one site. Secondly, it is data efficient in that it utilises many different methods to improve detection. Thirdly, it is especially important when considering interspecies interactions that can limit dispersal and occupancy of others (Moore & Swihart 2005). Lastly, by estimating parameters for both large, and for small scale occupancy, inference at two different scales can be achieved (Guillera-Arroita *et al.* 2014; Nichols *et al.* 2008). When there is little information available on the life history of the target species, combining more than one detection method (Parris *et al.* 1999; Rödel & Ernst 2004), along with incorporating environmental factors, can provide more accurate estimates of detectability (Guzy *et al.* 2014). This can allow the surveyor to identify the most appropriate sampling method (Guzy *et al.* 2014). If detection probability is influenced by the time of year or weather conditions, as is the case for many frog species, survey protocols can be adjusted to minimise the chance of false absences. Thus, despite some of its drawbacks, the use of the multiple detection method will probably become increasingly common in multi-species surveys (Eaton *et al.* 2011; Nichols *et al.* 2008.

Incomplete detection can cause bias in the final occupancy estimation (Eaton *et al.* 2011; Guillera-Arroita *et al.* 2014; Peterson & Mordecai 2006). Several methods have been developed to accommodate detection bias (Dorazio & Royle 2005; MacKenzie & Royle 2005; MacKenzie *et al.* 2002, 2003, 2004, 2005; Moore & Swihart 2005; Royle & Nichols 2003). An adaptation of the traditional occupancy model as described by MacKenzie *et al.* (2002), which allows for temporal variation in detection and abundance between sites, is suggested by Royle and Nichols

(2003). The original model assumed constant variance across all sites, which is often not the case in real life situations (Miller *et al.* 2011b; Royle & Nichols 2003). Complete detection is impossible as species-specific traits and the physical environment will often affect detectability (Miller *et al.* 2011b; Peterson & Mordecai 2006).

Often in ecological studies, fewer sites than is necessary are visited due to logistical constraints such as time and resources (Tyre *et al.* 2003). Sufficient presence-absence data is required to combat the variation found in detectability (Gibbons *et al.* 1997; Tyre *et al.* 2003; de Solla *et al.* 2005). Guillera-Arroita *et al.* (2014) hypothesised that the more sites surveyed, the less time that was needed searching for species at each of those sites, while a smaller number of sites required more intensive searching. When detection probabilities are low, as is the case for most rare species, increasing the number of site visits will improve the accuracy of the estimated occupancy (MacKenzie *et al.* 2002; Tyre *et al.* 2003). Field *et al.* (2005) further corroborated this, showing that a minimum of three surveys per site maximised the power to detect trends by minimising the variation in the estimation. However, Tyre *et al.* (2003) found that although three visits eliminated bias, occupancy estimates remained fairly inaccurate and that six visits would improve precision (Tyre *et al.* 2003). De Solla (2005) also found that three visits were not sufficient to detect all anuran species, even when rare or elusive species were excluded. Meanwhile, Miller *et al.* (2011b) indicated that five visits to sites would be considered adequate for infrequently detected species, but more visits and sites would be required if more habitat types were surveyed. It is not entirely clear whether it is better to increase the number of visits at the expense of the number of sites; the trade-off depending upon the cost of adding new sites versus the cost of revisiting the same sites, and on the objectives of the study (Tyre *et al.* 2003). However, Smith *et al.* (2006) recommended that for frogs, as many visits at as many different sites as possible should be made, especially when the survey involves few common species, so that environmental factors that affect detection can be modelled in conjunction with occupancy.

Contrary to previous studies regarding recommended number of visits (see de Solla *et al.* 2005; Field *et al.* 2005; Guillera-Arroita *et al.* 2014; Miller *et al*. 2011b; Tyre *et al.* 2003), a single-visit occupancy estimation method was developed by Lele *et al.* (2012). This method also accounts for detection, as seen in other occupancy methods (Lele *et al.* 2012; Solymos *et al.* 2012). Further, the single-visit occupancy method does allow for the inclusion of covariates, which can better demonstrate the dynamics between habitat variables and occupancy, and survey conditions and detection (Guillera-Arroita *et al.* 2014). The single-visit occupancy method is useful when assessing historical records as often, such records were recorded intermittently and opportunistically, with no structured repeat visits.

Another extension to the simple occupancy model is the two-species occupancy model developed by MacKenzie *et al.* (2004). This model can be used to address co-occurrence between two-species and to model species interactions, such as competition or predation, while still accounting for detectability (Lamothe *et al.* 2019; MacKenzie *et al.* 2004, 2018). Further, this method can also incorporate habitat and environmental information to account for other factors that may be affecting patterns of co-occurrence but are not related to species interactions (Lamothe *et al.* 2019; MacKenzie *et al.* 2004, 2018). The two-species occupancy model provides ecological understanding and greater insight into habitat and biotic relationships, which may be of critical understanding for future population assessments and conservation studies (Lamothe *et al.* 2019; Wisz *et al.* 2013).

Perhaps an integrated design which includes parts from the various adaptations will be evaluated in the future. Though it may be much more complex than any of the single methods describe here, it may be useful in addressing situations with multiple assumption violation (Alldredge *et al.* 2007; Nichols *et al.* 2008; Rota *et al.* 2009). Perhaps the best approach may be to choose an occupancy estimation method that best matches the objectives of the study, what violations of the assumptions could occur and the trade-off between the number of sites and the number of visits dictated by monetary and time constraints.

The standard single-species, single-season occupancy method with repeat visits and the inclusion of covariates was used in the present study to model current occupancy of the species found. However, several variations of the occupancy estimation method were also used. The single-visit occupancy estimation method (Lele *et al.* 2012; Solymos *et al.* 2012) was used to analyse the historical records. The two-species occupancy method (MacKenzie *et al.* 2018) was used to assess the influence of a potential predatory fish species, *G. holbrooki*, and a *B. dendrobatidis* reservoir host, *Cri. signifera*, on the occurrence of each of the frog species found in the New England Tablelands.

Chapter 2: The New England Tablelands Bioregion

2. The New England Tablelands Bioregion

The New England Tablelands bioregion is 3,004,202 ha (or 3,004 km^2) in area and is contained predominantly within the NSW borders. At the northern end, it extends from the Queensland border north of Tenterfield (29.0576° S, 152.0190° E) to south of Walcha (30.9852° S, 151.5933° E), and from immediately west of Bendemeer (30.8862° S, 151.1544° E) to east of Ebor (30.4000° S, 152.3500° E) across the widest part of the region (Fig. 2.1.1). Other notable population centres that can be found in this bioregion include Armidale (30.5036° S, 151.6523° E), Uralla (30.6424° S, 151.4991° E), Bundarra (30.1719° S, 151.0759° E), Glen Innes (29.7518° S, 151.7362° E) and Guyra (30.2168° S, 151.6676° E). Armidale is positioned roughly in the middle of the bioregion (Fig. 2.1.1). Except where referenced otherwise, the following descriptions of the topography and geology, the native vegetation and the climate of the New England Tablelands are sourced from Sahukar *et al.* (2003).

2.1 Topography and Geology

The New England Bioregion is a stepped plateau made up of hills and plains, with elevations varying between 600 m to 1500m (Heatwole & Simpson 1986; Sahukar *et al.* 2003). Elevations generally show a noticeable gradient, with higher altitudes in the East and lower altitudes in the west. The Great Dividing Ranges runs north to northeast along the eastern side of the New England Tablelands and there are some other lesser ranges and individual mountains in scattered throughout the plateau including the Moonbi range on the western edge (Heatwole & Simpson 1986).

Bedrock types vary with topography. The New England region bedrock primarily comprises of intrusive granite formed during the carboniferous and Permian sedentary rocks, along with tertiary basalts, gravels, and sands. Soils derived from the granites and sedentary rocks have low fertility and are prone to erosion. These soils are found mostly on areas with slopes, forming hills and ridges. The granite intrusions form boulder outcrops and tors, whilst the sedentary rocks form course, stony soils. The basalts are found predominantly on the plains, although there are some peaks where the origins of ancient eruptions occurred. The soils derived from the tertiary basalts are fertile and well-structured.

[redacted]

Fig. 2.1.1: The New England Tablelands Bioregion in NSW, Australia.

2.2 Native Vegetation

Native vegetation is dependent on soil types, geology and topography, often with a high degree of endemism for many of the species in the New England Tablelands (Sahukar *et al.* 2003). Rain forest and wet sclerophyll forest occur in the more humid, eastern margins in the New England Tablelands (Heatwole & Simpson 1986). Woodland and unforested habitat make up the majority of the vegetation cover throughout the region, with scattered localities of dry sclerophyll (Heatwole & Simpson 1989). In areas of cropping and grazing enterprises, the landscape has been highly modified (Heatwole & Simpson 1986).

Seventy species of Eucalypts occur in the Tablelands with around a third of them being endemic to the bioregion itself (Sahukar *et al.* 2003). The soils of granitic origin in the central part of the Tablelands support open forests and woodlands, predominantly comprising silver-top stringybark (*Eucalyptus laevopinea*), Blakely's red gum (*Eucalyptus blakelyi*), Youman's stringybark (*Eucalyptus youmanii*), yellow box (*Eucalyptus melliodora*), apple box (*Eucalyptus bridgesiana*), rough-barked apple (*Angophora floribunda*), black cypress pine (*Callitris endlicheri*), manna gum (*Eucalyptus viminalis*) and snow gum (*Eucalyptus pauciflora*). The western slopes support tumbledown gum (*Eucalyptus dealbata*), western New England blackbutt (*Eucalyptus andrewsii*), Caley's ironbark (*Eucalyptus caleyi*), red stringybark (*Eucalyptus macrorhynca*), McKie's stringybark (*Eucalyptus mckiena*), white cypress pine (*Callitris glaucophylla*), black cypress pine, rough-barked apple and silver-leaved ironbark (*Eucalyptus melanophloia nophloia*), with river oak (*Casuarina cunninghamiana*) lining rivers and streams below an elevation of 800 m. Sedgelands can be found around some of the smaller streams in the western part of the bioregion. Sites at higher altitudes are dominated by messmate (*Eucalyptus obliqua*), mountain gum (*Eucalyptus dalrympleana ssp.heptantha*), snow gum,black sallee (*Eucalyptus stellulata*) and ribbon gum (*Eucalyptus nobilis*), while orange gum (*Eucalyptus prava*) and black cypress pine are found in the north of the bioregion around rocky outcrops. High rainfall areas support some cool temperate rainforest species such as beech (*Notofagus moorei*).

Areas of the bioregion with tertiary basalt soils typically support open forests and woodlands of manna gum, snow gum, New England blackbutt (*Eucalyptus* *campanulata*), and narrow-leaved peppermint (*Eucalyptus radiata*) on the slopes. The valleys are dominated by New England stringybark (*Eucalyptus calignosa*), with yellow box, wattle-leaved peppermint (*Eucalyptus acaciiformis*), New England peppermint (*Eucalyptus nova-anglica*), snow gum, black sallee and ribbon gum. New England stringybark, yellow box, Blakely's red gum and rough-barked apple occur on tertiary sands.

Soils of Permian sediment origin support Youman's stringybark, tumble down gum, black cypress pine, silver-leaved ironbark, white cypress pine and the occasional kurrajong, with white box (*Eucalyptus albens*), grey box (*Eucalyptus moluccana*), yellow box, Blakely's red gum and localised occurrences of mugga (*Eucalyptus sideroxylon*) on the western stony ridges. In the cooler, higher regions, there are forests of snow gum and black sallee, while in higher moist areas, there can be found ribbon gum, mountain gum, silver-top stringybark, New England blackbutt and narrow-leaved peppermint. New England stringybark, ribbon gum and cool temperate rainforest species are found in moist, sheltered gullies.

2.3 Catchments and River Drainages

The New England Tablelands consist of six different water catchments (Fig. 2.2.1). The western side of the New England Tablelands is broken up into three catchments (Heatwole & Simpson 1986). From north to south, there are the Border Rivers catchment, Gwydir catchment and Namoi catchment. In the region, they extend to just west of Tenterfield, Glen Innes and Armidale, and lie beyond the New England Tablelands to the West. Past this, the eastern side of the region is divided between the Clarence catchment in the north, and the Macleay catchment, with the very southern tip of the region falling into the Manning catchment (Heatwole & Simpson 1986).

The major river of the border rivers catchment is the Macintyre River, which extends 300 km, the entirety of which is not contained within the New England bioregion (Department of Environment, Climate Change and Water, NSW [DECCW] 2010). Major tributaries of this river are the Severn River and Dumaresq River (Heatwole & Simpson 1986). Other notable waterbodies in the border rivers catchment are Pindari Dam which the Severn River flows into, Tenterfield Creek, Beardy River, Deepwater River, and Mole River (DECCW 2010).

The Gwydir River is the major river that flows through the Gwydir catchment (Heatwole & Simpson 1986). It has several tributaries: Copes creek, Moredun Creek. Georges Creek, Laura Creek, Horton Creek and Roumalla Creek (DECCW 2010). These rivers join at the base of the slopes and run into Copeton Dam on the very edge of the New England Tablelands bioregion (DECCW 2010).

The Clarence River catchment falls in a mountainous part of the New England bioregion. As such, its gorges, contain many major waterways; Maryland River, Cataract River, Timbara River, Mann River, Sara River, Aberfoyle River and Guy Fawkes River (Department of Environment, Climate Change and Water [DECCW], NSW (2006). These all flow into the Clarence River to the east outside of the bioregion.

The Macleay River catchment contains several major waterbodies; Gara River, Chandler River, Styx River, Apsley River and Rockvale Creek. All these flow down the eastern side of the range, meeting at the base of the mountains, outside of the bioregion, before flowing into the Macleay River.

The major waterway for the region in the Namoi River catchment is the Macdonald River. This river feeds into the Namoi River, outside the New England Tablelands bioregion. Finally, in the southern end of the New England bioregion, the Nowendoc River, runs outside the region and flows into the Manning River in the Manning River catchment.

Fig. 2.2.1: Catchments of the New England tablelands; Border-rivers catchment (A), Clarence Catchment (B), Gwydir catchment (C), Macleay Catchment (D), Namoi (E) and Manning catchment (F). NOTE: The borders of these catchments continue outside the bioregion.

2.3.1 Upland Wetlands

There are several upland wetlands in the New England Tablelands, many of which occur on private lands (Department of Environment and Heritage [DEH] 2005). These are not connected to any river system and are formed in depressions in the landscape (DEH 2005). They often occur on basalt soils but can be found on granitic or sedentary soils, at elevations from 700-1400m (DEH 2005). Water presence in these wetlands is impacted by several factors: depth of the depression, catchment area, rainfall, water run-off and disturbances (DEH 2005). As such, these areas can be near permanent, intermittent, or even ephemeral depending on these conditions (DEH 2005). Vegetation found at these sites include sedges, forbs, and grasses (DEH 2005). Though there are no naturally occurring shrubs or trees found at these locations, the presence of these in the surrounding area can have important implications for water run-off (DEH 2005). Examples of upland wetlands that were visited during this project were Racecourse Lagoon, Thomas Lagoon and Dangars Lagoon near Uralla and Little Llangothlin Lagoon near Glen Innes. Racecourse Lagoon, Thomas Lagoon and Dangars Lagoon all lie in the Gwydir River catchment, while Little Llangothlin Lagoon is in the Clarence catchment (DECCW 2006).

2.4 Climate

The majority of the region has a temperate to cool temperate climate, with a sub-humid climate occurring in the north of the region, closer to the Queensland border (Sahukar *et al.* 2003). This climate is characterised by warm summers, usually with uniform rainfall occurring throughout the summer months (Heatwole & Simpson 1986; Sahukar *et al.* 2003). Winters are generally cold with the presence of frost and a smaller rainfall peak associated from cold fronts from the South (Heatwole & Simpson 1986). The eastern side of the region is bordered by points of high elevations, showing a montane climate with milder summers and no distinct dry season (Sahukar *et al.* 2003). Climatic graphs for key towns within the New England Tablelands and for a town west and east of the New England Tablelands are shown in Fig. 3.2.1 and Fig. 3.2.2.

Temperatures vary only marginally within the region (Sahukar *et al.* 2003). Around Armidale, the average minimum temperature for the summer, autumn winter and spring for the years that the survey was conducted were: 14.4°C, 8.4°C, 1.9°C and 7.7°C, respectively (Bureau of Meteorology [BOM] 2021). The average maximum temperature was 27.7°C, 20°C, 13.6°C, 21.3°C, respectively, for the same periods (BOM 2021). These are higher than the long-term average temperature maxima of 25.5°C, 19.6°C, 12.9°C, 20.4°C, respectively, and minima of 13°C, 7.9°C, 1.8°C, 7.4°C, respectively (BOM 2021). The minimum and maximum temperatures for the areas around Tenterfield (13.9-26.6°C for summer, 8.6-21.4°C for autumn, 1.7-15.2°C for winter, 7.8-22.3°C for spring), Glen Innes (13.0-25.1°C for summer, 8-20°C for autumn, 1.3-13.4°C for winter, 7.1-20°C for spring) and Walcha (12.1-27°C for summer, 5.9-21°C for autumn, -0.6-13.6°C for winter, 5.2-21°C for spring) were also higher than the long-term averages (BOM 2021).

Rainfall patterns during the survey years was predominantly typical of the region. Of significant note, however, was the lower rainfall around the region during the project (2017-2019) (BOM 2022; Nguyen *et al.* 2021). Armidale’s annual rainfall for that year was 315.2 mm compared to the long-term average of 756.8 mm (BOM 2021). The areas around Glen Innes (339.4 mm compared to 837.3mm), Tenterfield (254.6 mm compared to 843.5 mm) and Walcha (252.3 mm compared to 773.4 mm) all showed similar reduced rainfall (BOM 2021).

There is a strong rainfall gradient as you move from the eastern edge of the New England tablelands westward (Heatwole & Simpson 1986). East of the New England Tablelands, Dorrigo (30.33°S, 152.72°E) has an average annual rainfall of 1896.8mm (BOM 2021). This is compared to west of the New England Tablelands, Inverell (29.78°S, 151.12°E) has an average yearly rainfall of 793.1mm (BOM 2021).

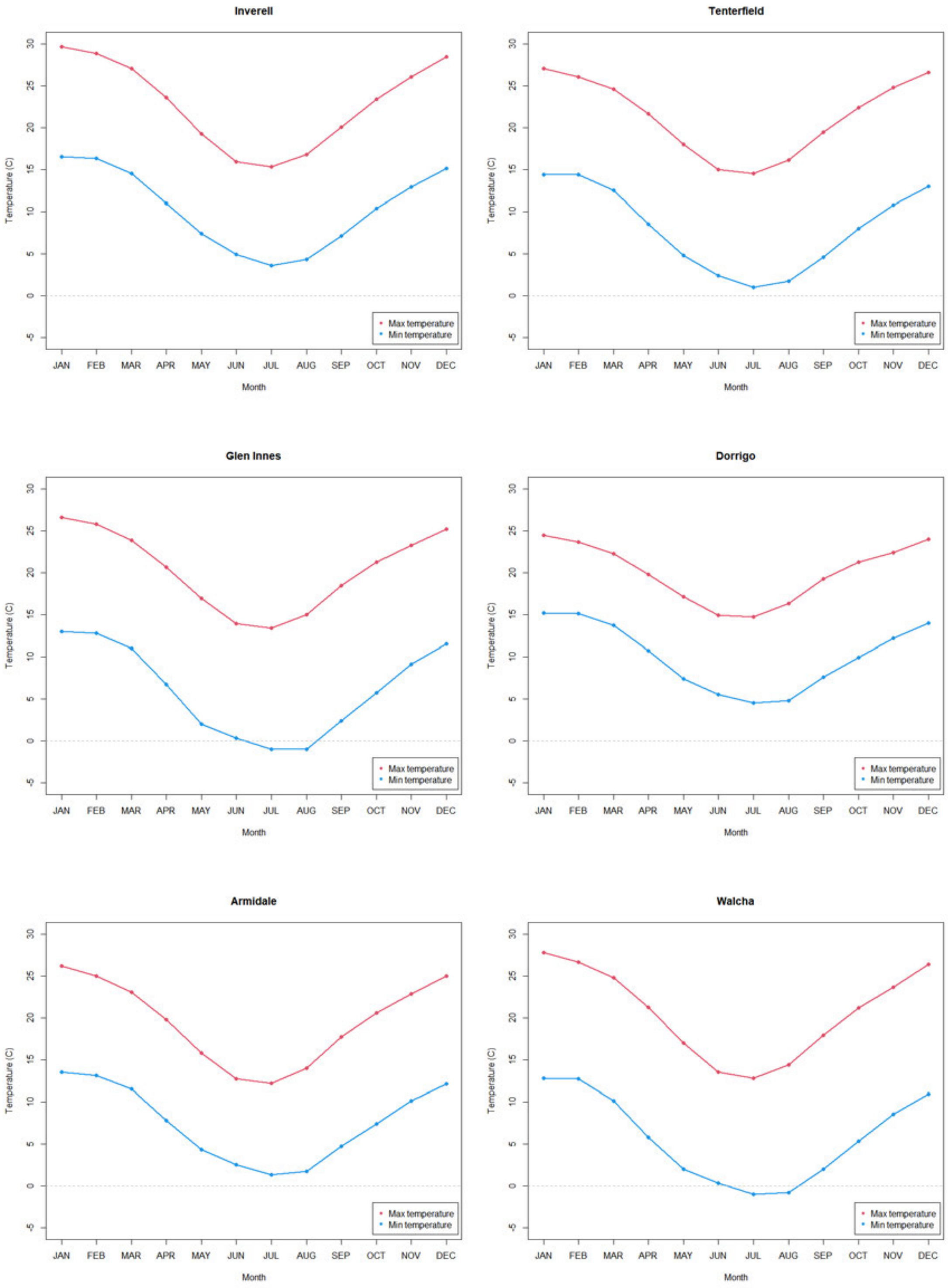


Fig. 2.3.1: Long-term average minimum (blue) and maximum (red) temperatures (°C) for each month in the New England Tablelands bioregion. New England Tablelands stations are located at Armidale, Glen Innes, Walcha and Tenterfield. Inverell station is located west of the New England Tablelands and Dorrigo station is located east of the New England Tablelands. NOTE: adapted from information supplied by Bureau of Meteorology [BOM] (2021, April 17). Climate statistics for Australian locations. http://www.bom.gov.au/climate/averages/tables

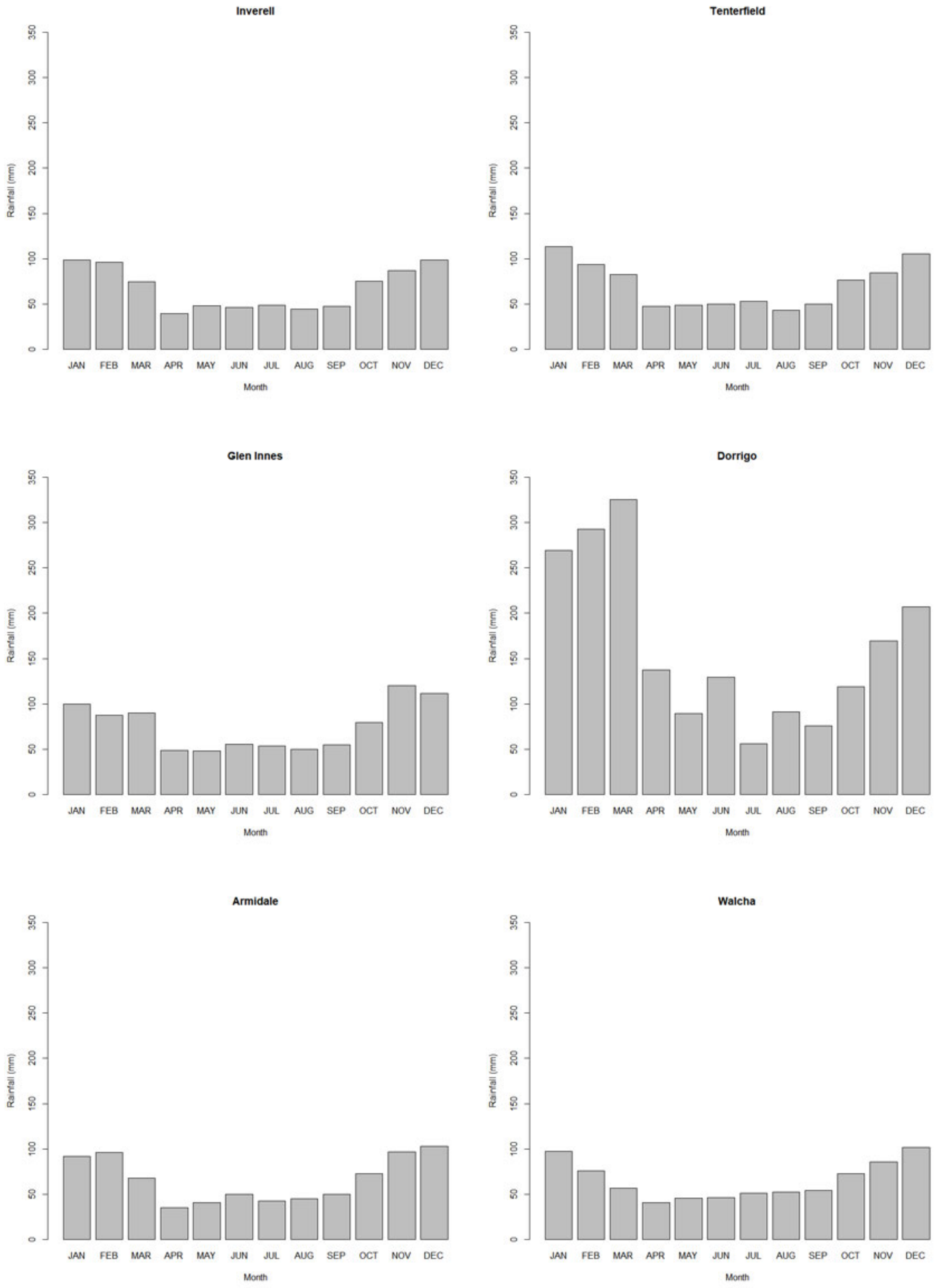


Fig. 2.3.2: Long-term average rainfall (mm) for each month in the New England Tablelands bioregion. New England Tablelands stations are located at Armidale, Glen Innes, Walcha and Tenterfield. Inverell station is located west of the New England Tablelands and Dorrigo station is located east of the New England Tablelands. NOTE: adapted from information supplied by Bureau of Meteorology [BOM] (2021, April 17). Climate statistics for Australian locations. http://www.bom.gov.au/climate/averages/tables

Chapter 3: The Historical surveys (Heatwole *et al*., 1995)

3. The Historical Surveys (Heatwole *et al*., 1995)

From 1966 through until 1975, a team from the University of New England (UNE) conducted extensive surveys of a number of faunal groups in the New England Tablelands of New South Wales (NSW) (Heatwole *et al.* 1995). These surveys targeted three major vertebrate groups, including the frogs (*Anura*), the major reptile groups, the lizards, snakes (*Squamata*) and tortoises (*Testudines*), and the birds (*Aves*). With regards to the present study, there will only be a focus on the historical presence of frogs at the sites that were originally sampled throughout the Tablelands. The overall outcome of this was that some 45 species of frogs, ranging across 13 genera, were found to be present in the Nandewar and New England Tablelands regions of northern NSW. For maps of the sites historically occupied by species found by Heatwole *et al.* (1995), see Appendices 1 and 2. All information presented here regarding the historical surveys are attributed to Heatwole *et al*. (1995), unless otherwise stated.

The original survey area comprised the federal electorate of New England based on the1975 boundaries (Simpson & Stanisic 1986), which covered parts of the Nandewar and New England Tablelands bioregions (Sahukar *et al.* 2003). The Nandewar bioregion is beyond the purview of the present study, so only those species records placed within the New England Tablelands have been referenced. The historical survey records were provided by the Australian Museum, where they were held in storage.

In relation to the UNE survey, the electoral map was divided into grid cells using the Australian Biogeographical Integrated Grid system (ABIGS) as outlined by Brook (1977). Each cell was 5’ latitude by 5’ longitude, and represented the smallest cell size in the ABIGS system (Simpson & Stanisic 1986). Apart from those that presented with accessibility issues each cell was visited opportunistically at least once (Simpson & Stanisic 1986). Some cells were deemed to have been visited more than once because surveyors of different faunal groups occasionally recorded the presence of frog species, particularly within easily accessible cells around population centres (Simpson & Stanisic 1986). In conducting the survey, collectors searched for frogs under logs and stones at sites with flowing water, in backwaters, marshes and farm dams (Simpson & Stanisic 1986).

The final anuran distribution paper published by Heatwole *et al.* (1995) also included extra records obtained from a collection held by the Department of Zoology at UNE, specimens brought into Zoology by members of the public (early citizen science), and historical collections maintained by the Australian Museum, the Queensland Museum and the Museum of Victoria. The historical records used here in the present study were confined only to data records that were collected opportunistically by the original UNE team during their surveys. Excluded were the extra records that were included from the other sources in the analysis for their final paper.

3.1 Species Discrepancies

Originally, the Heatwole *et al*. (1995) study recorded the presence of 39 frog species in the New England Tablelands bioregion. A number of these species were found outside their current predicted habitat range (Hoskin *et al.* 2015). These species included the knife-footed frog (*Cyclorana cultripes*), the water-holding frog (*Cyclorana platycehala*), the Blue Mountains tree frog (*Litoria citropa*), the green stream frog (*Litoria phyllochroa*), the giant barred frog (*Mixophyes iteratus*) and the red-crowned toadlet (*Pseudophryne australis*). A summary of the status of the 39 frog species found in the historical study is given in Table 3.1.1.

3.1.1 Misidentifications

There were four species whose current acknowledged distribution does not include the New England Tablelands. These were *Pseudophryne australis*, *Mixophyes iteratus* and two of the *Cyclorana sp.*, namely *Cyc. cultripes* and *Cyc. platycephala*. There is also some conflict with regard to a third *Cyclorana sp.*, namely *Cyc. brevipes*. Although not recorded as being endemic to the New England Tablelands by Anstis (2017), Hoskin *et al.* (2015) suggested that *Cyc. brevipes*, may be present at sites along the north-western edge of the bioregion. If *Cyc. brevipes* was known to be present in the north-west of the New England Tablelands, as suggested by Hoskin *et al.* (2015), then it is likely that the other two *Cyclorana sp.* were misidentified specimens of *Cyc. brevipes*. If the distribution proposed by Hoskin *et al.* (2015) does not reflect the actual distribution of *Cyc. brevipes*, then perhaps all three *Cyclorana sp.* were misidentified. Anstis (2017) suggests that these species are most likely to be mistaken for other *Cyclorana sp.*, although no other *Cyclorana sp*., apart from the possibility of *Cyc. brevipes* discussed above, have distributions that potentially include the New England Tablelands. The superficial appearance and behaviour of these species may be similar to other burrowing species found in the region, principally *Limnodynastes dumerilii*, *Neobatrachus sudellae* and *Platyplectum ornatum,* which could be some other, although less likely, options for misidentification.

Another species which may have been misidentified was the giant barred frog (*Mixophyes iteratus*). The acknowledged distribution of this species does not fall within the New England Tablelands (Anstis 2017, Hoskin *et al.* 2015). Further, Hines (2002) pointed out that this species did not occur at altitudes above 100 m above sea level (Lollback *et al.* 2021), which includes all parts of the New England Tablelands. Given the superficial similarity of their physical features and habitat preferences, a likely candidate for this misclassification would be one of the other *Mixophyes* species endemic to the region (Anstis 2017; Hoskin *et al.* 2015). Of these, the most likely candidate would be *Mixophyes balbus*, although *Mixophyes fasciolatus* is a possible but less likely option given its limited distribution within the New England Tablelands (see section 3.1.4).

Of the other misidentified species, *Pseudophryne australis* was likely to have been misidentified as one of the other *Pseudophryne* sp*.* common within the region. *Pseudophryne bibronii* or *Pseudophryne coriacea* are the most likely candidates, although *Pse. coriacea* is probably the more likely candidate since *Pse. bibronii* lacks the conspicuous red markings that the other two species possess (Anstis 2017; Hoskin *et al.* 2015). Anstis (2017) also suggests that tadpoles of *Pse. australis*, which are darker and with a less mottled colour, could potentially be mistaken for the tadpoles of the common eastern froglet (*Crinia signifera*), although these similarities disappear as the tadpole becomes a metamorph and develops the red crown of the adult frog.

The dainty green tree frog (*Litoria gracilenta*), another species whose distribution does not include the New England Tablelands (Anstis 2017; Hoskin et al. 2015) but was recorded by Heatwole *et al.* (1995), is known to be exported and translocated from its natural range along the eastern coast of Queensland and northern NSW through the transport of food products, primarily bananas (Anstis 2017). It is reasonable to suppose that this species may have been released into the New England Tablelands via transportation. The recording of the presence of this species could, however, have been a misclassification of the common green tree frog (*Litoria caerulea*), although this is less likely given that the two species' appearances are quite distinct from each other (Anstis 2017).

3.1.2 Taxonomic Changes

Since the undertaking of the original UNE surveys, the taxonomic classification of some species has been modified. Some species have been renamed, while some of the old species have been reclassified into more than one species. The species of note with regard to this are the green stream frog (*Litoria phyllochroa*), the New England tree frog (*Litoria subglandulosa)* and the Stony Creek frog (*Litoria lesueuri*).

Two species, *Litoria barringtonensis* and *Lit. subglandulosa*, were not present in the records of the historical survey. However, their presence was later noted in the Heatwole *et al.* (1995) paper. It is likely that both *Lit. barringtonenesis* and *Lit. subglandulosa* were present historically, but were likely misidentified as some other species in the historical records. Relevant to this is the fact that these two species were not described until 1961 for *Lit. subglandulosa* and 1975 for *Lit. barringtonenesis*, and their taxonomic placement was not fixed until after the historical survey in the New England Tablelands was complete (Donnellan *et al.* 1999; Mahony *et al.* 2001). *Litoria barringtonensis* and *Lit. subglandulosa* have both undergone subsequent rearrangements within their taxonomic complexes since their initial descriptions (Anstis 2017; Donnellan *et al.* 1999; Hoskin *et al.* 2015; Mahony *et al.* 2001).

A possible misclassification of *Lit. subglandulosa* is as *Litoria citropa*. *Litoria subglandulosa* is part of the *Lit. citropa* complex and shares many physical similarities with *Lit. citropa* (Mahony *et al.* 2001). Although these two species are similar in appearance, *Lit. citropa* does not have a distributional range that includes the New England Tablelands, whilst *Lit. subglandulosa* does (Anstis 2017). The New England tree frog, *Lit. subglandulosa*, is the only species from the *Litoria citropa* complex found in the New England Tablelands (Anstis 2017) and will be considered to be the species found in the historical study that was originally recorded as *Lit. citropa*.

A possible misclassification of *Lit. barringtonensis* was as *Lit. phyllochroa*. The single species originally identified as *Lit. phyllochroa* was later determined to comprise five distinct species: the Barrington Tops tree frog (*Litoria barringtonensis*), the Kroombit tree frog (*Litoria kroombitensis*), the southern green stream frog (*Litoria nudidigita*), Pearson's stream frog (*Litoria pearsoniana*) and the green stream frog (*Litoria phyllochroa*); with conjecture still surrounding a sixth species, the peppered tree frog (*Litoria piperata*) (Anstis 2017; Hoskin *et al.* 2015). The Barrington Tops tree frog, *Lit. barringtonensis*, is the only species from the *Lit. phyllochroa* complex that is likely still found in the New England Tablelands (Anstis 2017). *Litoria piperata* has also had a historical presence within the region (Anstis 2017; Heatwole *et al.* 1995). *Litoria piperata* has been the subject of several surveys dedicated to its rediscovery in the region but without success, so is possibly now extinct in the New England Tablelands (Anstis 2017). *Litoria piperata* is also yet to be verified as a separate species through DNA analysis (Anstis 2017; Donnellan *et al.* 1999). Further, there is some debate as to whether there are strong enough morphological differences from other members of the *Lit. phyllochroa* complex to support its classification of a separate species. Tyler and Davies (1985) did describe *Lit. piperata* as a separate species. However, Donnellan *et al.* (1999) and Gillespie and Hines (1999) suggest that such differences could be attributed to a fringe morphotype of *Litoria pearsoniana*. Given all this, records of *Lit. phyllochroa* will be considered as records of *Lit. barringtonensis*.

A similar taxonomic change has occurred for *Lit. lesueuri*. Originally, the distribution of *Lit. lesueuri* was thought to extend along the coast of northern Queensland all the way through to southern Victoria. Biochemical and chromosomal studies of individuals of *Lit. lesueuri* from different parts of this distributional range have determined that the original distribution of *Lit. lesueuri* was actually that of three separate species: the northern stony creek frog (*Litoria jungguy*) in northern Queensland, the eastern stony creek frog (*Litoria wilcoxii*) in southern Queensland to central NSW and *Lit. lesueuri* in southern NSW and Victoria (Anstis 2017; Donnellan & Mahony 2004). Since *Lit. wilcoxii* is the only one of these three species currently found within the New England Tablelands (Anstis 2017), it is likely that those individuals identified as *Lit. lesueuri* in the historical study, were actually *Lit. wilcoxii*. Within the context of the current study, all records of *Lit. lesueuri* will be considered as being records of *Lit. wilcoxii*.

Table 3.1.1: The 39 frog species detected in the historical study (Heatwole *et al*. 1995), with indications as to whether they were: 1) likely misclassified, 2) had undergone a taxonomic reclassification, 3) were transplanted via anthropogenic processes, or 4) had a known distribution that was on the margins of the New England Tablelands. NOTE: Frog species listed in **bold** are those recorded during the historical study that were also found in the present study.

Adelotus brevis	*Litoria gracilenta*[1,3]
Crinia parinsignifera	***Litoria latopalmata***
Crinia signifera	***Litoria peronii***
Cyclorana brevipes[4]	*Litoria piperata*
Cyclorana cultripes[1]	*Litoria phyllochroa*[2]
Cyclorana platycephala[1]	*Litoria rubella*
Lechriodus fletcheri	***Litoria subglandulosa***[2]
Limnodynastes dumerilii	***Litoria verreauxii***
Limnodynastes fletcheri	***Litoria wilcoxii***[2]
Limnodynastes peronii	***Mixophyes balbus***
Limnodynastes salmini	*Mixophyes fasciolatus*[4]
Limnodynastes tasmaniensis	*Mixophyes iteratus*[1]
Limnodynastes terraereginae	*Neobatrachus sudellae*
Litoria aurea	*Philora sphagnicola*[4]
Litoria barringtonensis[2]	*Platyplectrum ornatum*
Litoria booroolongensis	*Pseudophryne australis*[1]
Litoria caerulea	*Pseudophryne bibronii*
Litoria chloris[4]	***Pseudophryne coriacea***
Litoria citropa[2]	***Uperoleia laevigata***
Litoria dentata	*Uperoleia rugosa*
Litoria fallax	

3.1.3 Species whose Distribution Overlaps only on the Edge of the New England Tablelands

There were three species recorded in the historical study which have only a tiny part of their distribution within the bounds of the New England Tablelands. These include the red-eyed tree frog (*Litoria chloris*), the great barred frog (*Mixophyes fascioltaus*), and the sphagnum frog (*Philoria sphagnicola*). The distributions of all three of these species extend along the eastern edge of the New England Tablelands, within high altitude rainforests and wet sclerophyll forests (Anstis 2017; Hoskin *et al.* 2015). Two of these species, *Lit. chloris* and *M. fasciolatus*, are associated with streams (Anstis 2017; Hoskin *et al.* 2015). The other species, *Phi. sphagnicola,* has specific terrestrial breeding habitat requirements that need to be present at a site. *Philoria sphagnicola* is a terrestrial breeder that utilises moist areas such as cavities and seepage lines under rocks, logs, and at the base of sphagnum moss or trees (Anstis 2017; de Bavay 1993; Hoskin *et al.* 2015).

Only a small number of the sites (eight of 200) selected for the present study meet the specific habitat requirements of these species. As such, it is unlikely that any of these three species will be encountered in the present study.

A fourth species, the short-footed frog (*Cyclorana brevipes*), is a burrowing species which breeds opportunistically in response to suitable conditions (e.g., heavy rainfall). Potentially, it could be found on the north-western edge of the New England Tablelands (Anstis 2017; Hoskin *et al.* 2015). Apart from the conjecture on whether this species is present in the region or not (see section 3.1.1), the likelihood of encountering it is similar to that of other burrowing species in that it requires suitable meteorological conditions for activity (breeding, dispersal, foraging), principally heavy rainfall (Anstis 2017; Hoskin *et al.* 2015).

3.1.4 Species from within the New England Tablelands that were not Registered in the Historical Records

There are four species which have a historical distribution in the New England Tablelands but where not collected by the historical survey team. These were the yellow spotted tree frog (*Litoria castanea*), Tyler’s tree frog (*Litoria tyleri*), the striped rocket frog (*Litoria nasuta*) and the crucifix frog (*Notaden bennetti*) (Hoskin *et al.*

2015). Three of these species, *Lit. tyleri*, *Lit. nasuta* and *N. bennetti*, were included in the Heatwole *et al.* (1995) paper, although with only a small number of records (two, one and one record, respectively). Presumably, these inclusions were based on museum records rather than specimens the UNE team collected from 1966 to 1975. Although *Lit. tyleri* was not described until after the surveys had concluded, the other three had previously been described. *Litoria castanea* was also included in the Heatwole *et al.* (1995) paper, although its inclusion was not based on any records from the original survey team either.

Litoria tyleri was described in 1979 (Martin *et al.* 1979; Tyler & Davies 1978), after the historical surveys were concluded. It is possible that this species was encountered and listed as *Litoria peronii*, given the physical similarities between the two species and the overlap in their distributions on the eastern edge of the New England Tablelands (Anstis 2017; Hoskin *et al.* 2015).

The second species, *Litoria nasuta*, is found in a wide range of habitat types and, according to Hoskin *et al.* (2015), should be widespread throughout the region. It is possible that individuals of *Lit. nasuta* were mistaken for *Litoria latopalmata* (Anstis 2017), although this is less likely given its distinctly elongated head and long hind legs (Hoskin *et al.* 2015). This species is listed as least concern and has no documented declines in populations for the region (EPBC 2021; IUCN 2021), so at this point, there is no definitive reason that this species would not have been encountered historically.

The third species, *Notaden bennetti*, is a burrowing species which emerges opportunistically to breed on only one or two nights when climatic conditions are favourable (Anstis 2017). Since the surveys conducted by Heatwole *et al.* (2015) were opportunistic and did not target particular habitats in relation to specific conditions for explosive breeders (flooding after heavy rainfall), it is possible that the team just did not come across this species rather than it being absent from within the region. To potentially encounter this species, the researchers would have needed to choose strategic sites associated with clay soils in areas which were flood prone and then survey them on warm nights (spring to autumn) following heavy rainfall (Anstis 2017; Hoskin *et al.* 2015). Unless specifically targeting this species for study, taking such an approach is not feasible when undertaking a species-wide, relatively low intensity survey of the region, since it would be time-intensive with no guarantee of finding *N. bennetti*.

The fourth species, *Lit. castanea* was once a widespread species in the New England Tablelands but has not been recorded in the region since 1980 (Hamer *et al.* 2010) despite being the subject of several targeted studies (Mahony 1999). The cause of this decline is primarily attributed to the Amphibian chytrid fungus (*Batrachochytrium dendrobatidis*), with the degradation of suitable habitat playing a lesser role (Hazell *et al.* 2003; Hunter *et al.* 2018). There was a remnant population documented on the Southern Tablelands of New South Wales in 2009 (Hunter *et al.* 2018). However, this area is well outside of the New England Tablelands bioregion. It does, however, provide some support for the likelihood that this species may still persist in remote, undisturbed locations in the New England Tablelands, despite fears of its localised extinctions (Hunter *et al.* 2018; Mahony 1999). Although the team that surveyed the New England Tablelands from 1966 to 1975 did not collect this species, Heatwole *et al.* (1995) did note that a possible unconfirmed sighting for it may have occurred in 1991. Another potential issue with this species is its taxonomic uncertainty. Voros *et al.* (2010) had difficulty genetically distinguishing this species from another bell frog, *Litoria raniformis*, where the distributions of these overlapped. This taxonomic uncertainty is further compounded by the small number of *Lit. castanea* which still persist on the Southern Tablelands and is yet to be fully verified (Hunter *et al.* 2018).

3.2 Historical Occupancy

The historical surveys conducted from 1966 to 1975 involved mostly intermittent, opportunistic collecting over the course of those years, with very few repeat surveys of individual sites. MacKenzie and Royle (2005) recommended that a minimum of three visits to a site is needed in a standard occupancy design, but more visits are required when detection is low ($p < 0.5$). With only a single visit, standard occupancy estimation, as first proposed by MacKenzie *et al.* (2002), will not be a viable option for the purpose of analysing the historical data, especially for those species which have low detections. An alternative to this approach has been proposed and discussed by Solymos *et al.* (2010) and Lele *et al.* (2012).

3.2.1 Approaches to Historical Occupancy

Naïve occupancy estimation is one method that could be used to provide a historical estimate of the proportion of sites occupied. Naïve occupancy, however, assumes that detection is equal to one (Guillera-Arroita *et al.* 2014). That is, if the species was not detected at a site, then it does not occupy the site (Guillera-Arroita *et al.* 2010). Such an assumption could create biased estimates which do not reflect the true occupancy situation for this species and confound the occupancy dynamics with detection (Bailey *et al.* 2007; Guillera-Arroita *et al.* 2014; Guillera-Arroita *et al.* 2014). Where this could become problematic is for rare species or species whose behaviour makes them difficult to detect (Guillera *et al.* 2010).

The other analysis option for the historical data, is a single-visit occupancy estimation method developed by Lele *et al.* (2012). Single-visit occupancy analysis accounts for detection, so estimates do not have the same bias as seen with naïve estimation (Lele *et al.* 2012). Further, single-visit occupancy analysis allows for the inclusion of covariates, which can better demonstrate the dynamics between habitat variables and occupancy (Guillera-Arroita *et al.* 2014). The inclusion of covariates has two implicit conditions which must be met in order for this methodology to function. Firstly, when modelling, both detection and occupancy need to include at least one covariate that is a numerical variable. Secondly, there must be at least one covariate that is unique to either the occupancy or the detection model (Lele *et al.* 2012).

3.3 Methods

3.3.1 Site Selection

Of the 898 sites historically surveyed, 14 sites were missing covariate information. Since the inclusion of covariate information is required to conduct single-visit occupancy estimation, these sites were removed from further analysis. As such, 884 of the original 898 sites were used to calculate naïve occupancy estimates and in the single-visit occupancy analysis. From these 884 sites, 200 were selected to be revisited in the current study. To compare the historical occupancy with the current occupancy, these 200 sites will also be analysed as a subset of the total historical sites. For criteria used for the selection of these sites, see section 4.1

3.3.2 Naïve occupancy estimation

Naïve estimation (NE) of occupancy was generated for each of the species found in the historical study. Species which were suspected of being misidentifications were excluded from further analysis. These species included; *Cyclorana cultripes*, *Cyclorana platycephala*, *Litoria gracilenta*, *Mixophyes iteratus* and *Pseudophryne australis*. For all other species, naïve occupancy was calculated for two groups of sites: the 884 sites visited in the historical study and the selected 200 sites for revisitation in the current study. Standard errors (se) were calculated for each estimate. Naïve estimation of occupancy was calculated by dividing the number of sites a species (s) was collected from or detected at (x_s) by the total number of sites visited (T):

$$NE_s = \frac{x_s}{T} \qquad \text{(Eq. 3.01)}$$

3.3.3 Single-visit Occupancy Estimation

Single-visit occupancy estimation was used to analyse the detected (1) and non-detected (0) data for each species recorded in the historical survey. The method used was that described by Lele *et al.* (2012), where there are two true states possible for a site. If the i*th* site is occupied, then $Y_i = 1$. If the site is not occupied, then $Y_i = 0$. These two states, although true, are unobserved. In extending this, let $W_i = 1$ if the i*th* site is "observed to be occupied" and let $W_i = 0$ if the i*th* site is "observed to be unoccupied". Hence, for occupancy, $P(Y_i = 1) = \Psi_i$ and for detection, $P(W_i = 1 \mid Y_i = 1) = p_i$. The true state of a site can be defined by simple probability calculations. With this method, where a species is present, the probability of this event is described as

$$P(W_i = 1) = P(W_i = 1|Y_i = 1)P(Y_i = 1) = p_i\Psi_i \qquad \text{(Eq. 3.02)}$$

That is, the probability (P) that a species is detected at i*th* site (W_i), is equal to the probability that the species was detected at the i*th* site (W_i) given that it was present, multiplied by the probability that the species was present at the i*th* site (Y_i).

This is equal to the probability of detection (p_i) of the species multiplied by the probability of its occupancy ($\mathit{\Psi}_i$).

Where a species is absent, the simple probability calculation of this event can be expressed as:

$$P(W_i = 0) = 1 - p_i \mathit{\Psi}_i. \qquad \text{(Eq. 3.03)}$$

That is, the probability that the species was not detected at the *ith* site (W_i) is equal to one minus the combined probabilities of the detection and the occupancy of the species. Determination of these probabilities of occupancy and detection depend upon site-specific and survey-specific covariates, respectively.

The maximum likelihood estimator (*MLE*) function for single-visit occupancy can be used to estimate the coefficients for the occupancy and detection covariates (β, θ) for each species, given the detection records for each site, $\underline{W}$ = $\{W_1, W_2, \dots, W_N\}$. For both the total historical sites, N= 884, and for the selected sites, N= 200, the likelihood function can be described as:

$$MLE(\beta, \theta | \underline{W}) = \prod_{i=1}^{N} \left(\Psi\,(X_i, \beta) p(Z_i, \theta) \right)^{W_i} \left(1 - \Psi\,(X_i, \beta) p(Z_i, \theta) \right)^{1-W_i} \qquad \text{(Eq. 3.04)}$$

where β is the coefficients for the occupancy covariates, $x_i$is the *ith* covariate for occupancy, θ is the coefficients for the detection covariates, z_i is the *ith* covariate for detection and $\underline{W}$ is a vector of detection histories.

Improvements to the MLE can be obtained via penalisation as presented by Moreno and Lele (2010). The MLE can be penalised (MPLE) by initially determining (β, θ) using the MLE (β_M, θ_M), then maximising two inherent equations, the naïve estimator for occupancy (β_{naive}) and the naïve estimator for detection (θ_{naive}). The naïve estimator for occupancy is based on the assumption that there is no detection error and the naïve estimator of detection is based on the assumption that all sites are occupied.

$$L_{naive}(\beta_{naive} | \underline{W}) = \prod_{i=1}^{N} \Psi\,(X_i, \beta)^{W_i} \left(1 - \Psi\,(X_i, \beta) \right)^{1-W_i} \qquad \text{(Eq. 3.05)}$$

$$L_{naive}(\theta_{naive} | \underline{W}) = \prod_{i=1}^{N} p(Z_i, \theta)^{W_i} \left(1 - p(Z_i, \theta) \right)^{1-W_i} \qquad \text{(Eq. 3.06)}$$

Finally, the MLE for (β, θ) can be maximised using:

$$logMPLE(\beta,\theta|\underline{W}) = logMLE(\beta,\theta|\underline{W}) - \lambda_1|\beta - \beta_{naive}| - \lambda_2|\theta - \theta_{naive}| \quad \text{(Eq. 3.07)}$$

where $\lambda_1 = (1-\Psi_{naive})p_M\sqrt{tr(Var(\theta_M))}$, $\lambda_2 = (1-p_{naive})\Psi_M\sqrt{tr(Var(\beta_M))}$, Ψ_{naive} and p_{naive} are the average occupancy and detection probabilities under the naïve method and Ψ_M and p_M are the average occupancy and detection probabilities under the MLE.

Covariate information was included for both occupancy and detection. Latitude (LAT) and longitude ($LONG$) were the covariates used for occupancy and longitude, year ($YEAR$) and season (SEA) were the covariates used for detection. Longitude was modelled with detection to satisfy the numerical covariate requirement when fitting single-visit occupancy models. Latitude and longitude were scaled as a standard normal variable ($\bar{x}$ = 0, σ = 1). Year was classed as a factor, rather than a numerical covariate. The inclusion of these covariates satisfies the conditions for single-visit occupancy analysis. Altitude was not recorded in the historical data at the time of the surveys. Though this information could be determined presently from the latitude and longitude coordinates, it was not used in this instance for the reason that in the New England Tablelands, longitude is highly correlated with altitude (Sahukar *et al.* 2003).

Two base logistic regression models were generated; one for occupancy and one for detection using, as recommended by Solymos *et al.* (2020), a complementary Log-Log link (cLogLog) and logit link function, respectively. A cLogLog link is used when parameters lie in a unit interval (0,1) and when the sample has large differences in the number of 1s and 0s (Chen *et al.* 1999) as is the case for the detections in the historical data. A logistic regression model with a cLogLog link for the inclusion of covariate information for the probability of occupancy for the *ith* sampling unit for the *jth* covariate value can be calculated with:

$$cloglog(\Psi_{i,j}) = ln(\frac{\Psi_{ij}}{1-\Psi_{ij}}) = \beta_0 + \beta_1 * x_{i,1} + \beta_2 * x_{i,2} \quad \text{(Eq. 3.08)}$$

where x_{i1} is the covariate latitude, x_{i2} is the covariate longitude, β_0 is the baseline coefficient, β_1 is the coefficient for latitude and β_2 is the coefficient for longitude.

Occupancy and detection coefficients were generated using the detect package in **R** (https://cran.r-project.org/web/packages/detect/index.html)**.** These were used to calculate the occupancy probabilities given changes in the corresponding covariate values using the following expression:

$$\Psi_i = \frac{\exp(\beta_0+(\beta_1 * x_{i1})+(\beta_2 * x_{i2})}{1+\exp(\beta_0+(\beta_1 * x_{i1})+(\beta_2 * x_{i2}))} \qquad \text{(Eq. 3.09)}$$

A similar equation can be used to calculate the detection probabilities:

$$p_i = \frac{\exp(\theta_0+(\theta_1 * z_{i1})+(\theta_2 * z_{i2})}{1+\exp(\theta_0+(\theta_1 * z_{i1})+(\theta_2 * z_{i2}))} \qquad \text{(Eq. 3.10)}$$

where, z_{i1} is the covariate longitude, z_{i2} is the covariate season, θ_0 is the baseline coefficient, $\theta_1$is the coefficient for longitude and θ_2 is the coefficient for season.

The calculated occupancy and detection probabilities for each of the sites given the covariates are then averaged to give the final occupancy and detection probability.

$$\Psi = \frac{\sum_{i=1}^{n} \widehat{\Psi}_i}{n} \qquad \text{(Eq. 3.11)}$$

where, n is the number of sites (884) and $\widehat{\Psi}_i$ is the estimated occupancy for the *ith* site. A second average occupancy value for each of the species recorded was determined for the 200 sites selected for revisitation in the current study. To determine this, the same occupancy model used for the 884 sites was also used. The average occupancy value for the 200 sites was calculated using only the occupancy values generated for the subset of 200 sites (using Eq. 3.11 where n = 200).

3.4 Results

3.4.1 Naïve Occupancy Estimation

Naïve occupancy estimates were generated for 34 of the original 39 species recorded for all 884 sites (Heatwole *et al.* 1995), and for the 200 selected sites. Five species; *Cyc. cultripes*, *Cyc. platycephala*, *Lit. gracilenta*, *M. iteratus* and *Pseudophryne australis* were likely misidentifications during sampling, so any occupancy estimates generated for in the New England Tablelands would be unrealistic. These five species were excluded from modelling. The naïve estimates of occupancy are listed for each species in Table 3.4.1 for the 884 sites and in Table 3.4.2 for the 200 sites selected for the present study.

No species found in the historical study had a high (NE>0.500) naïve occupancy. For all 884 sites, only one species had a moderate (0.250<NE<0.500) naïve occupancy. That was *Limnodynatses tasmaniensis* (NE = 0.328±0.016). Other species which had notable naïve estimates of occupancy were *Adelotus brevis* (NE = 0.102±0.010), *Crinia signifera* (NE = 0.225±0.014), *Litoria boorolongensis* (NE = 0.143±0.012), *Litoria latopalmata* (NE = 0.111±0.011), *Litoria verreauxii* (NE = 0.126±0.011) and *Pseudophryne bibronii* (NE = 0.113±0.011).

For the 200 sites selected for the present study, four species had moderate naïve occupancy. These were *Cri. signifera* (NE = 0.290±0.032), *Lim. tasmaniensis* (NE = 0.335±0.034), *Lit. booroolongensis* (NE = 0.340±0.034) and *Pse. bibronii* (NE = 0.275±0.032). Other species with notable naïve occupancy in the selected 200 sites were *A. brevis* (NE = 0.240±0.030), *Litoria fallax* (NE = 0.100±0.021), *Lit. latopalmata* (NE = 0.150±0.025), *Lit. verreauxii* (NE = 0.145±0.025), *Litoria wilcoxii* (NE = 0.110±0.022) and *Uperoleia laevigata* (NE = 0.115±0.023). There were six species that were present overall that were not present at any of the 200 selected sites. These were *Cyclorana brevipes*, *Lechriodus fletcheri*, *Limnodynastes terraereginae*, *Litoria chloris*, *Litoria piperata* and *Philoria sphagnicola*.

3.4.2 Single-visit Occupancy Estimation

3.4.2.1 Occupancy

The initial model which fitted all 884 sites was a model where occupancy varied with LAT and $LONG$, and where detection varied with $LONG$, $YEAR$ and SEA. A stepwise protocol for single-visit occupancy, as developed by Solymos and Moreno (2020), removed $YEAR$ from many of the models for each of the species, indicating that detection did not vary with survey year and so this covariate was excluded from the models. The preferred model fitted for all the historically recorded species was therefore one whereby occupancy varied with LAT and $LONG$, and detection varied with $LONG$ and SEA.

For the species which occurred at the 884 sites, four had high single-visit occupancy (Ψ>0.500). These four species are indicated with two upwards arrows in Table 3.4.1. Sixteen species had moderate (0.250< Ψ<0.500) single-visit occupancy estimates. These sixteen are indicated with a single upwards arrow in Table 3.4.1. All other species at the 884 sites had a single-visit occupancy estimate that were <0.250, which was considered to be low. There were six species that were considered uncommon, with an occupancy estimates <0.05. These six species are indicated with an asterisk in Table 3.4.1.

Latitude and longitude influenced the occupancy of the 34 species modelled with single-visit occupancy estimation. For a summary of the influence of latitude and longitude on frog species occupancy, see Table 3.4.1. Twenty-four species had an occupancy that was positively associated with latitude. That is, they had a higher occupancy in the northern end of the New England Tablelands. The remaining ten species were negatively associated with latitude and had a higher occupancy in the southern end of the New England Tablelands. The occupancy for 20 frog species was positively associated with longitude. That is, these species had a higher occupancy on the eastern side of the New England Tablelands. The occupancy for the remaining 14 species was negatively associated with longitude and, therefore, had a higher occupancy towards the western parts of the tablelands.

Single-visit occupancy estimates were generated for the 34 species identified as occurring in the 200 selected sites. When single-visit occupancy was averaged over only the 200 sites for revisitation during the current study, most species were found to have occupancy values that were close to those for the 884 sites. Occupancy values of note which did change were those for *Lim. peronii* (Ψ = 0.237±0.171), *Lit. fallax* (Ψ = 0.544±0.165), *Lit. piperata* (Ψ = 0.254±0.015) and *Phi. sphagnicola* (Ψ = 0.219±0.016). *Limnodynastes peronii* and *Phi. sphagnicola* had occupancy values considered to be low (Ψ<0.250) in the 200 hundred sites, when compared to the moderate occupancy in the total 884 sites. *Litoria piperata* had a higher occupancy in the 200 selected sites when compared to the 884 site and was considered moderate ($0.250<\Psi<0.500$). *Litoria fallax* also had a higher single-visit occupancy in the 200 sites when compared to the 884 sites. The single-visit occupancy for *Lit. fallax* was considered to be high ($\Psi>0.500$) at the selected 200 sites. All other frog species recorded at the 200 sites had occupancy estimations similar to those of the 884 sites. Species which had a notable change in their occupancy at the 200 sites when compared to their occupancy at the 884 sites are indicated with an asterisk in Table 3.4.2.

3.4.3.2 Detection

For the species recorded at the 884 sites, seven had a high probability of detection. These species are indicated with two asterisks in Table 3.4.3. Nine species had a detection probability considered to be moderate. These species are indicated with a single asterisk in Table 3.4.3. All other frog species had a detection <0.250 and were therefore considered to have a low detection probability.

Season affected the detection of all the species found in the New England Tablelands. Most of the species were easier to detect in the warmer months. Species whose detection was highest in summer include *Cri. parinsignifera*, *Cyclorana brevipes*, *Lec. fletcheri*, *Lim. dumerilli*, *Lim. fletcheri*, *Lim. salmini*, *Lim. terreraginae*, *Lit. booroolongensis*, *Lit. caerulea*, *Litoria chloris*, *Lit. fallax*, *Lit. latopalmata*, *Lit. peronii*, *Lit. wilcoxii*, *M. fasciolatus* and *U. rugosa*. Species whose detection was highest in spring included *A. brevis*, *Lit. barringtonensis*, *Mixophyes balbus*, *N. sudellae*, *Phi. sphagnicola*, *Pla. ornatum*, *Pse. bibronii* and *Pse. coriacea*. A further three species were easier to detect in autumn, including *Lim. peronii*, *Lit. dentata* and *Lit. piperata*. Finally, there were seven species which were easier to detect during winter. These species included *Cri. signifera*, *Lim. tasmaniensis*, *Lit. aurea*, *Litoria rubella*, *Litoria subglandulosa*, *Lit. verreauxii* and *U. laevigata*.

Table 3.4.1: Naïve occupancy (NE) and single-visit occupancy estimates (Ψ) and their standard errors (*se*) for species found at all 884 sites in the historical study of the New England Tablelands. Species with moderate occupancy indicated with a "↑" and species with high occupancy are indicated with a "↟". Species which were uncommon are indicated with a "*". The influence of Latitude and Longitude on occupancy is indicated with a "+" (positive) and "-" (negative).

Species	Naïve Occupancy		Single-visit Occupancy estimation			
	NE	se	Ψ	se	Latitude	Longitude
Adelotus brevis↑	0.102	0.010	0.411	0.097	+	+
Crinia parinsignifera↑	0.016	0.004	0.357	0.109	+	+
Crinia signifera↑	0.225	0.014	0.273	0.121	+	–
_Cyclorana brevipes_*	0.002	0.002	0.016	0.007	+	–
_Lechriodus fletcheri_*	0.008	0.003	0.025	0.062	–	+
Limnodynastes dumerilii	0.070	0.009	0.149	0.109	+	+
Limnodynastes fletcheri	0.083	0.009	0.120	0.103	+	–
Limnodynastes peronii↑	0.042	0.007	0.262	0.119	+	–
Limnodynastes salmini↑	0.012	0.004	0.389	0.058	–	+
Limnodynastes tasmaniensis↑	0.328	0.016	0.339	0.126	–	+
Limnodynastes terraereginae↟	0.001	0.001	0.633	0.009	–	+
Litoria aurea	0.009	0.003	0.219	0.088	+	+
Litoria barringtonensis↑	0.014	0.004	0.364	0.115	–	–
Litoria booroolongensis↑	0.143	0.012	0.462	0.124	–	+
Litoria caerulea↑	0.036	0.006	0.383	0.115	+	–
Litoria chloris↑	0.001	0.001	0.342	0.012	+	+
_Litoria dentata_*	0.011	0.004	0.020	0.066	+	+
Litoria fallax↑	0.071	0.009	0.485	0.11	+	+
Litoria latopalmata↑	0.111	0.011	0.255	0.118	+	–
Litoria peronii↟	0.064	0.008	0.725	0.096	+	–
Litoria piperata	0.001	0.001	0.208	0.010	+	+
Litoria rubella	0.020	0.005	0.201	0.042	+	–
_Litoria subglandulosa_*	0.014	0.004	0.031	0.069	–	+
Litoria verreauxii↟	0.126	0.011	0.600	0.069	–	+
Litoria wilcoxii	0.084	0.009	0.110	0.101	+	–
Mixophyes balbus	0.014	0.004	0.114	0.103	+	+
_Mixophyes fasciolatus_*	0.009	0.003	0.019	0.065	+	+
_Neobatrachus sudellae_*	0.010	0.003	0.018	0.067	+	–
Philoria sphagnicola↑	0.001	0.001	0.303	0.008	+	+
Platyplectrum ornatum↑	0.063	0.008	0.343	0.097	+	–
Pseudophryne bibronii	0.113	0.011	0.172	0.100	–	–
Pseudophryne coriacea↟	0.025	0.005	0.849	0.059	+	–
Uperoleia laevigata↑	0.090	0.010	0.391	0.114	–	+
Uperoleia rugosa↑	0.014	0.004	0.456	0.015	+	+

Table 3.4.2: Naïve occupancy (NE) and single-visit occupancy estimates (Ψ) and their standard errors (*se*) for species found at the selected 200 sites from the historical study of the New England Tablelands. Species which had a notable change in their occupancy when compared to the total 884 are indicated with a "*".

Species	Naïve Occupancy		Single-visit Occupancy estimation	
	NE	se	Ψ	se
Adelotus brevis	0.240	0.030	0.469	0.146
Crinia parinsignifera	0.015	0.009	0.407	0.162
Crinia signifera	0.290	0.032	0.253	0.173
Cyclorana brevipes	-	-	0.005	0.007
Lechriodus fletcheri	-	-	0.024	0.092
Limnodynastes dumerilii	0.085	0.020	0.156	0.159
Limnodynastes fletcheri	0.070	0.019	0.112	0.147
*Limnodynastes peronii**	0.075	0.019	0.237	0.171
Limnodynastes salmini	0.005	0.005	0.343	0.085
Limnodynastes tasmaniensis	0.335	0.034	0.349	0.182
Limnodynastes terraereginae	-	-	0.654	0.010
Litoria aurea	0.020	0.010	0.247	0.135
Litoria barringtonensis	0.020	0.010	0.300	0.222
Litoria booroolongensis	0.340	0.034	0.461	0.181
Litoria caerulea	0.020	0.010	0.332	0.171
Litoria chloris	-	-	0.345	0.011
Litoria dentata	0.005	0.005	0.023	0.099
*Litoria fallax**	0.100	0.021	0.544	0.165
Litoria latopalmata	0.150	0.025	0.264	0.171
Litoria peronii	0.075	0.019	0.729	0.145
*Litoria piperata**	-	-	0.254	0.015
Litoria rubella	0.005	0.005	0.082	0.070
Litoria subglandulosa	0.020	0.010	0.028	0.099
Litoria verreauxii	0.145	0.025	0.653	0.110
Litoria wilcoxii	0.110	0.022	0.111	0.146
Mixophyes balbus	0.025	0.011	0.109	0.146
Mixophyes fasciolatus	0.010	0.007	0.020	0.096
Neobatrachus sudellae	0.010	0.007	0.018	0.096
*Philoria sphagnicola**	-	-	0.219	0.016
Platyplectrum ornatum	0.075	0.019	0.258	0.150
Pseudophryne bibronii	0.275	0.032	0.143	0.144
Pseudophryne coriacea	0.015	0.009	0.858	0.089
Uperoleia laevigata	0.115	0.023	0.399	0.171
Uperoleia rugosa	0.010	0.007	0.484	0.020

Table 3.4.3: Detection estimates (p) and their standard errors (*se*) for species found at the 884 sites from the historical study of the New England Tablelands. A "+" sign indicates that detection was higher than the average in that corresponding season and a "–" sign indicates that detection was lower during that season. Species which had very low detection in a season when compared to their average are indicated with a "*" in their corresponding season. Species which had high detection average are indicated with "**"on their species name and species which had a moderate average detection are indicated with a "*".

Species	Average Detection	se	Summer	Autumn	Winter	Spring
Adelotus brevis	0.224	0.118	+	-	-*	+
Crinia parinsignifera	0.196	0.067	+	-*	+	-*
*Crinia signifera***	0.776	0.109	-	+	+	-
Cyclorana brevipes	0.179	0.044	+	-*	-*	-*
*Lechriodus fletcheri**	0.408	0.089	+	-*	-*	-
*Limnodynastes dumerilli**	0.481	0.107	++	-	-*	-*
*Limnodynastes fletcheri***	0.530	0.021	++	-*	-	-
Limnodynastes peronii	0.214	0.095	-	-	++	+
Limnodynastes salmini	0.055	0.059	++	-*	-*	-*
*Limnodynastes tasmaniensis***	0.853	0.08	-	-	+	-
Limnodynastes terreraginae	0.018	0.001	+	-*	-*	-*
*Litoria aurea**	0.321	0.055	-	+	++	-*
Litoria barringtonensis	0.185	0.013	-	+	-*	++
*Litoria booroolongensis**	0.259	0.120	+	-	-	-
Litoria caerulea	0.060	0.083	++	-*	-	+
Litoria chloris	0.073	0.011	++	-	-	-
*Litoria dentata***	0.708	0.018	+	+	-*	-*
Litoria fallax	0.243	0.110	+	-	+	-*
*Litoria latopalmata**	0.365	0.115	++	-	-	-
Litoria peronii	0.080	0.095	+	-	-	.
Litoria piperata	0.005	0.035	-*	+	-*	-*
Litoria rubella	0.142	0.096	+	-*	++	-*
Litoria subgladulosa	0.208	0.020	-*	+	++	-
*Litoria verreauxii**	0.267	0.119	+	-	+	-
*Litoria wilcoxii***	0.694	0.030	++	-*	++	++
Mixophyes balbus	0.122	0.013	-	+	-*	+
*Mixophyes fasciolatus**	0.378	0.017	++	-*	-*	-*
*Neobatrachus sudellae***	0.554	0.020	-	+	-*	++
Philoria sphagnicola	0.030	0.008	-	+	-*	+
*Platyplectrum ornatum**	0.302	0.113	+	-*	-*	+
*Pseudophryne bibronii***	0.896	0.016	-	+	+	+
Pseudophryne coriacea	0.099	0.061	-	+	-*	++
*Uperoleia laevigata**	0.327	0.119	+	-	+	+
Uperoleia rugosa	0.181	0.073	++	-	-*	-*

3.5 Discussion

Historically, the New England Tablelands supported a large number of different frog species. These frog species range in habitat preference from generalists that are found in a wide range of habitat types, to species which have very specific habitat requirements (Anstis 2017; Hoskin *et al.* 2015). Associated with this is the fact that breeding strategies also vary between these species. Many of the historically recorded species have defined breeding seasons (Anstis 2017; Hoskin *et al.* 2015). There are also some species that are explosive breeders and require very specific meteorological conditions to trigger breeding (Anstis 2017; Hoskin *et al.* 2015). Other species show no preference and will breed during most parts of the year (Anstis 2017; Hoskin *et al.* 2015).

The naïve occupancy estimates for the historical survey data were lower than the single-visit occupancy estimates because naïve estimates assume detection is perfect (Guillera-Arroita *et al.* 2014). That is, if the species was not detected at a site, then it does not occupy that site (Guillera-Arroita *et al.* 2010). Detection is rarely perfect, especially for rare and cryptic species (Guillera *et al.* 2010), which many of the frog species found in the New England Tablelands are (Anstis 2017; Hoskin et al. 2015). Such an assumption could create biased estimates which do not reflect the true occupancy situation for frog species and confound the occupancy dynamics with detection (Bailey *et al.* 2007; Guillera-Arroita *et al.* 2014; Guillera-Arroita *et al.* 2014). An example of an elusive species found in the historical study was the red-backed toadlet (*Pseudophryne coriacea*), a common species on the eastern side of Australia (Hoskin *et al.* 2015). This species creates terrestrial chambers in moist soil, where the males call from during the warmer months when breeding is prevalent (Anstis 2017). Surveys outside of *Pse. coriacea*’s breeding period may not detect this species at all, as activity (calling in males and dispersal for breeding in females) will be low. Given this, their naïve occupancy may be underestimated. Such was the case with the historical survey. Heatwole *et al.* (1995) detected *Pse. coriacea* only a few times, resulting in a low naïve estimate (Table 3.4.1). However, when the data was analysed using single-visit occupancy estimation, the occupancy of this species was notably higher, and its corresponding detection was very low (Table 3.4.3).

Frog species that were found to have a high to moderate historical occupancy were predominantly generalists which utilise a wide range of habitats and have a wider range of tolerances to modified habitat (Callaghan *et al.* 2020; Keinanth *et al.* 2017; Liu *et al.* 2017; Simpkins *et al.* 2014). Two of these species, *Crinia signifera* and *Lim. tasmaniensis,* are both confirmed habitat generalists (Anstis 2017) which, according to Heatwole *et al.* (1995), were considered to be widespread throughout the New England Tablelands. Another habitat generalist, *Litoria verreauxii,* was thought to historically have a stronger presence in the eastern side of the New England Tablelands at sites above 800m asl (Heatwole *et al.* 1995) and the influence of longitude on its single-visit occupancy estimation reflects this. Despite the historical trend, the occupancy estimates from the historical records indicate that this species generally had a high occupancy throughout the region. Historically, the region had seen some modification and vegetation clearing due to agricultural practices (Heatwole & Simpson 1986). These changes are unlikely to have affected the occupancy of generalist species, since many generalists are known to tolerant of such changes in their habitat (Hamer & McDonnell; Lane & Burgh 2008). Also, some landscape modifications (e.g., the creation of dams) could actually favour them (Hamer & McDonnell; Lauck 2005).

There were a few species with moderate occupancy which had specific habitat requirements. One such species, *Lit. booroolongensis*, an obligate stream breeder was noted to be widespread in the region during the historical surveys (Heatwole *et al.* 1995) and the single-visit occupancy estimate corroborated this. Heatwole *et al.* (1995) noted further that this species was probably most likely to be associated with a particular habitat, but this information was not recorded with the historical data and so could not be modelled. Given that *Lit. booroolongensis* had a moderate historical occupancy, this species was likely once very common at many of the streams and rivers in the region.

Of particular note, however, are the moderate occupancy estimates for *Phi. sphagnicola* and *Lit. chloris*. These two species had a moderate occupancy in the New England Tablelands despite both species only having a small proportion of their distributional range overlapping with the New England Tablelands, principally along its eastern edge (Anstis 2017; Hoskin *et al.* 2015). This can be further compounded as both have very specific habitat requirements (Anstis 2017; Hoskin *et al.* 2015).

Further to this, both of these species were historically associated with either rainforest or wet sclerophyll forests which are only found in the eastern, higher rainfall parts of the tablelands (Heatwole *et al.* 1995). The characteristics of the habitat were not recorded at the time of the historical survey, and so its influence could not be modelled. Such an outcome has likely impacted the occupancy estimate for these two species and other species which have specific habitat requirements. It would be likely that habitat type would have an important influence on their occupancy (Faggioni *et al.* 2021; Mazerolle *et al.* 2005). This has been demonstrated by Faggioni *et al.* (2021) who found that occupancy was influenced by habitat and that this influence was often species specific. Further supporting this is the findings of Mazerolle *et al.* (2005), who determined that landscape characteristics were influential in determining frog species occupancy in ponds and such requirements differed depending on species. Wet sclerophyll forest and rainforest are only found along the high altitude, eastern edge of the New England Tablelands (Heatwole & Simpson 1986; Sahukar *et al.* 2003), so the estimates for *Lit. chloris* and *Phi. sphagnicola* are likely only relevant along this eastern edge where the habitat type requirements are met. This is further supported by the strong influence of longitude on occupancy for both *Lit. chloris* and *Phi. sphagnicola* (Table 3.4.1).

Another consideration with the single-visit occupancy estimates is that the analysis uses a zero-inflated Poisson model to account for the zero-inflated data where the number of zeros does not fit a normal distribution (Martin *et al.* 2005; Wenger & Freeman 2008). In situations such as here, three types of zeros can occur. These can be a zero that reflects the true state of the species at a site (i.e. a true absence), a zero that is false due to error in detection (i.e. a false absence), and a zero that occurs when a species is rare or where the species distribution is only partially covered by the region under study (Solymos *et al.* 2011; Wenger & Freeman 2008). It is possible that the estimates for species which are rare or have a limited distribution in the region have been overestimated due to the low number of presences (1) and the correspondingly high number of absences (0). Species which historically have only a small part of their total distribution in the New England Tablelands include *Limnodynastes terraeginae and Litoria chloris*, while species which were rare in the New England Tablelands include *Litoria piperata* and *Philoria sphagnicola* (Anstis 2017; Heatwole *et al.* 1995; Hoskin *et al.* 2015). The single-visit occupancy estimates for most of these species are much higher than are the naïve estimates (Table 3.4.1). To some extent, this is not surprising since single-visit occupancy estimates account for limitations in detection and the influence of geography on occupancy, whereas naïve estimates do not (Lele *et al.* 2012). However, when considering these species, which are only found in a small portion of the New England Tablelands, these estimates do perhaps appear somewhat high.

All species with low occupancy were species which had very specific habitat requirements. Two of these species, *Lit. subglandulosa* and *M. fasciolatus*, are found in association with streams in wet sclerophyll forests (Anstis 2017). Similarly, *Lit. dentata* was thought to be associated with wet sclerophyll forests and its presence in the New England Tablelands was thought to represent the western edge of its distribution (Heatwole *et al.* 1995). This corresponds with the coefficient for longitude covariate which pointed to *Lit. dentata* having a higher occupancy at sites in the eastern part of the New England Tablelands. There was some conjecture at the time that *Lit. dentata* may have had a westerly presence in the New England Tablelands (Moore 1961), but this was not supported by the survey data (Heatwole *et al.* 1995), nor by the occupancy estimates.

Burrowing species which were uncommon in the historical survey were *Neobatrachus sudellae* and *Cyc. brevipes,* two species which have extensive distributions throughout Australia (Anstis 2017; Hoskin *et al.* 2015). Both of these species are found in grassland or lightly wooded country (Anstis 2017; Hoskin *et al.* 2015), habitat that makes up a large proportion of the New England Tablelands (Heatwole & Simpson 1986). In relation to this, it could be assumed that these species are similarly common in the New England Tablelands, though this was not the case. *Cyclorana brevipes* only has a fraction of their distribution in the New England Tablelands, with a very low single-visit occupancy estimate (Table 3.4.1). However, the distribution of *N. sudellae* include a vast majority of the New England Tablelands (Anstis 2017; Hoskin *et al.* 2015). Something to consider in relation to this, however, is that *N. sudellae* is a burrowing species which breed opportunistically after heavy rain (Anstis 2017; Hoskin *et al.* 2015). It is possible that this species was common historically but due to their cryptic behaviour were not encountered as often as would have been expected. Rainfall was not recorded in relation to the historical presence-absence data and so could not be modelled in detection, which could lead to the historical occupancy of this species being underestimated.

Frog species which had a moderate or high detection were species which generally exhibit observable behaviours in the open or were species which occupy sites in high numbers (Anstis 2017; Hoskin *et al.* 2015). Two examples of species which exhibit obvious behaviours are *Lit. wilcoxii* and *Lit. booroolongensis*. Males of both these species, call from rocks and banks of creeks and streams (Anstis 2017). Further, juveniles of *Lit. wilcoxii* are often found moving around a site well into autumn (personal obs.). Such behaviour makes this species visible to collectors, supporting a high detection rate. *Crinia signifera*, is a small, brown, cryptic species (Anstis 2017; Hoskin *et al.* 2015). This in and of itself, should indicate that this species should have a low detection. However, at suitable habitat, this species can be found in high numbers (Anstis 2017; Hoskin *et al.* 2015), supporting the consistent high detection that the occupancy estimation determined for *Cri. signifera*. *Limnodynastes tasmaniensis* was another species which had constant high detection. This species too will occupy suitable sites in high densities (Anstis 2017; Hoskin *et al.* 2015).

One burrowing species, *Pse. bibronii,* also had a consistent high detection estimate throughout the year. *Pseudophryne bibronii* exhibit cryptic behaviour with males building concealed nests in moist soil and leaf litter from where they call (Anstis 2017; Bryne & Keogh 2007; O'Brien *et al.* 2018). Although this species behaviour is cryptic, the high detection was supported by the method on which the records were collected by Heatwole *et al.* (1995). Another burrowing species, *Lim. dumerilli*, also had a moderately high detection, but this was only during the warmer months. This species breeds during the warmer months (Anstis 2017, Heatwole *et al.* 2015), so a high detection during summer, corresponds to when there was a higher chance of activity for *Lim. dumerilli* above ground and consequently, a higher chance of encountering this species.

Detection for all species recorded historically varied with season (Table 3.4.3). Predominantly, species had higher detection during the months that corresponded with breeding activity. Such a pattern makes sense for many of the species which had set breeding seasons as activity (dispersal, feeding, calling) is highest during this period and so individuals are easier to find (Brander *et al.* 2007; Cook *et al.* 2011; Gooch *et al*. 2006). Such findings, support the need to consider ecological traits of frog species, such as breeding season when designing occupancy studies (Takahara *et al.* 2020). Interestingly, there were two summer breeding species which were easier to detect in winter; *Lit. aurea* and *Lit. rubella*. However, an aspect of the historical records, were that detection was only recorded based on physical sampling (e.g., the collection of specimens) and no detection records were made of frogs which were calling at the sites (Simpson & Stanisic 1986). Such an oversight could mean that the expectation is that these species could be easier to detect audibly during the warmer months. However, due to the method of surveying, specimens were only collected during the cooler months. Heatwole *et al.* (1995), searched under logs and in vegetation, places where these species could be found if they were hibernating over winter.

It should be noted that the occupancy estimates generated here were not modelled in relation to habitat characteristics nor was detection modelled in relation to meteorological conditions owing to the fact that such information was not recorded during the historical surveys. As such, the occupancy estimates generated from these analyses could be improved if the historical situation for species which have specific habitat requirements for occupancy or need specific meteorological conditions to trigger activity (breeding, foraging, dispersal) were recorded. This is something that future studies should consider including when doing large scale presence-absence surveys. This is especially important for species that are obligate stream breeders (*Lit. barringtonensis*, *Lit. booroolongensis*, *Lit. subglandulosa*, *Lit. wilcoxii* and *M. balbus*), terrestrial breeders which breed in moist areas (*Phi. sphagnicola*, *Pse. bibronii*, *Pse. coriacea*), and species which opportunistically breed following rain (*Cyc. brevipes*, *Lim. dumerilii*, *Lim. salmini*, *Limnodynastes terraeraginae*, *Neo. sudellae*, *Pla. ornatum* and *U. rugosa*) (Anstis 2017, Hoskin *et al.* 2015). However, for species which are habitat generalists with fixed breeding seasons, this is less likely to be an issue.

One way to improve the accuracy of occupancy estimates is to incorporate repeat surveys to sites to get an improved understanding of detection (Mackenzie *et al.* 2002). This is especially important when detection probabilities are low as is the case for the rare species discussed above, species with limited distribution in the survey area or in the case of anurans, outside of their breeding period when activity and calling incidence is low (Mackenzie *et al.* 2002). However, historical records do not usually include repeat visits, as is the case with these historical data. Despite this, the estimates generated using single-visit occupancy are still informative.

The single-visit occupancy estimates for the 884 sites reflect the general occupancy of frog species for the entire region during the ten-year period between 1966 and 1975 when the surveys were undertaken. The single-visit occupancy estimates for the 200 selected sites are representative of a subset of this larger data set that has been selected for species which are currently threatened and sites which historically had a large number of species present. This selection process favoured species which are currently considered to be threatened (Hoskin *et al.* 2015, ICUN 2022) or species which may share habitat preferences with threatened species. Despite this, the estimates for the 200 sites are quite similar to the estimates for the 884 sites, indicating that the subset selected for the current study was a good representation of the larger number of sites visited during the historical study.

For the occupancy analysis of the current species detected in the New England Tablelands for the 200 selected sites, single-species, single-season occupancy estimation was used. This incorporated repeat visits, as suggested by MacKenzie *et al.* (2002), as well as habitat and environmental covariate information which was limited in the historical records. This provided a stronger understanding of detection for the recorded species and, consequently, a more informative understanding of their current occupancy of which to base monitoring decisions.

Chapter 4: Field methods

4. Field Methods

4.1 Site Selection

Sites for the present study were chosen from those identified as supporting frog species during surveys carried out in the New England Tablelands region over the period extending from 1966 through to 1975 (Heatwole *et al.* 1995). The historical survey encompassed a total of 898 sites, each contained within the New England Tablelands or Nandewar bioregion. Due to time and labour constraints, only a subset from these sites was selected for the present study; each site to be visited on more than one occasion.

From the 898 sites historically surveyed, 200 were selected for revisiting in the current study. Site selection was based upon the following criteria. Firstly, all selected sites were restricted to the current New England Tablelands bioregion. Sites located in the Nandewar bioregion were excluded. Secondly, sites that supported more than two historical frog species were considered for selection. Lastly, if a site historically supported fewer than two frog species, but had previously recorded the presence of a threatened species, this site was considered for selection. Sites selected using these criteria were visited before surveying commenced in order to check their viability based on accessibility and the presence of water, permanent or ephemeral. Some sites had accessibility issues, whilst others could not be found due to changes in the habitat from human modification for farming, infrastructure or urban development. These sites were eliminated as potential survey sites. As such, all sites that were selected for the study were easily accessible or near roads and showed some degree of habitat disturbance. Those sites that were finally selected were assumed to have continued to support frog species to the present.

Sites for the present study were chosen from those identified as supporting frog species during surveys carried out in the New England Tablelands region over the period from 1966 to 1990 (Heatwole *et al.* 1995). The historical survey comprised a total of 898 sites, each contained within the New England Tablelands or Nandewar bioregion. Due to time and labour constraints, only a subset from these sites was selected for the present study (see Chapter 3).

Overall, 200 of the original sites in the New England Tablelands bioregion were revisited to determine principally whether or not previously-found species of frog could still found at them. Second, present day occupancy was going to be estimated for those species which were detected. This was determined within the framework of occupancy estimation (MacKenzie *et al* 2017). No other sites that could support frog species, but were not visited by Heatwole *et al.* (1995), were included for the present study.

Sites were aggregated into three regional clusters: a western cluster of 78 sites, a south-southeastern cluster of 64 sites and a north-northeastern cluster of 58 sites. The western cluster extended west from a defined eastern boundary extending from Guyra in the north to Uralla in the south out to the western boundary of the New England Tablelands, and further south to Bendemeer (Fig. 4.1.1). The south-southeastern cluster extended in its range east from Guyra to the eastern boundary of the bioregion and south towards Walcha and the southern boundary of the bioregion (Fig. 4.1.1). The north-northeastern cluster included all sites in the area found north of Guyra through to the northern boundary of the New England Tablelands (Fig. 4.1.1).

To assess the current presence (occupancy) of frog species, sites were sampled four times from the period extended from early summer (December) through to mid-autumn (May) in their respective years. The western cluster was sampled from 2017-2018, the south-southeastern cluster was sampled from 2018-2019 and the northern cluster was sampled from 2019-2020. Sites were visited of an evening from dusk till midnight. Order that the sites were visited in a night were random, but were stratified based on geological proximity. A minimum of 15 minutes was spent at each site, consisting of 5 mins listening for auditory calls, followed by at least 10 minutes of physical searching.

A number of habitat variables were recorded for each selected site (Table 4.1.1). It was assumed that these would not vary between surveys and would be used as covariates for modelling occupancy. These variables included the latitude, longitude and altitude of the site, the waterbody structure (if water was running, still or water was absent at the time of survey), proportion of emergent vegetation cover (%), proportion of riparian vegetation cover (%), agricultural disturbance (yes/no), caused principally by cattle in the form of bank trampling and organic pollution, and whether or not invasive fish species were present.

Fig. 4.1.1: The three clusters of selected study sites within the New England Tablelands Bioregion. These clusters are identified as the western cluster (orange), the south-southeastern cluster (purple) and the northern cluster (blue).

Vegetation cover percentages were determined by the proportion of an area dominated by that type of vegetation. Riparian vegetation was considered to be vegetation outside of the water and was assessed to 5 m distance from the water's edge. Emergent vegetation was considered as being all vegetation that was partially submerged within the waterbody and was assessed in relation to the proportion of the area occupied. For sites where water was absent, all vegetation was classified as being riparian.

Table 4.1.1: Description of habitat covariates and their associated occupancy modelling codes.

Code	Covariate description
$ripV$	Extent (% cover) of riparian vegetation; vegetation on the bank of the waterbody extending away from it for <5m.
emV	Extent (% cover) of emergent vegetation; vegetation partially submerged in the waterbody.
F	Presence of invasive fish species; principally *Gambusia* sp.
C	Signs of domestic livestock activity; principally cattle
rW	Running waterbody; streams and rivers.
sW	Still waterbody; dams, lagoons, marshes, ephemeral puddles
nW	Absent water; various waterbodies where there was no water present.
LAT	Latitude
$LONG$	Longitude
ALT	Altitude (m)

The presence of invasive fish species was determined using dip-netting. The gape of the net was 1450 cm^2 with 1 mm mesh diameter. The dip net was swept along the edge of a waterbody for a distance of one metre. For very small waterbodies (<1m length), the net was swept along their entire length. Following this, the net was inspected, and any fish captured were identified as being invasive or non-invasive. No native fish species were encountered but would have been immediately released unharmed at the point-of-capture.

Any netted fish that were identified as being invasive were subsequently euthanised. Euthanasia was carried out in accordance with the NSW Fisheries Guide to acceptable procedures and practices for Aquaculture and Fisheries Research (NSW DPI 2015). Invasive fish were transferred to an anaesthetic bath with an overdose of benzocaine (>100 mg L^{-1}) until individuals lost equilibrium and movement of opercula had ceased for 15 minutes, indicating that respiration had stopped.

4.2 Occupancy Sampling

At each visit to a selected site, to detect the presence of frogs, a maximum of 15 minutes was spent engaged in detection activities. The predominant method of detection was aural, with opportunistic visual detection generally supporting the original aural detection of the species. During visits, frog species presence was determined predominantly from their distinct call, and this generally occurred within the first few minutes of visiting a site. The remaining time was spent searching for individuals that were not calling, but were visible. This was particularly important for one species, *Litoria wilcoxii,* because often, its call could not be heard over the sound of the running water, but they were often visible sitting on the rocks at the sites. For species which had been found at the site in the original study, but not detected in the present, playback was implemented to stimulate calling. The software application (app) *Frogs of Australia* (Hoskin *et al.* 2015), was used to play a recording of the target species' call. The recording was played twice, with a minute of listening following each playback.

Along with site characteristics, a number of environmental (survey) variables were also recorded during each visit (Table 4.2.1). The information recorded during each visit included the date, time-of-visit, air temperature (°C), barometric pressure (mb), wind speed (km h^{-1}), relative humidity (%), cloud cover (%), if the ground was damp (yes/no), and if it was raining during the survey (yes/no).

Variables were also collected from the Bureau of Meteorology (BOM) website (http://www.bom.gov.au/climate/dwo/IDCJDW0201.shtml). Data was selected from the meteorological station (Armidale, Glenn Innes, Tenterfield or Walcha) closest to the field site. Data that was collected this way included; Rainfall for the week (mm), rainfall for the day of the survey (mm), number of days it had rained in the week preceding the visit (days), the occurrence of rainfall within the previous 48 hours before the visit (yes/no) and moon illumination (yes/no). For the final analysis models, the environmental variables used were; the occurrence of rainfall within the previous 48 hours, moon illumination, air temperature, relative humidity, wind speed and cloud cover. Barometric pressure was excluded as it caused models to have issues with convergence, creating extreme coefficients in the output.

Table 4.2.1: Environmental covariate descriptions and their codes.

Code	Description
AT	Air temperature (°C)
H	Relative humidity (%)
WS	Wind speed (km h^{-1})
CC	Cloud cover (%)
MI	Moon illumination; presence of light from the moon.
$R48$	Incidence of rainfall within the previous 48 hours

4.3 Amphibian Chytrid Fungus (*Batrachochytrium dendrobatidis*) Swabbing

From December 2020 through to February of 2021, a sample of frogs was swabbed for the Amphibian Chytrid fungus (*Batrachochytrium dendrobatidis*). A total of 292 swabs (DryswabMW100; Medical Wire & Equipment Co.) were collected from three different species at two sites in the New England Tablelands: Blue Hole (30°35’43”S, 151°47’56”E), a running water habitat and Thomas Lagoon, a still water habitat (30°32′44″S, 151°33′13″E). Three frog species were chosen for this part of the study based upon a comparison of their current average occupancy with their historical average occupancy and what sort of habitats they are typically found at. The eastern sedge frog (*Litoria fallax*) had an increase in its average occupancy when compared to the historical study and is found at both running and still water sites. The spotted marsh frog (*Limnodynastes tasmanienesis*) had a decrease in its average occupancy in the present study when compared to the historical and is found only at still sites. Finally, the eastern stony creek frog (*Litoria wilcoxii*) also had a decline in its average occupancy since the historical study but is found only at running sites. *Limnodynastes tasmaniensis* was collected and swabbed only from the Thomas Lagoon site, a still waterbody. *Litoria wilcoxii* was collected and swabbed only from the Blue Hole site, a running waterbody. *Litoria fallax*, however, was collected and swabbed from both sites.

Gloves were worn for the collection of these samples. Individual frogs were collected in separate plastic bags, which were disposed of after the frog's release. Upon capture, the swab was taken and the sex, age and snout-vent length of the frog was recorded. Swabs were taken from the ventral side of the animal; five each from the pelvic patch, thighs, and webbing of the feet. Frogs were held in the plastic bag until all swabbing was completed so as to prevent doubling up of samples. Once swabbing was completed, all frogs were then released at point-of-capture.

Snout-vent length was measured with a pair of Vernier callipers whilst the frog was held in the bag. Sex was predominantly determined by behaviour; if the individual was calling upon collection, it was identified as being male. For *Lit. wilcoxii*, sex was also confirmed by the colour of the individuals' skin. Male *Lit. wilcoxii,* change the colour of their skin during the breeding period to yellow (Anstis 2017; Rowley 2015). The males of the other two species, *Lit. fallax* and *Lim. tasmaniensis*, do not go through this colour change (Anstis 2017). Male frogs can also be identified by the presence of nuptial pads on their hands or the presence of a vocal sack (Rowley 2015). Individuals which were difficult to determine the sex of with certainty were listed as unknown. Age had three stages; adult, juvenile and metamorph. Adults were individuals which fell within the expected size range for each species; 31-42mm for male and 32-47 for female *Lim. tasmaniensis*, 22-26mm for male and 25-32mm for female *Lit. fallax*, and 40-48mm for male and 51-69mm for female *Lit. wilcoxii* (Anstis 2017; Hoskin et al. 2015). Juveniles were individuals which fell outside of that size range and metamorphs were individuals which still possessed some or all of their larval tail. No tadpoles were collected for swabbing. Minimum and Maximum temperatures for the days the swabs were collected were collected from the Bureau of Meteorology (BOM) website (http://www.bom.gov.au/climate/dwo/IDCJDW0201.shtml).

Swabs were stored at 4ºC until all swabs were collected from both sites. Once all swabs were collected, they were sent to the Australian Museum where they were stored at -20ºC before testing with diagnostic qPCR (Boyle *et al.* 2004; Hyatt *et al.* 2007). Swabs were tested both for *B. dendrobatidis* presence and zoospore load. Temperatures at which the swabs were stored are unlikely to affect the amount of *B. denrobatidis* sampled (Hyatt *et al.* 2007).

4.4 Site Hygiene

Prevention of contamination between sites and safe handling practices for the frogs were significant parts of the sampling procedure. Patterns in frog population decline indicate that disease is a major cause (Blaustein *et al.* 2018; Kriger *et al.* 2007; Murray *et al*. 2011). Recent research suggests that a water-borne pathogen, the Amphibian chytrid fungus (*Batrachochytrium dendrobatidis*), is the most likely cause (Blaustein *et al.* 2018; Gillespie *et al*. 2014; Kriger *et al.* 2007; McDonald *et al*. 2012; Murray *et al.* 2011; Scheele *et al.* 2014, 2017; Spark 2020). The aim of maintaining a strict hygiene protocol was to prevent the spread of contaminants such as chytrid fungus between sites and individuals as in accordance with the procedures suggested by Murray *et al.* (2011). To this end, when leaving a site, footwear was sprayed with bleach. Footwear was also washed between survey sessions. New disposable gloves were used when handling an individual frog, with any frogs caught being captured in a new, clean plastic bag so that human to frog skin contact was avoided.

4.5 Ethics

The project was undertaken with approval from the University of New England Animal Research Ethics Committee. The authority numbers were AEC17-048 and AEC 18-060. All procedures complied with the terms set down in the issued authorities. A New South Wales National Parks & Wildlife Service (NPWS) scientific license was also obtained for the conduct of the occupancy estimation surveys and collection of chytrid fungus samples. The license number was SL101963.

4.6 Copyright

Maps of the New England Tablelands were generated in Google maps (https://www.google.com/maps) using the “my maps” function. Attribution for the base map goes to Google Imagery and NASA, TerraMetrics (Map data ©2022 Google Imagery ©2022 NASA, TerraMetrics).

Chapter 5:

Single-species, Single-season Occupancy Estimation

5. Single-species, Single-season Occupancy Estimation

5.1 Data Analysis

The data collected was represented by the binary detected (1) or not detected (0) of a species at site i $(i = 1, \dots, 200)$, for j surveys $(j = 1, \dots, 4)$. Each species at each site had its own detection history that could be expressed by an intuitive equation representing the probability of the outcome of the sampling sequence. For example, a detection history for the common eastern froglet (*Crinia signifera*) at site FRG0030 was (0100). That is, it was found on the second sampling occasion, but not on the first, third or fourth occasions. A probability expression can be formulated for this detection history. This expression comprises two components. The first is the probability of occupancy (Ψ), that is the proportion of sites occupied by a species, and the second part is detection (p_j), likelihood of detecting a site given it is occupied. The probability statement for the above detection history would be as follows:

$$Pr(H_i=0100) = \Psi\,(1-p_1)\,p_2\,(1-p_3)\,(1-p_4) \qquad \text{(Eq. 5.01)}$$

The product of all detection history (H_i) probabilities forms the observed likelihood (L) model for the observed data. This differs from the complete data likelihood, as the values of the variables are calculated given the observed data for the observed model likelihood, whilst it is assumed values for the variables in the complete data likelihood are known. This equation can be solved for Ψ and p_j using the method of maximum likelihood:

$$L(\Psi, p_j \mid H_1, \dots, H_{200}) = Pr(H_1)\ x\ Pr(H_2)\ x\ \dots\ x\ Pr(H_{200}) \qquad \text{(Eq. 5.02)}$$

where, $i =$ site and, $j =$ sampling occasion.

Two hundred sites were visited. So, there are 200 detection histories for each of the frog species which were found. Keep in mind that although a species may not be found during the surveys, this does not necessarily mean that it was not present. This is why estimating detection probabilities become relevant.

The program **PRESENCE 7.1** (http://www.mbr-pwrc.usgs.gov/software/presence.html) was used to create the data files that were then analysed using the **R** package **RPresence** to determine the most likely model for estimating the probability of site occupancy. This package can be downloaded from https://www.mbr-pwrc.usgs.gov/software/presence.html. The standard single-season model proposed by Mackenzie *et al*. (2002) was expanded using, as covariates, the environmental and habitat variables recorded in the field. Environmental covariates were incorporated into the model for detection, while habitat covariates were incorporated into the model for occupancy.

5.1.1 Model Selection Procedure

In undertaking model selection, a series of *a priori* occupancy models were considered and compared. Model selection was based upon the Akaike's Information Criterion (AIC), an estimate of the expected, relative distance between a fitted model and the unknown true mechanism that actually generated the observed data (Burnham & Anderson 2002), in this case the occupancy and detection histories of the frog species under consideration. Akaike's Information Criterion was computed in **RPresence** for each model, with the model with the smallest AIC value being considered the preferred, most parsimonious model.

With regard to the model selection process, AIC values in and of themselves have no interpretable value for a single model. When comparing models, AIC values are ranked such that the value for a model is relative to the values for the other models in the comparison (Burnham & Anderson 2002). Therefore, it is the difference in AIC (ΔAIC) that becomes relevant. In comparing any two models, when $\Delta AIC >$ 2.00, the interpretation is that given the data, there is increasing evidence that the model with the smaller AIC is the better of the two models (Burnham & Anderson 2002). However, the converse is that when $\Delta AIC \leq$ 2.00, it can be thought that there is some level of empirical support for the model with the higher AIC in comparison with the one associated with the smaller AIC, given the data. An evidence ratio can be used to assess the weightings of each of the components (covariates) in the models (Mackenzie *et al.* 2018).

Single-species occupancy models were determined for each of the currently detected species for which there were enough data for analysis. The model selection process used is known as a secondary candidate set strategy which models sub-models independently and then combines the top set of models from each sub-model for selection in a final stage (Morin *et al.* 2020). In relation to the analysis here, it involved taking a hierarchical modelling approach that fitted separate candidate sets of sub-models for the probability of occupancy and the probability of detection (Arnold 2010; Morin *et al.* 2020). In doing this, the parameter for detection was held constant while fitting covariates to an occupancy model subset. Similarly, occupancy was then held constant while fitting covariates to a detection model subset. Unsupported variables in the separate occupancy and detection models were eliminated from further consideration (Morin *et al.* 2020). The final covariates in the occupancy and detection subsets from the most parsimonious models were combined to fit a secondary set of models for the final selection (Morin *et al.* 2020).

Initially with the analyses, models were created with the probability of occupancy being tested in relation to different combinations of habitat covariates, and constant probability of detection. Habitat covariates included; the extent of emergent vegetation (emV), the extent of riparian vegetation ($ripV$), the presence of invasive fish (F), and the existence of signs of domestic livestock disturbance of the site (C). Models were created using these covariates and by including, an indicator for two of the three different water site covariates: running water (rW) and still water (sW). Water absent (nW) was considered to be the baseline waterbody type to compare against the other two. These three types of sites were considered to be mutually exclusive. For the formulation of these models, see Table 5.1.1. Altitude (ALT) is then added to these model variations (Model 5, Table 5.1.1). Models were also created with the addition of latitude (LAT) and longitude ($LONG$), both without altitude (Model 8, Table 5.1.1) and with altitude (see Model 9, Table 5.1.1), and with only longitude and altitude (Model 7, Table 5.1.1) and with only longitude (Model 6, Table 5.1.1). Models created this way were also compared against a constant occupancy, constant detection model (Model 1, Table 5.1.1) and a global model (Model 2, Table 5.1.1) which contained all the habitat covariates.

For the habitat variables, invasive fish presence, signs of livestock activity, running water, still water and absent water were binary-valued covariates (0 or 1). The other variables were continuous-valued covariates. Riparian and emergent vegetation were given decimal values (scaled 0-1) indicative of their proportionate cover. Altitude was converted to kilometres above sea level and so was on a scale from 0.6 to 1.5. Latitude and longitude were standardised to decimal degrees distances centred on Armidale (30.5036° S, 151.6523° E), a population centre broadly in the middle of the New England Tablelands. This meant that positive scaled longitude values were indicative of sites west of Armidale and negative values indicative of sites east of Armidale. Similarly, positive scaled latitude values were indicative of sites north of Armidale and negative values indicative of sites south of Armidale.

Latitude alone was not considered as it had a confounding effect on model selection. Temperature, rainfall and altitude are relatively stable from north to south within the Tablelands (see section 2.4). Also, it was considered that any preferential models containing latitude would be a confounding correlation without longitude. Longitude was seen as a larger influencer of occupancy than latitude because of the existence of strong climatic and geographic gradients extending from east to west (increasing temperature, decreasing rainfall and decreasing altitude). Latitude does not exhibit these strong gradients from north to south without the context of longitude.

An example of a suite of models that initially tested the influences of emergent (emV) and riparian ($ripV$) vegetation (Model 3, Table 5.1.1) is listed in the table below (Table 5.1.1). This list of models does not include all the variable occupancy, constant detection models tested. All variable occupancy, constant detection models were compared using AIC and the covariates from the most parsimonious model were chosen to be included in the final AIC comparisons.

Table 5.1.1: Example of a suite of variable occupancy, constant detection models containing emergent (emV) and riparian vegetation ($ripV$). See Table 2.1.1 for the descriptions of the covariates associated with these abbreviated parameter names.

Model	Model formula
1	$\Psi(.), p(.)$
2	$\Psi(emV + ripV + F + C + ALT + LAT + LONG + rW + sW), p(.)$
3	$\Psi(emV + ripV), p(.)$
4	$\Psi(emV + ripV + rW + sW), p(.)$
5	$\Psi(emV + ripV + rW + sW + ALT), p(.)$
6	$\Psi(emV + ripV + rW + sW + LONG), p(.)$
7	$\Psi(emV + ripV + rW + sW + ALT + LONG), p(.)$
8	$\Psi(emV + ripV + rW + sW + LAT + LONG), p(.)$
9	$\Psi(emV + ripV + rW + sW + ALT + LAT + LONG), p(.)$

A second set of models was developed, each model with constant occupancy, but with detection varying in relation to a combination of environmental continuous-valued covariates including air temperature (AT), relative humidity (H), wind speed (WS), cloud cover (CC), and the binary-valued covariates of, moon illumination (MI) and the occurrence rain in the last 48 hours ($R48$). Each of these environmental covariates was added to a model of choice if not already included in the model. If the environmental covariates of interest were air temperature and humidity (Model 4, Table 5.1.2), then other models were created with these covariates and the addition of one other covariate: rain in the last 48 hours (Model 5, Table 5.1.2), or wind speed (Model 6, Table 5.1.2), or cloud cover (Model 7, Table 5.1.2), or moon illumination (Model 8, Table 5.1.2). Only one interaction covariate was included in any of the models, and that was the interaction between air temperature and humidity ($AT{:}H$). This term was only included in models where both these covariates, air temperature and humidity, were included. All these models were compared against the baseline constant occupancy, constant detection model (Model 1, Table 5.1.2), the constant occupancy, survey-specific detection model (Model 2, Table 5.1.2), and the global model that contained all the environmental variables (Model 3, Table 5.1.2), as well as models which contained the interaction between air temperature and humidity, if appropriate (Models 9-14, Table 5.1.2).

Table 5.1.2: Example of a suite of constant occupancy, variable detection models containing air temperature (AT) and humidity (H). See Table 2.2 for the descriptions of the covariates associated with these abbreviated parameter names.

Model	Model formula
1	$\Psi(.), p(.)$
2	$\Psi(.), p(SURVEY)$
3	$\Psi(.), p(AT + H + WS + CC + MI + R48)$
4	$\Psi(.), p(AT + H)$
5	$\Psi(.), p(AT + H + R48)$
6	$\Psi(.), p(AT + H + WS)$
7	$\Psi(.), p(AT + H + CC)$
8	$\Psi(.), p(AT + H + MI)$
9	$\Psi(.), p(AT + H + WS + CC + MI + R48 + AT{:}H)$
10	$\Psi(.), p(AT + H + AT{:}H)$
11	$\Psi(.), p(AT + H + R48 + AT{:}H)$
12	$\Psi(.), p(AT + H + WS + AT{:}H)$
13	$\Psi(.), p(AT + H + CC + AT{:}H)$
14	$\Psi(.), p(AT + H + MI + AT{:}H)$

For the environmental covariates, air temperature and wind speed were left as was initially recoded. Rainfall in the last 48 hours and moon illumination were both indicator variables; again a 1 indicating that there was light from the moon or that it had rained in the previous 48 hours, and a 0 indicating that there was neither moon illumination nor rain in the previous 48 hours. Finally, cloud cover and humidity were expressed as scaled proportions (0-1).

An example of a suite of models with constant occupancy and covariate-dependent detection with a focus on the environmental covariates; air temperature and humidity can be found in the table below (Model 4, Table 5.1.2). These models are a subset of all the constant occupancy, variable detection models that were tested with different environmental variables. All constant occupancy, variable detection models were compared using AIC, and the covariates from the most parsimonious model were chosen to be included in the final model selection process.

The covariates of the preferred models from the constant occupancy, variable detection, and from the constant detection, variable occupancy model comparisons were used to create a variable occupancy, variable detection model containing the covariates from both preferred models (Model 6, Table 5.1.3). This model was then compared against the constant occupancy, constant detection model (Model 1, Table 5.1.3), the constant occupancy, survey-specific detection model (Model 2, Table 5.1.3), the overall global model containing all the detection covariates and all the habitat covariates (Model 3, Table 5.1.3), the preferred constant occupancy, variable detection model (Model 4, Table 5.1.3); and the preferred variable occupancy, constant detection model from the two previous model selections (Model 5, Table 5.1.3). For example, the final model comparisons, assuming occupancy was influenced by emergent vegetation (emV), riparian vegetation $(ripV)$ running water (rW) and still water (sW), and detection was influenced by air temperature (AT) and humidity (H), are listed in Table 5.1.3.

Table 5.1.3: Example of a suite of variable occupancy, variable detection models containing the habitat covariates; emergent vegetation, riparian vegetation and still water, and the environmental covariates; air temperature and humidity. See Tables 2.1 and 2.2 for the descriptions of the covariates associated with these abbreviated parameter names.

Model	Model formula
1	$\Psi(.), p(.)$
2	$\Psi(.), p(SURVEY)$
3	$\Psi(emV + ripV + F + C + ALT + LAT + LONG + rW + sW),$ $p(AT + H + WS + CC + MI + R48)$
4	$\Psi(.), p(AT + H)$
5	$\Psi(emV + ripV + sW + rW), p(.)$
6	$\Psi(emV + ripV + sW + rW), p(AT + H)$

For the situation where there are multiple models with $\Delta AIC \leq 2.00$, an evidence ratio (ER) was calculated to test the weight rating of the covariates (Anderson 2008). Evidence ratios are calculated by dividing the AIC weight (w) for models containing specific covariates by the residual AIC weight (Mackenzie *et al*. 2018):

$$ER = \frac{w}{1-w} \tag{Eq. 5.03}$$

An $ER > 1.00$ (> 50% weight) provides evidence that a covariate is an influencing factor (Mackenzie *et al.* 2018). Covariates that have an $ER > 3.00$ (>75%) are considered particularly important (Mackenzie *et al.* 2018). In these analyses, it was only covariates with an $ER > 3.00$ that were included in the final model. An exception to this was when only one covariate was found to have an $ER > 1.00$ (> 50%). In this case, that single covariate was included in the model.

The exception to this was where the simplest model in a group of models, all with $\Delta AIC \leq 2.00$, was nested within the more complex models in the set, i.e. where all covariates present in the simple model were also present in the more complex models. If this were the case, then this simple model would be deemed to be the preferred model because there was not enough evidence to support acceptance of the more complex models with more covariates.

5.1.2 Logistic Regression Models for Occupancy and Detection

In the final models developed using these analyses, the included covariates were used to develop logistic regression models of occupancy and detection (MacKenzie *et al.* 2018). The probability of occupancy at potential sites can be calculated through the inclusion of information for the modelled covariates in these logistic regression models. The base logistic regression model with a logit link for the inclusion of covariate information for the probability of occupancy at a potential site can be calculated with:

$$logit(\theta_{i,j}) = ln(\frac{\theta_{ij}}{1- \theta_{ij}}) = \beta_0 + x_{1,j} * \beta_1 + x_{2,j} * \beta_2 \ldots + x_{n,j} * \beta_n \tag{Eq. 5.04}$$

where, θ is the probability of interest for the ith sampling unit for the jth covariate value, β_0 is the base coefficient of detection of the species, β_1 is the coefficient for the effect of a habitat covariate $x_{1,j}$ and β_n is the coefficient for the effect of the nth habitat covariate ($x_{n,j}$). A similar equation can be developed for the probability of detection with its corresponding environmental covariates. The above formula can be solved for occupancy or detection, once coefficients have been generated.

Occupancy and detection coefficients were generated using **RPresence.** These were used to calculate the detection probabilities and occupancy given changes in the corresponding covariate values. Using the hypothetical Model 8 from Table 5.1.3, to solve for the probability of occupancy would result in the following expression:

$$\Psi = \frac{\exp\left(\beta_0+(\beta_1 * emV)+(\beta_2 * ripV)+(\beta_3 * sW)+(\beta_4 * rW)+(\beta_5 * nW)\right)}{1+\exp\left(\beta_0+(\beta_1 * emV)+(\beta_2 * ripV)+(\beta_3 * sW)+(\beta_4 * rW)+(\beta_5 * nW)\right)} \qquad \text{(Eq. 5.05)}$$

where β_0 is the baseline coefficient, β_1 is the coefficient for emergent vegetation, β_2 is the coefficient for riparian vegetation, β_3 is the coefficient for still water, β_4 is the coefficient for running water and β_5 is the coefficient for habitats with no water. A similar equation can be used to generate detection probabilities given different values in the coefficients.

5.2 Results

Thirty two of the 39 frog species found in the historical study were present at the selected 200 sites historically. There were seven species which were recorded in the historical survey that were not present historically in the 200 selected sites. Overall, 18 of the 32 frogs species found historically at the 200 selected sites were found in the New England Tablelands in the current study (Table 5.2.1). Fourteen historical frog species which were present at the 200 selected sites were not detected during the current study.

Table 5.2.1: Total number of detections and sites at which each of the 18 species were detected in the current study. Also included are the percentage of historical sites at which the species was detected in the current study and the percentage of historical sites which were still occupied in the current study.

Species	Total detections	Total sites detected	Proportion of sites in the current study which were occupied historically (%)	Proportion of historical sites still occupied in the current study (%)
Crinia parinsignifera	146	56	2	33
Crinia signifera	233	92	33	52
Limnodynastes dumerilii	72	42	10	24
Limnodynastes fletcheri	11	4	0	0
Limnodynastes peronii	49	28	11	20
Limnodynastes tasmaniensis	132	64	44	41
Litoria barringtonensis	3	1	100	33
Litoria caerulea	2	1	0	0
Litoria dentata	26	13	0	0
Litoria fallax	182	90	13	60
Litoria latopalmata	93	52	23	40
Litoria peronii	85	54	15	53
Litoria subglandulosa	7	4	0	0
Litoria verreauxii	233	58	21	40
Litoria wilcoxii	46	13	15	9
Mixophyes balbus	2	2	0	0
Pseudophryne coriacea	13	12	17	67
Uperoleia laevigata	100	48	48	25

Of the 18 frog species detected in the current surveys, four of these species were detected at more than half of the sites at which they were known to have occupied historically (Table 5.2.1). Most species, however, were found at more sites than were found to be previously occupied in the historical survey (Table 5.2.1). In relation to this, there were five species which were only detected at sites which they had not previously occupied in the historical study. For maps of the historically occupied sites see Appendix 1 and for maps of sites occupied by species found in the current study, see Appendix 3.

5.2.1 Naïve Occupancy Estimation

Of the 18 frog species found, there were nine species that had a higher naïve occupancy in the current study than in the historical study. These species are indicated with two asterisks in Table 5.2.2. There was one species which had a noticeable decrease in naïve occupancy*, Litoria wilcoxii,* and one species which had maintained the same naïve occupancy in the current study, *Limnodynastes tasmaniansis*. The remaining seven species detected in the current study had very low naïve occupancy estimates for both the historical study and the current study, making it difficult to assess their changes in naïve occupancy.

5.2.2 Occupancy Estimation

Of the 18 frog species found in the New England Tablelands, 13 were able to be modelled using single-season occupancy analysis. It was found that in attempting to analyse the survey results for species with a small number of repeat detections over the 200 sites and four repeat visits resulted in issues with convergence and extreme model coefficient outputs. Frog species that exhibited this problem and were therefore not analysed using single-species occupancy models were the green tree frog, *Lit. caerulea* (two detections at two sites), *Lit. barringtonensis* (three detections at one site), *Lit. subglandulosa* (seven detections at four sites), the Southern barred frog, *M. balbus* (two detections at two sites) and the red backed toadlet, *Pse. coriacea* (13 detections at 12 sites).

Thirteen species were able to have their constant occupancy estimates calculated over the 200 selected sites. Constant occupancy estimates are a better indication of the true state of the occupancy of these species when compared to naïve occupancy estimates because the method of occupancy estimation used here accounts for detection. However, for those five species whose models did not converge, naïve estimates are still informative. The constant occupancy estimates along with the historical naïve estimates taken from Table 3.4.2 in Chapter 3 are given in Table 5.2.3.

Table 5.2.2: Naive occupancy (NE) and their standard errors (se) for frog species detected during the historical study and the current study. Total historical site naïve occupancy is the naïve occupancy of all sites visited in the historical survey. Selected historical site naïve occupancy is the naïve occupancy for the historical sites which were selected to be revisited in the current survey. Species who increased their naïve occupancy are indicated with an ** and species which decreased their naïve occupancy are indicated with a *.

Species	Total historical sites		Selected historical sites		Present selected sites	
	NE	se	NE	se	NE	se
Adelotus bevis	0.102	0.010	0.240	0.030	-	-
*Crinia parinsignifera***	0.016	0.004	0.015	0.009	0.280	0.032
*Crinia signifera***	0.225	0.014	0.290	0.032	0.460	0.035
Cyclorana brevipes	0.002	0.002	-	-	-	-
Lechriodus fletcheri	0.008	0.003	-	-	-	-
*Limnodynastes dumerilii***	0.070	0.009	0.085	0.020	0.210	0.029
Limnodynastes fletcheri	0.083	0.009	0.070	0.019	0.020	0.010
*Limnodynastes peronii***	0.042	0.007	0.075	0.019	0.140	0.025
Limnodynastes salmini	0.012	0.004	0.005	0.005	-	-
Limnodynastes tasmaniensis	0.328	0.016	0.335	0.034	0.320	0.033
Limnodynastes terraereginae	0.001	0.001	-	-	-	-
Litoria aurea	0.009	0.003	0.020	0.010	-	-
Litoria barringtonensis	0.014	0.004	0.020	0.010	0.005	0.005
Litoria booroolongensis	0.143	0.012	0.340	0.034	-	-
Litoria caerulea	0.036	0.006	0.020	0.010	0.005	0.005
Litoria chloris	0.001	0.001	-	-	-	-
Litoria dentata	0.011	0.004	0.005	0.005	0.065	0.018
*Litoria fallax***	0.071	0.009	0.100	0.021	0.450	0.035
*Litoria latopalmata***	0.111	0.011	0.150	0.025	0.260	0.031
*Litoria peronii***	0.064	0.008	0.075	0.019	0.270	0.032
Litoria piperata	0.001	0.001	-	-	-	-
Litoria rubella	0.020	0.005	0.005	0.005	-	-
Litoria subglandulosa	0.014	0.004	0.020	0.010	0.020	0.010
*Litoria verreauxii***	0.126	0.011	0.145	0.025	0.290	0.032
*Litoria wilcoxii**	0.084	0.009	0.110	0.022	0.065	0.018
Mixophyes balbus	0.014	0.004	0.025	0.011	0.010	0.007
Mixophyes fasciolatus	0.009	0.003	0.010	0.007	-	-
Neobatrachus sudellae	0.010	0.003	0.010	0.007	-	-
Philoria sphagnicola	0.001	0.001	-	-	-	-
Platyplectrum ornatum	0.063	0.008	0.075	0.019	-	-
Pseudophryne bibronii	0.113	0.011	0.275	0.032	-	-
Pseudophryne coriacea	0.025	0.005	0.015	0.009	0.060	0.017
*Uperoleia laevigata***	0.090	0.010	0.115	0.023	0.240	0.030
Uperoleia rugosa	0.014	0.004	0.010	0.007	-	-

Table 5.2.3: The average historical occupancy estimations (Ψ) and their standard errors (*se*) for the total 884 sites (Total historical sites) in the New England Tablelands, the 200 historical sites selected to be revisited in the current study (Selected historical sites) and the current average historical occupancy estimations and their standard errors (*se*) for the 200 selected sites (Present selected sites). Species who increased their average occupancy are indicated with an ** and species which decreased their average occupancy are indicated with a *. NOTE: Five species had models which did not converge (DNC), so averages could not be calculated for them.

Species	**Total historical sites**		**Selected historical sites**		**Present selected sites**	
	Ψ	**se**	**Ψ**	**se**	**Ψ**	**se**
Adelotus bevis	0.411	0.097	0.469	0.146	-	-
Crinia parinsignifera*	0.357	0.109	0.407	0.162	0.285	0.007
Crinia signifera**	0.273	0.121	0.253	0.173	0.468	0.012
Cyclorana brevipes	0.016	0.007	0.005	0.007	-	-
Lechriodus fletcheri	0.025	0.062	0.024	0.092	-	-
Limnodynastes dumerilii**	0.149	0.109	0.156	0.159	0.230	0.033
Limnodynastes fletcheri*	0.120	0.103	0.112	0.147	0.020	0.003
Limnodynastes peronii*	0.262	0.119	0.237	0.171	0.173	0.003
Limnodynastes salmini	0.389	0.058	0.343	0.085	-	-
Limnodynastes tasmaniensis	0.339	0.126	0.349	0.182	0.333	0.013
Limnodynastes terraereginae	0.633	0.009	0.654	0.010	-	-
Litoria aurea	0.219	0.088	0.247	0.135	-	-
Litoria barringtonensis	0.364	0.115	0.300	0.222	DNC	-
Litoria booroolongensis	0.462	0.124	0.461	0.181	-	-
Litoria caerulea	0.383	0.115	0.332	0.171	DNC	-
Litoria chloris	0.342	0.012	0.345	0.011	-	-
Litoria dentata	0.020	0.066	0.023	0.099	0.067	0.007
Litoria fallax	0.485	0.11	0.544	0.165	0.491	0.010
Litoria latopalmata	0.255	0.118	0.264	0.171	0.308	0.015
Litoria peronii*	0.725	0.096	0.729	0.145	0.282	0.006
Litoria piperata	0.208	0.010	0.254	0.015	-	-
Litoria rubella	0.201	0.042	0.082	0.070	-	-
Litoria subglandulosa	0.031	0.069	0.028	0.099	DNC	-
Litoria verreauxii*	0.600	0.069	0.653	0.110	0.294	0.013
Litoria wilcoxii*	0.110	0.101	0.111	0.146	0.065	0.006
Mixophyes balbus	0.114	0.103	0.109	0.146	DNC	-
Mixophyes fasciolatus	0.019	0.065	0.020	0.096	-	-
Neobatrachus sudellae	0.018	0.067	0.018	0.096	-	-
Philoria sphagnicola	0.303	0.008	0.219	0.016	-	-
Platyplectrum ornatum	0.343	0.097	0.258	0.150	-	-
Pseudophryne bibronii	0.172	0.100	0.143	0.144	-	-
Pseudophryne coriacea	0.849	0.059	0.858	0.089	DNC	-
Uperoleia laevigata*	0.391	0.114	0.399	0.171	0.250	0.032
Uperoleia rugosa	0.456	0.015	0.484	0.020	-	-

Of the 13 species, only two showed an increase in their averaged occupancy for the 200 selected sites when compared to their historical occupancy. These species are indicated with two asterisks in Table 5.2.3. Eight species had a decrease in their averaged occupancy when compared to the historical single-visit occupancy estimates. The remaining eight species; *Limnodynastes tasmaniensis, Lit. dentata* and *Lit. fallax,* had a similar averaged occupancy in the current study when compared to the historical.

Of the 13 species whose occupancy could be modelled, 11 had occupancy models which varied in relation to habitat and broad-scale geographical covariates (Table 5.2.4). Two species exhibited constant occupancy. These species were *Limnodynastes dumerilli* (Ψ = 0.230 ± 0.033) and *Uperoleia lavigata* (Ψ = 0.250 ± 0.032). For selection of the final model for each of these 13 species, see Appendix 4.

5.2.2.1 Geographical Covariates

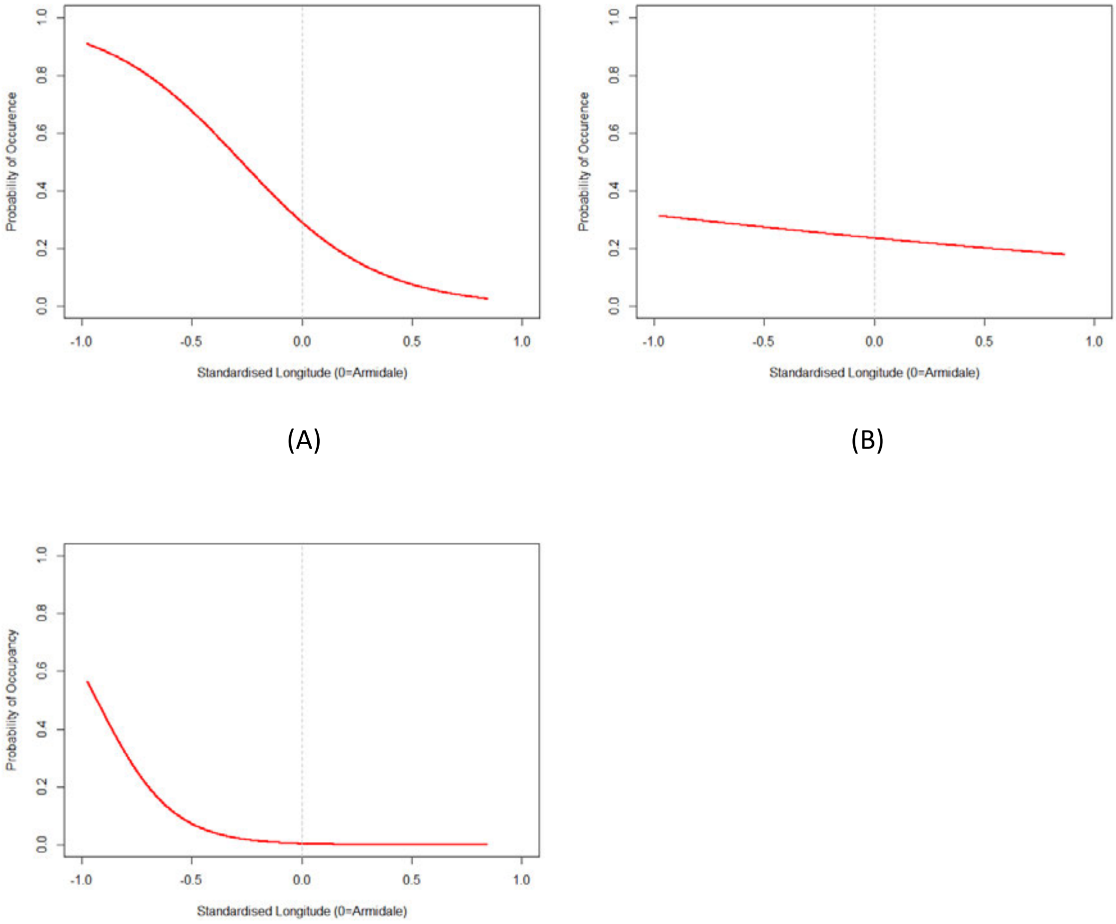
Of the 13 species modelled in the New England Tablelands during the current study, there were nine species whose occupancy was influenced by longitude (Fig. 5.2.1 and Fig. 5.2.2). For two of these species, *Crinia parinsignifera* and *Crinia signifera*, longitude had a positive association with occupancy. Positive coefficient values for longitude, indicate that the further east sites were located, the more likely they were to be occupied by these two species. The occupancy for the remaining seven species; *Limnodynastes fletcheri*, *Limnodynastes tasmaniensis*, *Litoria dentata*, *Litoria fallax*, *Litoria latopalmata*, *Litoria verreauxii* and *Litoria wilcoxii*, was negatively associated with longitude. Negative coefficient values for longitude, indicate that the further west sites were located, the more likely they were to be occupied by these species.

The occupancy of four frog species was influenced by altitude (Fig. 5.2.3). For two of these species, *Cri. signifera* and *Litoria wilcoxii,* occupancy had a negative association with altitude. Since altitude increased from 600 m to 1500 m asl, the likelihood of occupancy for *Cri. signifera* decreases in association with increasing altitude within these altitudinal limits. The occupancy of the other two species, *Lim. tasmaniensis* and *Lit. verreauxii.* had a positive association with altitude, increasing as altitude increases. Sites at higher altitudes had a higher likelihood of being occupied by *Lim. tasmaniensis* and *Lit. verreauxii.*

Table 5.2.4: Standardised occupancy and indication of the mode of influence where it occurred of habitat covariates on occupancy for each of the 13 species modelled in the current study. Covariates include: altitude (ALT), latitude (LAT), longitude ($LONG$), emergent vegetation (emV), riparian vegetation ($ripV$), livestock presence (C), *Gambusia holbrooki* presence (F) and waterbody structures, absent (nW), running (rW) and still water (sW). NOTE: The probability of occupancy (Ψ) is standardised for $ALT = 1$, $LAT = 0$, $LONG = 0$, $emV = 0$, $ripV = 0$, $rW = 0$, $sW = 0$, $C = 0$, $F = 0$.

Species	Ψ	ALT	LAT	$LONG$	emV	$ripV$	rW	sW	C	F
Crinia parinsignifera	0.239	.	.	+	.	.	−	+	.	.
Crinia signifera	0.315	−	.	+	+	.	.	.	.	.
Limnodynastes dumerilii	0.230	.	.	.	.	.	.	.	.	.
Limnodynastes fletcherai	0.004	.	.	−	.	.	.	.	.	.
Limnodynastes peronii	0.256	.	.	.	.	.	+	+	.	.
Limnodynastes tasmaniensis	0.298	+	.	−	+	.	.	.	.	.
Litoria dentata	0.146	.	+	−	+	.	.	.	.	.
Litoria fallax	0.252	.	.	−	.	.	+	+	.	.
Litoria latopalmata	0.290	.	.	−	.	.	.	.	.	.
Litoria peronii	0.237	.	.	.	.	+	.	.	−	.
Litoria verreauxii	0.235	+	+	−	.	.	.	.	.	.
Litoria wilcoxii	0.017	−	.	−	.	.	+	−	.	.
Uperoleia laevigata	0.250	.	.	.	.	.	.	.	.	.

There were two species which had a positive association between occupancy and latitude (Fig. 5.2.4). These two species were; *Lit.dentata* and *Lit. verreauxii*. Positive coefficient values for latitude, indicate that the further north sites were located, the more likely they were to be occupied by *Lit. dentata* and *Lit. verreauxii.*



(A) (B)

(C)

Fig. 5.2.1: Probability of occupancy for: (A) *Litoria latopalmata*, (B) *Litoria verreauxii*, (C) *Limnodynastes fletcheri*, against standardised longitude in the New England Tablelands. NOTE: Longitude is centralised at Armidale. Positive longitude values are sites east of Armidale and negative longitude values are west of Armidale.

5.2.2.2 Habitat characteristics

Of the 13 species modelled in the current study, the occupancy of three species was positively associated with emergent vegetation (Fig. 5.2.2, Fig. 5.2.3 & Fig 5.2.4). These three species were *Cri. signifera*, *Lim. tasmaniensis* and *Lit. dentata*. A positive coefficient for emergent vegetation indicates that these three species was more likely to be found at sites with a higher proportion of emergent vegetation.

Occupancy for *Cri. signifera, Lim. tasmaniensis* and *Lit. dentata* can be estimated using the coefficients from the most parsimonious model (see Appendix 5) and equation 5.04 (see Section 5.1.2).

Average occupancy for *Cri. signifera* at the 200 selected sites was Ψ = 0.468 (se = 0.012). Base probability of occupancy at a site at the reference location of Armidale ($LONG$ = 0, ALT = 1) with no emergent vegetation present (emV = 0), was Ψ = 0.315 (se = 0.033). For a site located at Armidale with a low proportion of emergent vegetation present (emV = 0.250), Ψ = 0.397 (se = 0.035), and for a site with a high proportion of emergent vegetation present (emV = 0.750), Ψ = 0.574 (se = 0.035).

Average occupancy for *Lim. tasmaniensis* at the 200 selected sites was Ψ = 0.333 (se = 0.013). Base probability of occupancy at a site at the reference location of Armidale ($LONG$ = 0, ALT = 1) with no emergent vegetation present (emV = 0), was Ψ = 0.298 (se = 0.032). For a site located at Armidale with a low proportion of emergent vegetation present (emV = 0.250), Ψ = 0.342 (se = 0.034), and for a site with a high proportion of emergent vegetation present (emV = 0.750), Ψ = 0.437 (se = 0.035).

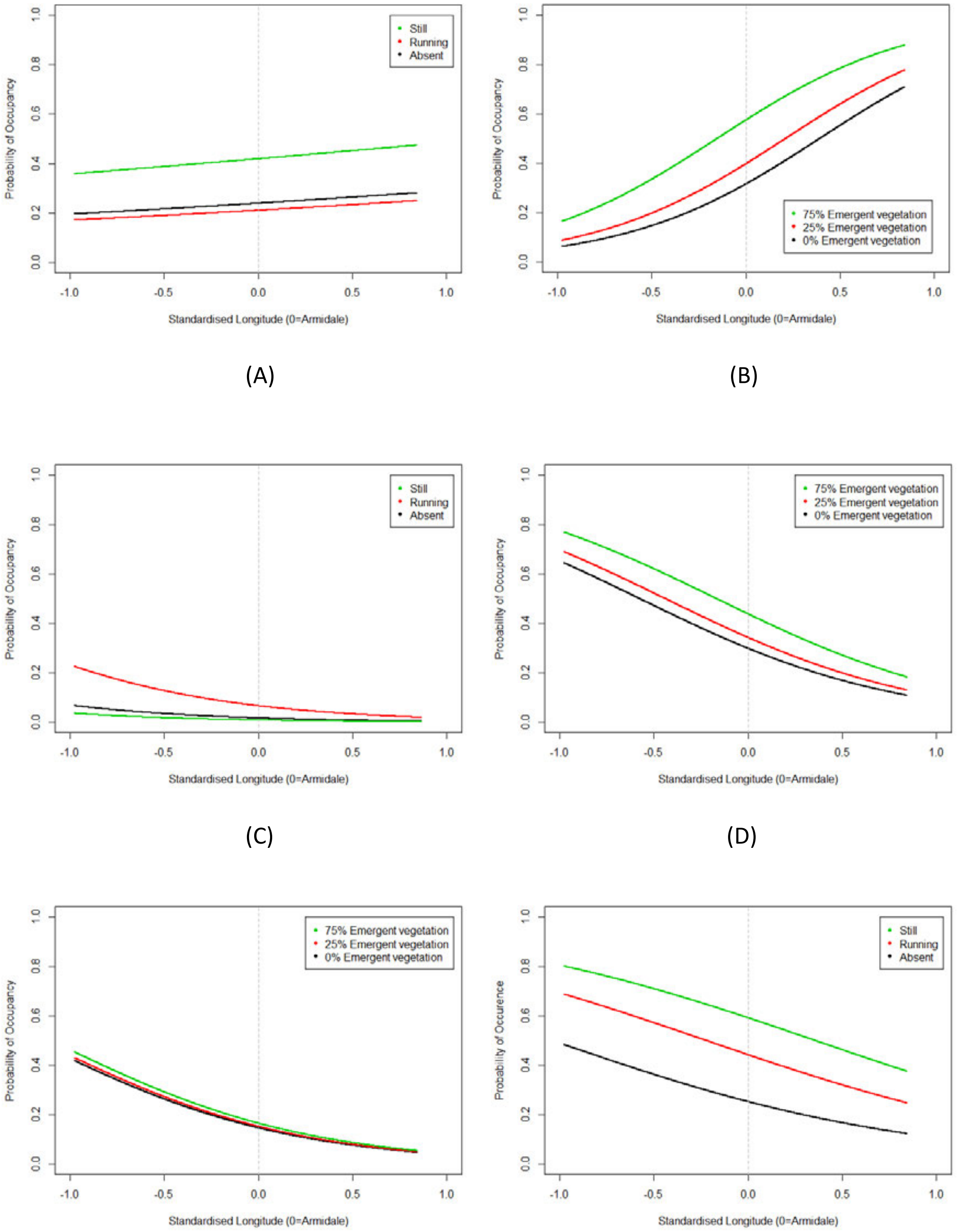
Average occupancy for *Lit. dentata* at the 200 selected sites was Ψ = 0.067 (se = 0.007). Base probability of occupancy at a site located at the reference location of Armidale ($LONG$ = 0, LAT = 0) with no emergent vegetation (emV), was Ψ = 0.146 (se = 0.025). For a site located at Armidale with a low proportion of emergent vegetation present (emV = 0.250), Ψ = 0.152 (se = 0.025), and for a site with a high proportion of emergent vegetation present (emV = 0.750), Ψ = 0.165 (se = 0.026).

There was a single species, *Lit. peronii*, whose occupancy was positively influenced by riparian vegetation (Fig. 5.2.5). As the proportion of riparian vegetation increases, so does the likelihood of *Lit. peronii* occupying a site. Occupancy estimation equations for *Lit. peronii* from the most parsimonious model can be calculated using equation 5.04 (see Section 5.1.2), using the coefficients from Appendix 5. Average occupancy for *Lit. peronii* at the 200 selected sites was Ψ = 0.282 (se = 0.006). Base probability of occupancy at a site with no livestock present (C = 0) and no riparian vegetation ($ripV$ = 0), was Ψ = 0.237 (se = 0.030).

The presence of livestock also had influenced the occupancy of *Lit. peronii* (Fig. 5.2.5). The presence of livestock had a negative association with occupancy. Negative coefficient values for livestock presence, indicate that *Lit. peronii* is more likely to occupy a site where there are no livestock, compared to one that does contain livestock (Fig. 5.2.5). For a site without livestock present and a low proportion of riparian vegetation ($ripV$ = 0.25), Ψ = 0.281 (se = 0.032). For a site without livestock present and with a high proportion of riparian vegetation present ($ripV$ = 0.75), Ψ = 0.380 (se = 0.034).

There were four species whose occupancy was influenced by the type of waterbody at a site (Fig. 5.2.1 & Fig 5.2.2). These four species were *Cri. parinsignifera*, *Lim*. *peronii*, *Lit. fallax* and *Lit. wilcoxii*. The occupancy for two of these species, *Lim. peronii and Lit fallax*, had a negative association with sites where no water was present. The presence of water, either running or still, had a positive effect on occupancy. Both *Lim. peronii* and *Lit. fallax* were much more likely to occupy a site where water was present than one where water was absent. Both these species were also more likely to occupy a site with a still waterbody, rather than a running waterbody.

Constant occupancy for *Lim. peronii* at the 200 selected sites was Ψ = 0.173 (se = 0.003). Base probability of occupancy at a site with no water present (aW), was Ψ = 0.094 (se = 0.064). For a site at Armidale that a running waterbody type (rW), Ψ = 0.141 (se = 0.040), and for a site that had a still waterbody type (sW), Ψ = 0.256 (se = 0.063). Constant occupancy for *Lit. fallax* at the 200 selected sites was Ψ = 0.456 (se = 0.010). Base probability of occupancy, at a site at the reference location of Armidale ($LONG$ = 0) with no water (aW), was Ψ = 0.252 (se = 0.033). For a site located at Armidale with a running waterbody type, Ψ = 0.442 (se = 0.035), and for a site with a still waterbody type, Ψ = 0.591 (se = 0.035).

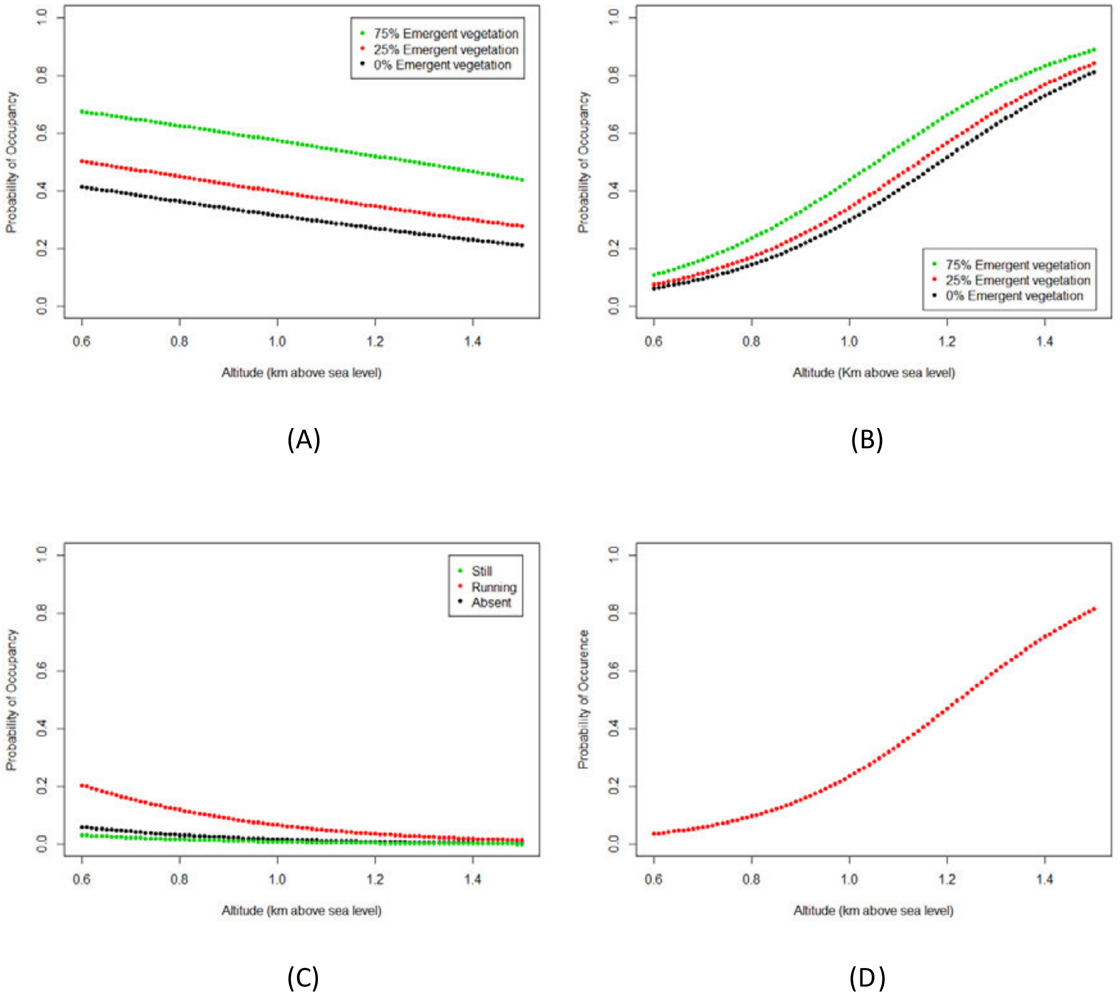


(A) (B)

(C) (D)

(E) (F)

Fig. 5.2.2: Probability of occupancy for: (A) *Crinia parinsignifera*, (B) *Crinia signifera*, (C) *Litoria wilcoxii*, (D) *Limnodynastes tasmaniensis*, (E) *Litoria dentata*, (F) *Litoria fallax*, against standardised longitude in the New England Tablelands at different habitat covariates. NOTE: Longitude is centralised at Armidale. Positive longitude values are sites east of Armidale and negative longitude values are west of Armidale.



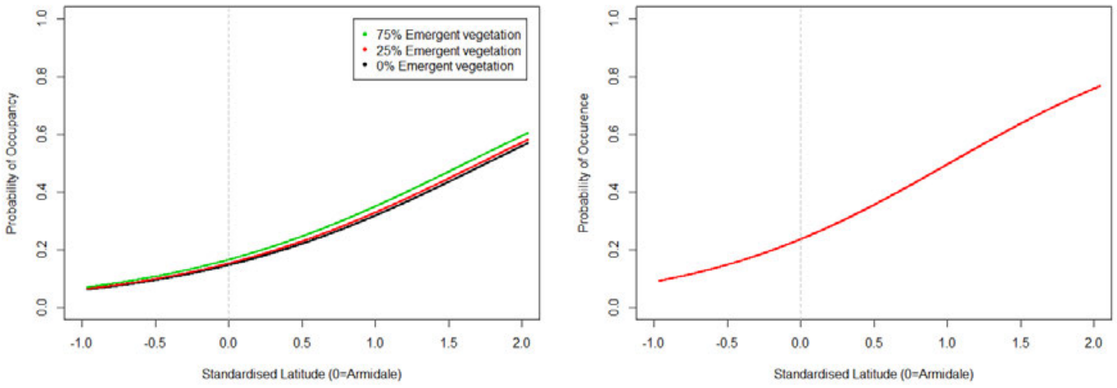
(A) (B)

(C) (D)

Fig. 5.2.3: Probability of occupancy for (A) *Crinia signifera*, (B) *Limnodynastes tasmaniensis*, (C) *Litoria dentata*, against standardised altitude at sites in the New England Tablelands with different habitat characteristics, and (D) *Litoria verreauxii* against standardised latitude. NOTE: Latitude is centralised at Armidale. Positive latitude values are sites north of Armidale and negative latitude values are south of Armidale. Standardised longitude was kept constant at 0 (Armidale).

The occupancy for one species was influenced by the type of waterbody at a site. *Crinia parinsignifera* was more positively associated with still waterbodies, rather than with running waterbodies. *Crinia parinsignifera* was much more likely to occupy a site where water was still rather than one where water was running. Further, running waterbodies (rW) that did have water present had a negative effect on occupancy, indicating that this species, was more likely to occupy a site with no water than one that was running. Base probability of occupancy at a site at the reference location of Armidale ($LONG = 0$) with no water (aW), was $\Psi = 0.239$ ($se =$

0.030). For a site located at Armidale with a running waterbody type, $\Psi = 0.210$ (se = 0.029), and for a site with a still waterbody type, $\Psi = 0.418$ ($se = 0.035$).



(A) (B)

Fig. 5.2.4: Probability of occupancy for (A) *Litoria dentata* against standardised latitude at sites in the New England Tablelands with three different emergent proportions; 75% (green), 25% (red) and 0% (black), and (B) *Litoria verreauxii* against standardised latitude. NOTE: Latitude is centralised at Armidale. Positive latitude values are sites north of Armidale and negative latitude values are south of Armidale. Standardised longitude was kept constant at 0 (Armidale).

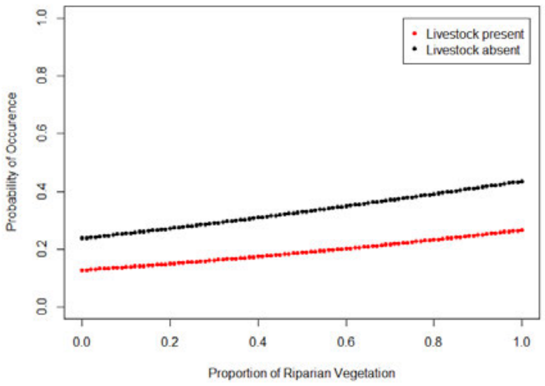


Fig. 5.2.5: Probability of occupancy for *Litoria peronii* against proportion of riparian vegetation at sites with livestock present (red) and absent (black) in the New England Tablelands.

Finally, the occupancy for the remaining species which was influenced by the type of waterbody at the site, *Lit. wilcoxii* was positive associated with running waterbodies. Still waterbodies had a negative association with occupancy, indicating that *Lit. wilcoxii* was much more likely to occupy a site where water was running rather than one where water was still regardless of whether waster was present or not. For *Lit. wilcoxii,* constant occupancy at the 200 selected sites was $\Psi = 0.065$ ($se = 0.006$). For a site located at Armidale with a running waterbody type, $\Psi = 0.066$ ($se = 0.018$), and with a still waterbody type, $\Psi = 0.009$ ($se = 0.007$).

5.2.3 Detection

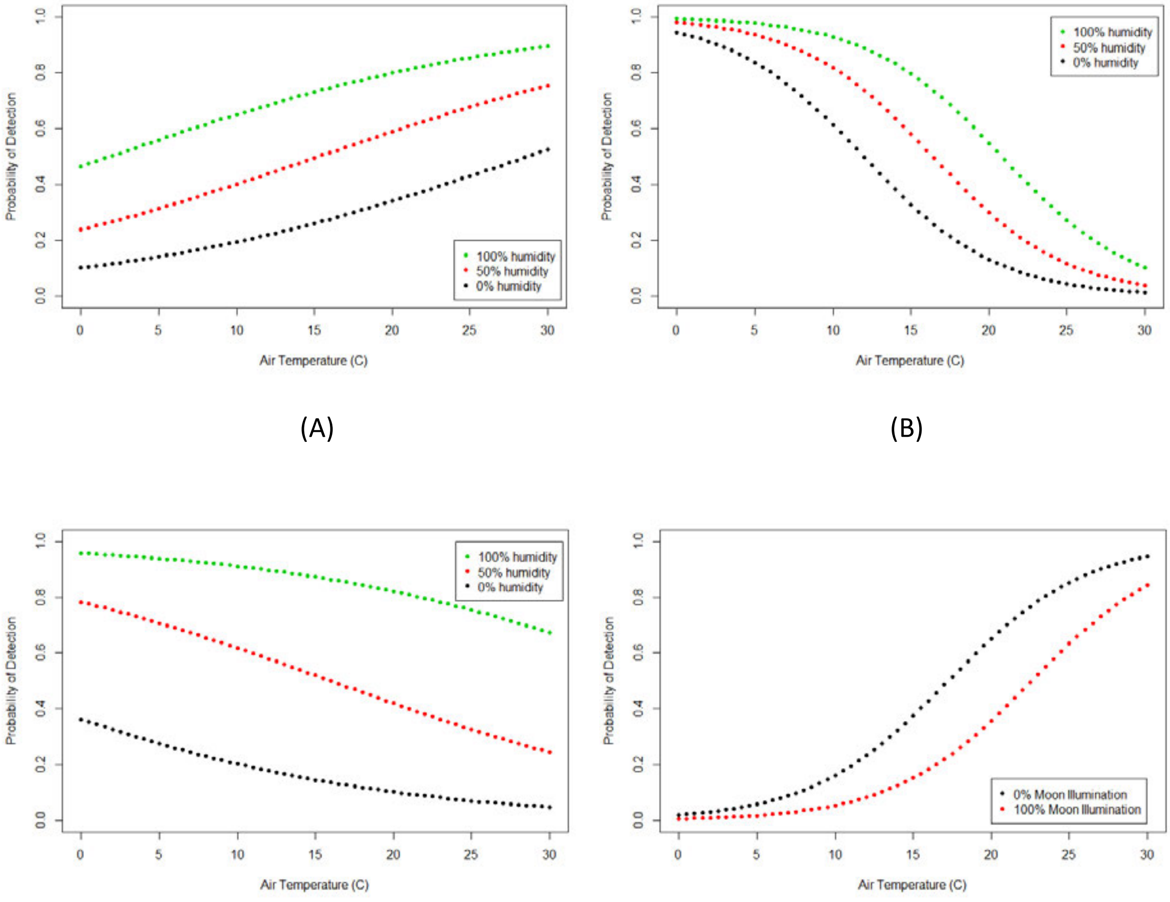
Eighteen of the 32 frog species detected in the historical study were detected on at least one occasion in the current study. Of these 18 species, only 13 were modelled using single-season occupancy estimation. None of these 13 species had constant detection (Table 5.2.5). The detection of eight species varied depending on climatic conditions. The detection of the remaining five varied depending on survey.

Table 5.2.5: Standardised detection and the effects of environmental covariates on detection for each of the 13 species detected in the current study. Covariates include: air temperature (AT), humidity (H), wind speed (WS), moon illumination (MI) and surveys, 2 ($SURV2$), 3 ($SURV3$) and 4 ($SURV4$). NOTE: Detection standardised with $AT = 15$, $H = 0.5$, $WS = 0$, $MI = 0$, and $SURVEY = 1$.

Species	p	AT	H	$R48$	WS	MI	$SURV\ 2$	$SURV\ 3$	$SURV\ 4$
Crinia parinsignifera	0.495	+	+	.	+	.	.	.	.
Crinia signifera	0.580	–	+	.	.	.	.	.	.
Limnodynastes dumerilii	0.697	.	.	.	.	.	–	–	–
Limnodynastes fletcherai	0.401	+	.	.	.	.	.	.	.
Limnodynastes peronii	0.380	+	.	.	.	–	.	.	.
Limnodynastes tasmaniensis	0.661	.	.	.	.	.	+	–	–
Litoria dentata	1.000	+	.	.	.	.	.	.	.
Litoria fallax	0.931	.	.	.	.	.	–	–	–
Litoria latopalmata	0.226	+	.	.	.	.	.	.	.
Litoria peronii	0.903	.	.	.	.	.	–	–	–
Litoria verreauxii	0.520	–	+	.	.	.	.	.	.
Litoria wilcoxii	0.781	+	.	.	.	.	.	.	.
Uperoleia laevigata	0.722	.	.	.	.	.	–	–	–

5.2.3.1 Climatic variables

There were eight species whose detection was associated with air temperature (Fig. 5.2.6 & Fig. 5.2.7). The detection for six of these species, *Cri. parinsignifera*, *Lim. fletcheri*, *Lim. peronii*, *Lit. dentata*, *Lit. latopalmata* and *Lit wilcoxii*, was positive associated with air temperature. The likelihood of detection for these species was higher when air temperatures were warmer. The detection for the remaining two species, *Cri. signifera* and *Lit. verreauxii,* was negatively associated with air temperature. As such, these two species had a higher detection when air temperatures were cooler.



(A)

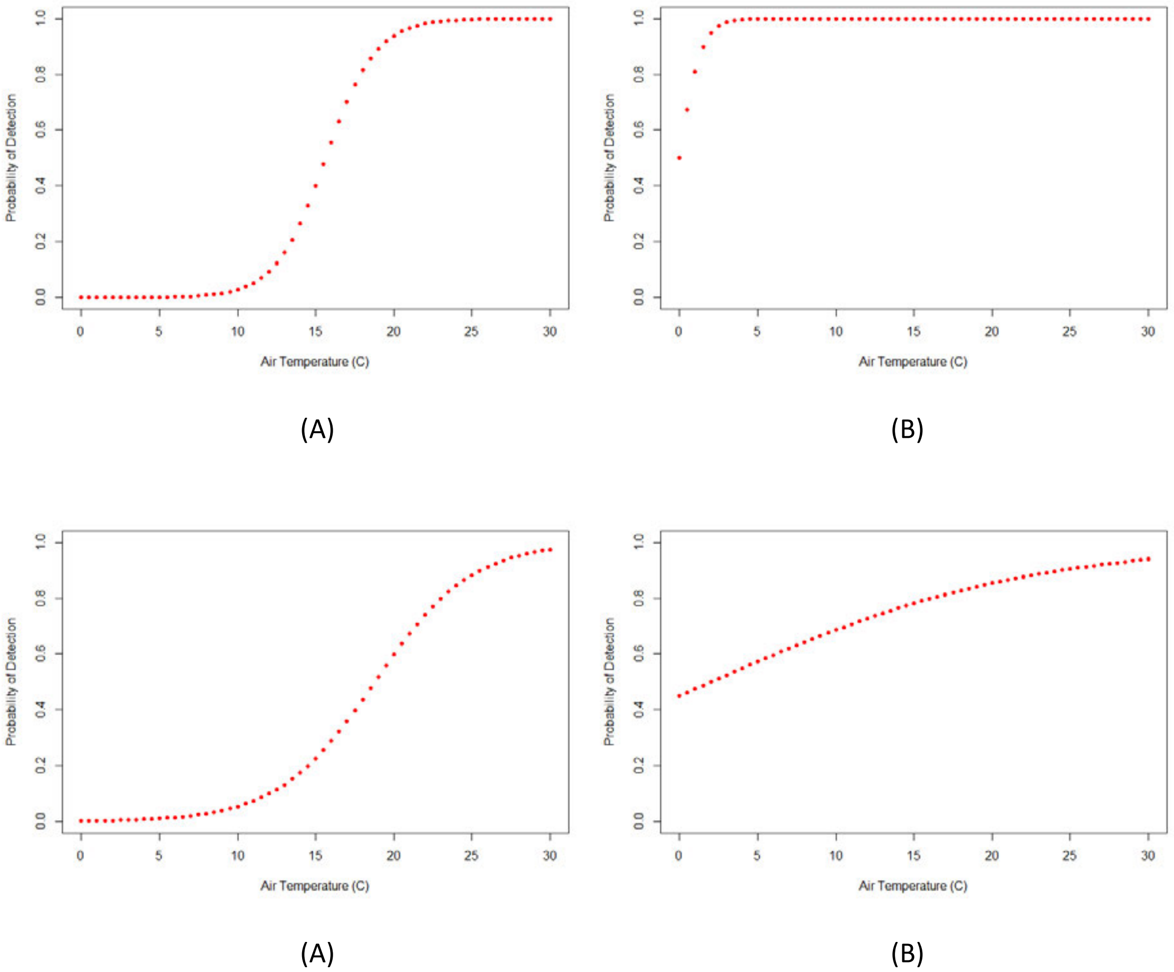
(B)

(C)

(D)

Fig. 5.2.6: Probability of detection for (A) *Crinia parinsignifera*, (B) *Crinia signifera*, (C) *Litoria verreauxii*, (D) *Limnodynastes peronii*, in the New England Tablelands at air temperatures between 0°C and 30°C .

The detection of three species was positively associated with humidity (Fig. 2.5.6 and Fig. 2.5.8). *Crinia parinsignifera*, *Cri. signifera* and *Lit. verreauxii* were more likely to be detected at occupied sites when humidity was high compared to when it was low.



(A) (B)

(A) (B)

Fig. 5.2.7: Probability of detection for (A) *Limnodynastes fletcheri*, (B) *Litoria dentata*, (C) *Litoria latopalmata*, (D) *Litoria wilcoxii*, in the New England Tablelands at air temperatures between 0°C and 30°C .

One species detection was positively associated with wind speed (Fig 5.2.8). The likelihood of detection for *Cri. parinsignifera* increased with increasing wind speed. Similarly, there was a single species whose detection was influenced by moon illumination (Fig. 5.2.6). Moon illumination had a negative association with detection of *Lim. peronii*. *Limnodynastes peronii* was more likely to be detected at occupied sites when moon illumination was absent compared to when it was present.

Incidence of rainfall in the previous 48 hours before the survey had no effect on detection. None of the species' detection varied depending on whether there had been rainfall in the last 48 hours.

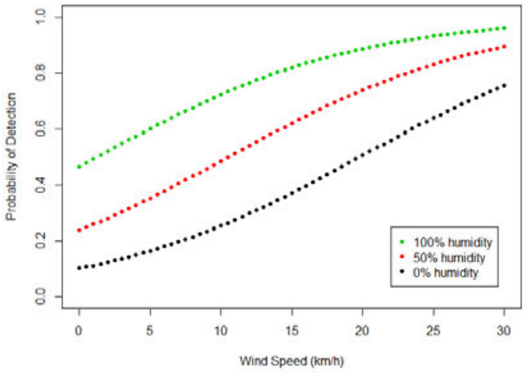


Fig. 5.2.8: Probability of detection for *Crinia parinsignifera* in the New England Tablelands at wind speeds between 0km^{-1}h and 30km^{-1}h for three different relative humidity values; 100% (green), 50% (red) and 0% (black). NOTE: Air temperature was standardised at 0°C.

5.2.3.2 Survey

Detection for five species varied with survey period. These five species were; *Lim. dumerilli*, *Lim. tasmaniensis*, *Lit. fallax*, *Lit. peronii* and *U. laevigata*. For *Lim. dumerilli, Lit. fallax, Lit. peronii* and *U. laevigata*, the detection coefficients for each subsequent survey had a larger negative value than the one previously. Since the survey periods proceeded from late spring through to early winter, the likelihood of detecting *Lim*. *dumerilii, Lit. fallax*, *Lit. peronii* and *U. laevigata* declined, with each subsequent survey. Detection for *Lim. dumerilli* was highest during the first survey period in late spring-early summer (p = 0.697, se = 0.079), with the final survey period (survey 4) in late autumn-early winter, having the lowest likelihood of detection (p = 0.022, se = 0.022). Detection for *Lit. fallax* was highest during the first survey period in late spring to early summer (p = 0.931, se = 0.030), with the final survey period (survey 4) in late autumn to early winter, having the lowest likelihood of detection (p = 0.077, se = 0.028). Detection for *Lit. peronii* was highest during the first survey period from early spring to summer (p = 0.903, se = 0.053), with the third survey period, in mid-autumn, having the lowest likelihood of detection (p = 0.124, se

= 0.044). Survey 4 was excluded during model analysis for *Lit. peronii* as its inclusion resulted in convergence issues, creating large standard errors for that survey. Detection for survey 4 is considered zero. Detection for *U. laevigata* was highest during the first survey period in late spring-early summer (p = 0.721, se = 0.068), with the final survey period (survey 4) in late autumn-early winter, having the lowest likelihood of detection (p = 0.060, se = 0.034).

Detection for *Lim. tasmaniensis* was highest during the second survey period during summer (p = 0.766, se = 0.061). From the end of summer to early winter, it became less likely to detect *Lim. tasmaniensis,* since the coefficients for each subsequent survey after the second had a larger negative value. The final survey period (survey 4) in late autumn to early winter, had the lowest likelihood of detecting *Lim. tasmaniensis* (p = 0.060, se = 0.029).

5.3. Discussion

5.3.1 Frog Species Occupancy and its Association with Environmental Covariates.

5.3.1.1 Geographical Covariates

Longitude ($LONG$) is a geographic coordinate that specifies the east-west position of a location on the surface of the earth. As such, it is likely to have little influence on the presence of frog species detected at sites in the New England Tablelands. However, within the context of the New England Tablelands it is associated with other identifiable climatic and geographical factors. In relation to this, the eastern side of the New England Tablelands is predominantly alpine, with higher rainfall and generally lower seasonal temperatures (Bureau of Meteorology [BOM] 2021; Sahukar *et al.* 2003). The western climes of the tablelands are lower, warmer and have lower seasonal rainfall (BOM 2021).

In relation to occupancy, both *Crinia* species, *Cri. signifera* and *Cri. parinsignifera,* were positively associated with longitude (Table 5.15.1). That is, they were more likely to be found occupying sites on the eastern side of the New England Tablelands, rather than sites on the western side. It is possible that it is linked to their breeding activity. Both *Crinia* species prefer cooler temperatures when breeding, *Cri. signifera* breeding in the winter months and *Cri. parinsignifera* breeding in the autumn and spring months (Anstis 2017). Frogs are generally easier to detect during their breeding season as males are calling and females are more mobile, moving towards calling males, potentially influencing detection of these species at sites they occupy. Both *Crinia* species may be more likely to be present at sites with cooler seasonal temperatures in comparison to sites with warmer seasonal temperatures during the same survey period.

An interesting contradiction in relation to the occupancy of *Cri. signifera*, is that altitude (ALT) had a negative association with the probability of occupancy at sites. That is, *Cri. signifera* was more likely to be found at sites lower than the reference altitude of 1000 m asl. Temperature typically decreases with increasing altitude (Berven *et al.*1979; Lauk *et al* 2005), with high altitudes running along the eastern edge of the New England Tablelands, indicating that there may be factors other than the variation of temperature associated with both longitude and altitude influences on the occupancy of *Cri. signifera*.

Conversely, the occupancy of *Lit. wilcoxii*, *Lit. vaerreauxii*, *Lit. latopalmata*, *Lit. fallax*, *Lit dentata*, *Lim. tasmaniensis* and *Lim. fletcherai* all had a negative association with longitude (Table 5.15.1). That is they were more likely to be present at sites on the western side of the New England Tablelands. Again, it is possible that this is linked to their preferred breeding season, with all seven of these species more likely to breed in the warmer months (Anstis 2017; Hoskin *et al.* 2015). Occupying sites with lower altitudes and lower temperatures is likely to provide a longer breeding period than sites at higher altitudes and cooler temperatures. The influence of altitude on *Lit. wilcoxii* further supports the western trend in relation to this species' occupancy, with altitude being negatively associated with occupancy of *Lit. wilcoxii* (Table 5.15.1). Contrary to this, *Lim. tasmaniensis* and *Lit. verreauxii* both had a positive associations with altitude (Table 5.15.1). That is, they are more likely to occupy sites at altitudes above 1000 m asl. Again, there may be factors other than the variation of temperature associated with both longitude and altitude that influence the occupancy of these two species.

Another consideration for frog species occupying sites at higher altitudes is the increased severity of Amphibian chytrid fungus (*B. dendrobatidis*) infection. A number of studies have modelled *B. dendrobatidis* growth in conjunction with temperature (Berger *et al.* 2004; Collins *et al.* 2003; Daszak *et al.* 2003; Johnson *et al.* 2003; Longcore *et al.* 1999). *Batrachochytrium dendrobatidis* grows best between 16-25°C, can survive freezing, stops growing at 28°C and dies at 30°C (Berger *et al.* 2004; Daszak *et al.* 2004; Piotrowski *et al.* 2004). At higher altitudes, temperatures rarely reach high enough to be fatal to *B. dendrobatidis* (Berger *et al.* 2004; Daszak *et al.* 2004; Piotrowski *et al.* 2004). As such, cooler daily temperatures consequently lead to higher infection intensities and correspondingly higher mortalities for species which are susceptible. *Batrochytrium dendrobatidis* will be further discussed in Section 7.3.

Another confounding factor for both altitude and longitude, is that during the survey years (2017-2020), the New England Tablelands region was experiencing a drought, with the severest conditions occurring during the second year of surveys (BOM 2021). Sites visited during this period were predominantly to sites on the eastern edge of the region, with many of them being either dry or with severely reduced volumes of water. The occurrence of drought could potentially skew the likelihood of detection, as many species may have chosen to aestivate rather than breed during this period. If this were the case, then individuals may well have been present at the site but were difficult to locate and, as a consequence, were recorded as being absent.

Latitude is a geographic coordinate that specifies the north-south position of a point on the Earth's surface. *Litoria verreauxii* and *Lit. dentata* were two species which had an increased likelihood of occupying sites with lower latitudes (LAT), i.e. sites north of Armidale compared to sites south of this reference location (Table 5.15.1). It is unclear what the determining factors may have been for these two species as there is not a strong north-south temperature or rainfall gradient along the latitudinal gradient like there is for longitude in the New England Tablelands. However, there may be vegetation-related factors unaccounted for during the survey which may be having an impact. *Litoria dentata* is a primarily arboreal species (Anstis 2017) and may have a preference for the type of vegetation present at sites it inhabits. In the north of the New England Tablelands, there is a higher density of dry sclerophyll forests (NSW Local Land Services Northern Tablelands region 2020), which *Lit. dentata* may prefer. *Litoria dentata* may also be under-represented in the dataset because this species shows a preference for breeding in ephemeral pools (Anstis 2017). Sites with water present were predominantly targeted during the survey. *Litoria verreauxi*, may possibly also have preferred vegetation types, although it is unlikely that it shows the same preferences as *Lit. dentata* because it is a species that prefers to call from low vegetation or emergent reeds (Anstis 2017).

There were no species which increased their occupancy with increasing latitude (Table 5.15.1). That is, no frog species detected were more likely to occupy sites south of Armidale because of increasing latitude (coded as negative latitude values in relation to Armidale).

5.3.1.2 Habitat Covariates

Habitat covariates are those that represent the physical structure of a site. These include emergent vegetation, riparian vegetation, waterbody structure and presence of livestock.

Litoria fallax and *Lim. peronii* are both more likely to occupy sites which have water present (Table 5.15.1). Frog reproduction stages and other life history traits are strongly linked to water, such as their eggs which are not amniotic and adult frogs which have moist, permeable skin, making them both susceptible to desiccation when little moisture is present (Baker & Lauck 2006; Hazell *et al*. 2001). Likewise, many species have a larval stage (tadpoles) which is reliant on water for habitat (Egan & Paton 2004; Hazell *et al.* 2001; Parris 2006; Welch & McMahon; Van Sluys *et al.* 2012), food sources (Schumutzer *et al.* 2008; Voshell 2002) and a medium for respiration (Barry & Syal 2013). In this way it makes sense for frog species to prefer a site that does have water present to maximise survival and reproductive success. In terms of site structure, both *Lit. fallax* and *Lim. peronii* show a preference for still (sW) over running (rW) waterbodies, but will still utilise a running waterbody site. This may be because these two species are able to utilise still pools within the structure of creeks and rivers.

Crinia parinsignifera similarly shows a preference for still waterbodies (Table 5.15.1). Also, *Cri. parinsignifera* is less likely to be found at running waterbody sites than sites without water (nW). This indicates that *Cri. parinsignifera* is perhaps more selective in its habitat preference than *Lit. fallax* and *Lim. peronii*. *Crinia signifera,* prefers standing water at occupied sites rather than running water (Baker & Lauck 2006), supporting this hypothesis. It should be noted, however, that the present study found no influence on occupancy for *Cri. signifera* between waterbody type.

Litoria wilcoxii occupied sites that had a running waterbody structure. It was also less likely to occupy still waterbody sites than a site with no water present (Table 5.15.1). *Litoria wilcoxii* have specific requirements for sites which they will occupy when breeding (Anstis *et al.* 1998). Males generally call from rocks and banks of creeks and streams (Anstis 2017). Higher probability of occupancy at running water sites makes sense; the survey period encompassing the peak breeding season for this species.

Vegetation structures are strong determinants of amphibian occupancy and abundance (Baker & Lauck 2006). Occupancy for *Lit. peronii* is positively associated with riparian vegetation ($ripV$) and negatively associated with presence of livestock (C, Table 8.1). Lemckert *et al.* (2005) also found that *Lit. peronii* preferred sites which had a higher proportion of bank cover, though particularly sites which had a high degree of larger trees. When choosing sites to occupy, *Lit, peronii* may prefer a site which is less disturbed by agricultural processes (clearing for cropping and livestock). Livestock can modify habitat around waterbodies (Agouridis *et al*. 2005; Belsky *et al*. 1999; O'Callaghan 2019) through the consumption or trampling of existing vegetation (Burton *et al*. 2008; Kauffman *et al*. 1983, O'Callaghan 2019; Ranganath *et al*. 2009; Scrimgeor & Kendell 2003), reduction of bank stability (Braccia & Voshell 2007; Zaimes & Schultz 2011), erosion of water banks (Evans *et al*. 2006), increased water turbidity (Herbst *et al*. 2012; Kauffman *et al*. 1983; Sovell *et al*. 2000; Schmutzer *et al*. 2008; Trimble 1994; Trimble & Mendel 1995), soil compaction (Trimble & Mendel 1995), and a reduction in overall water quality (O'Callaghan 2019; Schmutzer *et al.* 2008) and water temperature stability (Berven *et al*. 1979; Herbst *et al*. 2012; Lauk *et al*. 2005).

Hazell *et al*. (2001) found that in a modified environment, the terrestrial habitat is an important factor in determining habitat suitability for many species including *Lit. peronii*. Presence of vegetation in the riparian zone provides protection for vocalising males from predators during the breeding season (Hazell *et al.* 2001; Lauk *et al.* 2005). Increased complexity in vegetation may also reduce physical confrontations between conspecific breeding males (Lauk *et al*. 2005). Vegetation can also provide micro-habitats with stable temperatures and higher moisture retention both during the breeding season and outside of it (Hazell *et al.* 2001). Further, in temperate and alpine regions, the provision of vegetation offers protection from temperature drops when an individual is overwintering at a site, preventing freezing and improving survival chance (Hazell *et al.* 2001). Vegetation and its associated leaf litter also supplies habitat for a higher biomass of insects, the predominant food source of many anuran species (Schumutzer *et al*. 2008; Voshell 2002).

None of the other detected frog species had an association with riparian vegetation (Table 5.15.1).

Occupancy of *Lit. dentata*, *Lim. tasmaniensis* and *Cri. signifera* had a positive association with emergent vegetation (emV, Table 5.15.1). That is, these species preferred to occupy sites which had a higher proportion of emergent vegetation present. Villaseñor *et al.* (2017) found that the likelihood of finding *Cri. signifer*a increased with increased aquatic vegetation. Emergent vegetation is usually associated with higher amphibian occupancy (Hamer *et al.* 2012; Hazell *et al.* 2004; Sievers *et al.* 2019; Villaseñor *et al.* 2017; Wassens *et al.* 2010; Westgate *et al.* 2015) because it improves suitability of a breeding site (Egan & Paton 2004; Hazell *et al.* 2001; Parris 2006; Welch & McMahon 2005). Emergent vegetation is generally utilised as calling and oviposition sites (Anstis 2002; Hamer *et al.* 2021; Hazell *et al.* 2001; Semslitsch 2000; Villasenor *et al.* 2017), as is the case for *Cri. signifera* which attaches eggs to vegetation (Anstis 2017) and *Lim. tasmaniensis* which calls from the base of aquatic vegetation (Anstis 2017; Hamer *et al.* 2021; Hazell *et al.* 2001; Lemckert *et al.* 2006). However, emergent vegetation has also been found to offer shelter for the different life stages (Egan & Paton 2004; Hazell *et al.* 2001; Parris 2006; Welch & McMahon 2005), both eggs and larvae, protection from predators (Hamer & Parris 2011; Hazell *et al.* 2001; Lauk *et al.* 2005) and greater options for foraging (Lemckert *et al.* 2006). These may be the case for the positive occupancy association for *Lit. dentata*, as this species, neither deposits its eggs on aquatic vegetation, nor do males call from emergent vegetation (Anstis 2017). A distinction between vegetation types (e.g., floating or submerged) may increase an understanding of the complex relationship *Lit. dentata* may have with emergent vegetation. However, such distinctions were not made in the current study.

There have been some anuran species for which occupancy is associated with reduced emergent vegetation (Hamer *et al.* 2021). However, in the present study all other detected species' occupancy did not have a negative association with emergent vegetation (Table 5.15.1).

5.3.2 Frog Species Detection and its Association with Environmental Covariates

Detection of frogs during their breeding season reduces sampling effort, time and money during a survey (Perez-Grandados *et al.* 2020). This is because many anurans are cryptic with nocturnal behaviours, but auditory cues, such as calling, intensifies during the breeding season giving away the position of males and stimulating movement of females toward calling males (Guerra *et al*. 2018; Toledo *et al.* 2015). Many studies have found that changes in climatic factors can influence the calling behaviour of frogs (Almeida-Gomes *et al*. 2007; Baker & Lauck 2006; Hauselberger & Alford 2005; Milne *et al.* 2013; Oseen & Wassersug 2002; Ospina *et al.* 2013; Perez-Grandados *et al*. 2020; Pierce & Gutzwiller 2004; Van Sluys *et al.* 2012; Wong *et al.* 2004). Changes in environmental variables can indicate that conditions may be favourable for breeding, triggering different calling responses (Milne *et al.* 2013). Temperature and rainfall are the primary motivators of anuran breeding cycles (Almeida-Gomes *et al.* 2007; Van Sluys *et al.* 2012) and are usually positively associated with calling (Baker & Lauck 2006; Brooke *et al.* 2000; Wong *et al.* 2004), though some studies have found a negative relationship (Milne *et al.* 2013; Ospina *et al.* 2013). Other studies have linked calling activity to humidity (Almeida-Gomes *et al*. 2007; Baker & Lauck 2006), moonlight illumination (Buchanan 2006; Johnson & Batie 2001) and wind (Saenz *et al*. 2006; Steelman & Dorcas 2010).

5.3.2.1 Air Temperature

Detection of *Cri. parinsignifera*, *Lit. dentata*, *Lit. latopalmata*, *Lit. wilcoxii*, *Lim. peronii* and *Lim. fletcherai* increased with increasing air temperature (Table 482). It is generally accepted that calling activity of many frogs increase with temperature (Baker & Lauck 2006; Wong *et al.* 2004) and has been found in a wide range of species (Almeida-Gomes *et al*. 2007; Cui *et al*. 2011; Navas 1996; Van Sluys *et al.* 2012). Calling for summer breeders is triggered by warmer temperatures (Anstis 2017)

Litoria dentata, *Lit. latopalmata*, *Lit. wilcoxii*, *Lim fletcherai* and *Lim. peronii* are all summer breeders, with males intensifying their calling in the warmer months. Although *Cri. parinsignifera* calls in autumn and spring, the act of calling is still temperature dependent, with frogs gaining body heat from the environment (Narvas 1996; Van Dijk *et al*. 1990). Cui *et al.* (2011) suggested that if temperatures fall below a critical level, calling may cease, so it is possible that although *Cri. parinsignifera* mate during spring and autumn, it selects warmer nights to do so, thus calling only on warmer nights during this period. Another possibility is that with the increase in temperature, this species becomes more mobile at sites and is easier to spot regardless of whether it is breeding or not.

Conversely, increased detection of *Lit. verreauxii* and *Cri. signifera* was associated with lower temperatures (Table 5.15.2). *Crinia signifera* and *Lit. verreauxii* are both winter breeders, with calling of males intensifying during cool months. Some species of frogs utilise shallow pools for egg laying to reduce the impact of cool water on developing eggs (Oseen & Wassersug 2002), a possible behaviour for these two species. During their study, Wong *et al*. (2004) found that calling of *Cri. signifera* increased into winter before tapering off at the approach of spring. Although this period was not included in the present study, the increase in detection primarily by calling with the reduction in temperature is congruent with what Wong *et al.* (2004) found.

It should be noted that many studies have found an association of detection of anurans with water temperature (Almeida-Gomes *et al*. 2007; Oseen & Wassersug 2002; Perez-Grandados *et al*. 2020; Smith *et al.* 2014; Wong *et al.* 2004). Water temperature was not considered during the present study, as an increase in air temperature generally corresponds to an increase in water temperature. Highly correlated variables, such as water and air temperature, generate model choice issues during *a priori* model selection. Often the two models, each containing one of the correlated variables, will end up with a similar AIC and consequently a ΔAIC close to zero. In such cases, both models would be considered to be the most parsimonious model. Further, if the two correlated variables are in the same model, then overdispersion often becomes a problem (Royle 2006).

5.3.2.2 Relative Humidity

The present study found that increased detection of *Cri. parinsignifera*, *Cri. signifera* and *Lit. verreauxii* was associated with high humidity (Table 5.15.2). These findings are similar to those of Almeida-Gomes *et al*. (2007) and Baker and Lauck (2006), who found that calling and activity respectively decreased with decreasing humidity. High relative humidity is associated with higher amounts of moisture in the air, which, for frogs, reduces the risk of desiccation when calling or moving (Almeida-Gomes *et al.* 2007; Oseen & Wassersug 2002; Perez-Grandados *et al.* 2020). Further, sound travels better through humid rather than dry air, allowing for better transmission of the call to females (Oseen & Wassersug 2002) and, in the case of surveys, to observers.

5.3.2.3 Moon Illumination

The present study found that detection for one species, *Lim. peronii*, was negatively associated with moon illumination (Table 5.15.2). That is, this species was easier to detect on nights where there was little moon illumination. Hall (2016) suggested that there is a perceived increase in risk to calling individuals from predators when there is more ambient light, making frogs easier to spot. Another possibility is that *Lim. peronii* is easier to spot with eye shine on nights with little moon illumination. *Limnodynastes peronii* is a large frog (69-73 mm; Anstis 2017) which allows for the use of eye shine as a cue for locating this species. Lower ambient light, reduces shadowing and reflection, providing a better environment to utilise this method.

The response of moonlight illumination appears to be species-specific (Johnson & Batie 2001; Weir *et al.* 2005), with there being many contradictory findings reported in the literature. Perez-Grandados *et al.* (2020) found that moon illumination was not associated with calling behaviour of a Brazilian frog, *Elachistocleis matogrosso.* While Tuttle and Ryan (1982) found that calling in a Panama tree frog, *Smilisca sila*, was negatively associated with moon illumination, presumably as this frog used visual cues to spot predatory bats. Weir *et al.* (2005) had several Maryland (USA) frog species whose detection varied with moonlight illumination, though responses were mixed with some species responding positively with increasing moon illumination and some negatively. Studies conducted by Granda *et al.* (2008) and by Pierce and Gutzwiller (2007) found that low levels of moonlight increased the likelihood of detecting frog species.

5.3.2.4 Wind Speed

Only one species, *Cri. parinsignifera*, had their detection associated with wind speed (Table 5.15.2). Wind is generally thought to have a negative influence on calling of anurans, reducing detection (Saenz *et al.* 2006; Smith *et al.* 2014; Steelman & Dorcas 2010), due to the higher rate of desiccation or the auditory interference with the call (Oseen & Wassersug 2002; Steelman & Dorcas 2010). Other studies have found that wind has no effect on calling frequency of frog species (Halfwerk & Ryan 2016; Oseen & Wassersug 2002). However, the present study found that detection of *Cri. parinsignifera* was positively associated with wind speed. The mechanism behind this is as yet unknown. One theory is that the wind may disturb the frogs (Halfwerk & Ryan 2016) at a site, increasing mobility of individuals and hence likelihood of detection. Another theory is that, as higher wind speeds provide a higher ambient noise, the risk of predation is lower from predators using auditory cues to locate individuals (Tuttle & Ryan 1982). Alternatively, this association may be a random effect of the data. *Crinia parinsignifera* calls from the base of vegetation in the water (Anstis 2017), which may provide better shelter from windy conditions. It may have been that wind speed had very little to do with detection of this species and this species was detected regardless of wind speed, the association being spurious.

5.3.2.5 Survey Occasion

Finally, there were five frog species where detection varied with survey occasion. These were *Lim. dumerilii*, *Lim. tasmaniensis*, *Lit. fallax*, *Lit. peronii* and *U. laevigata* (Table 5.15.2). Where detection varies with survey, each survey period had a different likelihood of detection for each of the species. This indicates that variation in detection cannot be sufficiently explained by the other modelled or recorded parameters (MacKenzie *et al*. 2018), such as air temperature, relative humidity, wind speed, incidence of rainfall in the preceding 48 hours or moon illumination.

Most species had high detection in the earlier surveys (November to February), with likelihood of detection tapering off with each subsequent survey. This is likely linked to their breeding season as all five species are summer breeders (Anstis 2017). However, given that the other parameters were insufficient predictors of detection, there may be other factors having an effect which were not measured during the present study. Van Sluys *et al.* (2012) found that light intensity and photoperiod were both good predictors of calling in several Brazilian frog species.

The present study used incidence of rainfall the preceding 48 hours which had no effect on detection on any of the frog species modelled (Table 5.15.2). Tuttle and Ryan (1982) found that long-term seasonal rainfall was a better prediction of breeding in frog species than rainfall on the preceding day. They also found that this was more noticeable with opportunistic breeders than with those utilising permanent waterways. Perez-Grandados *et al.* (2020) also found that rainfall on the previous day had little impact on calling behaviour, suggesting that this may be less influential for species already at a site with water.

5.3.3 Changes in Frog Species Occupancy since the Historical Study

The occupancy of frog species in the New England Tablelands has changed from that found in relation to the historical survey conducted over the years 1966-1975 (Heatwole *et al.* 1995). Fewer species were detected in the current survey than in the historical survey. Two of these species, *M. balbus* and *Lit. subglandulosa,* are currently considered to be threatened by the Environmental Protection and Biodiversity (EPBC) Act (Department of Agriculture, Water and Environment [DAWE] 2020) and the International Union for the Conservation of Nature (IUCN)

(International union for the conservation of nature [IUCN] 2021). The rest of the species listed are all classed as being of least concern or unlisted (DAWE 2020; IUCN 2021).

Four of the species found in the current survey had a higher constant occupancy than they did in the historical survey. *Crinia parinsignifera*, *Cri. signifera*, *Lit. fallax* and *Lit. peronii* have all increased their average occupancy since the historical survey. Another two species; *Lim. peronii* and *U. laevigata* had an average occupancy in the current study similar to that of the historical study. Habitat loss and modification is generally considered a detrimental process for most species (Baker & Lauck 2006). However, it appears that these frog species are able to cope with some anthropogenic disturbance. Habitat generalists, which many of these species are (Anstis 2017), are able to utilise a wide range of habitats (Simpkins *et al.* 2014). Liu *et al.* (2017) found that habitat generalists are more tolerant of anthropogenic disturbance. Further, Callaghan *et al.* (2020) and Keinanth *et al.* (2017) found that it is habitat generalists that are better able to utilise modified habitat. This is likely to be the case for many of the species which increased their naïve occupancy in the current survey. Almost all the sites that were visited were easily accessible and showed some degree of disturbance from either urbanisation or agriculture, favouring habitat generalists. Other species such as *Lim. peronii* are known urban adapters (Hamer & McDonnell 2010). The most common species found, *Cri. signifera*, has been documented to utilise disturbed areas and has a wide range of habitat tolerances including moderate salinity (Hopkins *et al.* 2020), chemical pollution from run-off (Lane & Burgin 2008), noise pollution (Parris *et al.* 2009), habitat modification from logging (Lauck 2005) and chytridiomycosis (Scheele *et al.* 2016). *Crinia signifera* can also utilise shallow ephemeral pools after rain (Anstis 2017). It is likely that the other species which have increased their average occupancy since 1966-1975 share similar tolerances.

There is much in the literature on declining frog populations, but very little about increasing frog populations, outside of pest species (Dejean *et al.* 2012; Letnic *et al.* 2014; Sutherst *et al.* 1996). Another consideration is that the increase in these species occupancy could be a fluctuation. Blaustein *et al.* (1994), highlighted several long-term studies where frog populations have fluctuated, though this focus was predominantly on species which showed evidence of declines. Of interest would be the long-term monitoring of similar habitat-generalist species to see if such trends are the norm. This is especially important for *Cri. signifera* which is a known carrier of *B. dendrobatidis* (Brannelly *et al.* 2018; Burns *et al.* 2021; Scheele *et al.* 2016, 2017; Stockwell *et al.* 2016;). As such, increases in the occupancy of this species and other reservoir hosts will likely impact the occupancy of many other more susceptible species.

Another consideration when comparing the historical average occupancy to the present is the method of recording the presence of each species. The surveys undertaken by Heatwole *et al.* (1995) consisted of collecting individuals for preservation. They did not record species which were calling. When considering this, it is possible that there were species calling at the sites the Heatwole *et al.* (1995) survey team visited, but were not recorded due to difficulties in locating and capturing them. Species which might have been particularly difficult are both *Crinia* species; *Cri. parinsignifera* and *Cri. signifera*, given their small size and cryptic behaviour (Anstis 2017; Hoskin et al. 2015). As such, these species may have had a higher occupancy than was recorded historically.

Seven species found in the current survey have shown a decrease in average occupancy: *Lim. dumerilii*, *Lim. fletcheri*, *Lim. tasmaniensis*, *Lit. dentata, Litoria latopalmata, Lit. verreauxi* and *Lit. wilcoxii*. All seven of these species are listed as being of least concern, with no documented declines (DAWE 2020; Gillespie & Hines 1999; IUCN 2021), which makes these current declines in occupancy now of some relevance. Known causes of amphibian decline in Australia include habitat modification (Lehtinen *et al.*; 1999; MacNally *et al.* 2009), habitat fragmentation (Lehtinen *et al.* 1999; MacNally *et al.* 2009), pollution (Hero & Shoo, 2003), changes to hydrology (Wassens *et al.* 2011; Wilson *et al.* 2013), the Amphibian chytrid fungus (*Batrachochytrium dendrobatidis*) (Berger *et al.* 1998; Blaustein *et al.* 2018; Daszak *et al.* 1999; Daszak *et al.* 2003), invasive predators including fish (Gillespie & Hero, 1999; Gillespie, 2001; Knapp & Mathews, 2000), cane toads (*Rhinella marina*), cats (*Felis catus*) and foxes (*Vulpes vulpes*), and increased levels of UV radiation (Blaustein *et al.* 1998; Broomhall *et al.* 2000; Kiesecker *et al.*, 2001). These causes can be compounded by climate change, causing unpredictable weather patterns, increased evaporation, higher temperatures, and severe weather events such as flooding or drought (Evans *et al.* 2020; Wassens *et al.* 2013).

Declines associated with drought are not simply a matter of adult frog mortality. Although short-term declines are possible, with species recovering once conditions improve (Kupeberg *et al.* 2022), long-term declines induced by drought have also been reported (Evans *et al.* 2020; Osborne 1989; Osborne *et al.* 1999, Scheele *et al.* 2016). Long-term drought, such as the one experienced during this current study, can reduce recruitment (Scheele *et al.* 2016; Wilbur & Rudolf 2006), increase tadpole predation from introduced predators (Gillespie 2001; Scheele *et al.* 2016), produce less fit individuals with compromise immune systems (Kohli *et al.* 2019) and enhance the effects of disease (Kupeberg *et al.* 2022; Leidy *et al.,* 2009; Scheel *et al.* 2016). Long-term droughts result in early pond drying, reducing reproductive success (Scheele *et al.* 2016). Pond drying can result in either complete reproductive failure (Osborne 1989; Scheele *et al.* 2016) or drought stressed tadpoles which become froglets with impaired immune function (Kohli *et al.* 2019). One such case was seen with *Litoria verreauxii alpina*, which showed *B. dendrobatidis* associated declines in conjunction with drought stressors (Osborne 1989; Osborne *et al.* 1999, Scheele *et al.* 2016). These threats are not only limited to ephemeral ponds (Kupeberg *et al.* 2022). Stream intermittency associated with low rainfall, has also been demonstrated to correspond with peaks in *B. dendrobatidis* infection and population declines (Kupeberg *et al.* 2022).

During dry years, breeding success is limited, with a lower number of frogs calling and, consequently, lower numbers of tadpoles and metamorphs (Daszak *et al.* 2005; McCaffery *et al.* 2014; McGinness *et al.* 2014). If offspring recruitment into the population at a site is low, this can severely impact upon the persistence of these species at a site (Daszak *et al.* 2005; Pechmann *et al.* 1991). Since the end of the historical survey in 1975, there have been three drought events which affected the New England Tablelands. These were in 1982-1983, in 2002-2006 and, most recently, in 2017-2019, when the present study was being undertaken (BOM 2022). The occurrence of these events is likely to have challenged the persistence of these species at established sites. Daszak *et al.* (2005) found a similar trend for frog species in South Carolina, USA. Species which had low numbers of recruitment due to a reduced hydroperiod were more likely to be declining (Daszak *et al.* 2005). In an altered landscape, the effects of climate change have been linked to declines in common amphibian species (Hazell 2003; MacNally *et al.* 2009; Piha *et al.* 2007).

Activity, including breeding and movement, for *Lim. fletcheri* and *Lim. dumerilii* is strongly associated with high rainfall, leading to the inundation of flooded habitat (Anstis 2017; McGinness *et al.* 2014; Ocock *et al.* 2014). Littlefair *et al.* (2021) found that there was an increase in the abundance of *Lim. fletcheri* in areas of greater inundation, while McGinness *et al.* (2014) found that in central Victoria, *Lim. fletcheri* populations remained low, with spikes occurring during flooding of suitable habitat. These findings support what was found in the present study, with reduced average occupancy for this species in the period surveyed. The lower average occupancy of *Lim. fletcheri* and other species may have been influenced by the severe drought from 2017-2019, which occurred for all but the last year of the study (Nguyen *et al.* 2021). Nguyen *et al.* (2021) found that of the 36 months of the drought, only three months of that period exhibited normal rainfall in the region of which the New England Tablelands is a part. Further, that same period was the driest recorded for the region (Nguyen *et al.* 2021). Many frog species are reliant on periods of high rainfall and flooding to trigger breeding and other activity (Anstis 2017; Hoskin *et al.* 2015). It is likely that many individuals may have postponed breeding till conditions were more preferable, resulting in a low detectability for some of these species. Due to this, the species which declined in their average occupancy may be underrepresented in the data, given the lower detectability that comes with no breeding activity. Alternatively, given the drought and low water availability at some of the sites, these species may have experienced extirpation of some populations at sites which were severely affected by the low rainfall.

Another species which had a decline in its average occupancy in the current survey, *Lim. tasmaniensis*, is another habitat generalist (Anstis 2017). It can utilise a wide range of modified waterbodies as seen in an agricultural landscape (Hazell *et al.* 2001; Wassens 2006). Further, Woodham *et al.* (2007) reported that this species was resistant to infection from the Amphibian chytrid fungus due to secretions which were active against *B. dendrobatidis*. This makes it unlikely that the modification of the hydrological features of the landscape and the presence of *B. dendrobatidis* in the region will necessarily have a detrimental effect on the occupancy of this species. One possibility is that the drought of 2017-2019 had a negative effect on the occupancy of *Lim. tasmaniensis*. Along with permanent water sites, which were predominantly the sites visited during the present study, *Lim. tasmaniensis* can also utilise ephemeral pools during explosive breeding episodes (Wassens *et al.* 2013; Turner 2021). These episodes are primarily triggered by heavy rainfall during periods when temperatures are suitable for breeding (Anstis 2017; Turner 2021). During the years that the present study was conducted, there was very little precipitation in the region (Nguyen *et al.* 2021). *Limnodynastes tasmaniensis* may have remained in areas of core habitat where water remained to maximise breeding success during a period of low rainfall. Evans *et al.* (2020) determined that declines in *Lim. tasmaniensis* were associated with high maximum temperatures, low minimum temperatures and low rainfall. Such were the conditions during the current study. Potentially, this species could be found to occupy more sites when favourable conditions return to the region (Patla *et al.* 2009; Wassens *et al.* 2013; Turner *et al.* 2021).

Litoria wilcoxii, also had a lower naïve occupancy in the current study compared to the historical survey. A reduction in the occupancy of *Lit. wilcoxii* in the New England Tablelands is unusual in that this species is generally considered common and widespread (Anstis 2017; Donnellan & Mahony 2004; Portway *et al.* 2020) and no declines have previously been recorded (Gillespie & Hines 1999). This seems to be the consensus for the *Lit. wilcoxii* population in the New England Tablelands (Portway *et al.* 2020). The Amphibian chytrid fungus by itself is unlikely to be a significant factor decreasing the occupancy of *Lit. wilcoxii* (Kriger *et al.* 2007). This is further discussed in Section 7.3. Retallick *et al.* (2004) determined that *Lit. wilcoxii* did not show a decline in its population at the same time that two sympatric species, *Rheobatrachus vitellinus* and *Taudactylus eungellensis,* which were susceptible to *B. dendrobatidis* did. Further, Kriger and Hero (2006), and Berger *et al.* (2004) found that *Lit. wilcoxii* individuals were able to clear infections and that it did not appear to reduce survivorship in adults. This ability is thought to coincide with climatic changes, with individuals becoming infected in the cooler months and clearing the infection in the warmer months when the increase in temperature favours the frog by reducing the pathogens survival (Berger *et al.* 2004; Kriger & Hero 2006). Of note, however, is the impact of rising temperatures on the facilitation of *B. dendrobatidis* infection in alpine regions (Pounds *et al.* 2006), given the higher than average temperatures recorded (Nguyen *et al.* 2021). Pounds *et al.* (2006) found that rising temperatures in montane habitat caused local extinctions in high altitude harlequin frogs in Latin America. Kriger and Hero (2004b) conceded that although higher temperatures should reduce pathogenicity of *B. dendrobatidis* given its susceptibility to warmer temperatures, montane species may rely on cold temperatures (<4ºC) to slow fungal growth as diurnal temperatures may never reach a lethal threshold for *B. denrobatidis* in high altitude habitats. This supports the occupancy trend seen in *Lit. wilcoxii* as the occupancy models suggest that this species was more likely to occupy sites on the western side of the New England tablelands, which have lower altitudes and correspondingly higher diurnal temperatures.

Another factor to consider is the impact of invasive predatory species on frogs in the New England Tablelands. Foxes (*Vulpes Vulpes*) and feral cats (*Felis catus*) are present in the region and were spotted at sites during the present study. In studies conducted by Kirkwood *et al.* (2005), by Flemming *et al.* (2021), and by Mitchell and Banks (2005), frogs did not appear to make up a substantial part of the diet for foxes. However, these studies focused on remains found in stomach contents and scats. One problem with this method, is that frog remains may be difficult to detect when sampling predator stomach contents and scats, since frogs do not possess hard keratinised material and their bones are easily dissolved (Egeter *et al.* 2015a; Flemming *et al.* 2021; Woinarski *et al.*2020). As such, it is possible that the importance of frogs in a fox's diet has been underestimated to date.

Table 5.16.3: Frog species detected in the historical study (Heatwole *et al*. 1995), with indications if they were: 1) likely misclassified, 2) had undergone a taxonomic change, 3) were transplanted via anthropogenic processes, 4) had declined greatly, or 5) had a known distribution that was on the margins of the New England Tablelands. NOTE: Frog species in bold were those found in the present study. Frog species with no number indicator and are not in bold were species that are present in the New England Tablelands (Anstis 2017; Hoskin *et al.* 2015) and were expected to be found during the current study.

Adelotus brevis[4]

Crinia parinsignifera

Crinia signifera

Cylcorana brevipes[5]

Cylcorana cultripes[1]

Cyclorana platycephala[1]

Lechriodus fletcherai

Limnodynastes dumerilii

Limnodynastes fletcheri

Limnodynastes peronii

Limnodynastes salmini

Limnodynastes tasmaniensis

Limnodynastes terraereginae

Litoria aurea[4]

Litoria barringtonensis[2]

Litoria booroolongensis[4]

Litoria caerulea

Litoria chloris[5]

Litoria citropa[2]

Litoria dentata

Litoria fallax

Litoria gracilenta[3]

Litoria latopalmata

Litoria peronii

Litoria piperata[4]

Litoria phyllochroa[2]

Litroia rubella

Litoria subglandulosa[2]

Litoria verreauxii

Litoria wilcoxii[2]

Mixophyes balbus

Mixophyes fasciolatus[5]

Mixophyes iteratus[1]

Neobatrachus sudellae

Philora sphagnicola[5]

Platyplectrum ornatum

Pseudophryne australis[1]

Pseudophryne bibronii[4]

Pseudophryne coriacea

Uperoleia laevigata

Uperoleia rugosa

There are several reasons that feral cats may be a significant problem for frog species in the New England Tablelands. Firstly, frogs can make up a large part of a feral cat's diet (Doherty *et al.* 2015; Hernandez *et al.* 2018; McGregor *et al.* 2017), particularly during periods of high abundance such as during an explosive breeding event (Liberg 1984; McGregor et al. 2015; Molsher *et al.* 1999). Secondly, cats are often more active during the warmer months (Hernandez *et al.* 2018), when many frog species are undertaking breeding activity (Anstis 2017; Hoskin *et al.* 2015). Finally, it is the general consensus that feral cats will continue to hunt, even after feeding, and that these supplementary hunts are often not consumed (Egeter *et al.* 2015b; Hernandez *et al.* 2018; McGregor *et al.* 2015). This means that, for many frogs species, breeding behaviour makes them susceptible to hunting cats. Doherty *et al.* (2015) documented the successful capture and consumption by cats of several species of frog found in the New England Tablelands, namely *Cri. signifera*, *Lim. dumerilii*, *Lim. Fletcheri*, *Lim tasmaniensis*, *Lit. caerulea*, *Lit. fallax*, *Lit. latopalmata*, *Lit. peronii*, *Lit. rubella*, *Neobatachus sudelli* and *Platyplectrum ornatum*. A further consideration is that hunting success for feral cats is greater in less complex habitats, such as those modified for agriculture, or open wetlands with shallow water (McGregor *et al.* 2015, 2017). Such habitats are common in the New England Tablelands (Sahukar *et al.* 2003), with many of the sites visited in this survey close to or associated with agricultural enterprises.

The cane toad is another invasive species which could potentially affect frog species in the New England Tablelands. The effect of cane toads on native frogs is often complex and is not only limited to predation of native frogs by this species (Shine 2014). All stages of cane toad development are poisonous, leading to mortality in individuals which consume part of the eggs, tadpoles, metamorphs or adults (Crossland 2000; Crossland & Alford 1998; Crossland & Shine 2010; Greenlees *et al.* 2010). Further, cane toads are more fecund than native frog species (Tyler 1994; Shine 2014) and consume a greater amount of food (Crossland *et al.* 2009; Greenlees *et al.* 2007; Shine & Wiens 2010). As such, cane toad tadpoles can outcompete native tadpoles for food at sites where they are both present (Alford 1999; Williamson 1999). Williamson (1999) observed that *Lim. tasmaniensis* tadpoles grew slower and tadpole survival was reduced in the presence of cane toad tadpoles. No cane toads were recorded in the current study.

According to Anstis (2017) and Hoskin *et al.* (2015) their current distribution does include the New England Tablelands, although these have been stray individuals brought through anthropogenic practices then breeding populations. The impacts of invasive fish, particularly the plague minnow, *Gambusia holbrooki*, will be addressed in a later section of this thesis (see Section 6.3).

Another potential impact on the average occupancy of some of these species is that of pesticide and herbicide use (Spolyarich *et al.* 2010), although this is less likely given the low relative proportion of cropping systems in the region compared to grazing practices (Department of Agriculture, Water and the Environment [ABARES] 2021). Pesticides reduce fitness through the malformation of limbs inhibiting mobility of individuals, and limit reproductive success and recruitment through changes in sex ratios and feminisation of males (Hayes *et al.* 2003; McCoy *et al.* 2008; Taylor *et al.* 2005). Spolyarich *et al.* (2010) found that the presence of herbicides and pesticides associated with cropping led to an increase in limb malformation for *Lim. fletcheri*, though there was less evidence of modification to male genitalia. The present study did not record pesticide or herbicide use, so cannot comment on the prevalence of such pesticide and herbicide used at the sites visited. Neither was any limb malformations noted in the individuals that were observed, although auditory detection was the principal way to determine presence.

There were five species that were present at a small number of sites. These species were *Litoria barringtonensis*, *Litoria caerulea*, *Litoria subglandulosa*, *Mixophyes balbus* and *Pseudophryne coriacea*. The numbers of detections for these species were too low for occupancy models to converge. As such, naïve estimates of occupancy for the historical survey were compared to the naïve estimates of the current study instead of average occupancy. Three of these species, *Lit. barringtonensis*, *Lit. subglandulosa* and *M. balbus* are dedicated stream breeders. It is on record that *M. balbus* has disappeared from many of the sites in Victoria which had previously been found (Gillespie *et al*. 2014). In relation to this, Amphibian chytrid fungus is thought to be the most likely cause of decline for *M. balbus* and other stream breeding frogs (Gillespie *et al*. 2014; McDonald et al. 2012; Pounds *et al*. 2006), with other factors such as habitat loss, fragmentation and alteration or invasive fish being other valid causes (Gillespie & Hines 1999; Gillespie *et al*. 2011;).

Suitable breeding habitat is typically an important factor for occupancy of stream breeding frogs (Gillespie *et al* 2014). Loss of stream-side vegetation, logging close to stream banks, alteration to stream flow or water quality, habitat fragmentation and introduced fish are all thought to contribute to declines in many stream breeding species (Gillespie & Hines 1999; Hazell 2003; McDonald *et al.* 2012). Since the naïve occupancies of *M. balbus* and *Lit. subglandulosa* do not appear to have declined since the historical survey, it could be assumed that there is still some acceptable habitat available for these species to occupy and utilise for breeding in the New England Tablelands. However, those species should not be considered secure or stable in the New England Tablelands, given the small number of detections for these species, the correspondingly low naïve occupancy in the current study and that a stream breeder with similar habitat requirements, *Lit. barringtonensis* has shown a decrease in naïve occupancy in the current study than that recorded for the historical. A further consideration in relation to *Lit. subglandulosa* and *Lit. barringtonensis* is that they both have a restricted distribution (Anstis 2017; Hoskin et al. 2015). Species with narrow geographical ranges are more likely to face decline than would those with wider ranges (Murray & Hose 2005). An interesting feature of the occupancy of *M. balbus*, is that the larval stage (tadpole) is the most conspicuous stage of this species (Gillespie *et al.* 2014). In both the present and historical studies, focus was on the adult form, so it is possible that occupancy of *M. balbus* is under-represented in both studies.

Pseudophryne coriacea was another frog species that was found at only a small number of sites. *Pseudophryne coriacea* exhibits cryptic behaviour, with males building concealed nests in moist soil and leaf litter from where they call (Anstis 2017; Bryne & Keogh 2007; O'Brien *et al.* 2018). Of critical importance for this species is the moisture level in these nests, with drier nests leading to reduced calling by males (Mitchell 2001; O'Brien *et al.* 2020; O'Brien *et al.* 2018). Presumably, this is associated with the increased risk of desiccation for the calling male as they remain in their nests without access to external water sources (O'Brien *et al.* 2020). As such, breeding activity, when males of *Pse. coriacea* would be most conspicuous through calling, is associated with rainfall events (O'Brien *et al.* 2018). It is possible that the reduced rainfall for the period, as previously discussed, limited this species from undertaking breeding events, leading to low detectability at sites at which it might usually be present.

Finally, during the present study, *Litoria caerulea* was found to be present at only a few sites. Generally, activity (breeding, foraging and dispersal) of *Lit. caerulea* is influenced by local weather conditions, mostly long-term rather than short-term rainfall (Ocock *et al.* 2014). The majority of the present study was conducted under drought conditions, where rainfall was universally low for the region (Nguyen *et al.* 2021), so it is possible that activity for this species was reduced, making them less conspicuous and causing a larger number of absences for this species that did not reflect the actual situation.

Another issue to consider in relation to *Lit. caerulea* is that of anthropogenic disturbance, particularly noise from traffic (Kaiser *et al.* 2015). Noise from traffic has been shown to impact breeding in some species by masking the calls of males from females (Kaiser & Hammers 2009; Kaiser *et al.* 2011), inhibiting breeding migration (Tennessen *et al.* 2014) as well as triggering a stress response (Kaiser *et al.* 2015; Tennessen *et al.* 2014). Kaiser *et al.* (2015) found an increase in stress hormones, primarily cortisol, and a decrease in sperm count and viability in individuals exposed to higher levels of anthropogenic sound. Many of the sites surveyed were within 100 m of roads, which may have had the effect of reducing breeding success for *Lit. caerulea* at these sites and therefore inhibiting recruitment and persistence as the years progressed.

At present, *Lit. caerulea* is not considered a threatened species, given its wide distribution. However, there have been reports of widespread mass deaths of this species, and many others, of which the driving force behind this is as yet to be explicitly confirmed (Australian Museum 2017; Rowley & Rose 2021). Some suggestions for the cause behind this, is the ever-present Amphibian chytrid fungus or some other pathogen in concert with climatic conditions (Rowley & Rose 2021). A pathogen induced decline is probable for this species since *Lit. caerulea* is susceptible to *B. denrobatidis* infection, often followed by a high rate of mortality (Woodhams *et al.* 2007; Young *et al.* 2012) and a *B. dendrobatidis* induced decline has been recorded in the past (Berger *et al.* 2004). Sudden population declines, as seen recently in *Lit. cearulea*, could be the influence of the Amphibian chytrid fungus with the extra stressors preceding from the drought. Pounds *et al.* (2006) and

Laurence (2008) found that higher mean minimum temperatures predispose montane amphibian populations in rainforest habitat to a higher infection chance and increased mortality from *B. dendrobatidis*. These findings are supported by Daszak *et al.* (2003), Berger *et al.* (2004) and Piotrowski *et al.* (2004), who determined *B. dendrobatidis* grows best from 16 to 25^{o}C, can survive in temperatures as low as 4^{o}C, stops growing at 28^{o}C and dies at 30^{o}C. Therefore, daily temperatures within the peak growth temperatures would encourage higher infection intensity in affected individuals, leading to greater mortality. In the New England Tablelands, maximum daily temperatures rarely consistently reach higher than 30^{o}C, though minimum temperatures can and often do fall below 4^{o}C (BOM 2021), providing some support for temperature induced chytrid declines in the region. A further consideration with temperature-induced chytrid decline, is the higher temperatures associated with the drought from 2017-2019, which may have induced stress in individuals, making them more susceptible to disease in general (Pounds *et al.* 2006), though these high temperatures would also reduce survivorship for *B. dendrobatidis*.

There were 21 species that were not found in the present survey but were present at the time of the historical survey (Table 5.16.3). These were the tusked frog (*Adelotus brevis*), the short-footed frog (*Cyclorana brevipes*), the knife-footed frog (*Cyclorana cultripes*), the water-holding frog (*Cyclorana platycephala*), Fletcher's frog (*Lechriodus fletcherai*), the salmon-striped frog (*Limnodynastes salmini*), the northern banjo frog (*Limnodynastes terraereginae*), the green and golden bell frog (*Litoria aurea*), the Booroolong frog (*Litoria booroolongensis*), the red-eyed tree frog (*Litoria chloris*), the dainty green tree frog (*Litoria gracilenta*), the peppered tree frog (*Litoria piperata*), the red tree frog (*Litoria rubella*), the great barred frog (*Mixophyes fasciolatus*), the giant barred frog (*Mixophyes iteratus*), Sudell's frog (*Neobatrachus sudellae*), the sphagnum frog (*Philoria sphagnicola*), the ornate burrowing frog (*Platyplectrum ornatum*), the red-crowned toadlet (*Pseudophryne australis*), Bibron's toadlet (*Pseudophyryne bibronii*) and the wrinkled toadlet (*Uperoilea rugosa*). This finding is similar to that of MacNally *et al.* (2009) who, during their study in Central Victoria, detected only seven of 15 species that had been recorded previously.

Cyclorana cultipes, *Cyc. Platycehpala*, *M. iteratus* and *Pse. australis* are likely misclassifications and would therefore have been unlikely to be found during the present study (see Section 3.1.1). Similarly, *Lit. gracilenta* was most likely an anthropogenic transplant at the time of the historical survey or another misclassification. There were four species, *Lec. fletcheri*, *Lit. chloris*, *M. faciolatus* and *Phi. sphagnicola*, which were unlikely to be found in the present study given the very small overlap in their distribution that these species have with the New England Tablelands region (see Section 3.1.3). This low likelihood of detections was likely to be compounded to some extent by the drought of 2017-2019. The eastern edge of the New England Tablelands, where all these three species' limited distributions are, were sampled during the second year of the drought (2018-2019), when it was most severe (Nguyen *et al.* 2021).

Of further note is the susceptibility of these species to the Amphibian chytrid fungus (Berger *et al*. 2004; Murray & Hose 2005; Ohmer *et al*. 2017; Woodhams *et al*. 2007). Both *Lit. chloris* and *M. fasciolatus* are susceptible to *B. dendrobatdidis*, although have not recorded declines (Berger et al. 2004; IUCN 2022; Woodhams *et al*. 2007). The susceptibility of *Lec. fletcheri* and *Phi. sphagnicola* to *B. dendrobatidis* is yet to be determined (Murray & Hose 2005; Ohmer *et al*. 2017).

Along with the *Cyclorana* species, there were another four burrowing frog species found in the historical survey which were not found in the present survey. These were *Lim. salmini*, *Lim terreaginae*, *N. sudellae* and *Pla. ornatum* (Heatwole *et al.* 1995), and all four species are believed to have their distribution in at least some part of the New England Tablelands (Anstis 2017; Hoskin *et al.* 2015). Activity (breeding, foraging and dispersal) of burrowing frog species is linked to meteorological conditions, primarily temperature (Ocock *et al.* 2014), rainfall (Ocock *et al.* 2014; Paltridge & Southgate 2001; Penman *et al.* 2006) and humidity (Penman *et al.* 2006; Wassens *et al.* 2013). This makes these species particularly difficult to observe during periods of low rainfall (Penman *et al.* 2006), as seen during the period the present study was conducted (Nguyen *et al*. 2021).

The alteration of the hydrological environment by agricultural practices (creation of dams, diversion of rivers for irrigation and the creation of drainage channels and reservoirs) has generated large numbers of similar habitats with greater water permanence (MacNally *et al.* 2009). This shift in land management has created an environment which has changed the dispersal ability of many species which is to the advantage of some species and the disadvantage of others (Hazell 2003; Hazell *et* *al.* 2003). MacNally *et al.* (2009) and Wassens *et al.* (2013) found that it is the frog species that are habitat generalists, rather than burrowing frog species, which dominate in a landscape modified by agriculture, especially after periods of extended drought as occurred during the period 2017-2019 (Nguyen *et al*. 2021). This is supported by what was found in the present study, as only one burrowing species, *Lim. dumerilii,* was found and this species was recorded as having a lower average occupancy in the present study, than was recorded for the historical study.

The impact of the 2017-2019 drought coupled with the alteration of the hydrological environment was likely to have also affected *Lit. rubella* and *U. rugosa*. Both these species are widely distributed throughout the New England Tablelands (Anstis 2017; Hoskin *et al*. 2015). However, breeding activity, when these two species are most likely to be detected, occurs in ephemeral pools after a heavy rain event (Anstis 2017; Hoskin *et al*. 2015). The low and unreliable amount of rain during the survey period (Nguyen *et al*. 2021), may have been insufficient to trigger breeding for these species. It is also possible that given their short breeding period, the sites at which they were breeding at were not visited during this window. Ceron *et al*. (2020) determined that explosive breeders such as *U. rugosa* and *Lit. rubella* (Anstis 2017; Hoskin *et al*. 2015), have shorter breeding events. Opportunistic sampling after rain, which was not part of the sampling method used in the present study, could have improved detectability of *Lit. rubella* and *U. laevigata*.

Of most particular concern are the apparent disappearances of the tusked frog (*A. brevis*), the Booroolong frog (*Lit. boorolongensis*) and Bibron's toadlet (*Pse. bibronii*). These three species were common when the historical survey was conducted (Heatwole *et al.* 1995) and other reports noted that they were also common and secure before the 1990s (Barker 1995; Gillespie & Hines 1999; Mahony 1999; Tyler 1992). The decline of *Lit. booroolongensis* in the New England Tablelands is well documented (Clulow *et al.* 2009; Gillespie 2000; Hunter *et al.* 2018; Hunter & Smith 2013; Spark 2020; Tyler 1992), with only a recent, single report of a small population still existing at a single site in the New England Tablelands (Rowley & Cutajar 2017). Similarly, in recent years both *A. brevis* and *Pse. bibronii* appear to have declined significantly in the New England Tablelands (Anstis 2017; Gillespie & Hines 1999; Hunter *et al.* 2018; Mahony 1999; Thumm & Mahony 1997). The causes of the declines of *A. brevis* and *Pse. bibronii* in the New

England Tablelands has not been completely established (Howard *et al.* 2010; Mahony 1999; McDonald *et al.* 2012), although the threats facing them are thought to be similar to those facing *Lit. booroolongensis*. A fourth species, the green and golden bell frog (*Litoria aurea*), was also thought to be widespread and secure (Mahony 1999; White & Pyke, 1996), but was not as common during the historical survey (Heatwole *et al.* 1995). Another species, the peppered tree frog (*Litoria piperata*), was uncommon during the historical survey and is possibly extinct in the New England Tablelands (see Section 3.1.2) (Anstis 2017; Gillespie & Hines 1999).

Suggested threats to these five species include the Amphibian chytrid fungus (Hamer *et al.* 2010; McFadden *et al.* 2010; Mahony 1999; Spark 2020), habitat loss and alteration (Gillespie & Hines 1999; Hunter & Smith 2013; Hunter *et al.* 2018; Mahony 1999; McFadden *et al.* 2010; Spark 2020), introduced fish (Gillespie & Hero 1999; Hunter *et al.* 2011; Hunter & Gillespie 1999; McFadden *et al.* 2010; Mahony 1999; Spark 2020), invasive weeds (Hunter & Gillespie 1999; Hunter & Smith 2013; McFadden *et al.* 2010; Spark 2020) and the reduction and disappearance of available water at waterbody sites (Hunter & Smith 2013; McFadden *et al.* 2010; Spark 2020).

The high susceptibility of these species to *B. dendrobatidis* is predominantly based on their decline at sites that are relatively pristine with little in the way of habitat disturbance (Gillespie & Hines 1999; Howard *et al.* 2010; Mahony 1999; McDonald *et al.* 2012). Testing for the susceptibility of *Lit. booroolongensis* to the Amphibian chytrid fungus, showed that this species was only moderately susceptible (Cashins *et al*. 2013). However, these relatively recent experiments were on individuals that may have inherited some level of resistance from previous *B. dendrobatidis* survivors (Cashins *et al.* 2013). *Litoria aurea* is also susceptible to infection by *B. dendrobatidis,* with a high mortality rate if left untreated (Mahony *et al.* 2013; Stockwell *et al.* 2010). This provides support for *B. dendrobatidis* being a major contributor to *Lit. aurea* decline. McDonald *et al.* (2012) also suspected that the Amphibian chytrid fungus played a part in the decline of *A. brevis*, as dead and dying individuals were positive for *B. dendrobatidis*. The susceptibility of *Pse. bibronii* to *B. dendrobatidis* has not been experimentally addressed and remains a consideration for future study. Of further importance is that most of the sites visited contained frog species that are known carriers of the Amphibian chytrid fungus; *Lit.*

fallax and Cri. signifera, potentially acting as a reservoir for the fungus at sites that were revisted during the current study (Burns *et al.* 2021; Scheele *et al.* 2016).

The suitability of habitat for *Lit. booroolongensis* is critical for its persistence in the New England Tablelands. For successful breeding, *Lit. booroolongensis* requires rocky crevices to deposit eggs (Hunter & Smith 2013). Sedimentation, stream erosion and stream drying, along with encroachment of vegetation into rocky banks degrade stream habitats, making them unsuitable for successful breeding of *Lit. booroolongensis* (Hunter & Gillespie 1999; Hunter & Smith 2013).

There is some conflict in the literature as to the impact of habitat alteration through urbanisation on *A. brevis* and *Lit. aurea*. Gillespie and Hines (1999), and Hines *et al.* (1999) suggests that habitat loss through land clearing of suitable habitat for *A. brevis* is a major threat, while Lemckert (1999) determined that this species was dependent on patches of undisturbed forest. However, McDonald *et al.* (2012) observed that this species could utilise highly modified and man-made habitats. *Litoria aurea* is also known to utilise modified still water habitat and will persist at sites that have undergone a great degree of disturbance (Mahony 1999). Size of the waterbody, connectivity to other breeding sites and availability of terrestrial vegetation in the surrounding area are considered more important predictors for *Lit. aurea* occupancy than the extent of disturbance (Hamer & Mahony 2010; Hamer *et al.* 2002a; Hamer *et al.* 2008; Heard *et al.* 2012; Pyke & White 1996; Pyke *et al.* 2002). *Pseudophryne bibronii* has specific habitat requirements for breeding being a terrestrial egg-laying species (Anstis 2017; Hoskin *et al.* 2015; Wassens *et al.* 2013). As such, clearing for housing, intensive agriculture, overgrazing, changes to hydrology, construction of new roads and tracks, logging, and firewood collection could have the effect of reducing availability of suitable nesting sites for *Pse. bibronii* (Howard *et al.* 2010). As almost all of the sites visited in the current study were sites with some degree of disturbance, it is possible that these species may still yet occupy protected isolated sites in the New England Tablelands that have not been greatly disturbed.

Another consideration is the presence of invasive fish in the region. Hunter *et al*. (2011) found that redfin perch (*Perca fluviatilis*) and the eastern mosquito fish, (*Gambusia holbrooki*), both of which are present in the New England Tablelands (Department of Primary industries NSW [DPI] 2022), will consume the tadpoles of

Lit. booroolongensis, while Pyke and White (1996) found a similar predation of *G. holbrooki* on *Lit. aurea* tadpoles. Gillespie and Hero (1999) have suggested that the presence of *G. holbrooki* contributed to the decline of *A. brevis*, although experimental studies have not yet been undertaken to verify predation of *A. brevis* tadpoles by *G. holbrooki*.

Finally, the effects of water availability in river systems likely reduced survivorship of *Lit. booroolongensis* over time. Long-term factors affecting water availability include the creation of dams and the diverting of water for agriculture. Spark (2020) found that *Lit. booroolongensis* was abundant at areas of inflow from a river into a dam, but were absent at sites below dam walls. This suggests that the alteration to the river flow following a dam may reduce survivorship of individuals at that site. Another consideration with water flow is that of drought. Extended droughts can greatly reduce frog populations (Piha *et al.* 2007). Given the reportedly low numbers of *Pse. bibronii*, *A. brevis*, *Lit. booroolongensis* and *Lit. aurea* in recent years, it is unlikely that the most recent drought of 2017-2019 could have influenced these declines. However, previous droughts may have contributed to the decline of populations already under stress from the other factors discussed. This is supported by Hunter and Smith (2006), who reported a local extinction of a *Lit. booroolongensis* population in Maragle creek, Victoria during the 2006 drought. Also, Hazell *et al.* (2003) linked large scale declines of both *Pse. bibronii* and *Lit. aurea* in southern NSW to severe droughts lasting longer than two years.

Chapter 6: Single-season, Two-species Occupancy Analysis

6. Single-season, Two-species Occupancy Analysis

6.1 Data Analysis

In this chapter, a second single-season, single-visit occupancy model (Mackenzie *et al*. 2004) was used to assess the influence of occupancy of *Crinia signifera* on the other 12 frog species found in the current survey. Co-occurrence of this species with other frog species was of particular interest because *Cri. signifera* is a known carrier of the Amphibian chytrid fungus (*Batrachochyytrium dendrobatidis*, Scheele *et al.* 2016). Further, *Cri. signifera* is a habitat generalist that utilises a wide range of waterbody types (Anstis 2017), suggesting that this species may overlap in habitat choice with other frog species found in the New England Tablelands. It would be of interest to determine if the presence of such a species has resulted in the absence or low co-occurrence of other frog species found in the New England Tablelands at sites that *Cri. signifera* also occupies.

Models were also created to compare co-occurrence of 13 frog species with another possible key species, the invasive fish *Gambusia holbrooki*. There have been many reports of invasive fish species being predators of tadpoles (Hamer *et al.* 2021, Remon *et al.* 2016, Shulse *et al.*2013). *Gambusia holbrooki*, is a common invasive fish in the New England Tablelands, which has been reported prey upon the tadpoles of *Litoria latopalmata*, *Platyplectrum ornatum*, *Limnodynastes peronii*, *Litoria dentata* and *Litoria peronii*, and both the tadpoles and eggs of *Litoria aurea* (Hamer *et al.* 2021). Understanding whether or not the presence of predatory fish species is associated with absences of adult frogs at sites will aid in conservation efforts.

6.1.1 *Crinia signifera* Comparisons

For the analyses, *Cri. signifera* was labelled species A and the other frog species tested with it was labelled species B. In relation to this, the co-occurrence parameterisation used assumes that one species (species A) is the dominant species and the other (species B) is the subdominant species (Richmond *et al.* 2010). The aim of the analysis was to explore the influence of *Cri. signifera* on the occupancy of the other frog species in the New England Tablelands. Therefore, it makes sense to analyse these data with *Cri. signifera* as the dominant species.

As was the case with the single-species, single season models developed in Chapter 5, the program **PRESENCE 7.1** was used to create the data files that were then analysed using the R package **RPresence**. The standard single-species model was expanded by incorporating the covariates which were chosen from the preferred single-species model analysis in Chapter 5 for the frog species in each anlaysis. Principally, these covariates were longitude ($LONG$), latitude (LAT), altitude (ALT), still waterbody (sW), running waterbody (rW), emergent vegetation (emV), riparian vegetation ($ripV$) and presence of livestock (C). The decision to include these covariates was based on the final single-species occupancy model for each of the frog species as described in Chapter 5. An additional covariate, occupancy of *Cri. signifera* (sigO), was also included in the models. The occupancy of *C. signifera* was calculated for each of the sites, using the occupancy equation described in Chapter 5 and the habitat covariates recorded form each site. This fitted probablity of occupancy was included in the models for the other frog species as a covariate for occupancy fo the second frog species.

Five models were tested along with models which included covariate data and, in some cases, an interaction between covariate data and the fitted probability of occupancy for *Cri. signifera*. No interactions between geographical covariates (LAT, $LONG$, ALT) and fitted occupancy of *Cri. signifera* were tested, nor with *Cri. signifera* and presence of liverstock (C), as it was deemed that the influence of these covaraites on the second species were unlikely to vary whether *Cri. signifera* was present or not. If the main effects of vegetation and waterbody type were important influences of occupancy for the second frog species, interactions were fitted between waterbody type (sW, rW) and fitted occupancy of *Cri. signifiera,* and vegetation type (emV, $ripV$) and fitted occupancy of *Cri. signifera*.

Included in the modelling for detection were the covariates determined in Chapter 5 that were found to influence the detection of each species. For an example of a suite of two-species models including *Cri. signifera* and another frog species, see Table 6.1.2. A similar calculation was made for the fitted detection of

Cri. signifera at each of the sites for each of the sampling occasions (*sigD*). No interactions were included between the environmental covariates and fitted detection of *Cri. signifera*. These values were included as a covariate for detection. A description of the five standard models and an example of an interaction model are given in Table 6.1.1.

Table 6.1.1: Example of a suite of variable occupancy, constant detection models containing x_n covariates, the fitted occupancy of *Crinia signifera* (*sigO*) and the fitted detection of *Cri. signifera* (*sigD*). NOTE: not all suites of models included interaction models, only those which also contained the covariates; *sW*, *rW, emV* or *ripV*.

Model	Model formula
1	$\Psi(.), p(.)$
2	$\Psi(x_1 + ... + x_n), p(x_1 + ... + x_n)$
3	$\Psi(x_1 + ... + x_n + sigO), p(x_1 + ... + x_n)$
4	$\Psi(x_1 + ... + x_n), p(x_1 + ... + x_n + sigD)$
5	$\Psi(x_1 + ... + x_n + sigO), p(x_1 + ... + x_n + sigD)$
6	$\Psi(x_1 + ... + x_n + sigO + x_n{:}sigO), p(x_1 + ... + x_n + sigD)$

Model selection was based on *AIC*, with the model with the smallest *AIC* value being considered the preferred, most parsimonious model. For the situation where there are competing models for which $\Delta AIC \leq 2.00$, the simplest model in a group of nested models was deemed to be the preferred model because there was not enough evidence to support acceptance of the more complex models with more covariates. If the preferred model, was one where *sigO* was not included, occupancy for the second species was deemed to be independent of the occupancy of *Cri. signifera*. The same determination was made for detection. That is, if the preferred model, was one where *sigD* was not included, detection for the second species was deemed to be independent of the detection of *Cri. signifera*.

The final preferred models were used to develop logistic regression models of occupancy for each of the second species modelled with *Cri. signifera*. The base logistic regression model with a logit link for the inclusion of covariate information for the probability of occupancy at a potential site can be calculated with:

$$logit\ (\Psi^{A}) = ln(\frac{\psi^{A}}{1-\psi^{A}}) = 0.30 + 1.97LONG - 1.08ALT + 1.43emV \quad \text{(Eq. 6.01)}$$

$$logit\ (\Psi^{Ba}) = ln(\frac{\psi^{Ba}}{1-\psi^{Ba}}) = \beta_0 + \beta_1 x_1 + \cdots + \beta_n x_n \quad \text{(Eq. 6.02)}$$

$$logit\ (\Psi^{BA}) = ln(\frac{\psi^{Ba}}{1-\psi^{Ba}}) = \beta_2 + \beta_3 x_3 + \beta_4 sigO + \cdots + \beta_k x_k \quad \text{(Eq. 6.03)}$$

where, Ψ^{A} is the probability of occupancy for *Cri. signifera* generated from the preferred model in Chapter 5, Ψ^{Ba} is the probability of occupancy for species B, given *Cri. signifera* is absent, Ψ^{BA} is the probability of occupancy for species B, given *Cri. signifera* is present, β_0 is the base coefficient for occupancy of species B when *Cri. signifera* is absent, β_1 is the coefficient for the effect of a habitat covariate x_1 when *Cri. signifera* is absent, β_2 is the base coefficient for occupancy of species B when *Cri. signifera* is present, β_3 is the coefficient for the effect of a habitat covariate x_3 when *Cri. signifiera* is present, β_4 is the coefficient for the effect of *Cri. signifera* on occupancy of species B.

The final preferred models can also be used to develop logistic regression models of detection for the two species. The base logistic regression model with a logit link for the probability of detection at a potential site can be calculated with:

$$logit\ (p^{A}) = ln(\frac{p^{A}}{1-p^{A}}) = 2.80 - 0.23AT + 2.07H \quad \text{(Eq. 6.04)}$$

$$logit\ (p^{Ba}) = ln(\frac{p^{Ba}}{1-p^{Ba}}) = \beta_0 + \beta_1 x_1 + \cdots + \beta_n x_n \quad \text{(Eq. 6.05)}$$

$$logit\ (p^{BA}) = ln(\frac{p^{Ba}}{1-p^{Ba}}) = \beta_2 + \beta_3 x_3 + \beta_4 sigO + \cdots + \beta_k x_k \quad \text{(Eq. 6.06)}$$

Where p^{A} is the probability of detection for *Cri. signifera*, p^{Ba} is the probability of detection for species B, given *Cri. signifera* is absent, p^{BA} is the probability of detection for species B, given *Cri. signifera* is present, β_0 is the base coefficient for detection of species B when *Cri. signifera* is absent, β_1 is the coefficient for the effect of an environmental covariate x_1 when *Cri. signifera* is absent, β_2 is the base coefficient for the detection of species B when *Cri. signifera* is present, β_3 is the coefficient for the effect of an environmental covariate x_3 when *Cri. signifiera* is present, β_4 is the coefficient for the effect of *Cri. signifera* on detection of species B.

6.1.2 *Gambusia holbrooki* Comparisons

The same general method used for the *Cri. signifera* two-species analysis was used for the *G. holbrooki* two-species analysis. The two methods differed in that a single-season, single-species was initially fitted for *G. holbrooki*. The procedure for fitting an occupancy model for *G. holbrooki*, followed the same process as that described in Chapter 5 for the other single-season, single-visit occupancy models generated for the 18 frog species. The fitted occupancy and detection values were calculated from the preferred model and used in the same fashion as those for *Cri. signifera*. As such, five *a priori* models were created and tested using AIC to find the preferred model (Table 6.1.2).

Table 6.1.2: Example of a suite of variable occupancy, constant detection models containing x_n covariates, the fitted occupancy of *Gambusia holbrooki* ($gamO$) and the fitted detection of *G. holbrooki* ($gamD$). NOTE: not all suites of models included interaction models, only those which also contained the covariates; sW, rW, emV or $ripV$.

Model	Model formula
1	$\Psi(.), p(.)$
2	$\Psi(x_1 + ... + x_n), p(x_1 + ... + x_n)$
3	$\Psi(x_1 + ... + x_n + gamO), p(x_1 + ... + x_n)$
4	$\Psi(x_1 + ... + x_n), p(x_1 + ... + x_n + gamD)$
5	$\Psi(x_1 + ... + x_n + gamO), p(x_1 + ... + x_n + gamD)$
6	$\Psi(x_1 + ... + x_n + gamO + x_n{:}gamO), p(x_1 + ... + x_n + gamD)$

Model selection followed the same process that was use for *Cri. signifera.* If the preferred model, was one where $gamO$ was not included, occupancy for the second species was deemed to be independent of the occupancy of *G. holbrooki*. The same determination was made for detection. That is, if the preferred model, was one where $gamD$ was not included, detection for the second species was deemed to be independent of the detection of *G. holbrooki*.

The final preferred models were used to develop logistic regression models of occupancy for each of the second species modelled with *Cri. signifera*. The base logistic regression model with a logit link for the inclusion of covariate information for the probability of occupancy at a potential site can be calculated with:

$$logit\ (\Psi^{A}) = ln(\frac{\psi^{A}}{1-\psi^{A}}) = \beta_0 + \beta_1 x_1 + \cdots + \beta_n x_n \qquad \text{(Eq. 6.07)}$$

$$logit\ (\Psi^{Ba}) = ln(\frac{\psi^{Ba}}{1-\psi^{Ba}}) = \beta_2 + \beta_3 x_3 + \cdots + \beta_j x_j \qquad \text{(Eq. 6.08)}$$

$$logit\ (\Psi^{BA}) = ln(\frac{\psi^{Ba}}{1-\psi^{Ba}}) = \beta_4 + \beta_5 x_5 + \beta_6 gamO + \cdots + \beta_k x_k \qquad \text{(Eq. 6.09)}$$

where, Ψ^{A} is the probability of occupancy for *G. holbrooki* generated from the preferred single-season, single-visit model, Ψ^{Ba} is the probability of occupancy for species B, given *G. holbrooki* is absent, Ψ^{BA} is the probability of occupancy for species B, given *G. holbrooki* is present, β_0 is the base coefficient for occupancy of *G. holbrooki*, β_1 is the coefficient for the effect of a habitat covariate x_1 for *G. holbrooki*, β_2 is the base coefficient for occupancy of species B when *G. holbrooki* is absent, β_3 is the coefficient for the effect of a habitat covariate x_3 when *G. holbrooki* is absent, β_4 is the base coefficient for occupancy of species B when *G. holbrooki* is present, β_5 is the coefficient for the effect of a habitat covariate x_3 when *G. holbrooki* is present, β_6 is the coefficient for the effect of *G. holbrooki* on occupancy of species B.

The final preferred models can also be used to develop logistic regression models of detection for the two species. The base logistic regression model with a logit link for the probability of detection at a potential site can be calculated with:

$$logit\ (p^{A}) = ln(\frac{p^{A}}{1-p^{A}}) = \beta_0 + \beta_1 x_1 + \cdots + \beta_n x_n \qquad \text{(Eq. 6.10)}$$

$$logit\ (p^{Ba}) = ln(\frac{p^{Ba}}{1-p^{Ba}}) = \beta_2 + \beta_3 x_3 + \cdots + \beta_n x_n \qquad \text{(Eq. 6.11)}$$

$$logit\ (p^{BA}) = \ ln(\frac{p^{Ba}}{1-p^{Ba}}) = \ \beta_4 + \beta_5 x_5 + \beta_6 sigO + \cdots + \beta_k x_k \qquad \text{(Eq. 6.12)}$$

Where p^A is the probability of detection for *G. holbrooki*, p^{Ba} is the probability of detection for species B, given *G. holbrooki* is absent, p^{BA} is the probability of detection for species B, given *G. holbrooki* is present, β_0 is the base coefficient for detection of *G. holbrooki*, β_1 is the coefficient for the effect of a habitat covariate x_1 for *G. holbrooki,* β_2 is the base coefficient for detection of species B when *G. holbrooki* is absent, β_3 is the coefficient for the effect of a habitat covariate x_3 when *G. holbrooki* is absent, β_4 is the base coefficient for detection of species B when *G. holbrooki* is present, β_5 is the coefficient for the effect of a habitat covariate x_3 when *G. holbrooki* is present, β_6 is the coefficient for the effect of *G. holbrooki* on detection of species B.

6.2 Results

Single-species, single-season analysis models were developed for the co-occurrence of *Crinia signifera* with the other frog species found in the current study. A second set of single-species, single-season models were developed for the co-occurrence of *Gambusia holbrooki* and all frog species found in the current study. For the development of these models, *Litoria barringtonensis*, *Litoria caerulea*, *Litoria subglandulosa*, *Mixophyes balbus* and *Pseudophryne coriacea* were deemed to have too few detections for the analysis to function properly, so were excluded from the two-species, single-season analysis. Occupancy estimation and detection probability equations developed from the general forms of these equations, i.e. equations 6.01- 6.06 for *Cri. signifera* and 6.07-6.12 for *G. holbrooki* (see Section 6.1), respectively, were used to generate specific estimates of the probability of occupancy and the probability of detection in relation to the co-occurring species being examined.

6.2.1 Comparison of Occupancy for Frog Species with *Crinia signifera*

Crinia signifera was found at 92 of the 200 sites surveyed in the present study. Sites at which *Cri. signifera* were detected overlapped with all but one of the other frog species, *Lim. fletcheri,* found in the current survey (Table 6.2.1). However, it should be noted that this species was detected at only a small number of sites (n=4). Twelve frog species had a high proportion ($P \geq 0.5$) of sites at which they overlapped with *Cri. signifera*. The remaining four frog species had a low proportion ($P < 0.5$) of sites at which they overlapped with *Cri. signifera*. For maps of the overlap in sites at which these species were detected at and all following species, see Appendix 3.

Single-species, single-season models with *Cri. signifera* included as a covariate were developed for 12 frog species: *Crinia parinsignifera*, *Limnodynastes dumerilii*, *Limnodynastes fletcheri*, *Limnodynastes peronii*, *Limnodynastes tasmaniensis*, *Litoria dentata*, *Litoria fallax*, *Litoria latopalmata*, *Litoria peronii*, *Litoria verreauxii*, *Litoria wilcoxii* and *Uperoleia laevigata*. The occupancy of two of these frog species was found to be associated with the presence of *Cri. signifera*. These two species were *Lim. fletcheri* and *U. laevigata* (Tables 6.2.2). *Limnodynastes fletcheri* was positively associated with *Cri. signifera* and *U. laevigata* was negatively associated with *Cri. signifera* (Table 6.2.2). This indicates that *Lim. fletcheri* is more likely to occupy sites at which *Cri. signifera* also has a high probability of occupying (Fig. 6.2.1). Similarly, *U. laevigata* is less likely to occupy sites at which *Cri. signifera* has a high probability of occupying (Fig. 6.2.2). Occupancy for *U. laevigata* when *Cri. signifera* is also present was $\Psi = 0.01$ and when Cri. signifera is absent, it was $\Psi = 0.23$. Detection for *U. laevigata* was found to be positively associated with *Cri. signifera* (Table 6.2.3). Detection of *U. laevigata* is only slightly more likley when *Cri. signifera* detection is also high, given the small magnitude of the coefficient (Table 6.2.3). Detection for *U. laevigata* when *Cri. signifera* is also present was highest during $SURVEY$ 1 and $SURVEY$ 3 (Fig. 6.2.3). The occupancy and detection of the remaining ten species was found to be independent of the presence of *Cri. signifera* (Tables 6.2.2 & 6.2.3). That is, for these species, occupancy and detection was not influenced by the likelihood of the occupancy or detection of *Cri. signifera*. For the model selection which determined the influence of *Cri. signifera* on occupancy of the other frogs species, see Appendix 4.

Table 6.2.1: Proportion of sites at which *Crinia signifera* overlapped with the other 17 frog species found in the current study. Listed here are the number of sites (n) at which each of the frog species were found and the proportion of these sites at which these frog species were found in association with *Cri. signifera.* NOTE: total number of sites surveyed was 200. Five species had a low proportion of sites at which they were also found in association with *Cri. signifera: Limnodynastes fletcheri*, *Limnodynastes peronii*, *Litoria fallax*, *Litoria latopalmata* and *Litoria wilcoxii*.

Species	**n**	**Proportion of sites at which *Crinia signifera* was also found**
Crinia parinsignifera	56	0.60
Linodynastes dumerilii	42	0.57
Limnodynastes fletcheri	4	0.00
Limnodynastes peronii	28	0.46
Limnodynastes tasmaniensis	64	0.61
Litoria barringtonensis	1	1.00
Litoria caerulea	1	1.00
Litoria dentata	13	0.77
Litoria fallax	90	0.40
Litoria latopalmata	52	0.37
Litoria peronii	54	0.50
Litoria subglandulosa	4	1.00
Litoria verreauxii	58	0.67
Litoria wilcoxii	13	0.31
Mixophyes balbus	2	0.50
Pseudophryne coriacea	12	0.75
Uperoleia laevigata	48	0.58

Table 6.2.2: Estimates of the occupancy coefficients and their standard errors (se) for the covariates of the most parsimonious occupancy models for the 12 frog species modelled with *Crinia signifera*. NOTE: only 13 of the 18 detected species are presented because for five species, the occupancy models did not converge.

Species	**Occupancy Parameter**									
	β_0	$sigO$	LAT	$LONG$	ALT	sW	rW	emV	$ripV$	C
Crinia parinsignifera	-1.16 (0.47)	–	–	0.26 (0.47)	–	0.83 (0.53)	-0.16 (0.53)	–	–	–
Crinia signifera	0.30 (0.73)	–	–	1.97 (0.48)	-1.08 (0.77)	–	–	1.43 (0.56)	–	–
Limnodynastes dumerilli	-1.21 (0.18)	–	–	–	–	–	–	–	–	–
Limnodynastes fletcheri	-10.22 (3.50)	8.55 (4.52)	–	-10.15 (4.11)	–	–	–	–	–	–
Limnodynastes peronii	-2.26 (0.75)	–	–	–	–	1.2 (0.81)	0.45 (0.81)	–	–	–
Limnodynastes tasmaniensis	-5.48 (1.08)	–	–	-1.48 (0.59)	4.62 (1.07)	–	–	0.81 (0.59)	–	–
Litoria dentata	-4.07 (0.73)	–	2.30 (0.67)	-1.47 (1.06)	–	–	–	0.19 (1.07)	–	–
Litoria fallax	-1.09 (0.46)	–	–	-1.04 (0.43)	–	1.46 (0.52)	0.85 (0.51)	–	–	–
Litoria latopalmata	-0.89 (0.21)	–	–	-3.25 (0.68)	–	–	–	–	–	–
Litoria peronii	-1.17 (0.50)	–	–	–	–	–	–	–	0.91 (0.70)	-0.75 (0.34)
Litoria verreauxii	-6.46 (1.33)	–	1.15 (0.43)	-0.40 (0.67)	5.28 (1.24)	–	–	–	–	–
Litoria wilcoxii	-0.83 (1.58)	–	–	-1.45 (0.78)	-3.23 (1.41)	-0.66 (1.47)	1.41 (1.13)	–	–	–
Uperoleia laevigata	-1.21 (0.77)	-3.42 (1.85)	–	–	–	–	–	–	–	–

Table 6.2.3: Estimates of the detection coefficients and their standard errors (se) for the covariates of the most parsimonious occupancy models for the 12 frog species modelled with *Crinia signifera*. NOTE: only 13 of the 18 detected species are presented because for five species, the occupancy models did not converge.

Species	**Detection Parameter**									
	β_0	*sigD*	*AT*	*H*	*WS*	*MI*	*R48*	*SURVEY 2*	*SURVEY 3*	*SURVEY 4*
Crinia parinsignifera	-2.18 (0.68)	–	0.08 (0.03)	2.04 (0.99)	0.11 (0.04)	–	–	–	–	–
Crinia signifera	2.80 (0.66)	–	-0.23 (0.03)	2.07 (0.79)	–	–	–	–	–	–
Limnodynastes dumerilli	0.83 (0.37)	–	–	–	–	–	–	-0.29 (0.44)	-2.11 (0.49)	-4.64 (1.07)
Limnodynastes fletcheri	-9.79 (5.21)	–	0.63 (0.32)	–	–	–	–	–	–	–
Limnodynastes peronii	-3.90 (0.94)	–	0.23 (0.05)	–	–	-1.21 (0.46)	–	–	–	–
Limnodynastes tasmaniensis	0.67 (0.27)	–	–	–	–	–	–	0.52 (0.39)	-0.80 (0.36)	-3.42 (0.58)
Litoria dentata	-22.86 (12.04)	–	1.46 (0.76)	–	–	–	–	–	–	–
Litoria fallax	2.61 (0.46)	–	–	–	–	–	–	-1.81 (0.50)	-3.47 (0.51)	-5.09 (0.60)
Litoria latopalmata	-6.11 (0.90)	–	0.33 (0.05)	–	–	–	–	–	–	–
Litoria peronii	2.22 (0.61)	–	–	–	–	–	–	-2.31 (0.62)	-4.18 (0.70)	*
Litoria verreauxii	-0.56 (0.76)	–	-0.08 (0.03)	3.69 (1.02)	–	–	–	–	–	–
Litoria wilcoxii	-0.19 (1.21)	–	0.10 (0.07)	–	–	–	–	–	–	–
Uperoleia laevigata	2.39 (1.04)	0.001 (<0.001)	–	–	–	–	–	-1.19 (1.23)	0.09 (1.47)	-1.92 (1.19)

* NOTE: Survey 4 omitted from model as it caused convergence errors.

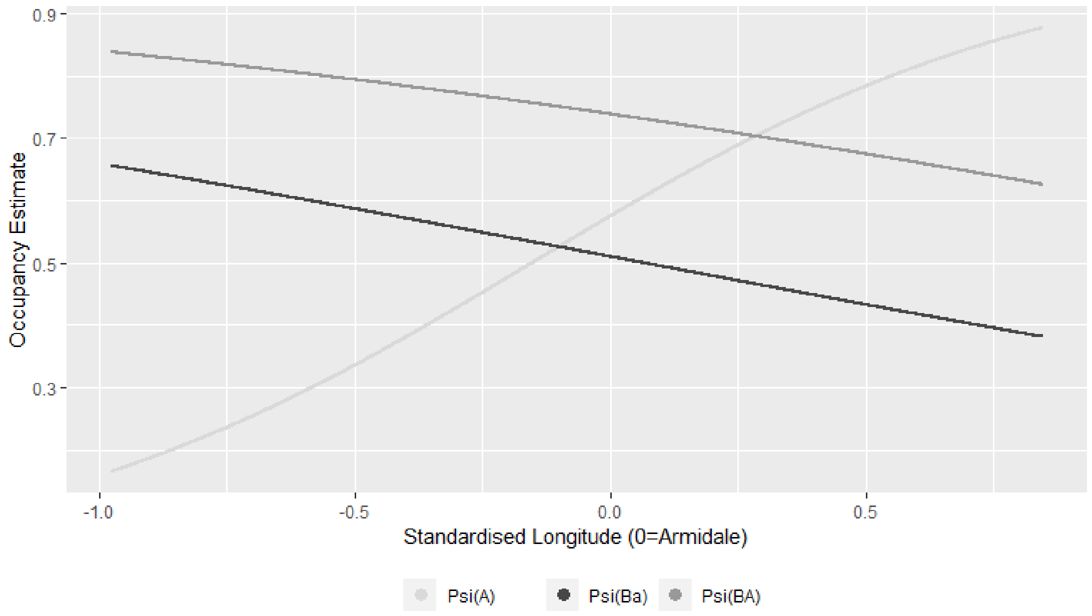


Fig 6.2.1: Influence of the presence or absence of *Crinia signifera* on the occupancy of *Limnodynastes fletcheri* at sites extending from west (-1) to east (1) across the New England Tablelands. Psi(A) is the independent occupancy of *Cri. signifera*, Psi(BA) is the occupancy of *Lim. fletcheri* when *Cri. signifera* is present and Psi(Ba) is the occupancy of *Lim. fletcheri* when *Cri. signifera* is present. NOTE: Longitude was standardised, so that Armidale=0.

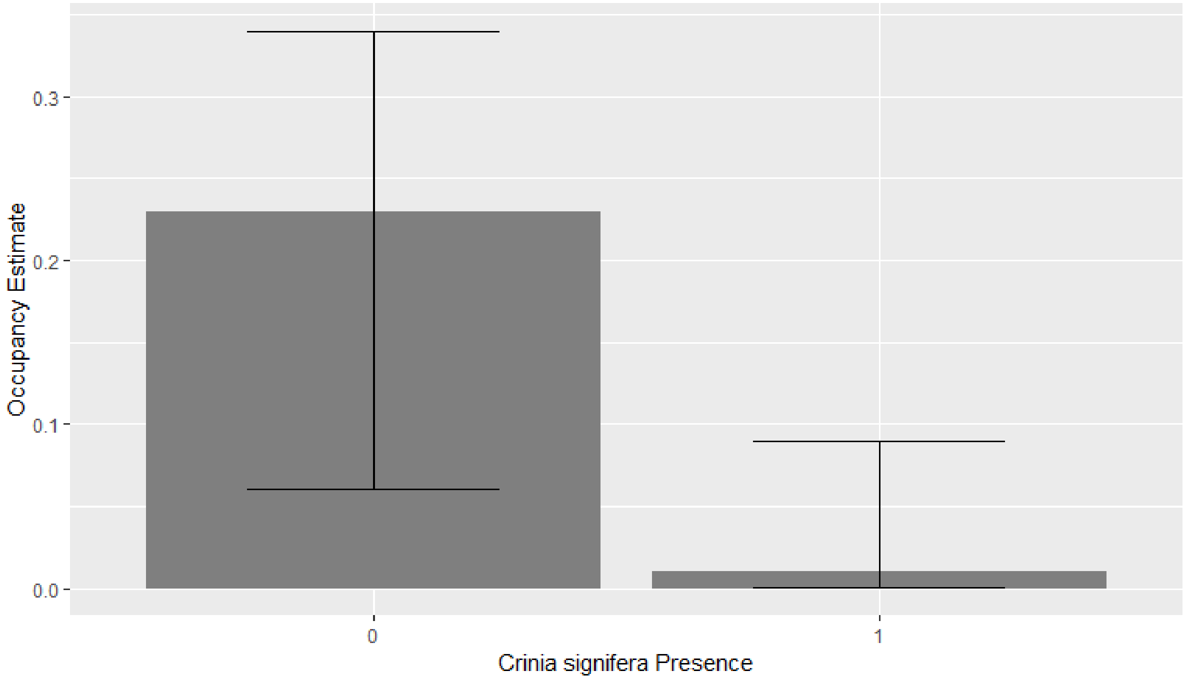


Fig. 6.2.2: Influence of the presence (1) or absence (0) of *Crinia signifera* on the occupancy of *Uperoleia laevigata* at sites within the New England Tablelands. Also included are the confidence intervals for the estimates.

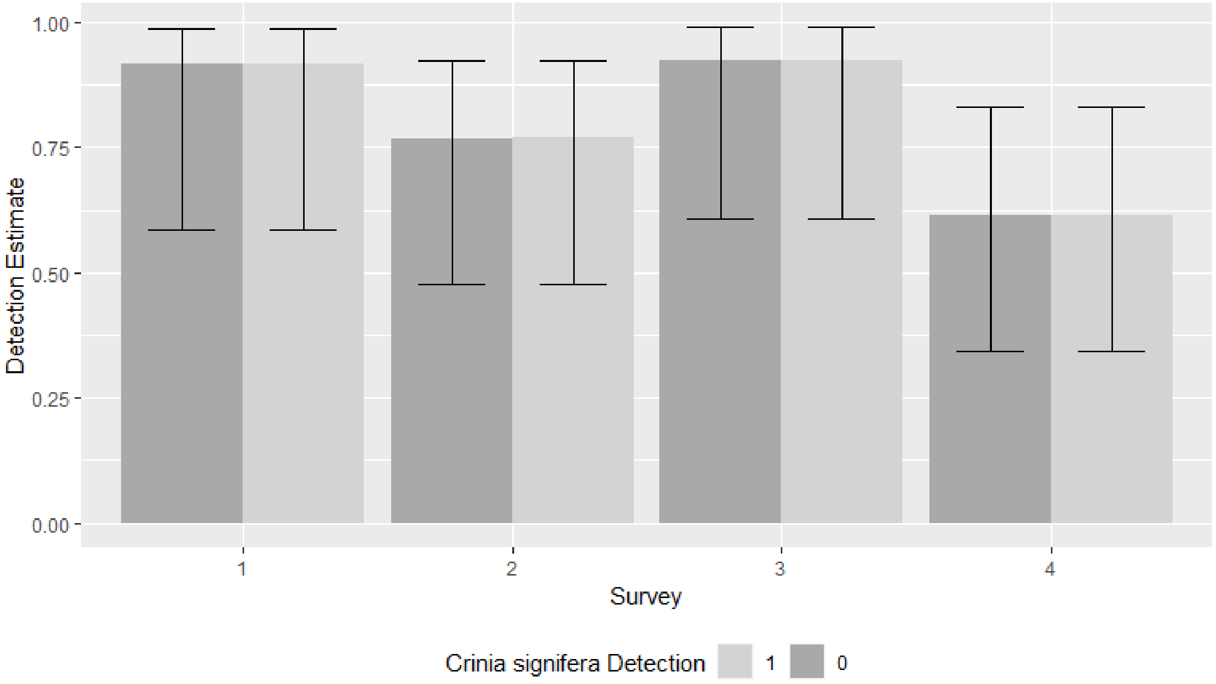


Fig.6.2.3: Influence of the detection (1) or non-detection (0) of *Crinia signifera* on the detection of *Uperoleia laevigata* at sites within the New England Tablelands during the separate survey seasons. Also included are the confidence intervals for the estimates.

6.2.1 Comparison of Occupancy for Frog Species with *Gambusia holbrooki*

6.2.1.1 single-season, single-visit occupancy model for *Gambusia holbrooki*

For the analysis of the variable occupancy, constant detection models for *G. holbrooki*, there were two models for which $\Delta AIC \leq$ 2.00 (Table 6.2.4). These two models had similar Akaike weights (w_i). However, because these models were nested and the simpler model had a slightly larger Akaike weight, the simpler of the three was considered the preferred model. This model was one where occupancy varied with waterbody type (rW, sW), latitude (LAT) and longitude ($LONG$), and detection was constant. The constant occupancy, constant detection model ($\Psi(.), p(.)$) had a ΔAIC = 79.88 (Table A4.1.4), supporting the inclusion of covariates for occupancy.

The occupancy coefficients for LAT and $LONG$ were both positive, indicating that *G. holbrooki* has a higher occupancy in the north-east part of the New England Tablelands (Table 6.2.5). Similarly, the coefficients for sW and rW were positive, indicating that this species is more likely to occur at sites where water is present.

The coefficients are similar for both sW and rW, so waterbody type does not influence occupancy of *G. holbrooki*, as long as there is water present. The logistic regression model for *G. holbrooki* with a logit link for the probability of occupancy at a potential site can be calculated using equation 6.07 and the coefficients from Table 6.2.5:

$$logit\ (\Psi^A) = ln(\frac{\psi^A}{1-\psi^A}) = -28.46 + 0.56LAT + 1.86LONG + 26.16sW + 28.52rW$$

(Eq. 6.13)

Table 6.2.4: Top-ranked constant occupancy, variable detection models with combinations of habitat variables used to model occupancy for *Gambusia holbrooki.* Listed are the number of parameters (n) AIC, ΔAIC, Akaike weights (w_i) and maximised log-likelihood ($2Log(l)$) for each of the top-ranked models.

Model	n	AIC	ΔAIC	w_i	$2Log(l)$
$\Psi(LAT + LONG + rW + sW), p(.)$	6	220.04	0.00	0.50	208.04
$\Psi(LAT + LONG + rW + sW), p(emV)$	7	220.28	0.24	0.44	206.28
$\Psi(LAT + LONG + rW + sW), p(SURVEY)$	9	224.32	4.28	0.06	206.32
$\Psi(.), p(.)$	**2**	**299.91**	**79.88**	**0.00**	**295.91**

Table 6.2.5: Coefficient estimates and their standard errors (se) of occupancy from the most parsimonious model for *Gambusia holbrooki* found in the current study.

Parameter	Estimate	se
β_0	-28.46	1.92
LAT	0.56	0.36
$LONG$	1.86	0.55
$RUNNING$	28.52	1.92
$STILL$	26.16	1.98

Fitted occupancy values for each of the sites was calculated using equation 6.13 and incorporated into the single-visit single-season occupancy models for the 13 frog species whose occupancy was modelled in Chapter 5. Detection for *G. holbrooki* was constant with a detection probability of 0.99. This detection value was also used in the single-visit single-season occupancy models for the 13 frog species

6.2.1.2 Influence of *Gambusia holbrooki* on occupancy for frog species

Gambusia holbrooki was found at 73 of the 200 sites surveyed in the present study. Sites at which *G. holbrooki* were detected overlapped with all but two of the frog species, namely *Lit. barringtonensis* and *Lit. caerulea,* found in the current survey (Table 6.2.6). It should be noted though that both these species were detected at only a single site each. Two frog species had a high proportion (P≥0.5) of sites at which they overlapped with *G. holbrooki*, namely *Lit. subgladulosa* and *M. balbus*. However, both if these species were also only found at a small number of sites (n=4 and n=2, respectively). The remaining 14 frog species had a low proportion (P<0.5) of sites at which they overlapped with *G. holbrooki*. For maps of the overlap in sites at which these species were detected at and all following species, see Appendix 3.

Single-species, single-season models with *G. holbrooki* included as a covariate were developed for 13 frog species: *Cri. parinsignifera, Cri. signifera*, *Lim. dumerilii*, *Lim. fletcheri*, *Lim. peronii*, *Lim. tasmaniensis*, *Lit. dentata*, *Lit. fallax*, *Lit. latopalmata*, *Lit. peronii*, *Lit. verreauxii*, *Lit. wilcoxii* and *U. laevigata*. None of the frog species was found to have their occupancy or detection associated with the presence of *G. holbrooki*. Both the occupancy and detection of these 13 frog species was found to be independent of the presence of *G. holbrooki*. For the model selection which determined the influence of *G. holbrooki* on occupancy of the frog species found in the current survey, see Appendix 4.

Table 6.2.6: Proportion of sites at which *Gambusia holbrooki* overlapped with the other 17 frog species found in the current study. Listed here are the number of sites (n) at which each of the frog species were found and the proportion of these sites at which these frog species were found in association with *G. holbrooki.* NOTE: total number of sites surveyed was 200. All species had a low proportion of sites at which they were also found with *G. holbrooki* apart from; *Litoria subglandulosa* and *Mixophyes balbus*.

Species	**n**	**Proportion of sites at which *Crinia signifera* was also found**
Crinia parinsignifera	56	0.32
Crinia signifera	92	0.38
Linodynastes dumerilii	42	0.43
Limnodynastes fletcheri	4	0.25
Limnodynastes peronii	28	0.39
Limnodynastes tasmaniensis	64	0.27
Litoria barringtonensis	1	0.00
Litoria caerulea	1	0.00
Litoria dentata	13	0.31
Litoria fallax	90	0.38
Litoria latopalmata	52	0.31
Litoria peronii	54	0.41
Litoria subglandulosa	4	0.50
Litoria verreauxii	58	0.43
Litoria wilcoxii	13	0.46
Mixophyes balbus	2	0.50
Pseudophryne coriacea	12	0.33
Uperoleia laevigata	48	0.29

6.3 Discussion

6.3.1 Co-occurrence of Frog Species with *Crinia signifera*

For the two-species single season analysis, the occupancy of 12 frog species was able to be modelled in relation to the presence of the common eastern toadlet (*Crinia signifera*). There were another five species that had too few detections in relation to the presence of *Cri. signifera* to be modelled successfully. These species were *Litoria barringtonensis*, *Litoria caerulea*, *Litoria subgandulosa*, *Mixophyes balbus* and

Pseudophryne coriacea. Of the 12 species above, there were two whose occupancy was influenced by *Cri. signifera. These were Lim. fletcheri* and *U. laevigata* (Table 6.2.2). Neither of these two species showed an interaction between habitat covariates and *Cri. signifera*. For the remaining ten species it was found that their occupancy was independent of the presence of *Cri. signifera*. Hence, the presence or absence of *Cri. signifera* at a site did not influence whether each of these ten species would also occupy that site.

The composition of an anuran community can influence the disease dynamics of the Amphibian chytrid fungus (*Batrachochytrium dendrobatidis*). Disease dynamics are often complex because the severity of *B. dendrobatidis* infection on an individual can differ depending on frog species, the environment and strain of *B. dendrobatidis* (Van Rooij *et al.* 2015; Lips 2016). A major concern for frog species which co-occur with *Cri. signifera* is its status as a competent reservoir host for the Amphibian chytrid fungus (Brannelly *et al.* 2018; Burns *et al.* 2021). Competent reservoir hosts for *B. dendrobatidis* share several characteristics. These include a high prevalence of *B. dendrobatidis* infection in the population; hosts can maintain a high infection intensity over a long period of time; hosts suffer no fitness cost from infection; and, as a species, hosts have not seen a decline in numbers or changes in demographics from the disease (Brannelly *et al.* 2018; Scheele *et al.* 2017; Stockwell *et al.* 2016). Prevalence of *Cri. signifera* at a site can cause chytridiomycosis in other species which are also present and which may be more susceptible to the fungus.

In the New England Tablelands, *Cri. signifera* is one of the few species which has increased its average occupancy since the time of the historical study (see Section 5.1 and Section 5.3.3). When infected with *B. dendrobatidis*, individuals of *Cri. signifera* are often asymptomatic, rarely developing clinical signs of chytridiomycosis, and have a very low chance of morbidity from the fungus (Brannelly *et al.* 2018; Burns *et al.* 2021; Scheele *et al.* 2017). Further, the continued presence of reservoir species at a site can maintain zoospore densities, even when other frog species which are present are declining (Brannelly *et al.* 2018; Scheele *et al.* 2017). Only one species, *U. laevigata,* was determined to be less likely found with *Cri. signifera*. This species has showed a decrease in its average occupancy since the historical study (see Section 5.1 and Section 5.3.3). *Crinia signifera* can carry high zoospore loads without mortality and the density of *Cri. signifera* at a suitable breeding site is often high. This can create high densities of *B. dendrobatidis* zoospores at habitats *Cri. signifera* occupies, or sites that it is moving through. Higher zoospore density is linked to quicker deaths in species which are susceptible to the disease (Burns *et al.* 2021). The continued presence of *Cri. signifera* at sites inhabited by susceptible species may have caused local extinctions at these sites.

Several studies have implicated the presence of *B. dendrobatidis* infected *Cri. signifera* to the decline of other species. Burns *et al.* (2021) found that populations of the frog *Philoria frosti* were only present at sites where *Cri. signifera* was absent, and in the laboratory, mortality rate of *Phi. frosti* was found to increase with higher infection intensity of *B. dendrobatidis* in *Cri. signifera*. Brannelly *et al.* (2018) determined that high densities of *Cri. signifera* were present at sites where three alpine frog species had previously been recorded and were declining or had extirpated locally. Further, the infection intensity of *B. dendrobatidis* in *Cri. signifera* was much higher than those of the declining species (Brannelly *et al.* 2018). *Uperoleia laevigata* was one of the species determined to have a lower occupancy in the current study than in the historical study (Chapter 5). One possibility is that co-occurrence of U. laevigata with Cri. signifera may have caused local extinctions at these sites (Brannelly *et al.* 2018; Scheele *et al.* 2017). There is no documentation that *U. laevigata* is susceptible to *B. dendrobatidis* infection. However, this does not preclude susceptibility, since testing often focuses on frog species which are already in crisis.

Crinia signifera is also more likely to occupy sites in the eastern side of the New England Tablelands. The eastern side of the New England Tablelands with higher altitudes has a montane habitat with correspondingly lower temperatures and higher rainfall compared to further west in the region (Sahukar *et al.* 2003). Such meteorological conditions provide optimum growing conditions for *B. dendrobatids* (Kriger & Hero 2008; Kriger & Hero 2007a; Kriger & Hero 2004b; Kriger *et al.* 2007; Pounds *et al.* 2006). When temperature and rainfall is optimal for *B. dendrobatidis* growth, infection intensity is high (Kriger & Hero 2007a; Kriger *et al.* 2007), possibly applying extra pressure to species which are more susceptible to *B. dendrobatidis* than are *Cri. signifera* when *Cri. signifera* is present. However, longitude appears not to influence the occupancy of *U. laevigata*.

Interspecies competition may be another reason for the lower occupancy of *U. laevigata* at sites with a high probability of occupancy for *Cri. signifera. Crinia signifera* and *U. laeivigata* have similar habitat requirements (Anstis 2017; Hoskin *et al.* 2015). This may lead to interspecies competition for shelter and breeding space, and for food resources (Freeland & Kerin 1988). More complex habitat, for example where there is a higher proportion of emergent vegetation, can provide greater resources and therefore support a larger diversity of frog species (Bazzaz 1975; Tews *et al.* 2004). A higher proportion of emergent vegetation would increase the space that males of each species can use for calling and females can use for depositing eggs (Hettyey *et al.* 2014). A greater proportion of emergent vegetation would also support a greater bioload of insects and algae which would supply greater food resources for both the adults and tadpoles at a site (Bazzaz 1975; Tews *et al.* 2004). Sites with a higher proportion of emergent vegetation would ultimately reduce competition pressure between members of *Cri. signifera* and *Lim tasmaniensis* at all life stages for sites where they both occur. Despite this, the influence of *Cri. signifera* on occupancy for *U. laevigata* did not interact with emergent vegetation.

Another possible problem for species which are less likely to co-occur with *Cri. signfera* is signal jamming. Mixed signal jamming occurs when there are multiple males of different species calling in a chorus (Shimoyama 1999). *Crinia signifera* males will respond when males from other species begin to call, even responding to call playback (pers. obs). This behaviour may interfere with the successful reproduction of the other species breeding at the same site (Nakanishi *et al.* 2020).

There is not a lot of documented evidence that the other frog species modelled with *Cri. signifera* in the current study are susceptible to *B. dendrobatidis* infection. *Litoria wilcoxii* is a species that is believed to have some resistance to *B. dendrobatidis* infection (Kriger & Hero 2006) and has been implicated as a reservoir host for the fungus at sites where *Litoria booroolongensis* has declined (Franklinos *et al.* 2020). Such previous findings support the independence of *Lit. wilcoxii* in relation to the presence of *Cri. signifera*. Further, independent co-occurrence for *Lit. wilcoxii* and *Cri. signifera* could be supported by differences in habitat requirements. *Litoria wilcoxii* is more likely to be found at sites with running water, while *Cri. signifera* is more likely to be found at sites with still water (Anstis 2017; Hoskin *et al.* 2015).

Interestingly, another species, *Lit. verreauxii* is thought to be susceptible to *B. dendrobatidis* infection (Scheele *et al*. 2014), so you would expect to see a response for occupancy similar to that found in *U. laevigata*. This provides some support that *Lit. verreauxii* may not be able to identify *B. dendrobatidis* host reservoirs or does not choose habitats which are free of them.

Limnodynastes fletcheri was more likely to be found with *Cri. signifera* at sites in the New England Tablelands. Scheele *et al.* (2014) suggested that the impact of *B. dendrobatidis* may be limited by higher quality habitat. However, this may not necessarily be the case for the present study, given the degree of disturbance seen at many of the sites surveyed. It is also possible that the presence of *Cri. signifera* at sites may provide some advantage to *Lim. fletcheri* that is yet to be explored, such as functioning as an indicator for suitability of habitat (juang *et al.* 2017), or perhaps, *Cri. signifera* provide a food source for *Lim. fletcheri* (Crossland 1998; Werner *et al.* 1995). It is more likely, however, that the co-occurrence of *Cri. signifera* and *Lim. fletcheri* is linked to the similarities in breeding behaviour and habitat requirements (Hartmam *et al.* 2014; Iwai *et al.* 2018; Thomas *et al.* 2011). *Crinia signifiera* and *Lim. fletcheri* have similarities in the type of waterbody they utilise for breeding, breeding time and placement of eggs during oviposition (Anstis 2017; Hoskin *et al.* 2015). Males of *Cri. signifera* and *Lim. fletcheri* should select sites that would maximise their reproductive success and increase the chance of their offspring survival (Kats & Sih 1992; Resetarits & Wilbur 1989), thus leading to the utilisation of the same sites for breeding. A further factor to consider with this analysis was that *Lim. fletcheri* was found at only a very small number of sites. A future study targeting the co-occurrence of these two species would aid in confirming that the influence of *Cri. signifera* may, in fact, be positive.

6.3.2 Co-occurrence of Frog Species with an Invasive Fish; *Gambusia holbrooki*

For the two-species single season analysis, 13 frog species were able to be modelled with the eastern mosquito fish *(Gambusia holbrooki*). Five species had too few detections to be modelled successfully. These include *Litoria barringtonensis*, *Litoria caerulea*, *Litoria subgandulosa*, *Mixophyes balbus* and *Pseudophryne* *coriacea*. Of the 13 species that could be modelled, none of the frog species found had occupancy affected by the presence of the eastern mosquito fish (*G. holbrooki*). This indicates that the presence or absence of *G. holbrooki* at a site did not affect the presence or absence of these species in the New England Tablelands.

Under other circumstances, *G. holbrooki* has been found to influence a number of aspects of frog ecology (Hamer & Parris 2013; Hamer *et al.* 2002b; Klop-Toker *et al.* 2018; Komak & Crossland 2000; Littlefair *et al.* 2021; Morgan & Buttemer 1996). A number of studies have linked *G. holbrooki* presence to the decline of amphibians in Australia through predation on eggs and tadpoles (Hamer *et al.* 2002b; Littlefair *et al.* 2021; Morgan & Buttlemar 1996; Pyke & White 2000). *Gambusia holbrooki* can negatively influence abundance and occurrence of tadpoles (Littlefair *et al.* 2021) and reduce reproductive success of frogs (Hamer 2021). Further, the presence of *G. holbrooki* at a site may influence the behaviour of tadpoles leading to difficulties in their detection (Klop-Toker *et al.* 2018; Sanders *et al.* 2015). This is less likely to be an issue in the current study as it focused on detecting adult frogs, rather than tadpoles.

The presence of *G. holbrooki* at a site did not affect the likelihood of some species whose tadpoles have been reported to be preyed upon by *G. holbrooki* (Hamer & Parris 2013; Hamer *et al.* 2002b; Klop-Toker *et al.* 2018; Komak & Crossland 2000; Littlefair *et al.* 2021; Morgan & Buttemer 1996). Hamer (2021) determined that reproduction for *Lim. peronii* was significantly reduced at sites where *G. holbrooki* was present. This is supported by Morgan and Buttemer (1996), and by Pyke and White (2000) who found that tadpoles belonging to *Lim peronii* were vulnerable to predation by *G. holbrooki*. Klop-Toker *et al.* (2018) reported a negative association between abundance of *Lim. peronii* tadpoles and presence of *G. holbrooki*. *Litoria lesueuri* has also shown to be susceptible to predation by *G. holbrooki* (Harris 1995). Given that *Lit. lesueuri* is closely related to *Lit. wilcoxii* (Anstis 2017; Donnellan & Mahony 2004) and the study by Harris (1995) was conducted in the New England Tablelands before the taxonomic reclassification of the *Lit. lesueuri* complex occurred (See Section 3.1.2), it is likely that the tadpoles of *Lit. wilcoxii* would be heavily preyed upon by *G. holbrooki* if they were both present at a site. This would appear to be the first report of occupancy for *Lim. fletcheri* and *Lit. latopalmata* being influenced by *G. holbrooki*. Litllefair *et al.* (2021) determined that there was a negative association between *Cri. parinsigignifera* tadpole density and the presence of *G. holbrooki*. This concurs with the outcome of a study conducted by Komak and Crossland (2000) who observed that *G. holbrooki* reduced the number of *Cri. parinsignifera* tadpoles in enclosed ponds. *Litoria verreauxii*, *Lit. fallax* and *Lit dentata* tadpoles have also been found to be vulnerable to predation by *G. holbrooki* (Hamer & Parris 2013; Harris 1995; Klop-Toker *et al.* 2018; Morgan & Buttemer 1996; Webb & Joss 1997). There was a negative association of *Lit. fallax* tadpoles with the presence of *G. holbrooki,* but not with adult frogs (Klop-Toker *et al.* 2018).

A large number of studies have documented the predation of *Lit. peronii* by *G. holbrooki* (Hamer 2021; Klop-Toker *et al.* 2018; Morgan & Buttemer 1996; Pyke & White 2000). These contradict the findings of the present study. The presence of *G. holbrooki* at sites where *Lit. peronii* was also present, reduced the abundance of tadpoles and reproductive success of adults (Klop-Toker *et al.* 2018; Morgan & Buttemer 1996; Pyke & White 2000). Further, the predation rate did not change if there were other species of tadpoles present (Hamer *et al.* 2021). Klop-Toker *et al.* (2018) found that the adult *Lit. peronii* would alter its breeding behaviour, selecting sites which were absent of *G. holbrooki*. Another potential cause of the differences between the present and other studies is the meteorological conditions at the time the present study was conducted. Given the low rainfall in the region (Nguyen *et al.* 2021), *Lit. peronii* and the other species may have been limited in site choice for breeding. These species may have been restricted to breeding in permanent waterbodies regardless of *G. holbrooki* presence.

An increase in emergent vegetation may provide an increase in refuge habitat for tadpoles and eggs against predation from *G. holbrooki* (Babbitt & Tanner 2000; Hecnar & M'Closkey 1997), leading to increased survival success. The present study found that *Cri. signifera*, *Lim. tasmaniensis* and *Lit. dentata* were more likely to occur at sites with a higher proportion of emergent vegetation. Morgan and Buttemer (1996) determined that predation of *Lit. dentata* and *Litoria aurea* tadpoles were reduced in the presence of emergent vegetation, indicating that vegetation provides some protection from predation. Klop-Toker *et al.* (2018) suggested that dense aquatic vegetation provides shelter for and reduces visibility of tadpoles by *G. holbrooki*, reducing predation success.

The difference found in the present study for *Cri. parinsignifera*, *Lit. dentata*, *Lit. fallax* and *Lit. verreauxii* occupancy responses to the presence of *G. holbrooki* when compared to other studies is likely linked to the differences in the targeted life stages. The studies by Hamer and Parris (2013), Harris (1995), Komak and Crossland (2000), Littlefair *et al.* (2021), and by Morgan and Buttemer (1996) focused on tadpole assemblages, while adult frogs were the predominant life stage encountered in the present study. Some species of tadpoles have been shown to have very little change in behaviour in response to invasive fish (Hamer *et al.* 2002b; Petranka *et al.* 1987; Lawler 1989; Stauffer & Semlitsch 1993; Relyea 2001a, 2001b). Further, the adults of *Lit. aurea* and *Lit. fallax*, have also shown no modified behaviour in selecting habitats free of *G. holbrooki* when breeding (Klop-Toker *et al.* 2018). However, *Lim. tasmaniensis* adults do modify their behaviour to avoid *G. holbrooki* in an experimental setting (Hamer *et al.* 2002b). This contradicts what the present study found for *Lim. tasmaniensis*, as co-occurrence with *G. holbrooki* was independent, with the presence or absence of *G. holbrooki* at a site not influencing the likelihood of occupancy of *Lim. tamsaniensis* at the same site. Hamer (1998) did find that *Lim. tasmaniensis* could co-exist with *G. holbrooki* in the wild, potentially relating to their evolutionary history. Frog species which share an evolutionary history with predatory fish could identify *G. holbrooki* as a potential predator of their offspring and avoid breeding at sites where the fish are present (Klop-Toker *et al.* 2018). Adults of frog species which cannot recognise fish as a threat, could still select sites for breeding where *G. holbrooki* may also be present.

There is some conflict in the literature as to the response of *Cri. signifera* to the presence of *G. holbrooki*. Webb & Joss (1997) observed predation of *Cri. signifera* tadpoles by *G. holbrooki*. However, Klop-Toker *et al.* (2018) found there was no relationship between *G. holbrooki* presence and that of *Cri. signifera*, similar to the findings of the present study. Since *Cri. signifera* is a habitat generalist (Anstis 2017; Hoskin *et al.* 2015), it would likely occupy sites that are occupied by other frog species. Potentially, *G. holbrooki* may have a greater preference for the other species of tadpoles that may be present or alternatively, behaviour of *Cri. signifera* tadpoles allows for greater survivorship when compared to other species of tadpoles (Baber & Babbitt 2004).

Some generalist frog species have shown to have a higher tadpole survival rate when in the presence of invasive fish (Gunzburger & Travis 2004; Smith *et al.* 1999). However, none of the New England Tablelands frog species modelled in relation to *G. holbrooki* showed a particular preference for occupying sites that *G. holbrooki* also occupied.

Chapter 7. The Amphibian Chytrid Fungus (*Batrachochytrium dendrobatidis*) Swab Analysis

7. The Amphibian Chytrid Fungus (*Batrachochytrium dendrobatidis*) Swab Analysis

7.1 Swab Analysis

Two hundred and ninety-two swabs were collected and sent to the Australian Museum to test for the presence and infection intensity of the Amphibian chytrid fungus (*Batrachochytrium dendrobatidis*). For the swab collection and storage protocol, see Section 4.3.

7.1.1 Quantitative Polymerase Chain Reaction (qPCR) Protocol

The extraction of *B. dedrobatidis* DNA from each swab was undertaken using PrepMan™ Ultra Sample Preparation Reagent (Applied Biosystems) as outlined by Portway *et al.* (2020). Briefly, the tip of the swab was removed and added to a 2-ml tube, with 40 mg of 0.5-mm diameter Zirconium/silica beads (Qiagen) and 100-µl PrepMan™ reagent. The samples were vortexed for ten seconds, homogenised twice in a Qiagen Tissuelyser 11, each time for 45 seconds, centrifuged for a further one minute and then incubated at 100˚C for ten minutes. The resulting supernatant was then extracted, with 20 µl of it being decanted into a new, sterile, 1.5-ml microcentrifuge tube, where the sample was then diluted by 1/10 and stored at -20^{o}C before thermal cycling.

Prepared samples were tested for *B. dendrobatidis* in singlicate using Taqman qPCR (Boyle *et al.* 2004; Portway *et al.* 2020). The qPCR reactions were run on an ABI Quantstudio3 qPCR Machine using the ITS1-3 and ITS1/5.8s primers (Boyle *et al.* 2004). ITS1 standard curves were generated from five $\log_{10}$ dilutions of ITS1 ranging from 10^9 to 10^1 copies. These curves were used to quantify the number of copies in each sample.

In this analysis, it is the internal transcribed spacer (ITS1) that the primer/probe binds to during qPCR analysis and is considered an effective means of species-level identification (Boyle *et al.* 2004; Schoch *et al.* 2010). A sample was considered positive if the number of amplified ITS1 copies were registered as being greater than zero (Briggs *et al.* 2010; DiRenzo *et al.* 2018). The reason that the number of ITS1 copies was used instead of the zoospore count was that the *B.*

dendrobatidis strains vary in the number of target ITS1 copies between sites (Kirshtein *et al.* 2007; Longo *et al.* 2013). Longo *et al.* (2013) suggested that this was due to genetic changes in *B. denrobatidis* DNA from duplications or deletions. Varying numbers of ITS1 copies can lead to either underestimation or overestimation of zoospore counts because the number of copies is linearly related to florescence during analysis (Boyle *et al.* 2004).

7.1.2 Data Analysis

A generalised linear model with a binomial error distribution using a log-link function was fitted to the data using the glm function in R (R Core Team 2020) to test the relationship between the number of individuals (prevalence) infected with *B. dendrobatidis* and the species of frog, the site the sampled replicate individual occupied, the age class of the individual, its body size (snout-vent length), its sex, and month the swab was collected. Infection status ($CHYTRID$) was designated with either a 1 (infected) or a 0 (uninfected). These values were determined based on the zoospore load obtained from the qPCR. The qualitative predictor variables fitted to the model were species (SP: *Limnodynastes tasmaniensis*, *Litoria fallax* and *Litoria wilcoxii*), age (AGE: metamorph, juvenile and adult), gender type (SEX: female or male) and site from which the swab was collected from ($SITE$: Thomas Lagoon and Blue Hole). Quantitative predictor variables were also fitted to the model and these included snout vent length (SVL) measured in mm, and minimum temperature ($MinT$) and maximum temperature ($MaxT$). A binomial error term is appropriate when assessing infected-uninfected data as there are only two potential outcomes, which are mutually exclusive. An example of a generalised linear model with second order interactions and quadratic terms with a log-link function can be defined as:

$$\log(\mu_{ijk}) = \beta_0 + \beta_1 x_1 + \cdots + \beta_k x_k + \beta_{1k} x_1 x_k + \cdots + \beta_{ik} x_i x_k + \beta_2 x_1^2 \ldots + \beta_j x_j^2 + \epsilon_{ijk}$$

(Eq. 7.01)

where, β_0, is the intercept, β_1 is the coefficient for the first covariate (x_1), β_k is the coefficient for the kth covariate (x_k), β_{1k} is the coefficient for the interaction between the first and kth covariate, β_{ik} is the coefficient for the interaction between the ith $and\, kth$ covariate, β_2 is the coefficient for the polynomial of the first covariate (x_1^2), and β_j is the coefficient for the polynomial of the jth covariate (x_j^2).

A backwards stepwise regression was used to determine the final model. A stepwise regression procedure uses AIC statistic to determine model preference (Burnham & Anderson 2002). The initial model was one fitted with all predictor main effects, an interaction term between SVL and SP, and an added quadratic term for each of non-binary variables: $MinT$, $MaxT$ and SVL.

A second set of generalised linear models using a Gaussian error distribution was fitted to test for infection intensity in the three species, *Lim. tasmaniensis*, *Lit. fallax* and *Lit. wilcoxii*. Infection intensity, the number of ITS1 copies (see Section 7.1.1), were $\log_{10}(X + 1)$ transformed to ensure that the data conformed to a normal distribution, thus ensuring that a Gaussian error distribution was suitable for the analysis. Infection intensity (II) was modelled using the same predictor variables as infection prevalence. The procedure used to determine the most parsimonious model for these data followed the same steps as that for modelling infection prevalence.

7.2 Results

7.2.1 Infection Prevalence

Infection prevalence for *Lim. tasmaniensis* was 23.7%. For *Lit. fallax* it was 14.3%, and for *Lit. wilcoxii* it was 16.5%. *Limnodynastes tasmaniensis* specimens were only collected from Thomas Lagoon and not from Blue Hole. *Litoria wilcoxii* specimens were collected only from Blue Hole and not from Thomas Lagoon. *Litoria fallax* specimens were collected from both sites. The infection prevalence determined for *Lit. wilcoxii* and *Lim. tasmaniensis* were exclusively for the sites from which they had been collected.

The preferred prevalence model was one whereby infection prevalence was related to three variables: frog species, maximum daily temperature and body size (SVL). The site which a frog inhabited, its age and its sex had no influence on infection prevalence; nor did minimum daily temperature. The parameter coefficients for the most parsimonious model are listed in Table 7.1.3. Positive coefficients for *Lit. fallax* and *Lim. tasmaniensis*, indicate that both species are likely to have a higher infection prevalence than that of *Lit. wilcoxii*. However, the influence of species on infection prevalence differs depending on the body size of the individual. The quadratic term for SVL is negative indicating that infection prevalence increases as SVL increases, reaching a peak and then declining. Prevalence peaked at a SVL of 20 mm for *Lim. tasmaniensis*, a SVL of 25 mm for *Lit. fallax* and a SVL of 35 mm for *Lit. wilcoxii* (Fig. 7.2.1). The parameter coefficient for the quadratic of maximum temperature is negative, indicating that infection prevalence reaches a peak and then begins to decline. A regression equation can be generated using Eq 7.01 and the coefficients from Table 7.1.3:

$$\begin{aligned}\log(\mu_{infection\ prevalence}) &\\ = -69.041 - 0.003(MaxT^2) + 3.846(SVL) - 0.052(SVL^2) &\\ + 48.759(SP_{Lim.tasmaniensis}) + 35.839(SP_{Lit.fallax}) &\\ - 1.750(SVL{:}SP_{Lim.tasmaniensis}) - 1.206(SVL{:}SP_{Lit.fallax}) &\end{aligned}$$

(Eq. 7.02)

where, factors = 1 where the state is true and 0 where the state is false.

Table 7.1.3: Estimated coefficients and their standard errors (*se*) of the log linear regression for the most parsimonious generalised linear model for infection prevalence. Parameter subscripts represent the level of the covariate. Coefficients for all parameters are significant at <0.001.

Parameter	Estimate	se	t-statistic
β_0	-69.041	22.232	-3.105
$SP_{Lim.tasmaniensis}$	48.759	16.377	2.977
$SP_{Lit.\ fallax}$	35.839	13.711	2.614
SVL	3.846	1.190	3.233
$MaxT^2$	-0.003	0.001	-2.370
SVL^2	-0.052	0.016	-3.293
$SP_{Lim.tasmaniensis}{:}SVL$	-1.750	0.576	-3.038
$SP_{Lit.\ fallax}{:}SVL$	-1.206	0.455	-2.648

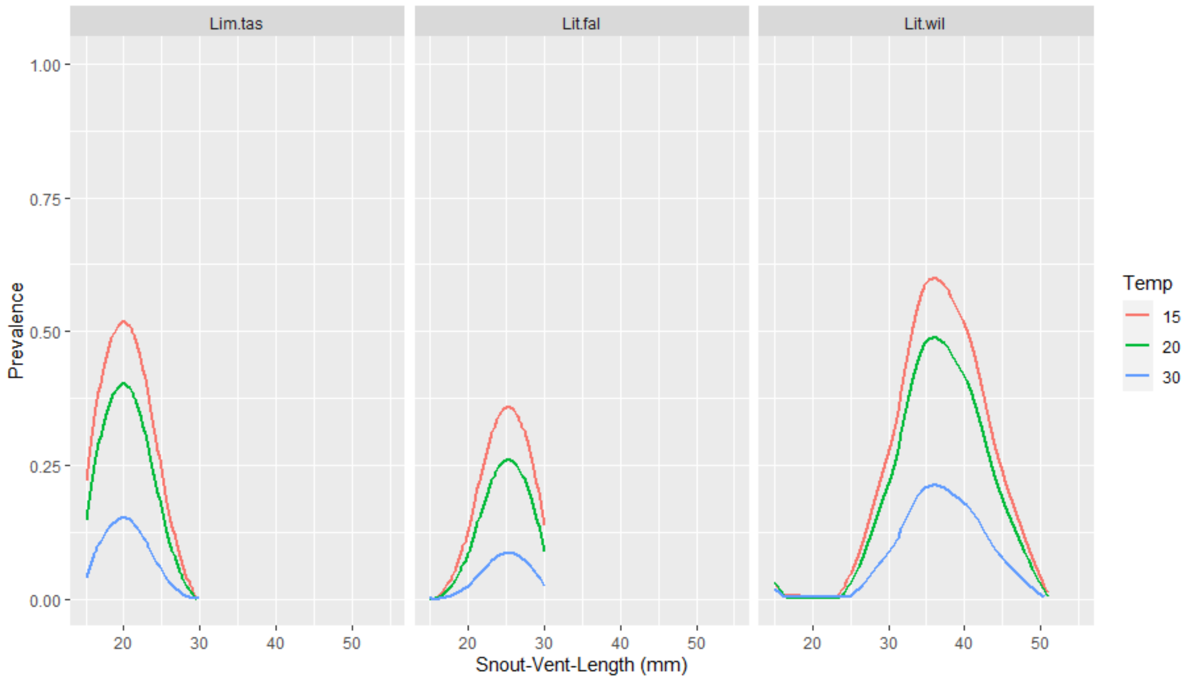


Figure 7.2.1: The infection prevalence for *Batrachochytrium dendrobatidis* in three New England Tablelands frog species; *Limnodynastes tasmaniensis* (Lim.tas), *Litoria fallax* (Lit.fal) and *Litoria wilcoxii* (Lit.wil), given increasing snout-vent length at three different maximum daily temperatures; 15°C, 20°C and 30°C.

7.2.2 Infection Intensity

Mean infection intensity was highest for *Lim. tasmaniensis* (1438.3 ± 2432.8). Mean infection intensity for *Lit. fallax* infected with *B. dendrobatidis* was 568.1 ± 729.1 and for *Lit. wilcoxii*, mean infection intensity was 543.2 ± 589.0.

The preferred model for infection intensity, based on copies of ITS-1 gene, was one whereby infection intensity was influenced by frog species, maximum daily temperature and body size. The site which a frog inhabited, its age and its sex had no effect on infection prevalence; nor did daily temperature. The parameter coefficients for the most parsimonious model for infection intensity are listed in Table 7.2.3. Positive coefficients for the species *Lit. fallax* and *Lim. tasmaniensis* in the model, indicate that both species are likely to have a higher infection intensity than that of *Lit. wilcoxii*. The negative coefficient for maximum temperature indicates that infection intensity decreases with increasing maximum temperatures. The quadratic term for SVL is negative indicating that infection prevalence increases as SVL increases, reaching a peak and then declining.

Table 7.2.3: Estimated coefficients and their standard errors (se) of the log linear regression for the most parsimonious generalised linear model for infection prevalence. Coefficients for all parameters are significant at <0.001.

Parameter	Estimate	se	t-statistic
β_0	-4.822	1.601	-3.008
$MaxT$	-0.035	0.016	-2.143
$SP_{Lim.tasmaniensis}$	3.578	1.123	3.185
$SP_{Lit.\ fallax}$	3.389	1.347	2.516
SVL	0.351	0.086	4.067
SVL^2	-0.004	0.001	-4.078
$SP_{Lim.tasmaniensis}{:}SVL$	-0.120	0.044	-2.753
$SP_{Lit.\ fallax}{:}SVL$	-0.126	0.052	-2.410

A regression equation can be generated for male frogs using Eq. 7.01 and the coefficients from Table 7.2.3:

$$\begin{aligned}\log\mathrm{it}\left(\mu_{infection\ intensity}\right) \\ &= -4.822 - 0.035(MaxT) + 0.351(SVL) - 0.004(SVL^2) \\ &+ 3.578(SP_{Lim.tasmaniensis}) + 3.389\left(SP_{Lit.fallax}\right) \\ &- 0.120(SVL{:}SP_{Lim.tasmaniensis}) - 0.126\left(SVL{:}SP_{Lit.fallax}\right)\end{aligned}$$

(Eq. 7.03)

where factors = 1 where the state is true and 0 where the state is false. The regression equation can be solved for each species given a particular maximum temperature (Fig. 7.2.2). From Fig. 7.2.1, all three species showed an increase in infection intensity with increasing snout-vent length. *Limnodynastes tasmaniensis* and *Lit. wilcoxii* have higher, similar infection intensities than *Lit. fallax* for the same body size.

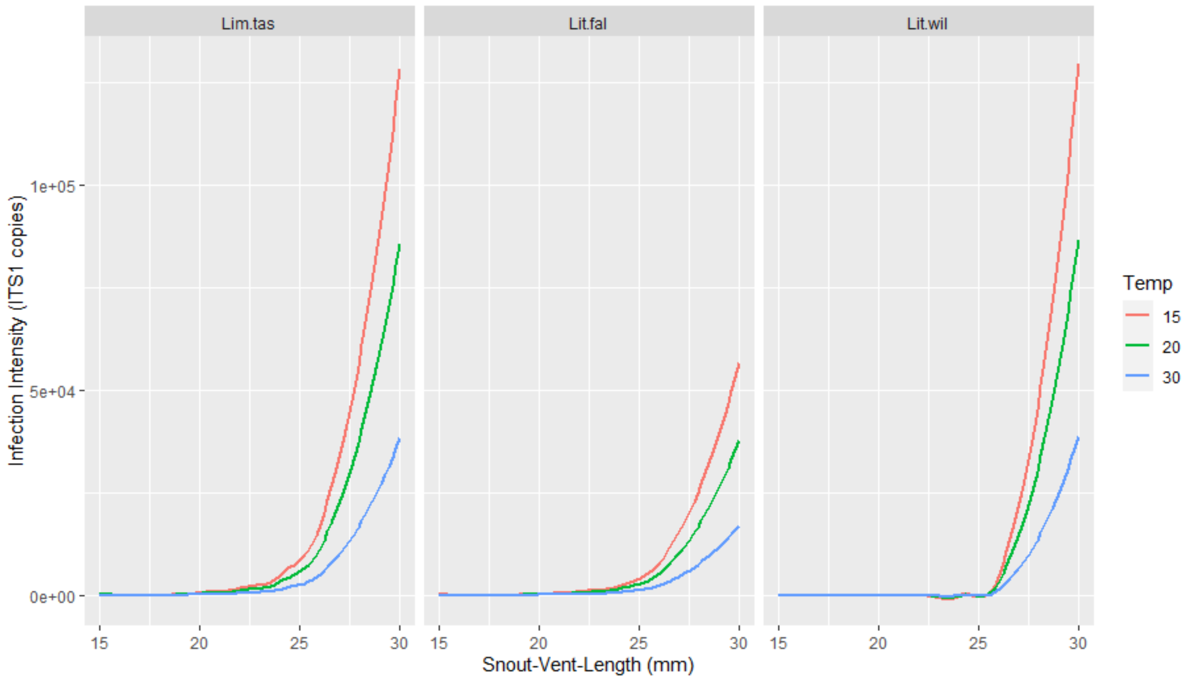


Fig. 7.2.2: The infection intensity for *Batrachochytrium dendrobatidis* in three New England Tablelands frog species; *Limnodynastes tasmaniensis* (Lim.tas), *Litoria fallax* (Lit.fal) and *Litoria wilcoxii* (Lit.wil), given increasing snout-vent length at three different maximum daily temperatures; 15°C, 20°C and 30°C.

7.3 Discussion

Individuals infected with the Amphibian chytrid fungus (*Batrachochytrium dendrobatidis*) were present at both sites and across all three species sampled. All three species have been known to be resistant to *B. dendrobatidis* infection, or have not shown any population declines in the past (Kriger & Hero 2006; Kriger *et al.* 2007; Miaud *et al.* 2016; Portway *et al.* 2020; Scheele *et al.* 2017; Stockwell *et al.* 2008; Woodhams *et al.* 2007). In response to *B. dendrobatidis*, these species can secrete peptides through their skin which, coupled with increased skin shedding, reduces infection intensity and the likelihood of mortality (Berger *et al.* 2004; Kriger & Hero 2006; Woodhams *et al.* 2007). Both *Lit. wilcoxii* and *Lim. tasmaniensis* have been documented to clear themselves of *B. dendrobatidis* infections (Berger *et al.* 2004; Kriger & Hero 2006). While populations of *Lit. fallax* infected with *B. dendrobatidis* did not show a decline in numbers, populations of another, sympatric species did (Stockwell *et al.* 2008).

Infection prevalence of *B. dendrobatidis* differed between the three frog species. *Litoria wilcoxii* had the highest infection prevalence and *Lit. fallax* had the lowest infection prevalence. The prevalence of *B. dendrobatidis* infection for *Lit. wilcoxii* determined here was similar to what has previously been recorded in this species, 32-70% by Portway *et al.* (2020), 22-77% by Van Sluys and Hero (2010) and 33% by Kriger and Hero (2006). Similarly, infection prevalence for *Lit. fallax* and for *Lim. tasmaniensis* was also similar to that previously reported; between 15-50% for *Lit. fallax* (Kriger & Hero 2007; Stockwell *et al.* 2016) and 57% for *Lim. tasmaniensis* (Kalvas 2014).

Infection intensity also differed with species. *Limnodynastes tasmaniensis* and *Lit. wilcoxii* had a higher infection intensity than *Lit. fallax,* which had a much lower infection intensity than the other two species. *Litoria wilcoxii* has been found to have reduced occupancy in the current study compared to the historical study (Heatwole *et al.* 1995). *Litoria fallax* and *Lim. tasmaniensis*, on the other hand, have both maintained their occupancy since the historical study. Previous studies have suggested that all three of these species are known to be tolerant of *B. dendrobatidis* infection (Kriger & Hero, 2006; Kriger *et al.* 2007; Miaud *et al.* 2016; Portway *et al.* 2020; Scheele *et al.* 2017; Stockwell *et al.* 2008; Woodhams *et al.* 2007). However, the present study found that one of the frog species which have reduced average occupancy also show a higher infection intensity of *B. dendrobatidis* than did the one species which increased its average occupancy. This suggests that there may be a negative influence of *B. dendrobatidis* infection on frog species which are declining in their occupancy, despite previously suggested tolerances. Briggs *et al.* (2010) determined that populations which do persist with *B. dendrobatidis* have lower infection loads, whilst populations facing decline had considerably higher infection loads as is the case for *Lit. wilcoxii* in the present study.

This study found that there was no overall difference in infection prevalence or intensity between the two different types of sites. Other studies have determined that infection prevalence and intensity of *B. dendrobatidis* can be specific to the type of site occupied (Kirshtein *et al.* 2007; Longo *et al.* 2013). Only one type of each site was sampled in the current study and two of the frog species were swabbed exclusively from each site. Given that there was no replication of site type, it is possible that the differences in infection intensity and prevalence between the species was a stronger predictor than that of site.

Sex was also not an important predictor of infection prevalence or intensity. However, this was confounded by the fact that no female frogs were found to be infected with *B. dendrobatidis.* Other studies have found that female and male *Lit. wilcoxii* had similar prevalence when similar numbers of both were sampled (Retallick *et al*. 2004; Van Sluys & Hero 2010). Some studies have found that infection intensity and prevalence for *B. dendrobatidis* differs between sites (Kirshtein *et al.* 2007; Kriger & Hero 2007b; Longo *et al.* 2013). Lips *et al.* (2006) observed that fewer dead individuals were found along streams than around ponds. Kriger and Hero (2007b) also found that frog species at permanent streams were more likely to be infected with *B. dendrobatidis* than permanent ponds. However, there was no difference in infection intensity between pond breeders and stream breeders (Kriger & Hero 2007b). The difference in prevalence was also not as drastic as it was found to be when comparing permanent streams to ephemeral ponds (Kriger & Hero 2007b). One proposed reason for the similarity in infection intensity and prevalence between the present studies sites, is that they were close enough to each other (<25 km apart) so that their broader geographical differences were similar and that they were part of the same catchment area (Sahukar *et al.* 2003). A repeat study, focusing on multiple replicates of the two different site types could potentially test this difference with more precision.

Site structure could also have an effect on Infection prevalence (Van Sluys & Hero 2010). Both sites sampled are surrounded by substantial farming enterprises, predominantly grazing cattle, although cattle were excluded from the sites themselves. The vegetation at Thomas Lagoon is predominantly composed of low-lying marsh plants, while the vegetation at Blue Hole forms riparian forest. Van Sluys and Hero (2010) found that prevalence of *B. dendrobatidis* in *Lit. wilcoxii* was higher in closed habitats. This is perhaps linked to difference in daytime temperatures caused by microhabitats, with closed habitats providing cooler temperatures during the day, benefitting *B. dendrobatidis*.

Body size was another predictor of infection prevalence, with prevalence being highest in individuals of ~20 mm for *Lim. tasmaniensis*, ~25 mm for *Lit. fallax* and ~35 mm for *Lit. wilcoxii*. However, as the size of the individual increased above or decreased below this size, infection prevalence reduced. This is contrary to what Kriger *et al.* (2006) found. They determined that there was a negative relationship between the likelihood of infection with the body length of juveniles, indicating that smaller individuals had a higher infection intensity. However, it should be noted that this particular study focused only on juveniles, so this association may not hold true for individuals that reach adulthood (Kriger *et al.* 2006). The findings of this contemporary study indicates that infection prevalence was highest in juvenile individuals for all three species. This is supported by other studies which reported a high intensity of infection in juveniles (Lamirande & Nichols 2006; Van Sluys & Hero 2010). A possible reason for this is that chytrid- induced mortality in juveniles and metamorphs is higher than it is in infected adults (Lamirande & Nichols 2006). Kriger and Hero (2006) determined that chytrid-induced mortality in *Lit. wilcoxii* was restricted to metamorphs and juveniles, with adults able to survive infection. The findings of Rachowicz and Vrendenburg (2004) support this suggestion in that they found that post-metamorphic *Rana muscosa* died while tadpoles remained clinically healthy. This may be the case for individuals of *Lit. wilcoxii* that were found in the present study where all infected *Lit. wilcoxii* were found to be adults. However, there were juvenile *Lim. tasmaniensis* which were infected, possibly indicating that susceptibility of juveniles to chytrid-induced mortality may vary between species. The lower infection prevalence in adults could be due to two different interpretations. Either, individuals that survive to adulthood are able to successfully clear themselves of infection, or fewer infected juveniles are able to survive to adulthood, or a combination of the two. It should be noted that tadpoles, the life stage that is most at risk of infection from *B. dendrobatidis* (Kriger & Hero 2006; Rachowicz & Vredenburg 2004), were not collected during the present study.

Infection intensity and prevalence in all three species differed depending on maximum daily temperature. This is supported by a number of studies which have modelled *B. dendrobatidis* growth in conjunction with temperature (Berger *et al.* 2004; Collins *et al.* 2003; Daszak *et al.* 2003; Johnson *et al.* 2003; Longcore *et al.* 1999). *Batrachochytrium dendrobatidis* grows best between 16-25^{o}C, can survive freezing, stops growing at 28^{o}C and dies at 30^{o}C (Berger *et al.* 2004; Daszak *et al.* 2004; Piotrowski *et al.* 2004). Longcore *et al.* (1999) found that growth of *B. dendrobatidis* was greatly reduced at 29^{o}C, but would resume once temperatures declined. This is a significant factor when considering *B. dendrobatidis* in an alpine environment. Daily maximum temperatures rarely exceed 30^{o}C, nor are daily temperatures maintained at which it would be fatal to the fungus (32ºC for four days, Johnson *et al.* 2003). As such, a montane environment, of which many parts of the New England Tablelands comprise, with cooler daily temperatures consequently lead to higher infection intensities and correspondingly higher mortalities for species which are susceptible.

Minimum daily temperature was not as good a predictor of infection intensity and prevalence as was maximum temperatures. This is different to what both Pounds *et al.* (2006) and Laurence (2008) found in their studies, where it was higher mean minimum temperatures that predisposed montane amphibian populations to higher infection intensity. However, the study conducted by Drew *et al.* (2006) did find that maximum daily temperature was a significant predictor of *B. dendrobatidis* infection across a large geographical scale. The studies conducted by Pounds *et al.* (2006) and by Laurence (2008) were conducted in rainforest habitat rather than an open, agricultural landscape. This possibly accounts for the difference in predictors, since habitat structure has been documented to influence infection intensity (Van Sluys & Hero 2010).

The present study found no evidence which suggests that infection prevalence varied depending on time of year. This is contrary to what Portway *et al.* (2020) found, where prevalence was lowest in October and January and highest in December in the New England Tablelands. One suggestion for the findings of the present study, is that these swabs were collected after a severe drought which extended from 2017 through to the end of 2019 (Nguyen *et al.* 2021). It is possible that given the reduced rainfall, individuals were less likely to be engaging in breeding activities, when they are thought to be more susceptible to infection (Muths *et al.* 2003). Further, Kriger *et al.* (2007) found that rainfall was a strong predictor of *B. dendrobatidis* infection, with wetter areas corresponding to higher *B. dendrobatidis* abundance. Another consideration linked to the drought, is that given the extra stressors associated with limited water availability, individuals already infected with *B. dendrobatidis* may have been more susceptible to chytridiomycosis induced mortality (Berger *et al.* 2004). These circumstances could lead to a reduced likelihood of infection or could decrease the number of infected individuals, which would lower infection prevalence.

Chapter 8: Conclusion

8. Conclusion

There were a number of locations in the New England Tablelands that were identified by Heatwole *et al.* (1995) as sites at which a number species of frog were variously found. The principal aim of this study was to revisit these sites and determine the current occupancy for frog species at them.

Overall, the diversity of the frog species communities found in the present study was somewhat diminished compared to those in the historical study. Three former common species from the historical study, the tusked frog (*Adelotus brevis*), the Booroolong frog (*Litoria booroolongensis*) and Bibron's toadlet (*Pseudophryne bibronii*) (Barker 1995; Gillespie & Hines 1999; Heatwole *et al.* 1995; Mahony 1999; Tyler 1992), were not found at all during the present study. Contrary to this, habitat generalists such as, the common eastern froglet (*Crinia signifera)*, the spotted marsh frog (*Limnodynastes tasmaniensis*) and the dwarf sedge frog (*Litoria fallax*) all maintained or had increased their current average occupancy in the New England Tablelands. Some other frog species, those which were habitat specialists, opportunistic breeders or burrowing species, were either found to have had decreased average occupancy, or were not found at all. Many habitat specialists are sensitive to changes in their environment and may also have a restricted distribution because of the narrow requirements of their breeding habitat (Filer *et al.* 2022; Wassens *et al.* 2013; Williams & Hero 2001), while explosive breeders are particularly sensitive to the unpredictability in weather conditions as projected for a world under the effects of climate change (Wassens *et al.* 2013; Ulloa *et al.* 2019).

Many of the frog species that still persist in the New England Tablelands have a lower average occupancy now than they were estimated to have during the period over which the historical study was conducted. This was not restricted to known threatened species, as there were seven species listed as being of least concern that have shown a decline in occupancy. Many previous studies have related the decline of frog species to the presence of the invasive, predatory eastern mosquito fish (*Gambusia holbrooki*) (Gillespie & Hero 1999; Gillespie & Hines 1999; Hamer *et al.* 2002b; Hamer *et al.* 2021; Hunter *et al.* 2011; Littlefair *et al.* 2021; Pyke & White 1996) and a known Amphibian chytrid fungus (*Batrachochytrium dendrobatidis*) reservoir host, the common eastern froglet (*Cri. signifera*) (Burns *et al.* 2021;

Scheele *et al.* 2016). However, the present study found that neither of these two species appeared to influence many of the frogs species in the New England Tablelands which showed a decline in occupancy. *Uperoleia laevigata* was the only frog species whose occupancy declined and also showed a negative association with *Cri. signifera*. The likelihood of *U. laevigata* occupying a site which was also occupied by *Cri. signifera* was much lower than at a site that was not occupied by *Cri. signifera*. The occupancy of none of the frog species was influenced by the presence of *G. holbrooki*, despite there being extensive literature to contrary (Gillespie & Hero 1999; Gillespie & Hines 1999; Hamer *et al.* 2002b; Hamer *et al.* 2021; Hunter *et al.* 2011; Littlefair *et al.* 2021; Pyke & White 1996).

The most important predictors of occupancy in the New England Tablelands were altitude, longitude (possibly a surrogate for rainfall and temperature gradients) and emergent vegetation. Most species which had a lower current occupancy compared to their historical occupancy were more likely to occupy sites at lower altitudes and with higher proportions of emergent vegetation. Similarly, species which exhibited lower average occupancy currently than when compared to the historical study where more likely to occupy sites which were in a warmer temperature and lower rainfall zone. Species which may be more susceptible to chytrid fungus may be less likely to persist at sites at higher altitudes where conditions are cooler and wetter. Such sites are more likely to favour *B. dendrobatidis* growth and consequently results in a higher risk of mortality for infected individuals (Berger *et al.* 2004; Daszak *et al.* 2003; Kriger & Hero 2006; Piotrowski *et al.* 2004). This is in keeping with other studies that found alpine species were more likely to suffer declines during the same period than those found at lower altitudes (Gillespie & Hero 1999; Gillespie & Hines 1999; Kriger & Hero 2004b; Laurance 2008; Pounds *et al.* 2006).

Detection was generally high for all species modelled during this study. Detection was also primarily influenced by air temperature as previous studies have found (Almeida-Gomes *et al*. 2007; Baker & Lauck 2006; Cui *et al*. 2011; Navas 1996; Van Sluys *et al.* 2012; Wong *et al.* 2004). These temperatures often corresponded to breeding season, with summer breeders having a higher detection during warmer temperatures and winter breeders have a higher detection during cooler temperatures (Baker & Lauck 2006; Wong *et al.* 2004). As such, future monitoring of frog species in the New England Tablelands should coincide with the breeding seasons of such species and carried out at sites where habitat variables maximise the likelihood of occupancy. However, there were several species which were only detected a handful of times at a small number of sites and as such were unable to be modelled. Further efforts should be made to determine the current occupancy of these species, to form a baseline for future modelling.

One method which is becoming more popular as a way of enhancing detection is the use of digital recorders (Blumstein *et al.* 2011; Darras *et al.* 2019; Forest 2007; Hill *et al.* 2018; Lapp *et al.* 2021; Xie *et al.* 2018). Digital recorders have been demonstrated to be useful in detecting species whose calls may be masked by louder species (Forest 2007; Lapp *et al.* 2021), species with short breeding windows (Forest 2007), rarer species or species with low detection (Forest 2007), or at sites located in remote areas which are difficult to access regularly (Larsen *et al.* 2018). Further, digital recorders may identify species at new, previously unoccupied locations (Bridges & Dorcas 2000) or provide can provide new information on long-term changes in phenology (Larsen *et al.* 2018). They are also reported to be less time and personnel intensive than manual sampling (Larsen *et al.* 2018; Xie *et al.* 2018). However, digital recorders generate large quantities of data which need to be analysed, either by hand or with a program (Lapp *et al.* 2021; Xie *et al.* 2018). Identification programs are in development and have been used previously to assist with this, but there are still limitations as to their efficacy in identifying specific frog calls (Lapp *et al.* 2021; Xie *et al.* 2018). Identification programs are also limited in that they need recordings of the target frog species on which to train, which are often not available for many frog species (Lapp *et al.* 2021; Xie *et al.* 2018). As such, using sound recorders in future studies may be useful in targeting more cryptic species or explosive breeders in the New England Tablelands, provided suitable analysis software becomes available.

Infection prevalence of *B. dendrobatidis* was higher in a habitat specialist species that had reduced its occupancy, than for a habitat generalist species which had maintained its historical occupancy. Similarly, it was found that a species which decreased their average occupancy since the historical study had a higher *B. dendrobatidis* infection load than that of one which had maintained its historical occupancy. That is a habitat specialist species with reduced occupancy, was more likely to be infected with *B. dendrobatidis* and at higher zoospore counts. The likelihood of *B. dendrobatidis* infection resulting in mortality differs with species, often with more susceptible species exhibiting a lower infection load threshold (Blaustein *et al.* 2005; Stockwell *et al.* 2010). Potentially, species which are exhibiting a decrease in their average occupancy in the New England Tablelands are also subjected to higher infection intensities leading to an increased risk of mortality and, consequently, reducing populations and therefore occupancy.

There are some final factors to consider in association with the present study. Firstly, it should be noted that due to the time and logistical constraints, not all historical sites were surveyed. The sites that were chosen to be surveyed were selected so as to include species that were known to be threatened or, alternatively, were identified as sites supporting a relatively large number of species in the historical study. Further, historical and current average occupancy was only compared between the 200 selected sites, which were considered to be representative of the region. It is possible, however, that species which were not detected at the 200 selected sites may have been occupying those sites that were not selected to be sampled. In relation to this, sites were also picked based on accessibility. Due to this, almost all sites showed some degree of anthropogenic disturbance, either agricultural or from the impact of urbanisation. Sites were also close to roads, so there was a high degree of disturbance associated with this as well. Species which require undisturbed habitat may still be present in areas that were more isolated in the New England Tablelands.

A second factor to consider is that almost all of the sites selected, were permanent or semi-permanent waterbodies. Areas that may have flooded, given sufficient rainfall, were a very small proportion of the sites surveyed. Given the drought which extended over the period 2017-2019 (Nguyen *et al.* 2021), species that could be present at ephemeral sites may not have been well represented in the present study. These particular frog species might have been present at these sites, but due to the lack of rainfall, were not engaged in activities (breeding, foraging, dispersal) that would allow them to be detected. Further, there was no opportunistic surveying conducted after rain, so observers may not have been present at ephemeral sites to detect the frog species that might have been there. Also associated with the drought is the timing of the surveys. Surveys were conducted in clusters over the three years when the drought was most severe (Nguyen *et al.* 2021). MacNally *et al.* (2009) and Wassens *et al.* (2013) found that it is the frog species that are habitat generalists, rather than burrowing frog species, which dominate in a landscape modified by agriculture, especially after periods of extended drought as occurred during the survey period for this study (Nguyen *et al*. 2021).

Thirdly, there was a difference in the methods to which the historical study was conducted when compared to the current study. The surveys conducted by Heatwole *et al.* (1995) consisted of collecting individuals for preservation (Simpson & Stanisic 1986). They did not record species which were calling (Simpson & Stanisic 1986). When considering this, it is possible that there were species calling at the sites the Heatwole *et al.* (1995) survey team visited, but were not recorded due to difficulties in locating and capturing them. As such, the historical occupancy for some species may have been underrepresented by the records. One such example could be *Cri. parinsignifera*, which is generally calling at a site when present, but given their colouration and size (Anstis 2017) are difficult to locate (*pers. obs*).

Finally, the majority of surveying was undertaken in the warmer months of the year (November to May) to maximise the number of species to potentially detect. No surveying was undertaken during the winter months. As such, it is possible that the true occupancy of species which breed in winter may be higher than estimated. This could have been relevant in relation to the common eastern froglet (*Cri. signifera)*, the whistling tree frog (*Litoria verreauxii*) and the crucifix frog (*Notaden bennetti*). It should be noted that *N. bennetti* was not detected at all in the present study.

Ultimately, the present study has documented a substantial diminution in frog biodiversity in the New England Tablelands. There were fewer species found currently than what was historically recorded in the region. Some species which were once common have declined. Further, species which are listed as having secure populations are also beginning to show reductions in their occupancy and it is predominantly habitat generalists which have maintained or, in a few instances, increased their occupancy in the New England Tablelands. Additionally, species that have exhibited higher infection prevalence and intensities are also more likely to have reduced their occupancy since the historical study as seen in other *B. dendrobatidis* studies (Brannelly *et al*. 2018; Burns *et al.* 2021; Laurance 2008;

Mahony *et al.* 2013; Scheele *et al.* 2017; Stockwell *et al.* 2010; Woodhams *et al.* 2007; Young *et al.* 2012).

The patterns observed in the New England Tablelands are likely not to be exclusive to this region. Since species which were once thought to be common in the New England Tablelands are now showing a decrease in their average occupancy, there should be some emphasise placed on monitoring all frog species, not just species with documented declines. The persistence of frog species in a freshwater ecosystem is important for its overall health. Given this, the initiation of any conservation efforts for declining frog species should not be postponed until that species is in crisis, as is the case with *Lit. booroloongensis* in the New England Tablelands. Such species that may require further monitoring in the region include the barking marsh frog (*Limnodynestes fletcheri*), the broad-palmed rocket frog (*Litoria latopalmata*) and the eastern stony creek frog (*Litoria wilcoxii*). All three species had lower average occupancy in the present study when compared to the historical study.

Broad-scale monitoring of frog populations should be undertaken to improve the understanding of the current occupancy of frog species and form the basis of future conservation efforts. Such methods may become more critical with the shifting precipitation patterns and frequency of extreme droughts (Mann & Gleick, 2015) which may have negative effects on amphibians (Kupeberg et al. 2022; Walls et al., 2013). Given the findings of the present study, future monitoring efforts should be made during seasonal breeding of the target species, at sites which maximise the likelihood of occupancy. Such habitat characteristics which should be targeted at sites are a high degree of vegetation with sampling to occur at either still or running waterbodies depending on the breeding requirements of the target species. Further, more effort is required to target species with low detection and or explosive breeders to determine their state of occupancy before monitoring can begin. The use of innovations such a digital recorders could assist with this endeavour.

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Appendix 1

Sites occupied by frog species found during the current survey and their historically occupied sites. NOTE: historical sites are from the selected 200 sites visited in the current survey, not the total 898 sites visited by Heatwole et al. (1995).

Fig. A1.1: A map of the sites historically occupied (H, red) by *Crinia parinsignifera*, and sites where *Cri. parinsignifera* were found in the current study at historical (CH, purple) and new sites (C, blue).

[redacted]

Fig. A1.2: A map of the sites historically occupied (H, red) by *Crinia signifera*, and sites where *Cri. signifera* were found in the current study at historical (CH, purple) and new sites (C, blue).

[redacted]

Fig. A1.3: A map of the sites historically occupied (H, red) by *Limnodynastes dumerilii*, and sites where *Lim. dumerilii* were found in the current study at historical (CH, purple) and new sites (C, blue).

[redacted]

Fig. A1.4: A map of the sites historically occupied (H, red) by *Limnodynastes fletcheri*, and sites where *Lim. fletcheri* were found in the current study at historical (CH, purple) and new sites (C, blue).

[redacted]

Fig. A1.5: A map of the sites historically occupied (H, red) by *Limnodynastes peronii*, and sites where *Lim. peroniii* were found in the current study at historical (CH, purple) and new sites (C, blue).

[redacted]

Fig. A1.6: A map of the sites historically occupied (H, red) by *Limnodynastes tasmaniensis*, and sites where *Lim. tasmaniensis* were found in the current study at historical (CH, purple) and new sites (C, blue).

[redacted]

Fig. A1.7: A map of the sites historically occupied (H, red) by *Litoria barringtonensis*, and sites where *Lit. barringtonensis* were found in the current study at historical (CH, purple) and new sites (C, blue).

[redacted]

Fig. A1.8: A map of the sites historically occupied (H, red) by *Litoria caerulea*, and sites where *Lit. caerulea* were found in the current study at historical (CH, purple) and new sites (C, blue).

[redacted]

Fig. A1.9: A map of the sites historically occupied (H, red) by *Litoria dentata*, and sites where *Lit. dentata* were found in the current study at historical (CH, purple) and new sites (C, blue).

[redacted]

Fig. A1.10: A map of the sites historically occupied (H, red) by *Litoria fallax*, and sites where *Lit. fallax* were found in the current study at historical (CH, purple) and new sites (C, blue).

[redacted]

Fig. A1.11: A map of the sites historically occupied (H, red) by *Litoria latopalmata*, and sites where *Lit. latopalmata* were found in the current study at historical (CH, purple) and new sites (C, blue).

[redacted]

Fig. A1.12: A map of the sites historically occupied (H, red) by *Litoria peronii*, and sites where *Lit. peronii* were found in the current study at historical (CH, purple) and new sites (C, blue).

[redacted]

Fig. A1.13: A map of the sites historically occupied (H, red) by *Litoria subglandulosa*, and sites where *Lit. subglandulosa* were found in the current study at historical (CH, purple) and new sites (C, blue).

[redacted]

Fig. A1.14: A map of the sites historically occupied (H, red) by *Litoria verreauxii*, and sites where *Lit. verreauxii* were found in the current study at historical (CH, purple) and new sites (C, blue).

[redacted]

Fig. A1.15: A map of the sites historically occupied (H, red) by *Litoria wilcoxii*, and sites where *Lit. wilcoxii* were found in the current study at historical (CH, purple) and new sites (C, blue).

[redacted]

Fig. A1.16: A map of the sites historically occupied (H, red) by *Mixophyes balbus*, and sites where *M. balbus* were found in the current study at historical (CH, purple) and new sites (C, blue).

[redacted]

Fig. A1.17: A map of the sites historically occupied (H, red) by *Pseudophryne coriacea*, and sites where *Pse. coriacea* were found in the current study at historical (CH, purple) and new sites (C, blue).

[redacted]

Fig. A1.18: A map of the sites historically occupied (H, red) by *Uperoleia laevigata*, and sites where *U. laevigata* were found in the current study at historical (CH, purple) and new sites (C, blue).

Appendix 2

Historical sites occupied by frog species which were not found during the current survey. NOTE: some historical sites are outside the current borders of the New England Tablelands, owing to the fact that the Heatwole et al. (1995) team used an electoral map from 1977 with different borders for the New England Tablelands than those of today.

Fig. A2.1: A map of the sites occupied by *Adelotus brevis* during the historical study (Heatwole *et al.* 1995).

[redacted]

Fig. A2.2: A map of the sites occupied by *Cyclorana sp.* during the historical study (Heatwole *et al.* 1995); *Cyc. brevipes* (yellow), *Cyc. cultripes* (red) and *Cyc. platycephala* (blue).

[redacted]

Fig. A2.3: A map of the sites occupied by *Lechriodus fletcheri* during the historical study (Heatwole *et al.* 1995).

[redacted]

Fig. A2.4: A map of the sites occupied by two *Limnodynastes sp.* during the historical study (Heatwole *et al.* 1995); *Lim. salmini* (red) and *Lim. terraereginae* (yellow).

[redacted]

Fig. A2.5: A map of the sites occupied by *Litoria aurea* during the historical study (Heatwole *et al.* 1995).

[redacted]

Fig. A2.6: A map of the sites occupied by *Litoria booroolongensis* during the historical study (Heatwole *et al.* 1995).

[redacted]

Fig. A2.7: A map of the sites occupied by *Litoria rubella* during the historical study (Heatwole *et al.* 1995).

[redacted]

Fig. A2.8: A map of the sites occupied by *Litoria sp.* with only a couple of detections during the historical study (Heatwole *et al.* 1995); *Lit. chloris* (yellow), *Lit. gracilenta* (red) and *Lit. piperata* (blue)

[redacted]

Fig. A2.9: A map of the sites occupied by two *Mixophyes sp.* with only a couple of detections during the historical study (Heatwole *et al.* 1995); *M. iteratus* (yellow) and *M. fasciolatus* (red).

[redacted]

Fig. A2.10: A map of the sites occupied by *Neobatrachus sudellae* during the historical study (Heatwole *et al.* 1995).

[redacted]

Fig. A2.11: A map of the single site occupied by *Philoria sphagnicola* during the historical study (Heatwole *et al.* 1995).

[redacted]

Fig. A2.12: A map of the single site occupied by *Platyplectrum ornatum* during the historical study (Heatwole *et al.* 1995).

[redacted]

Fig. A2.13: A map of the sites occupied by two *Pseudophryne sp.* during the historical study (Heatwole *et al.* 1995); *Pse. australis* (yellow) and *Pse. bibronii* (red).

[redacted]

Fig. A2.14: A map of the single site occupied by *Uperoleia rugosa* during the historical study (Heatwole *et al.* 1995).

Appendix 3

Maps of frog species detected in the current study. Also included is a map of sites where Gambusia holbrooki was and was not found, two species maps showing overlap of sites at which the other frog species were found with Crinia signifera and two species maps at which the frog species were found with Gambusia holbrooki.

A3.1 Maps for the single-species, single-season occupancy estimation for individual frog species (Chapter 5)

[redacted]

Fig. A3.1.1: Sites where *Crinia parinsignifera* was found during the current survey (blue) and sites where they were not found in the current survey (orange).

[redacted]

Fig. A3.1.2: Sites where *Crinia signifera* was found during the current survey (Blue) and sites where they were not found in the current survey (orange).

[redacted]

Fig. A3.1.3: Sites where *Limnodynastes dumerilli* was found during the current survey (Blue) and sites where they were not found in the current survey (orange).

[redacted]

Fig. A3.1.4: Sites where *Limnodynastes fletcheri* was found during the current survey (Blue) and sites where they were not found in the current survey (orange).

[redacted]

Fig. A3.1.5: Sites where *Limnodynastes peronii* was found during the current survey (Blue) and sites where they were not found in the current survey (orange).

[redacted]

Fig. A3.1.6: Sites where *Limnodynastes tasmaniensis* was found during the current survey (blue) and sites where they were not found in the current survey (orange).

[redacted]

Fig. A3.1.7: Sites where *Litoria barringtonensis* was found during the current survey (blue) and sites where they were not found in the current survey (orange).

[redacted]

Fig. A3.1.8: Sites where *Litoria caerulea* was found during the current survey (blue) and sites where they were not found in the current survey (orange).

[redacted]

Fig. A3.1.9: Sites where *Litoria dentata* was found during the current survey (Blue) and sites where they were not found in the current survey (orange).

[redacted]

Fig. A3.1.10: Sites where *Lit. fallax* was found during the current survey (blue) and sites where they were not found in the current survey (orange).

[redacted]

Fig. A3.1.11: Sites where *Litoria latopalmata* was found during the current survey (blue) and sites where they were not found in the current survey (orange).

[redacted]

Fig. A3.1.12: Sites where *Litoria peronii* was found during the current survey (Blue) and sites where they were not found in the current survey (orange).

[redacted]

Fig. A3.1.13: Sites where *Crinia parinsignifera* was found during the current survey (blue) and sites where they were not found in the current survey (orange).

[redacted]

Fig. A3.1.14: Sites where *Litoria verreauxii* was found during the current survey (blue) and sites where they were not found in the current survey (orange).

[redacted]

Fig. A3.1.15: Sites where *Litoria wilcoxii* was found during the current survey (Blue) and sites where they were not found in the current survey (orange).

[redacted]

Fig. A3.1.16: Sites where *Mixophyes balbus* was found during the current survey (blue) and sites where they were not found in the current survey (orange).

[redacted]

Fig. A3.1.17: Sites where *Pseudophryne coriacea* was found during the current survey (blue) and sites where they were not found in the current survey (orange).

[redacted]

Fig. A3.1.18: Sites where *Uperoleia laevigata* was found during the current survey (Blue) and sites where they were not found in the current survey (orange).

A3.2 Maps for the Comparison of Occupancy for Frog Species with *Crinia signifera* (Chapter 6)

[redacted]

Fig. A3.2.1: Sites where *Crinia signifera* and *Crinia parinsignifera* were found together (BA, purple), where only *Cri. signifera* was found (A, red) and where only *Cri. parinsignifera* (Ba, blue) was found during the current survey.

Fig. A3.2.2: Sites where *Crinia signifera* and *Limnodynastes dumerilii* were both found (BA, purple), only *Cri. signifera* was found (A, red), and only *Lim. dumerilii* (Ba, blue) was found during the current survey.

[redacted]

Fig. A3.2.3: Sites where *Crinia signifera* and *Limnodynastes fletcheri* were both found (BA, purple), only *Cri. signifera* was found (A, red), and only *Lim. fletcheri* (Ba, blue) was found during the current survey. NOTE: There were no sites where *Cri. signifera* and Lim. fletcheri were found together.

[redacted]

Fig. A3.2.4: Sites where *Crinia signifera* and *Limnodynastes peronii* were both found (BA, purple), only *Cri. signifera* was found (A, red), and only *Lim. peronii* (Ba, blue) was found during the current survey.

[redacted]

Fig. A3.2.5: Sites where *Crinia signifera* and *Limnodynastes tasmaniensis* were both found (BA, purple), only *Cri. signifera* was found (A, red), and *Lim. tasmaniensis* (Ba, blue) was found during the current survey.

Fig. A3.2.6: Sites where *Crinia signifera* and *Litoria barringtonensis* were found together (BA, purple), where only *Cri. signifera* was found (A, red) and where only *Lit. barringtonensis* (Ba, blue) was found during the current survey.

[redacted]

Fig. A3.2.7: Sites where *Crinia signifera* and *Litoria caerulea* were found together (BA, purple), where only *Cri. signifera* was found (A, red) and where only *Lit. caerulea* (Ba, blue) was found during the current survey.

[redacted]

Fig. A3.2.8: Sites where *Crinia signifera* and *Litoria dentata* were both found (BA, purple), only *Cri. signifera* was found (A, red), and only *Lit. dentata* (Ba, blue) was found during the current survey.

[redacted]

Fig. A3.2.9: Sites where *Crinia signifera* and *Litoria fallax* were both found (BA, purple), only *Cri. signifera* was found (A, red), and only *Lit. fallax* (Ba, blue) was found during the current survey.

[redacted]

Fig. A3.2.10: Sites where *Crinia signifera* and *Litoria latopalmata* were both found (BA, purple), only *Cri. signifera* was found (A, red), and only *Lit. latopalmata* (Ba, blue) was found during the current survey.

Fig. A3.2.11: Sites where *Crinia signifera* and *Litoria peronii* were both found (BA, purple), only *Cri. signifera* was found (A, red), and only *Lit. peronii* (Ba, blue) was found during the current survey.

[redacted]

Fig. A3.2.12: Sites where *Crinia signifera* and *Litoria subglandulosa* were found together (BA, purple), where only *Cri. signifera* was found (A, red) and where only *Lit. subglandulosa* (Ba, blue) was found during the current survey.

[redacted]

Fig. A3.2.13: Sites where *Crinia signifera* and *Litoria verreauxii* were both found (BA, purple), only *Cri. signifera* was found (A, red), and only *Lit. verreauxii* (Ba, blue) was found during the current survey.

Fig. A3.2.14: Sites where *Crinia signifera* and *Litoria wilcoxii* were both found (BA, purple), only *Crinia signifera* was found (A, red), and only *Litoria wilcoxii* (Ba, blue) was found during the current survey.

[redacted]

Fig. A3.2.15: Sites where *Crinia signifera* and *Mixophyes balbus* were found together (BA, purple), where only *Cri. signifera* was found (A, red) and where only *Cri. parinsignifera* (Ba, blue) was found during the current survey.

[redacted]

Fig. A3.2.16: Sites where *Crinia signifera* and *Pseudophryne coriacea* were found together (BA, purple), where only *Cri. signifera* was found (A, red) and where only *Pse. coriacea* (Ba, blue) was found during the current survey.

[redacted]

Fig. A3.2.17: Sites where *Crinia signifera* and *Uperoleia laevigata* were both found (BA, purple), only *Cri. signifera* was found (A, red), and only *U. laevigata* (Ba, blue) was found during the current survey.

A3.3 Maps for the Comparison of Occupancy for Frog Species with *Gambusia holbrooki* (Chapter 6)

[redacted]

Fig. A3.3.1: Sites where *Gambusia holbrooki* and *Crinia parinsignifera* were found together (BA, purple), where only *G. holbrooki* was found (A, red) and where only *Cri. parinsignifera* (Ba, blue) was found during the current survey.

[redacted]

Fig. A3.3.2: Sites where *Gambusia holbrooki* and *Crinia signifera* were found together (BA, purple), where only *G. holbrooki* was found (A, red) and where only *Cri. signifera* (Ba, blue) was found during the current survey.

[redacted]

Fig. A3.3.3: Sites where *Gambusia holbrooki* and *Limnodynastes dumerilii* were found together (BA, purple), where only *G. holbrooki* was found (A, red) and where only *Lim. dumerilii* (Ba, blue) was found during the current survey.

[redacted]

Fig. A3.3.4: Sites where *Gambusia holbrooki* and *Limnodynastes fletcheri* were found together (BA, purple), where only *G. holbrooki* was found (A, red) and where only *Lim. fletcheri* (Ba, blue) was found during the current survey.

Fig. A3.3.5: Sites where *Gambusia holbrooki* and *Limnodynastes peronii* were found together (BA, purple), where only *G. holbrooki* was found (A, red) and where only *Lim. peronii* (Ba, blue) was found during the current survey.

Fig. A3.3.6: Sites where *Gambusia holbrooki* and *Limnodynastes tasmaniensis* were found together (BA, purple), where only *G. holbrooki* was found (A, red) and where only *Lim. tasmaniensis* (Ba, blue) was found during the current survey.

[redacted]

Fig. A3.3.7: Sites where *Gambusia holbrooki* and *Litoria barringtonensis* were found together (BA, purple), where only *G. holbrooki* was found (A, red) and where only *Lit. barringtonensis* (Ba, blue) was found during the current survey.

Fig. A3.3.8: Sites where *Gambusia holbrooki* and *Litoria caerulea* were found together (BA, purple), where only *G. holbrooki* was found (A, red) and where only *Lit. caerulea* (Ba, blue) was found during the current survey.

[redacted]

Fig. A3.3.9: Sites where *Gambusia holbrooki* and *Litoria dentata* were found together (BA, purple), where only *G. holbrooki* was found (A, red) and where only *Lit. dentata* (Ba, blue) was found during the current survey.

[redacted]

Fig. A3.3.10: Sites where *Gambusia holbrooki* and *Litoria fallax* were found together (BA, purple), where only *G. holbrooki* was found (A, red) and where only *Lit. fallax* (Ba, blue) was found during the current survey.

[redacted]

Fig. A3.3.11: Sites where *Gambusia holbrooki* and *Litoria latopalmata* were found together (BA, purple), where only *G. holbrooki* was found (A, red) and where only *Lit. latopalmata* (Ba, blue) was found during the current survey.

[redacted]

Fig. A3.3.12: Sites where *Gambusia holbrooki* and *Litoria peronii* were found together (BA, purple), where only *G. holbrooki* was found (A, red) and where only *Lit. peronii* (Ba, blue) was found during the current survey.

Fig. A3.3.13: Sites where *Gambusia holbrooki* and *Litoria subglandulosa* were found together (BA, purple), where only *G. holbrooki* was found (A, red) and where only *Lit. subglandulosa* (Ba, blue) was found during the current survey.

[redacted]

Fig. A3.3.14: Sites where *Gambusia holbrooki* and *Litoria verreauxii* were found together (BA, purple), where only *G. holbrooki* was found (A, red) and where only *Lit. verreauxii* (Ba, blue) was found during the current survey.

[redacted]

Fig. A3.3.15: Sites where *Gambusia holbrooki* and *Litoria wilcoxii* were found together (BA, purple), where only *G. holbrooki* was found (A, red) and where only *Lit. wilcoxii* (Ba, blue) was found during the current survey.

[redacted]

Fig. A3.3.16: Sites where *Gambusia holbrooki* and *Mixophyes balbus* were found together (BA, purple), where only *G. holbrooki* was found (A, red) and where only *M. balbus* (Ba, blue) was found during the current survey.

[redacted]

Fig. A3.3.17: Sites where *Gambusia holbrooki* and *Pseudophryne coriacea* were found together (BA, purple), where only *G. holbrooki* was found (A, red) and where only *Pse. coriacea* (Ba, blue) was found during the current survey.

Fig. A3.3.18: Sites where *Gambusia holbrooki* and *Uperoleia laevigata* were found together (BA, purple), where only *G. holbrooki* was found (A, red) and where only *U. laevigata* (Ba, blue) was found during the current survey.

A3.4 Map for the single-species, single-season occupancy estimation for *Gambusia holbrooki* (Chapter 6)

[redacted]

Fig. A4.4.1: Sites where *Gambusia holbrooki* was found during the current survey (Blue) and sites where they were not found in the current survey (orange).

Appendix 4

Model selection for the top ranked models for single-season, single-species models created for 13 of the 18 species found in the New England Tablelands (Chapter 5) and the single-season, single-species models which included Crinia signifera and Gambusia holbrooki to model co-occurrence with the other frog species (Chapter 6).

The model selection process used is known as a secondary candidate set strategy which models sub-models independently and then combines the top set of models from each sub-model for selection in a final stage (Morin *et al.* 2020). In relation to the analysis conducted here, it involved taking a hierarchical modelling approach that involved fitting separate candidate sets of sub-models for the probability of occupancy and the probability of detection (Arnold 2010; Morin *et al.* 2020). As such, occupancy model comparison tables are presented for each step of the secondary candidate set procedure. A description of each of the covariates used is provided in Table A4.1.

Akaike's Information Criterion (AIC) was used to determine the most parsimonious model. Included in each of the occupancy comparison tables is the AIC statistic, the difference in AIC for a given model and the model in the set with the smallest AIC (i.e. the ΔAIC), the numbers of parameters including the intercepts for occupancy and detection (n), the Akaike weight for the model (w_i) and the maximised log-likelihood ($2Log(l)$). AIC statistics were computed for each model and, following comparisons, the model with the smallest AIC value was considered to be the preferred, most parsimonious model. In comparing any two models, when $\Delta AIC >$ 2.00, the interpretation is that given the data, there is increasing evidence that the model with the smaller AIC is the better of the two models (Burnham & Anderson 2002). Contrary to this, when $\Delta AIC <$ 2.0 for any two model, then it was considered that there was equal support for either model being considered to be the preferred model. The Akaike weight (w_i) provides a measure of the relative likelihood of the model being the best model, given the candidate set (Burnham & Anderson 2002). These weights can be combined and tested for each covariate using evidence ratios (ER). For the situation where there are multiple models with $\Delta AIC \leq$ 2.00, an evidence ratio (ER) was calculated to test the weight rating of the covariates (Anderson 2008). The $2Log(l)$ is a measure of model fit, with larger values indicating a better fit for the model (Burnham & Anderson 2002).

Table A4.1: Description of covariates and their associated occupancy modelling codes.

Code	Covariate description
Occupancy	
$ripV$	Extent (% cover) of riparian vegetation; vegetation on the bank of the waterbody extending away from it for <5m.
emV	Extent (% cover) of emergent vegetation; vegetation partially submerged in the waterbody.
F	Presence of invasive fish species; principally *Gambusia* sp.
C	Signs of domestic livestock activity; principally cattle
rW	Running waterbody; i.e. streams and rivers.
sW	Still waterbody; i.e. dams, lagoons, marshes, ephemeral puddles
nW	Absent water; i.e. various waterbodies where there was no water present.
LAT	Latitude
$LONG$	Longitude
ALT	Altitude (m)
$sigO$	Calculated occupancy probability for *Crinia signifera* at each of the 200 sites.
$gamO$	Calculated occupancy probability for *Gambusia holbrooki* at each of the 200 sites.
Detection	
AT	Air temperature (°C)
H	Relative humidity (%)
WS	Wind speed (km h^{-1})
CC	Cloud cover (%)
MI	Moon illumination; i.e. presence of light from the moon.
$R48$	Incidence of rainfall within the previous 48 hours
$sigD$	Calculated detection probability *Crinia signifera* for each of the 200 sites on each of the four sampling occasions.
$gamD$	Calculated detection probability *Gambusia holbrooki* for each of the 200 sites on each of the four sampling occasions.

Occupancy model comparison tables presented in this section show all models in the AIC comparison with a $\Delta AIC \leq 2.00$. Alternatively, tables were limited to the top six best performing models when comparisons had less than six models within $\Delta AIC \leq 2.00$. Other models were tested, but were not included in the following tables, due to having a $\Delta AIC > 2$. Not all variables listed in Table A4.1 will be represented in the top performing models. The ΔAIC for the baseline constant occupancy, constant detection model ($\Psi(.), p(.)$) indicates the strength of support for the inclusion of the covariates for both occupancy and detection that were included in the final model for each of the species. These values are included in the results for each species as a comparison to the preferred model where applicable. A $\Delta AIC > 2$ in comparison with the baseline model indicates strong support for the inclusion of covariates.

A4.1 Model selection for the single-species, single-season occupancy estimation for individual frog species (Chapter 5)

A4.1.1 Crinia parinsignifera

For the analysis of the variable occupancy, constant detection models, there were seven models for which $\Delta AIC \leq 2.00$ (Table A4.1.2). Evidence ratios were calculated for each of the variables included in these seven top models. Habitat covariates which had an $ER > 3.00$ were running waterbody (rW), still waterbody (sW) and longitude ($LONG$). These variables were considered for inclusion in the variable occupancy, variable detection model. All the other variables had an $ER <$ 3.00 and were not considered.

For the analysis of the constant occupancy, variable detection models there were five models with $\Delta AIC \leq 2.00$ (Table A4.1.3). Evidence ratios were calculated for each of the detection variables included in these five top models. Environmental covariates that had an $ER > 3.00$ were air temperature (AT), humidity (H) and wind speed (WS). These variables were considered for inclusion in the variable occupancy, variable detection model. All the other variables had an $ER < 3.00$ and were not considered.

Table A4.1.2: Top-ranked variable occupancy, constant detection models ($\Delta AIC \leq$ 2.00) with combinations of habitat variables used to model occupancy for *Crinia parinsignifera*. Listed are the number of parameters (n) AIC, ΔAIC, Akaike weights (w_i) and maximised log-likelihood ($2Log(l)$) for each of the top-ranked models.

Model	n	AIC	ΔAIC	w_i	$2Log(l)$
$\Psi(ripV + rW + sW + LONG), p(.)$	6	521.44	0.00	0.23	507.44
$\Psi(emV + ripV + rW + sW + LONG), p(.)$	7	521.95	0.52	0.18	505.95
$\Psi(C + rW + sW + LONG), p(.)$	6	522.49	1.05	0.14	508.49
$\Psi(emV + ripV + C + rW + sW + LONG), p(.)$	8	522.60	1.16	0.13	504.60
$\Psi(rW + sW + LONG), p(.)$	5	522.74	1.30	0.12	510.74
$\Psi(ripV + ALT + rW + sW + LONG), p(.)$	7	522.84	1.41	0.12	506.84
$\Psi(emV + ripV + ALT + rW + sW + LONG), p(.)$	8	523.44	2.00	0.09	505.44

Table A4.1.3: Top-ranked constant occupancy, variable detection models ($\Delta AIC \leq$ 2) with combinations of habitat variables used to model occupancy for *Crinia parinsignifera.* Listed are the number of parameters (n) AIC, ΔAIC, Akaike weights (w_i) and maximised log-likelihood ($2Log(l)$) for each of the top-ranked models.

Model	n	AIC	ΔAIC	w_i	$2Log(l)$
$\Psi(.), p(AT + H + WS)$	5	508.56	0.00	0.32	498.56
$\Psi(.), p(AT + H + WS + CC)$	6	509.41	0.85	0.21	497.41
$\Psi(.), p(AT + H + WS + R48)$	6	510.39	1.83	0.13	498.39
$\Psi(.), p(AT + H + WS + AT{:}H)$	6	510.41	1.85	0.13	498.41
$\Psi(.), p(AT + H + WS + MI)$	6	510.51	1.95	0.12	498.51
$\Psi(.), p(AT + WS)$	4	510.84	2.28	0.10	502.84

There was only one variable occupancy, variable detection model with $\Delta AIC \leq$ 2.00 (Table A4.1.4). This model was one where occupancy varied with waterbody type (rW, sW) and longitude ($LONG$), and detection varied with air temperature (AT), humidity (H) and wind speed (WS). The constant occupancy, constant detection model ($\Psi(.), p(.)$) had a $\Delta AIC =$ 23.46 (Table A4.1.4).

Table A4.1.4: Top six best performing variable occupancy, variable detection models with combinations of habitat and environmental variables used to model occupancy and detection for *Crinia parinsignifera*. Listed are the number of parameters (n) AIC, ΔAIC, Akaike weights (w_i) and maximised log-likelihood ($2Log(l)$) for each of the top-ranked models. NOTE: Constant occupancy, constant detection model ($\Psi(.), p(.)$) included as a reference.

Model	n	AIC	ΔAIC	w_i	$2Log(l)$
$\Psi(sW + rW + LONG), p(AT + H + WS)$	8	506.26	0.00	0.53	490.26
$\Psi(.), p(AT + H + WS)$	5	508.56	2.30	0.17	498.56
$\Psi(sW + rW + LONG), p(AT + WS)$	7	508.62	2.36	0.16	494.62
$\Psi(emV + ripV + F + C + ALT + wR + sW + LAT + LONG), p(AT + H + WS + MI + CC + R48)$	17	510.11	3.86	0.08	476.11
$\Psi(sW + rW + LONG), p(AT + H)$	7	511.36	5.10	0.04	497.36
$\Psi(.), p(.)$	**2**	**528.98**	**23.46**	**0.00**	**524.98**

A4.1.2 Crinia signifera

For the analysis of the variable occupancy, constant detection models, there were ten models for which $\Delta AIC \leq 2.00$ (Table A4.1.5). Evidence ratios were calculated for each of the variables included in these ten top models. Habitat covariates which had an $ER > 3.00$ were emergent vegetation (emV), altitude (ALT) and longitude ($LONG$). These variables were considered for inclusion in the variable occupancy, variable detection model. All the other variables had an $ER < 3.00$ and were not considered.

For the analysis of the constant occupancy, variable detection models there were four models with $\Delta AIC \leq 2.00$ (Table A4.1.6). Evidence ratios were calculated for each of the detection variables included in these four top models. Environmental covariates which had an $ER > 3.00$ were air temperature (AT), humidity (H) and the interaction between air temperature and humidity ($AT{:}H$). These variables were considered for inclusion in the variable occupancy, variable detection model. All the other variables had an $ER < 3.00$ and were not considered.

Table A4.1.5: Top-ranked variable occupancy, constant detection models ($\Delta AIC \leq 2.00$) with combinations of habitat variables used to model occupancy for *Crinia signifera*. Listed are the number of parameters (n) AIC, ΔAIC, Akaike weights (w_i) and maximised log-likelihood ($2Log(l)$) for each of the top-ranked models.

Model	n	AIC	ΔAIC	w_i	$2Log(l)$
$\Psi(emV + F + C + ALT + LAT + LONG), p(.)$	8	737.57	0.00	0.17	721.57
$\Psi(emV + F + C + ALT + rW + sW + LAT + LONG), p(.)$	10	738.48	0.91	0.11	718.48
$\Psi(emV + F + C + ALT + rW + sW + LONG), p(.)$	9	738.53	0.96	0.10	720.53
$\Psi(emV + ALT + LONG), p(.)$	5	738.64	1.07	0.10	728.64
$\Psi(emV + LONG), p(.)$	4	738.70	1.13	0.10	730.70
$\Psi(emV + F + C + ALT + LONG), p(.)$	7	738.91	1.34	0.09	724.91
$\Psi(emV + ripV + C + ALT + LAT + LONG), p(.)$	8	739.23	1.66	0.07	723.23
$\Psi(emV + F + C + rW + sW + LONG), p(.)$	8	739.25	1.67	0.07	723.25
$\Psi(emV + ALT + LAT + LONG), p(.)$	6	739.34	1.77	0.07	727.34
$\Psi(emV + ripV + F + C + ALT + LAT + LONG), p(.)$	9	739.42	1.84	0.07	721.42

Table A4.1.6: Six top-ranked constant occupancy, variable detection models with combinations of habitat variables used to model occupancy for *Crinia signifera*. Listed are the number of parameters (n) AIC, ΔAIC, Akaike weights (w_i) and maximised log-likelihood ($2Log(l)$) for each of the top-ranked models.

Model	n	AIC	ΔAIC	w_i	$2Log(l)$
$\Psi(.), p(AT + H + AT{:}H)$	5	657.36	0.00	0.33	647.36
$\Psi(.), p(AT + H + CC + AT{:}H)$	6	658.04	0.68	0.24	646.04
$\Psi(.), p(AT + H)$	4	658.65	1.29	0.17	650.65
$\Psi(.), p(AT + H + WS + AT{:}H)$	6	658.90	1.54	0.15	646.90
$\Psi(.), p(AT + H + CC)$	5	659.63	2.27	0.00	649.63
$\Psi(.), p(AT + H + MI + CC + AT{:}H)$	5	659.63	2.27	0.00	647.36

There were two variable occupancy, variable detection models with $\Delta AIC \leq 2.00$ (Table A4.1.7). A $\Delta AIC \leq 2.00$ for both models indicates that there is insufficient evidence to unequivocally distinguish between the two models. Since both these models were nested, the simplest model was considered the preferred model. This model was one where occupancy varied with emergent vegetation (emV), altitude (ALT) and longitude ($LONG$), and detection varied with air temperature (AT) and humidity (H). The constant occupancy, constant detection model ($\Psi(.), p(.)$) had a ΔAIC = 120.85 (Table A4.1.7).

Table A4.1.7: Top five best performing variable occupancy, variable detection models with combinations of habitat and environmental variables used to model occupancy and detection for *Crinia signifera*. Listed are the number of parameters (n) AIC, ΔAIC, Akaike weights (w_i) and maximised log-likelihood ($2Log(l)$) for each of the top-ranked models. NOTE: Constant occupancy, constant detection model ($\Psi(.), p(.)$) included as a reference.

Model	n	AIC	ΔAIC	w_i	$2Log(l)$
$\Psi(emV + ALT + LONG), p(AT + H + AT{:}H)$	8	639.26	0.00	0.63	623.26
$\Psi(emV + ALT + LONG), p(AT + H)$	7	640.38	1.13	0.36	626.38
$\Psi(emV + ripV + F + C + ALT + rW + sW + LAT + LONG),$ $p(AT + H + WS + MI + CC + R48)$	17	646.50	7.24	0.02	612.50
$\Psi(.), p(AT + H + AT{:}H)$	5	657.36	18.10	0.00	647.36
$\boldsymbol{\Psi(.), p(.)}$	**2**	**760.11**	**120.85**	**0.00**	**756.11**

A4.1.3 Limnodynastes dumerilii

For the analysis of the variable occupancy, constant detection models, there were 21 models for which $\Delta AIC \leq$ 2.00 (Table A4.1.8). Evidence ratios were calculated for each of the variables included in these 21 models. The only habitat covariate considered for occupancy included in the variable occupancy, variable detection model was emergent vegetation (emV). Although this covariate had an $ER <$ 3.00 (ER = 2.19), it was the only covariate that had an $ER >$ 1.00. All other covariates had an $ER <$ 1.00 and were not considered for the final model.

For the analysis of the constant occupancy, variable detection models there was only one model with $\Delta AIC \leq$ 2.00 (Table A4.1.9). This model was one with constant occupancy and detection varying with survey ($SURVEY$). A model with constant occupancy, detection varying with survey is a standard model included in most model likelihood comparisons (MacKenzie *et al.* 2018, p. 132). A model with detection varying with survey indicates that there is some component of variation in detecting this species which all other proposed models in the comparison cannot explain. The mechanism by which this species may be easier or harder to detect remains elusive, and the covariates selected in an attempt to model these differences are insufficient predictors. The omnibus covariate of survey ($SURVEY$) was included in the final variable occupancy, variable detection model.

Table A4.1.8: Top-ranked variable occupancy, constant detection models ($\Delta AIC \leq$ 2.00) with combinations of habitat variables used to model occupancy for *Limnodynastes dumerilli*. Listed are the number of parameters (n) AIC, ΔAIC, Akaike weights (w_i) and maximised log-likelihood ($2Log(l)$) for each of the top-ranked models.

Model	n	AIC	ΔAIC	w_i	$2Log(l)$
$\Psi(emV + LONG), p(.)$	4	426.01	0.00	0.08	418.01
$\Psi(emV), p(.)$	3	426.14	0.14	0.08	420.14
$\Psi(emV + ripV + LONG), p(.)$	5	426.63	0.63	0.06	416.63
$\Psi(emV + ALT), p(.)$	4	426.83	0.83	0.05	418.83
$\Psi(.), p(.)$	2	426.94	0.94	0.05	422.94
$\Psi(emV + ripV), p(.)$	4	426.96	0.95	0.05	418.96
$\Psi(LONG), p(.)$	3	426.98	0.97	0.05	420.98
$\Psi(emV + ripV + C)\ , p(.)$	5	427.28	1.28	0.04	417.28
$\Psi(emV + ripV + F), p(.)$	5	427.29	1.29	0.04	417.29
$\Psi(C), p(.)$	3	427.44	1.43	0.04	421.44
$\Psi(ripV + LONG), p(.)$	4	427.46	1.46	0.04	419.46
$\Psi(emV + F + C), p(.)$	5	427.52	1.52	0.04	417.52
$\Psi(emV + ripV + ALT), p(.)$	5	427.58	1.58	0.04	417.58
$\Psi(emV + ripV + C + LONG), p(.)$	6	427.59	1.58	0.04	415.59
$\Psi(ripV), p(.)$	3	427.63	1.62	0.04	421.63
$\Psi(emV + ALT + LONG), p(.)$	5	427.64	1.64	0.04	417.64
$\Psi(ALT), p(.)$	3	427.67	1.67	0.04	421.67
$\Psi(emV + ripV + F + C), p(.)$	6	427.68	1.68	0.04	415.68
$\Psi(emV + ripV + F + ALT), p(.)$	5	427.87	1.87	0.03	417.84
$\Psi\ (F), p(.)$	6	427.88	1.87	0.03	415.87
$\Psi(emV + ripV + F + LONG), p(.)$	3	427.96	1.96	0.03	421.88

There were two models in the final comparison which had a $\Delta AIC \leq 2.00$ (Table A4.1.10). A $\Delta AIC \leq 2.00$ for both models indicates that there is insufficient evidence to unequivocally distinguish between the two models. Since both these models were nested, the simpler model was selected as the preferred model. This model was where occupancy was constant, and detection varied with survey ($SURVEY$). The constant occupancy, constant detection model ($\Psi(.), p(.)$) had a $\Delta AIC = 64.60$ (Table A4.1.10).

Table A4.1.9: Top-ranked constant occupancy, variable detection models ($\Delta AIC \leq 2.00$) with combinations of habitat variables used to model occupancy for *Limnodynastes dumerilli*. Listed are the number of parameters (n) AIC, ΔAIC, Akaike weights (w_i) and maximised log-likelihood ($2Log(l)$) for each of the top-ranked models.

Model	n	AIC	ΔAIC	w_i	$2Log(l)$
$\Psi(.), p(SURVEY)$	5	363.34	0.00	1.00	353.34
$\Psi(.), p(H)$	3	426.77	63.43	0.00	420.77
$\Psi(.), p(CC)$	3	426.84	63.49	0.00	420.84
$\Psi(.), p(.)$	2	426.94	63.60	0.00	422.94
$\Psi(.), p(WS)$	3	426.98	63.63	0.00	420.98
$\Psi(.), p(AT)$	3	426.99	63.65	0.00	420.99

Table A4.1.10: Top five best performing variable occupancy, variable detection models with combinations of habitat and environmental variables used to model occupancy and detection for *Limnodynastes dumerilli*. Listed are the number of parameters (n) AIC, ΔAIC, Akaike weights (w_i) and maximised log-likelihood ($2Log(l)$) for each of the top-ranked models. NOTE: Constant occupancy, constant detection model ($\Psi(.), p(.)$) included as a reference.

Model	n	AIC	ΔAIC	w_i	$2Log(l)$
$\Psi(emV), p(SURVEY)$	6	362.34	0.00	0.62	350.34
$\Psi(.), p(SURVEY)$	5	363.34	1.00	0.38	353.34
$\Psi(emV), p(.)$	3	426.14	63.80	0.00	420.14
$\Psi(emV), p(AT)$	4	426.20	63.86	0.00	418.20
$\Psi(.), p(.)$	**2**	**426.94**	**64.60**	**0.00**	**422.94**

A4.1.4 *Limnodynastes fletcheri*

For the analysis of the variable occupancy, constant detection models, there were six models for which $\Delta AIC \leq 2.00$ (Table A4.1.11). Evidence ratios were calculated for each of the variables included in these top six models. The only habitat covariate which had an $ER > 3.00$ was longitude ($LONG$). This variable was included for occupancy in the variable occupancy, variable detection model. All the other variables had an $ER < 3.00$ and were not considered.

Table A4.1.11: Top-ranked variable occupancy, constant detection models ($\Delta AIC \leq 2.00$) with combinations of habitat variables used to model occupancy for *Limnodynastes fletcheri*. Listed are the number of parameters (n) AIC, ΔAIC, Akaike weights (w_i) and maximised log-likelihood ($2Log(l)$) for each of the top-ranked models.

Model	n	AIC	ΔAIC	w_i	$2Log(l)$
$\Psi(LONG), p(.)$	3	53.77	0.00	0.28	47.77
$\Psi(ALT + LONG), p(.)$	4	54.16	0.39	0.23	46.16
$\Psi(C + ALT + LONG), p(.)$	5	55.28	1.51	0.13	45.28
$\Psi(C + LONG), p(.)$	4	55.44	1.66	0.12	47.44
$\Psi(ripV + LONG), p(.)$	4	55.53	1.76	0.12	47.53
$\Psi(F + LONG), p(.)$	4	55.60	1.83	0.11	47.60

For the analysis of the constant occupancy, variable detection models there were two models with $\Delta AIC \leq 2.00$ (Table A4.1.12). Evidence ratios were calculated for each of the detection variables included in these top two models. Environmental covariates which had an $ER > 3.00$ were air temperature (AT), moon illumination (MI) and cloud cover (CC). These variables were considered to be included for detection in the variable occupancy, variable detection model. All the other variables had an $ER < 3.00$ and were not considered.

There were three variable occupancy, variable detection models with $\Delta AIC \leq 2.00$ (Table A4.1.13). A $\Delta AIC \leq 2.00$ for all three models indicates that there is insufficient evidence to unequivocally distinguish between them. Since these three models were nested, the simplest model was considered the preferred model. This model was one where occupancy varied with longitude ($LONG$), and detection varied with air temperature (AT). The constant occupancy, constant detection model ($\Psi(.), p(.)$) had a ΔAIC = 14.73 (Table A4.1.13).

Table A4.1.12: Top six constant occupancy, variable detection models with combinations of habitat variables used to model occupancy for *Limnodynastes fletcheri*. Listed are the number of parameters (n) AIC, ΔAIC, Akaike weights (w_i) and maximised log-likelihood ($2Log(l)$) for each of the top-ranked models.

Model	n	AIC	ΔAIC	w_i	$2Log(l)$
$\Psi(.), p(AT + MI + CC)$	5	46.78	0.00	0.49	36.78
$\Psi(.), p(AT + MI + CC + R48)$	6	48.44	1.66	0.21	36.44
$\Psi(.), p(AT + H + MI + CC)$	6	49.46	2.68	0.13	37.46
$\Psi(.), p(AT + H + MI + CC + AT{:}H)$	7	50.56	3.78	0.07	36.56
$\Psi(.), p(AT + WS + MI + CC)$	6	50.89	4.11	0.06	38.89
$\Psi(.), p(AT + H + MI + CC + R48 + AT{:}H)$	8	52.56	5.78	0.03	36.56

Table A4.1.13: Top six best performing variable occupancy, variable detection models with combinations of habitat and environmental variables used to model occupancy and detection for *Limnodynastes fletcheri*. Listed are the number of parameters (n) AIC, ΔAIC, Akaike weights (w_i) and maximised log-likelihood ($2Log(l)$) for each of the top-ranked models. NOTE: Constant occupancy, constant detection model ($\Psi(.), p(.)$) included as a reference.

Model	n	AIC	ΔAIC	w_i	$2Log(l)$
$\Psi(LONG), p(AT)$	4	48.28	0.00	0.34	40.28
$\Psi(LONG), p(AT + CC)$	5	49.05	0.77	0.23	39.05
$\Psi(LONG), p(AT + H)$	5	49.47	1.19	0.19	39.47
$\Psi(emV + ripV + F + C + ALT + rW + sW + LAT + LONG),$ $p(AT + H + WS + MI + CC + R48)$	17	50.79	2.51	0.10	16.79
$\Psi(LONG), p(AT + H + AT{:}H)$	6	51.10	2.82	0.08	39.10
$\Psi(.), p(.)$	**2**	**63.01**	**14.73**	**0.00**	**59.01**

A4.1.5 Limnodynastes peronii

For the analysis of the variable occupancy, constant detection models, there were fifteen models for which $\Delta AIC \leq 2.00$ (Table A4.1.14). Evidence ratios were calculated for each of the variables included in these fifteen top models. Habitat covariates considered for inclusion in the variable occupancy, variable detection model were running water (rW) and still water (sW). Although these two covariates had an $ER < 3.00$ (1.83), they were, however, the only covariate that had an $ER > 1.00$. All other covariates had an $ER < 1.00$ and were not considered significant.

Table A4.1.14: Top-ranked variable occupancy, constant detection models ($\Delta AIC \leq 2.00$) with combinations of habitat variables used to model occupancy for *Limnodynastes peronii*. Listed are the number of parameters (n) AIC, ΔAIC, Akaike weights (w_i) and maximised log-likelihood ($2Log(l)$) for each of the top-ranked models.

Model	n	AIC	ΔAIC	w_i	$2Log(l)$
$\Psi(rW + sW), p(.)$	4	311.71	0.00	0.11	303.71
$\Psi(.), p(.)$	2	312.04	0.32	0.10	308.04
$\Psi(emV + rW + sW), p(.)$	5	312.04	0.33	0.10	302.04
$\Psi(F + rW + sW), p(.)$	5	312.41	0.70	0.08	302.41
$\Psi(ALT + rW + sW), p(.)$	5	312.55	0.84	0.07	302.55
$\Psi(LAT + LONG), p(.)$	4	312.71	1.00	0.07	304.71
$\Psi(ALT), p(.)$	3	313.07	1.35	0.06	307.07
$\Psi(emV + ALT + rW + sW), p(.)$	6	313.25	1.54	0.05	301.25
$\Psi(F + ALT + rW + sW), p(.)$	6	313.26	1.54	0.05	301.26
$\Psi(ripV + rW + sW), p(.)$	5	313.46	1.75	0.05	303.46
$\Psi(emV), p(.)$	3	313.51	1.80	0.05	307.51
$\Psi(rW + sW + LONG), p(.)$	5	313.55	1.83	0.05	303.55
$\Psi(LONG), p(.)$	3	313.64	1.92	0.04	307.64
$\Psi(rW + sW + LAT + LONG), p(.)$	6	313.64	1.92	0.04	301.64
$\Psi(C + rW + sW), p(.)$	5	313.66	1.95	0.04	303.66

For the analysis of the constant occupancy, variable detection models there were six models with $\Delta AIC \leq 2.00$ (Table A4.1.15). Evidence ratios were calculated for each of the detection variables included in these six top models. Environmental covariates which had an $ER > 3.00$ were air temperature (AT) and moon illumination (MI). These two variables were considered to be included for detection in the variable occupancy, variable detection model. Cloud cover (CC) had a $1.00 < ER < 3.00$ (2.20) and was considered for inclusion in the variable occupancy, variable detection model. All the other variables had an $ER < 2.00$ and were not considered.

Table A4.1.15: Top-ranked constant occupancy, variable detection models ($\Delta AIC \leq 2.00$) with combinations of habitat variables used to model occupancy for *Limnodynastes peronii*. Listed are the number of parameters (n) AIC, ΔAIC, Akaike weights (w_i) and maximised log-likelihood ($2Log(l)$) for each of the top-ranked models.

Model	n	AIC	ΔAIC	w_i	$2Log(l)$
$\Psi(.), p(AT + MI + CC)$	5	272.58	0.00	0.27	262.58
$\Psi(.), p(AT + MI + CC + R48)$	6	273.29	0.71	0.19	261.29
$\Psi(.), p(AT + WS + MI + CC)$	6	274.01	1.43	0.13	262.01
$\Psi(.), p(AT + MI)$	4	274.20	1.63	0.12	266.20
$\Psi(.), p(AT + WS + MI + CC + R48)$	7	274.23	1.66	0.12	260.23
$\Psi(.), p(AT + H + MI + CC)$	6	274.51	1.94	0.10	262.51

There were three variable occupancy, variable detection model with $\Delta AIC \leq 2.00$ (Table A4.1.16). The habitat covariates for occupancy were running waterbody (rW) and still waterbody (sW), and the environmental covariates for detection air temperature (AT) and moon illumination (MI) all had an $ER > 3.00$. This suggests strong evidence for models which included these four covariates to be most suitable. Cloud cover (CC) had and $ER < 3.00$ (1.08) and so there was insufficient evidence for a model which included cloud cover to be more suitable than models without cloud cover. The preferred model was therefore one where occupancy varied with waterbody type and detection varied with air temperature and moon illumination. The constant occupancy, constant detection model ($\Psi(.), p(.)$) had a $\Delta AIC = 39.52$ (Table A4.1.16).

Table A4.1.16: Top six best performing variable occupancy, variable detection models with combinations of habitat and environmental variables used to model occupancy and detection for *Limnodynastes peronii*. Listed are the number of parameters (n) AIC, ΔAIC, Akaike weights (w_i) and maximised log-likelihood ($2Log(l)$) for each of the top-ranked models. NOTE: Constant occupancy, constant detection model ($\Psi(.), p(.)$) included as a reference.

Model	n	AIC	ΔAIC	w_i	$2Log(l)$
$\Psi(rW + sW), p(AT + CC + MI)$	7	272.52	0.00	0.52	258.52
$\Psi(.), p(AT + MI)$	4	274.20	1.68	0.22	266.20
$\Psi(rW+sW), p(AT + MI)$	6	274.26	1.73	0.22	262.26
$\Psi(rW +sW), p(AT)$	5	279.52	7.00	0.02	269.52
$\Psi(.), p(AT)$	3	279.80	7.28	0.01	273.80
$\boldsymbol{\Psi(.), p(.)}$	**2**	**312.04**	**39.52**	**0.00**	**308.04**

A4.1.6 Limnodynastes tasmaniensis

For the analysis of the variable occupancy, constant detection models, there were five models for which $\Delta AIC \leq 2.00$ (Table A4.1.17). Evidence ratios were calculated for each of the variables included in these five top models. Habitat covariates which had an $ER > 3.00$ were emergent (emV), altitude (ALT), and longitude ($LONG$). These variables were considered to be included for occupancy in the final variable occupancy, variable detection model. All the other variables had an $ER < 3.00$ and were not considered.

Table A4.1.17: Six top-ranked variable occupancy, constant detection models ($\Delta AIC \leq 2$) with combinations of habitat variables used to model occupancy for *Limnodynastes tasmaniensis*. Listed are the number of parameters (n) AIC, ΔAIC, Akaike weights (w_i) and maximised log-likelihood ($2Log(l)$) for each of the top-ranked models.

Model	n	AIC	ΔAIC	w_i	$2Log(l)$
$\Psi(emV + ALT + LONG), p(.)$	5	576.26	0.00	0.30	566.26
$\Psi(emV + rW + sW + ALT + LONG), p(.)$	7	577.22	0.96	0.19	563.22
$\Psi(emV + ALT + LAT + LONG), p(.)$	6	577.61	1.35	0.15	565.61
$\Psi(rW + sW + ALT + LONG), p(.)$	6	577.78	1.52	0.14	565.78
$\Psi(emV + ripV + ALT + LONG), p(.)$	6	578.00	1.74	0.13	566.00
$\Psi(ALT + LONG), p(.)$	4	578.58	2.32	0.09	570.58

For the analysis of the constant occupancy, variable detection models there was only one model with $\Delta AIC \leq 2.00$ (Table A4.1.18). This model was one with constant occupancy and detection varying with the omnibus variable survey ($SURVEY$). The covariate of survey ($SURVEY$) was included in the final variable occupancy, variable detection model.

Table A4.1.18: Six top-ranked constant occupancy, variable detection models ($\Delta AIC \leq 2.00$) with combinations of habitat variables used to model occupancy for *Limnodynastes tasmaniensis*. Listed are the number of parameters (n) AIC, ΔAIC, Akaike weights (w_i) and maximised log-likelihood ($2Log(l)$) for each of the top-ranked models.

Model	n	AIC	ΔAIC	w_i	$2Log(l)$
$\Psi(.), p(SURVEY)$	5	518.88	0.00	1.00	508.88
$\Psi(.), p(AT + H + MI + AT{:}H)$	6	548.67	29.79	0.00	536.67
$\Psi(.), p(AT + H + WS + MI + AT{:}H)$	7	548.67	29.79	0.00	534.67
$\Psi(.), p(AT + H + WS + AT{:}H)$	6	548.79	29.91	0.00	536.79
$\Psi(.), p(AT + H + AT{:}H)$	5	549.17	30.29	0.00	539.17
$\Psi(.), p(AT + H + WS + MI + R48 + AT{:}H)$	8	549.74	30.86	0.00	533.74

There was a single variable occupancy, variable detection model with $\Delta AIC \leq 2.00$ (Table A4.1.19). This model was one where occupancy varied with emergent vegetation (emV), altitude (ALT) and longitude ($LONG$), and detection varied with the omnibus variable survey ($SURVEY$). The reference constant occupancy, constant detection model ($\Psi(.), p(.)$) had a $\Delta AIC = 106.07$ (Table A4.1.19).

Table A4.1.19: Top six best performing variable occupancy, variable detection models with combinations of habitat and environmental variables used to model occupancy and detection for *Limnodynastes tasmaniensis*. Listed are the number of parameters (n) AIC, ΔAIC, Akaike weights (w_i) and maximised log-likelihood ($2Log(l)$) for each of the top-ranked models. NOTE: Constant occupancy, constant detection model ($\Psi(.), p(.)$) included as a reference.

Model	n	AIC	ΔAIC	w_i	$2Log(l)$
$\Psi(emV + ALT + LONG), p(SURVEY)$	8	494.45	0.00	1.00	478.45
$\Psi(.), p(SURVEY)$	5	518.88	24.43	0.00	508.88
$\Psi(emV + ALT + LONG), p(AT + H + AT{:}H)$	8	525.08	30.63	0.00	509.08
$\Psi(emV + ALT + LONG), p(AT + H)$	7	528.08	33.63	0.00	514.08
$\Psi(emV + ALT + LONG), p(AT)$	6	537.72	43.27	0.00	525.72
$\Psi(.), p(.)$	**2**	**600.51**	**106.07**	**0.00**	**596.51**

A4.1.7 Litoria dentata

For the analysis of the variable occupancy, constant detection models, there were ten models for which $\Delta AIC \leq 2.00$ (Table A4.1.20). Evidence ratios were calculated for each of the variables included in these ten top models. Habitat covariates which had an $ER > 3.00$ were emergent vegetation (emV), latitude (LAT) and longitude ($LONG$). These variables were considered for inclusion in the variable occupancy, variable detection model. All the other variables had an $ER < 3.00$ and were not considered.

For the analysis of the constant occupancy, variable detection models there were 11 models with $\Delta AIC \leq 2.00$ (Table A4.1.21). Evidence ratios were calculated for each of the detection variables included in these top 11 models. The only environmental covariate which had an $ER > 3.00$ was air temperature (AT). This variable was considered for inclusion in the variable occupancy, variable detection model. All the other variables had an $ER < 3.00$ and were not considered.

Table A4.1.20: Top-ranked variable occupancy, constant detection models ($\Delta AIC \leq 2.00$) with combinations of habitat variables used to model occupancy for *Litoria dentata*. Listed are the number of parameters (n) AIC, ΔAIC, Akaike weights (w_i) and maximised log-likelihood ($2Log(l)$) for each of the top-ranked models.

Model	n	AIC	ΔAIC	w_i	$2Log(l)$
$\Psi(emV + ripV + C + LAT + LONG), p(.)$	7	154.36	0.00	0.18	140.36
$\Psi(emV + ripV + LAT + LONG), p(.)$	6	155.21	0.85	0.12	143.21
$\Psi(emV + LAT + LONG), p(.)$	5	155.22	0.86	0.11	145.22
$\Psi(emV + F + C + LAT + LONG), p(.)$	7	155.69	1.33	0.09	141.69
$\Psi(emV + ripV + C + ALT + LAT + LONG), p(.)$	8	155.75	1.40	0.09	139.75
$\Psi(emV + ALT + LAT + LONG), p(.)$	6	155.90	1.54	0.08	143.90
$\Psi(emV + ripV + ALT + LAT + LONG), p(.)$	7	156.09	1.73	0.07	142.09
$\Psi(emV + ripV + F + C + LAT + LONG), p(.)$	8	156.31	1.95	0.07	140.31
$\Psi(ALT + LAT + LONG), p(.)$	5	156.33	1.97	0.07	146.33
$\Psi(ripV + LAT + LONG), p(.)$	5	156.33	1.97	0.07	146.33

Table A4.1.21: Top-ranked constant occupancy, variable detection models ($\Delta AIC \leq 2.00$) with combinations of habitat variables used to model occupancy for *Litoria dentata*. Listed are the number of parameters (n) AIC, ΔAIC, Akaike weights (w_i) and maximised log-likelihood ($2Log(l)$) for each of the top-ranked models.

Model	n	AIC	ΔAIC	w_i	$2Log(l)$
$\Psi(.), p(AT + MI + CC + R48)$	6	110.85	0.00	0.14	98.85
$\Psi(.), p(AT)$	3	110.92	0.07	0.14	104.92
$\Psi(.), p(AT + R48)$	4	111.35	0.50	0.11	103.35
$\Psi(.), p(AT + WS)$	4	111.67	0.81	0.10	103.67
$\Psi(.), p(AT + CC + R48)$	5	111.94	1.09	0.08	101.94
$\Psi(.), p(AT + H + CC)$	5	112.03	1.17	0.08	102.03
$\Psi(.), p(AT + WS + CC + R48)$	6	112.55	1.70	0.06	100.55
$\Psi(.), p(AT + WS + R48)$	5	112.62	1.77	0.06	102.62
$\Psi(.), p(AT + WS + MI + R48)$	6	112.62	1.77	0.06	100.62
$\Psi(.), p(AT + MI)$	4	112.65	1.80	0.06	104.65
$\Psi(.), p(AT + H + MI + R48)$	6	112.80	1.95	0.05	100.80

There was only one variable occupancy, variable detection model with $\Delta AIC \leq 2.00$ (Table A4.1.22). This model was one where occupancy varied with emergent vegetation (emV), latitude (LAT) and longitude ($LONG$), and detection varied with air temperature (AT). The constant occupancy, constant detection model ($\Psi(.), p(.)$) had a $\Delta AIC = 52.16$ (Table A4.1.22).

Table A4.1.22: Top six best performing variable occupancy, variable detection models with combinations of habitat and environmental variables used to model occupancy and detection for *Litoria dentata*. Listed are the number of parameters (n) AIC, ΔAIC, Akaike weights (w_i) and maximised log-likelihood ($2Log(l)$) for each of the top-ranked models. NOTE: Constant occupancy, constant detection model ($\Psi(.), p(.)$) included as a reference.

Model	n	AIC	ΔAIC	w_i	$2Log(l)$
$\Psi(emV + LAT + LONG), p(AT)$	6	96.57	0.00	0.90	84.57
$\Psi(emV + ripV + F + C + ALT + rW + sW + LAT + LONG),$ $p(AT + H + WS + MI + CC + R48)$	17	100.87	4.31	0.10	66.87
$\Psi(.), p(AT)$	3	110.71	14.14	0.00	104.71
$\Psi(.), p(SURVEY)$	4	118.31	21.74	0.00	110.31
$\Psi(emV + LAT + LONG), p(.)$	5	133.57	37.01	0.00	123.57
$\boldsymbol{\Psi(.), p(.)}$	**2**	**148.73**	**52.16**	**0.00**	**144.73**

A4.1.8 Litoria fallax

For the analysis of the variable occupancy, constant detection models there were nine models for which $\Delta AIC \leq 2.00$ (Table A4.1.23). Evidence ratios were calculated for each of the variables included in these top nine models. Those habitat covariates which had an $ER \geq 3.00$ were running water (rW), still water (sW) and longitude ($LONG$). These variables were considered for the inclusion for occupancy in the final variable occupancy, variable detection model. All the other variables had an ER < 3.00, and were therefore not considered in the final modelling process.

For the analysis of the constant occupancy, variable detection models there was only one model with $\Delta AIC \leq 2.00$ (Table A4.1.24). This model was one with constant occupancy and detection varying with the omnibus variable survey

($SURVEY$). The covariate of survey ($SURVEY$) was included in the final variable occupancy, variable detection model.

Table A4.1.23: Top-ranked variable occupancy, constant detection models ($\Delta AIC \leq 2.00$) with combinations of habitat variables used to model occupancy for *Litoria fallax*. Listed are the number of parameters (n) AIC, ΔAIC, Akaike weights (w_i) and maximised log-likelihood ($2Log(l)$) for each of the top-ranked models.

Model	n	AIC	ΔAIC	w_i	$2Log(l)$
$\Psi(F + rW + sW + LONG), p(.)$	6	754.82	0.00	0.15	742.82
$\Psi(emV + ripV + F + rW + sW + LONG), p( )$	8	755.08	0.27	0.13	739.08
$\Psi(rW + sW + LONG), p(.)$	5	755.30	0.48	0.12	745.30
$\Psi(F + ALT + rW + sW + LONG), p(.)$	7	755.73	0.92	0.10	741.73
$\Psi(emV + rW + sW + LONG), p(.)$	6	755.82	1.01	0.09	743.82
$\Psi(ripV + ALT + rW + sW + LONG), p(.)$	7	756.74	1.93	0.06	742.74
$\Psi(ALT + rW + sW + LONG), p(.)$	6	756.77	1.95	0.06	744.77
$\Psi(emV + ripV + ALT + rW + sW + LONG), p(.)$	8	756.80	1.98	0.06	740.80
$\Psi(ripV + F + C + rW + sW + LONG), p(.)$	7	756.81	1.99	0.06	742.80

Table A4.1.24: Top-ranked constant occupancy, variable detection models ($\Delta AIC \leq 2.00$) with combinations of habitat variables used to model occupancy for *Litoria fallax*. Listed are the number of parameters (n) AIC, ΔAIC, Akaike weights (w_i) and maximised log-likelihood ($2Log(l)$) for each of the top-ranked models.

Model	n	AIC	ΔAIC	w_i	$2Log(l)$
$\Psi(.), p(SURVEY)$	5	590.78	0.00	1.00	580.78
$\Psi(.), p(AT)$	3	615.55	24.77	0.00	609.55
$\Psi(.), p(AT + R48)$	4	616.73	25.95	0.00	608.73
$\Psi(.), p(AT + MI)$	4	617.11	26.32	0.00	609.11
$\Psi(.), p(AT + H)$	4	617.30	26.52	0.00	609.30
$\Psi(.), p(AT + WS)$	4	617.53	26.75	0.00	609.53

There was only one variable occupancy, variable detection model with $\Delta AIC \leq 2.00$ (Table A4.1.25). This model was one where occupancy varied with water body type (rW, sW) and longitude ($LONG$), and detection varied with survey

($SURVEY$). The reference model of constant occupancy, constant detection ($\Psi(.)$, $p(.)$) had a ΔAIC = 184.34 (Table A4.1.25).

Table A4.1.25: Top six best performing variable occupancy, variable detection models with combinations of habitat and environmental variables used to model occupancy and detection for *Litoria fallax*. Listed are the number of parameters (n) AIC, ΔAIC, Akaike weights (w_i) and maximised log-likelihood ($2Log(l)$) for each of the top-ranked models. NOTE: Constant occupancy, constant detection model ($\Psi(.), p(.)$) included as a reference.

Model	n	AIC	ΔAIC	w_i	$2Log(l)$
$\Psi(rW + sW + LONG), p(SURVEY)$	8	580.92	0.00	0.83	564.92
$\Psi(rW + sW), p(SURVEY)$	7	585.11	4.19	0.10	571.11
$\Psi(LONG), p(SURVEY)$	6	585.96	5.04	0.07	573.96
$\Psi(.), p(SURVEY)$	5	590.78	9.86	0.01	580.78
$\Psi(rW + sW + LONG), p(AT)$	6	608.07	27.15	0.00	596.07
$\Psi(.), p(.)$	**2**	**765.26**	**184.34**	**0.00**	**761.26**

A4.1.9 Litoria latopalmata

For the analysis of the variable occupancy, constant detection models, there were eight models for which $\Delta AIC \leq$ 2.00 (Table A4.1.26). Evidence ratios were calculated for each of the variables included in these eight top models. The only habitat covariate which had an ER > 3.00 was longitude ($LONG$). This variable was considered for inclusion in the variable occupancy, variable detection model. All the other variables had an ER < 3.00 and were not considered.

For the analysis of the constant occupancy, variable detection models there were 12 models with $\Delta AIC \leq$ 2.00 (Table A4.1.27). Evidence ratios were calculated for each of the detection variables included in these top 12 models. The only environmental covariate which had an ER > 3.00 was air temperature (AT). This variable was considered for inclusion in the variable occupancy, variable detection model. All the other variables had an ER < 3.00 and were not considered.

Table A4.1.26: Top-ranked variable occupancy, constant detection models ($\Delta AIC \leq 2.00$) with combinations of habitat variables used to model occupancy for *Litoria latopalmata*. Listed are the number of parameters (n) AIC, ΔAIC, Akaike weights (w_i) and maximised log-likelihood ($2Log(l)$) for each of the top-ranked models.

Model	n	AIC	ΔAIC	w_i	$2Log(l)$
$\Psi(LONG), p(.)$	3	468.66	0.00	0.22	462.66
$\Psi(F + LONG), p(.)$	4	469.41	0.75	0.15	461.41
$\Psi(C + LONG), p(.)$	4	469.79	1.13	0.12	461.79
$\Psi(emV + LONG), p(.)$	4	469.97	1.31	0.11	461.97
$\Psi(F + C + LONG), p(.)$	5	470.58	1.92	0.08	460.58
$\Psi(LAT + LONG), p(.)$	4	470.62	1.96	0.08	462.62
$\Psi(ALT + LONG), p(.)$	4	470.63	1.97	0.08	462.63
$\Psi(ripV + LONG), p(.)$	4	470.65	1.99	0.08	462.65

Table A4.1.27: Top-ranked constant occupancy, variable detection models ($\Delta AIC \leq 2.00$) with combinations of habitat variables used to model occupancy for *Litoria latopalmata*. Listed are the number of parameters (n) AIC, ΔAIC, Akaike weights (w_i) and maximised log-likelihood ($2Log(l)$) for each of the top-ranked models.

Model	n	AIC	ΔAIC	w_i	$2Log(l)$
$\Psi(.), p(AT + MI)$	4	425.21	0.00	0.12	417.21
$\Psi(.), p(AT + CC)$	4	425.40	0.19	0.11	417.40
$\Psi(.), p(AT)$	3	425.41	0.20	0.11	419.41
$\Psi(.), p(AT + MI + CC)$	5	425.48	0.27	0.11	415.48
$\Psi(.), p(AT + R48)$	4	426.09	0.87	0.08	418.09
$\Psi(.), p(AT + H + MI)$	5	426.09	0.88	0.08	416.09
$\Psi(.), p(AT + H)$	4	426.16	0.95	0.08	418.16
$\Psi(.), p(AT + CC + R48)$	5	426.57	1.36	0.06	416.57
$\Psi(.), p(AT + MI + R48)$	5	426.66	1.45	0.06	416.66
$\Psi(.), p(AT + H + R48)$	5	427.04	1.83	0.05	417.04
$\Psi(.), p(AT + WS + MI)$	5	427.20	1.99	0.05	417.20
$\Psi(.), p(AT + MI + CC + R48)$	6	427.20	1.99	0.05	415.20

There was only one variable occupancy, variable detection model with $\Delta AIC \leq 2.00$ (Table A4.1.28). This model was one where occupancy varied with emergent longitude ($LONG$), and detection varied with air temperature (AT). The constant occupancy, constant detection model ($\Psi(.), p(.)$) had a ΔAIC = 111.92 (Table A4.1.28).

Table A4.1.28: Top six best performing variable occupancy, variable detection models with combinations of habitat and environmental variables used to model occupancy and detection for *Litoria latopalmata*. Listed are the number of parameters (n) AIC, ΔAIC, Akaike weights (w_i) and maximised log-likelihood ($2Log(l)$) for each of the top-ranked models. NOTE: Constant occupancy, constant detection model ($\Psi(.), p(.)$) included as a reference.

Model	N	AIC	ΔAIC	w_i	$2Log(l)$
$\Psi(LONG), p(AT)$	4	394.59	0.00	1.00	386.59
$\Psi(emV + ripV + F + C + ALT + rW + sW + LAT + LONG),$ $p(AT + H + WS + MI + CC + R48)$	17	412.31	17.72	0.00	378.31
$\Psi(.), p(AT)$	3	425.41	30.82	0.00	419.41
$\Psi(.), p(SURVEY)$	5	434.70	40.11	0.00	424.70
$\Psi(LONG), p(.)$	3	468.66	74.07	0.00	462.66
$\Psi(.), p(.)$	**2**	**506.51**	**111.92**	**0.00**	**502.51**

A4.1.10 Litoria peronii

For the analysis of the variable occupancy, constant detection models, there were fifteen models for which $\Delta AIC \leq$ 2.00 (Table A4.1.29). Evidence ratios were calculated for each of the variables included in these fifteen top models. The only habitat covariate which had an ER > 3.00 was the presence of livestock (C). This variable was considered for inclusion in the variable occupancy, variable detection model. Riparian vegetation ($ripV$) had a 1.00 < ER < 3.00 (2.21) and was also considered for inclusion in the variable occupancy, variable detection model. All the other variables had an ER < 2.00 and were not considered.

For the analysis of the constant occupancy, variable detection models, there was only one model with $\Delta AIC \leq$ 2.00 (Table A4.1.30). This model was one with constant occupancy and detection varying with the omnibus variable survey ($SURVEY$). The covariate of survey ($SURVEY$) was included in the final variable occupancy, variable detection model.

Table A4.1.29: Top-ranked variable occupancy, constant detection models ($\Delta AIC \leq 2.00$) with combinations of habitat variables used to model occupancy for *Litoria peronii*. Listed are the number of parameters (n) AIC, ΔAIC, Akaike weights (w_i) and maximised log-likelihood ($2Log(l)$) for each of the top-ranked models.

Model	n	AIC	ΔAIC	w_i	$2Log(l)$
$\Psi(emV + ripV + C), p(.)$	5	442.97	0.00	0.10	432.97
$\Psi(C), p(.)$	3	443.23	0.26	0.09	437.23
$\Psi(ripV + F + C), p(.)$	5	443.40	0.43	0.08	433.40
$\Psi(ripV + F + C + LONG), p(.)$	6	443.54	0.57	0.07	431.54
$\Psi(emV + ripV + C + ALT), p(.)$	6	443.68	0.71	0.07	431.68
$\Psi(emV + ripV + C + LONG). p(.)$	6	443.68	0.71	0.07	431.68
$\Psi(C + LAT + LONG), p(.)$	5	443.69	0.72	0.07	433.69
$\Psi(emV + ripV + C + LAT + LONG), p(.)$	7	443.74	0.77	0.07	429.74
$\Psi(C + LONG), p(.)$	4	443.85	0.89	0.06	435.85
$\Psi(C + ALT), p(.)$	4	444.09	1.12	0.06	436.09
$\Psi(ripV + F + C + LAT + LONG), p(.)$	7	444.18	1.21	0.05	430.18
$\Psi(ripV + F + C + ALT), p(.)$	6	444.21	1.25	0.05	432.21
$\Psi(emV + ripV + F + C), p(.)$	6	444.68	1.72	0.04	432.68
$\Psi(emV + ripV + F + C + LONG), p(.)$	7	444.80	1.84	0.04	430.80
$\Psi(ripV), p(.)$	3	444.85	1.88	0.04	438.85

Table A4.1.30: Top-ranked constant occupancy, variable detection models ($\Delta AIC \leq 2.00$) with combinations of habitat variables used to model occupancy for *Litoria peronii*. Listed are the number of parameters (n) AIC, ΔAIC, Akaike weights (w_i) and maximised log-likelihood ($2Log(l)$) for each of the top-ranked models.

Model	n	AIC	ΔAIC	w_i	$2Log(l)$
$\Psi(.), p(SURVEY)$	4	377.44	0.00	1.00	369.44
$\Psi(.), p(AT)$	3	402.60	25.16	0.00	396.60
$\Psi(.), p(AT + CC)$	4	403.11	25.67	0.00	395.11
$\Psi(.), p(AT + WS)$	4	404.18	26.74	0.00	396.18
$\Psi(.), p(AT + H)$	4	404.19	26.74	0.00	396.19
$\Psi(.), p(AT + CC + R48)$	5	404.31	26.86	0.00	394.31

There were two variable occupancy, variable detection model with $\Delta AIC \leq$ 2.00 (Table A4.1.31). A $\Delta AIC \leq$ 2.00 for both models indicates that there is insufficient evidence to unequivocally distinguish between the two. When both models are nested, the simplest model is usually considered the preferred model. However, since the model which included riparian vegetation had a ΔAIC = 1.77, it was considered sufficiently close to two, providing sufficient evidence for the support of a model including riparian vegetation. The preferred model was therefore, the model where occupancy varied with riparian vegetation ($ripV$) and livestock presence (C), and detection varied with survey ($SURVEY$). The constant occupancy, constant detection model ($\Psi(.), p(.)$) had a ΔAIC = 71.53 (Table A4.1.31).

Table A4.1.31: Top six best performing variable occupancy, variable detection models with combinations of habitat and environmental variables used to model occupancy and detection for *Litoria peronii*. Listed are the number of parameters (n) AIC, ΔAIC, Akaike weights (w_i) and maximised log-likelihood ($2Log(l)$) for each of the top-ranked models. NOTE: Constant occupancy, constant detection model ($\Psi(.), p(.)$) included as a reference.

Model	n	AIC	ΔAIC	w_i	$2Log(l)$
$\Psi(ripV + C), p(SURVEY)$	6	373.69	0.00	0.64	361.69
$\Psi(C), p(SURVEY)$	5	375.45	1.77	0.26	365.45
$\Psi(.), p(SURVEY)$	4	377.44	3.76	0.10	369.44
$\Psi(ripV + C), p(AT)$	5	398.15	24.46	0.00	388.15
$\Psi(C), p(AT)$	4	399.77	26.09	0.00	391.77
$\Psi(.), p(.)$	**2**	**445.22**	**71.53**	**0.00**	**441.22**

A4.1.11 Litoria verreauxii

For the analysis of the variable occupancy, constant detection models, there were six models for which $\Delta AIC \leq$ 2.00 (Table A4.1.32). Evidence ratios were calculated for each of the variables included in these six top models. Habitat covariates which had an ER > 3.00 were altitude (ALT), latitude (LAT) and longitude ($LONG$). These variables were considered to be included for occupancy in the variable occupancy, variable detection model. All the other variables had an ER < 3.00 and were not considered.

Table A4.1.32: Top-ranked variable occupancy, constant detection models ($\Delta AIC \leq 2.00$) with combinations of habitat variables used to model occupancy for *Litoria verreauxii*. Listed are the number of parameters (n) AIC, ΔAIC, Akaike weights (w_i) and maximised log-likelihood ($2Log(l)$) for each of the top-ranked models.

Model	n	AIC	ΔAIC	w_i	$2Log(l)$
$\Psi(emV + ALT + LAT + LONG), p(.)$	6	501.46	0.00	0.26	489.46
$\Psi(ALT + LAT + LONG), p(.)$	5	501.80	0.34	0.22	491.80
$\Psi(F + ALT + LAT + LONG), p(.)$	6	503.01	1.55	0.12	491.01
$\Psi(emV + rW + sW + ALT + LAT + LONG), p(.)$	7	503.09	1.63	0.11	489.09
$\Psi(ripV + ALT + LAT + LONG), p(.)$	8	503.10	1.64	0.11	487.10
$\Psi(C + ALT + LAT + LONG), p(.)$	6	503.43	1.96	0.10	491.43

For the analysis of the constant occupancy, variable detection models there were ten models with $\Delta AIC \leq 2.00$ (Table A4.1.33). Evidence ratios were calculated for each of the detection variables included in these ten top models. Environmental covariates which had an $ER > 3.00$ were air temperature (AT) and humidity (H). These variables were considered to be included for detection in the variable occupancy, variable detection model. All the other variables had an $ER < 3.00$ and were not considered.

There were two variable occupancy, variable detection model with $\Delta AIC \leq$ 2.00 (Table A4.1.34). A $\Delta AIC \leq 2.00$ for both models indicates that there is insufficient evidence to unequivocally distinguish between the two. When both models are nested, the simplest model is usually considered the preferred model. However, since the model which included an interaction between air temperature and humidity had a $\Delta AIC = 1.92$, it was considered sufficiently close a value to 2.00, providing sufficient evidence for the support of a model including air temperature. The preferred model was therefore, the model where occupancy varied with altitude (ALT), latitude (LAT) and longitude ($LONG$), and detection varied with air temperature (AT) and humidity (H). The constant occupancy, constant detection model ($\Psi(.), p(.)$) had a $\Delta AIC = 43.93$ (Table A4.1.34).

Table A4.1.33: Top-ranked constant occupancy, variable detection models ($\Delta AIC \leq$ 2.00) with combinations of habitat variables used to model occupancy for *Litoria verreauxii*. Listed are the number of parameters (n) AIC, ΔAIC, Akaike weights (w_i) and maximised log-likelihood ($2Log(l)$) for each of the top-ranked models.

Model	n	AIC	ΔAIC	w_i	$2Log(l)$
$\Psi(.), p(AT + H + WS)$	5	508.67	0.00	0.19	498.67
$\Psi(.), p(AT + H)$	4	508.75	0.07	0.18	500.75
$\Psi(.), p(AT + H + WS + R48)$	6	510.26	1.58	0.08	498.26
$\Psi(.), p(AT + H + R48)$	5	510.30	1.63	0.08	500.30
$\Psi(.), p(AT + H + WS + CC)$	6	510.53	1.86	0.07	498.53
$\Psi(.), p(AT + H + MI)$	5	510.55	1.88	0.07	500.55
$\Psi(.), p(AT + H + WS + MI)$	6	510.55	1.88	0.07	498.55
$\Psi(.), p(AT + H + CC)$	5	510.59	1.92	0.07	500.59
$\Psi(.), p(AT + H + AT{:}H)$	5	510.65	1.97	0.07	500.65
$\Psi(.), p(AT + H + WS + AT{:}H)$	6	510.65	1.98	0.07	498.65

Table A4.1.34: Top six best performing variable occupancy, variable detection models with combinations of habitat and environmental variables used to model occupancy and detection for *Litoria verreauxii*. Listed are the number of parameters (n) AIC, ΔAIC, Akaike weights (w_i) and maximised log-likelihood ($2Log(l)$) for each of the top-ranked models. NOTE: Constant occupancy, constant detection model ($\Psi(.), p(.)$) included as a reference.

Model	n	AIC	ΔAIC	w_i	$2Log(l)$
$\Psi(ALT + LAT + LONG), p(AT + H)$	7	484.04	0.00	0.72	470.04
$\Psi(ALT + LAT + LONG), p(AT + H + AT{:}H)$	8	485.96	1.92	0.28	469.96
$\Psi(emV + ripV + F + C + ALT + rW + sW + LAT + LONG),$ $p(AT + H + WS + MI + CC + R48)$	17	496.07	12.03	0.00	462.07
$\Psi(ALT + LAT + LONG), p(AT)$	6	496.37	12.33	0.00	484.37
$\Psi(ALT + LAT + LONG), p(.)$	5	501.80	17.76	0.00	491.80
$\Psi(.), p(.)$	**2**	**527.97**	**43.93**	**0.00**	**523.97**

A4.1.12 Litoria wilcoxii

For the analysis of the variable occupancy, constant detection models, there were seven models for which $\Delta AIC \leq$ 2.00 (Table A4.1.35). Evidence ratios were calculated for each of the variables included in these seven top models. Habitat covariates which had an ER > 3.00 were running water (rW), still water (sW), altitude (ALT) and longitude ($LONG$). These variables were considered to be included for occupancy in the variable occupancy, variable detection model. All the other variables had an ER < 3.00 and were not considered.

Table A4.1.35: Top-ranked variable occupancy, constant detection models ($\Delta AIC \leq 2.00$) with combinations of habitat variables used to model occupancy for *Litoria wilcoxii*. Listed are the number of parameters (n) AIC, ΔAIC, Akaike weights (w_i) and maximised log-likelihood ($2Log(l)$) for each of the top-ranked models.

Model	n	AIC	ΔAIC	w_i	$2Log(l)$
$\Psi(ALT + rW + sW + LONG), p(.)$	6	143.52	0.00	0.24	131.52
$\Psi(emV + ALT + rW + sW + LONG), p(.)$	7	144.34	0.82	0.16	130.34
$\Psi(ripV + ALT + rW + sW + LONG), p(.)$	7	144.98	1.45	0.12	130.98
$\Psi(ALT + rW + STILL\ P\ LAT\ P\ LONG), p(.)$	7	145.03	1.51	0.11	131.03
$\Psi(ALT + rW + sW), p(.)$	5	145.20	1.68	0.11	135.20
$\Psi(C + ALT + rW + sW + LONG), p(.)$	7	145.48	1.96	0.09	131.48
$\Psi(F + ALT + rW + sW + LONG), p(.)$	7	145.50	1.98	0.09	131.50

For the analysis of the constant occupancy, variable detection models there were nine models with $\Delta AIC \leq 2.00$ (Table A4.1.36). Evidence ratios were calculated for each of the detection variables included in these nine top models. The only environmental covariate considered for detection inclusion in the variable occupancy, variable detection model was air temperature (AT). Although this covariate had an ER < 3.00 (2.69), it was the only covariate that had an ER > 1.00. All other covariates had an ER < 1.00 and were not considered significant.

There were two variable occupancy, variable detection model with $\Delta AIC \leq$ 2.00 (Table A4.1.37). A $\Delta AIC \leq 2.00$ for both models indicates that there is insufficient evidence to unequivocally distinguish between the two. When both models are nested, the simpler model is usually considered the preferred model. However, Since the model which excluded air temperature had a $\Delta AIC = 1.95$, it was considered sufficiently close to 2.00, providing sufficient evidence for the support of a model including air temperature. The preferred model was therefore, the model where occupancy varied with waterbody type (rW, sW), altitude (ALT) and longitude

($LONG$), and detection varied with air temperature (AT). The constant occupancy, constant detection model ($\Psi(.), p(.)$) had a ΔAIC = 2.99 (Table A4.1.37).

Table A4.1.36: Top-ranked constant occupancy, variable detection models ($\Delta AIC \leq$ 2.00) with combinations of habitat variables used to model occupancy for *Litoria wilcoxii*. Listed are the number of parameters (n) AIC, ΔAIC, Akaike weights (w_i) and maximised log-likelihood ($2Log(l)$) for each of the top-ranked models.

Model	n	AIC	ΔAIC	w_i	$2Log(l)$
$\Psi(.), p(AT)$	3	150.80	0.00	0.22	144.80
$\Psi(.), p(AT + R48)$	4	152.39	1.59	0.10	144.39
$\Psi(.), p(AT + WS)$	4	152.45	1.65	0.10	144.45
$\Psi(.), p(WS)$	3	152.48	1.68	0.10	146.48
$\Psi(.), p(H)$	3	152.65	1.84	0.09	146.65
$\Psi(.), p(CC)$	3	152.65	1.84	0.09	146.65
$\Psi(.), p(AT + CC)$	4	152.74	1.93	0.08	144.74
$\Psi(.), p(AT + H)$	4	152.76	1.96	0.08	144.76
$\Psi(.), p(AT + MI)$	4	152.80	1.99	0.08	144.80

Table A4.1.37: Top six best performing variable occupancy, variable detection models with combinations of habitat and environmental variables used to model occupancy and detection for *Litoria wilcoxii*. Listed are the number of parameters (n) AIC, ΔAIC, Akaike weights (w_i) and maximised log-likelihood ($2Log(l)$) for each of the top-ranked models. NOTE: Constant occupancy, constant detection model ($\Psi(.), p(.)$) included as a reference.

Model	n	AIC	ΔAIC	w_i	$2Log(l)$
$\Psi(sW + rW + ALT + LONG), p(AT)$	7	143.24	0.00	0.52	126.53
$\Psi(sW + rW + ALT + LONG), p(.)$	6	145.19	1.95	0.19	131.52
$\Psi(.), p(AT)$	3	145.71	2.48	0.15	144.80
$\boldsymbol{\Psi(.), p(.)}$	**2**	**146.23**	**2.99**	**0.12**	**149.81**
$\Psi(.), p(SURVEY)$	5	150.80	7.57	0.01	145.76
$\Psi(emV + ripV + F + C + ALT + rW + sW + LAT + LONG),$ $p(AT + H + WS + MI + CC + R48)$	17	152.76	9.52	0.00	123.25

A4.1.13 Uperoleia laevigata

For the analysis of the variable occupancy, constant detection models, there were eleven models for which $\Delta AIC \leq$ 2.00 (Table A4.1.38). Evidence ratios were calculated for each of the variables included in these top eleven models. No habitat covariates had an $ER \geq 1.00$, indicating that there is little support for the inclusion of covariates in the modelling of occupancy. However, since riparian vegetation ($ripV$) had the highest ER (0.86), it was considered as a possible key covariate of occupancy in the variable occupancy, variable detection model. All the other variables had an $ER < 0.86$ and were not considered.

Table A4.1.38: Top-ranked variable occupancy, constant detection models ($\Delta AIC \leq 2.00$) with combinations of habitat variables used to model occupancy for *Uperoleia laevigata*. Listed are the number of parameters (n) AIC, ΔAIC, Akaike weights (w_i) and maximised log-likelihood ($2Log(l)$) for each of the top-ranked models.

Model	n	AIC	ΔAIC	w_i	$2Log(l)$
$\Psi(ripV), p(.)$	3	483.85	0.00	0.14	477.85
$\Psi(F), p(.)$	3	484.00	0.15	0.13	478.00
$\Psi(.), p(.)$	2	484.25	0.40	0.12	480.25
$\Psi(ripV + rW + sW), p(.)$	5	485.11	1.26	0.08	475.11
$\Psi(emV + ripV + F), p(.)$	5	485.29	1.44	0.07	475.29
$\Psi(emV + ripV), p(.)$	4	485.30	1.45	0.07	477.30
$\Psi(F + LAT + LONG), p(.)$	5	485.45	1.60	0.06	475.45
$\Psi(rW + sW), p(.)$	4	485.48	1.63	0.06	477.48
$\Psi(F + LONG), p(.)$	4	485.63	1.79	0.06	477.63
$\Psi(emV), p(.)$	3	485.78	1.93	0.05	479.78
$\Psi(ripV + LONG), p(.)$	4	485.83	1.98	0.05	477.83

For the analysis of the constant occupancy, variable detection models there was only one model with $\Delta AIC \leq 2.00$ (Table A4.1.39). This model was one with constant occupancy and detection varying with the omnibus variable survey ($SURVEY$). The covariate of survey ($SURVEY$) was included in the final variable occupancy, variable detection model.

There were two models in the final comparison which had a $\Delta AIC \leq 2.00$ (Table A4.1.40). The close weight rating (w_i) for both models indicates that there is insufficient evidence for one model being better than the other. Because these models were nested, the simpler of the two was considered the preferred model.

This model was where occupancy was constant, and detection varied with survey ($SURVEY$). The reference constant occupancy, constant detection model had a ΔAIC = 57.40 (Table A4.1.40).

Table A4.1.39: Top six best performing constant occupancy, variable detection models ($\Delta AIC \leq 2$) with combinations of habitat variables used to model occupancy for *Uperoleia laevigata*. Listed are the number of parameters (n) AIC, ΔAIC, Akaike weights (w_i) and maximised log-likelihood ($2Log(l)$) for each of the top-ranked models.

Model	n	AIC	ΔAIC	w_i	$2Log(l)$
$\Psi(.), p(SURVEY)$	5	427.31	0.00	0.82	417.31
$\Psi(.), p(AT + H + WS + CC + AT{:}H)$	7	432.89	5.58	0.05	418.89
$\Psi(.), p(AT + H + WS + AT{:}H)$	6	433.19	5.88	0.04	421.19
$\Psi(.), p(AT + WS)$	4	433.57	6.27	0.04	425.57
$\Psi(.), p(AT + WS + CC)$	5	434.04	6.74	0.03	424.04
$\Psi(.), p(AT + H + WS + CC)$	6	434.08	6.77	0.03	422.08

Table A4.1.40: Top six best performing variable occupancy, variable detection models with combinations of habitat and environmental variables used to model occupancy and detection for *Uperoleia laevigata*. Listed are the number of parameters (n) AIC, ΔAIC, Akaike weights (w_i) and maximised log-likelihood ($2Log(l)$) for each of the top-ranked models. NOTE: Constant occupancy, constant detection model ($\Psi(.), p(.)$) included as a reference.

Model	n	AIC	ΔAIC	w_i	$2Log(l)$
$\Psi(ripV), p(SURVEY)$	6	426.85	0.00	0.56	414.85
$\Psi(.), p(SURVEY)$	5	427.31	0.46	0.44	417.31
$\Psi(.ripV), p(AT + H + AT + H)$	6	440.26	13.41	0.00	428.26
$\Psi(.), p(AT + H + AT + H)$	5	440.70	13.85	0.00	430.70
$\Psi(ripV), p(AT + H)$	5	443.91	17.05	0.00	433.91
$\Psi(.), p(.)$	**2**	**484.25**	**57.40**	**0.00**	**480.25**

A4.2 Model selection for Comparison of Occupancy for Frog Species with *Crinia signifera* (Chapter 6)

Occupancy model comparison tables presented in this section show all models in the AIC comparisons for modelling frog species occupancy with *Cri. signifera*. The ΔAIC for the independent occupancy, independent detection model ($\Psi(.), p(.)$), indicates the strength of support for the inclusion of the covariates for both occupancy and detection that were included in the final model for each of the species. These values are included in the results for each species as a comparison to the preferred model where applicable. In a comparison of models, a $\Delta AIC > 2.00$, indicates strong support for one or a combination of factors included in the preferred model; the effect of *Cri. signifera* on the occupancy and detection of the other frog species and the inclusion of the other habitat and environmental covariates. A description of each of the covariates used in the following models are provided in Table A4.1.

A4.2.1 Crinia parinsignifera

For the single-species occupancy analysis with *Cri. signifera* included as a covariate, there were three models for which $\Delta AIC \leq 2.00$ (Table A4.2.1). The Akaike weights (w_i) for the simplest model was more than twice that of the other two more complex models. Therefore, because these models were nested, the simplest of the three was considered the preferred model. This was the model without $sigO$ influencing occupancy, and without $sigD$ affecting detection.

Table A4.2.1: Top-ranked variable occupancy, variable detection models with combinations of habitat variables and *Crinia signifera* used to model occupancy for *Crinia parinsignifera*. Listed are the number of parameters (n) AIC, ΔAIC, Akaike weights (w_i) and maximised log-likelihood ($2Log(l)$) for each of the top-ranked models.

Model	n	AIC	ΔAIC	w_i	$2Log(l)$
$\Psi(rW + sW + LONG), p(AT + H + WS)$	8	506.26	0.00	0.50	490.26
$\Psi(rW + sW + LONG + sigO), p(AT + H + WS)$	9	507.90	1.64	0.22	489.90
$\Psi(rW + sW + LONG), p(AT + H + WS + sigD)$	9	508.22	1.96	0.19	490.22
$\Psi(rW + sW + LONG + sigO), p(AT + H + WS + sigD)$	10	509.86	3.61	0.08	489.86
$\Psi(rW + sW + LONG + sigO + sigO{:}rW + sigO{:}sW)$, $p(AT + H + WS + sigD)$	12	513.46	7.21	0.01	489.46
$\Psi(.), p(.)$	**2**	**528.98**	**22.72**	**0.00**	**524.98**

A6.2.2 Limnodynastes dumerilii

For the single-species occupancy analysis with *Cri. signifera* included as a covariate, there were four models for which $\Delta AIC \leq 2.00$ (Table A4.2.2). The Akaike weights (w_i) for the model including $sigO$ and for the model which did not include $sigO$ for occupancy were approximately the same. Because these models were nested, the simplest of the three was considered the preferred model. This was the model without $sigO$ influencing occupancy and without $sigD$ affecting detection.

Table A4.2.2: Top-ranked variable occupancy, variable detection models with combinations of habitat variables and *Crinia signifera* used to model occupancy for *Limnodynastes dumerilli*. Listed are the number of parameters (n) AIC, ΔAIC, Akaike weights (w_i) and maximised log-likelihood ($2Log(l)$) for each of the top-ranked models.

Model	N	AIC	ΔAIC	w_i	$2Log(l)$
$\Psi(sigO), p(SURVEY)$	6	363.26	0.00	0.35	351.26
$\Psi(.), p(SURVEY)$	5	363.34	0.08	0.34	353.34
$\Psi(.), p(SURVEY + sigD)$	6	364.93	1.67	0.15	352.93
$\Psi(sigO), p(SURVEY + sigD)$	7	364.94	1.68	0.15	350.94
$\Psi(.), p(.)$	**2**	**426.94**	**63.68**	**0.00**	**422.94**

A4.2.3 Limnodynastes fletcheri

For the single-species occupancy analysis with *Cri. signifera* included as a covariate, there were three models for which $\Delta AIC \leq 2.00$ (Table A4.2.3). The Akaike weights

(w_i) for the model including *sigO* for occupancy but not *sigD* for detection was approximately twice that of the next model. Because these models were nested, the simplest of the three was considered the preferred model. This was the model with *sigO* influencing occupancy and without *sigD* affecting detection.

Table A4.2.3: Top-ranked variable occupancy, variable detection models with combinations of habitat variables and *Crinia signifera* used to model occupancy for *Limnodynastes fletcheri*. Listed are the number of parameters (n) *AIC*, ΔAIC, weight rating (w_i) and maximised log-likelihood (*2Log(l)*) for each of the top-ranked models.

Model	n	*AIC*	ΔAIC	w_i	*2Log(l)*
$\Psi(LONG+sigO), p(AT)$	5	47.09	0.00	0.40	37.09
$\Psi(LONG + sigO), p(AT + sigD)$	6	48.09	1.00	0.24	36.09
$\Psi(LONG), p(AT)$	4	48.28	1.19	0.22	40.28
$\Psi(LONG), p(AT + sigD)$	5	49.28	2.19	0.13	39.28
$\Psi(.), p(.)$	**2**	**63.01**	**15.92**	**<0.01**	**59.01**

A4.2.4 Limnodynastes peronii

For the single-species occupancy analysis with *Cri. signifera* included as a covariate, there were three models for which $\Delta AIC \leq 2.00$ (Table A4.2.4). The Akaike weights (w_i) for the model that did not include *sigO* for occupancy and did not include *sigD* for detection was approximately twice that of the next model. Because these models were nested, the simplest of the three was considered the preferred model. This was the model without *sigO* influencing occupancy and without *sigD* affecting detection.

Table A4.2.4: Top-ranked variable occupancy, variable detection models with combinations of habitat variables and *Crinia signifera* used to model occupancy for *Limnodynastes peronii*. Listed are the number of parameters (n) AIC, ΔAIC, Akaike weights (w_i) and maximised log-likelihood ($2Log(l)$) for each of the top-ranked models.

Model	n	AIC	ΔAIC	w_i	$2Log(l)$
$\Psi(sW + rW), p(AT + M)$	6	274.26	0.00	0.44	262.26
$\Psi(sW + rW), p(AT + M + sigD)$	7	275.49	1.23	0.24	261.49
$\Psi(sW + rW + sigO), p(AT + M)$	7	276.01	1.75	0.18	262.01
$\Psi(sW + rW + sigO), p(AT + M + sigD)$	8	277.13	2.87	0.11	261.13
$\Psi(sW + rW + sigO + sW{:}sigO + rW{:}sigO), p(AT + M + sigD)$	10	279.99	5.74	0.02	259.99
$\Psi(.), p(.)$	**2**	**312.04**	**37.78**	**0.00**	**308.04**

A4.2.5 Limnodynastes tasmaniensis

For the single-species occupancy analysis with *Cri. signifera* included as a covariate, there were three models for which $\Delta AIC \leq 2.00$ (Table A4.2.5). The Akaike weights (w_i) for the model that did not include $sigO$ for occupancy and did not include $sigD$ for detection was approximately twice that of the next model. Because these models were nested, the simplest of the three was considered the preferred model. This was the model without $sigO$ influencing occupancy and without $sigD$ affecting detection.

Table A4.2.5: Top-ranked variable occupancy, variable detection models with combinations of habitat variables and *Crinia signifera* used to model occupancy for *Limnodynastes tasmaniensisi*. Listed are the number of parameters (n) AIC, ΔAIC, Akaike weights (w_i) and maximised log-likelihood ($2Log(l)$) for each of the top-ranked models.

Model	n	AIC	ΔAIC	w_i	$2Log(l)$
$\Psi(LONG + ALT + emV), p(SURVEY)$	8	494.45	0.00	0.49	478.45
$\Psi(LONG + ALT + emV + sigO), p(SURVEY)$	9	495.95	1.50	0.23	477.95
$\Psi(LONG + ALT + emV), p(SURVEY + sigD)$	9	496.32	1.87	0.19	478.32
$\Psi(LONG + ALT + emV + sigO), p(SURVEY + sigD)$	10	497.81	3.36	0.09	477.81
$\Psi(.), p(.)$	**2**	**600.51**	**106.07**	**0.00**	**596.51**

A4.2.6 Litoria dentata

For the single-species occupancy analysis with *Cri. signifera* included as a covariate, there were three models for which $\Delta AIC \leq 2.00$ (Table A4.2.6). The Akaike weights (w_i) for the model that did not include $sigO$ for occupancy and did not include $sigD$ for detection was greater than that of the next model. Because these models were nested, the simplest of the three was considered the preferred model. This was the model without $sigO$ influencing occupancy and without $sigD$ affecting detection.

Table A4.2.6: Top-ranked variable occupancy, variable detection models with combinations of habitat variables and *Crinia signifera* used to model occupancy for *Litoria dentata.* Listed are the number of parameters (n) AIC, ΔAIC, Akaike weights (w_i) and maximised log-likelihood ($2Log(l)$) for each of the top-ranked models.

Model	n	AIC	ΔAIC	w_i	$2Log(l)$
$\Psi(LONG + LAT + emV), p(AT)$	6	96.58	0.00	0.38	84.58
$\Psi(LONG + LAT + emV + sigO), p(AT)$	7	97.17	0.58	0.28	83.17
$\Psi(LONG + LAT + emV), p(AT + sigD)$	7	97.92	1.34	0.20	83.92
$\Psi(LONG + LAT + emV + sigO), p(AT + sigD)$	8	98.60	2.01	0.14	82.60
$\Psi(LONG + LAT + emV + sigO + sigO{:}emV), p(AT + sigD)$	9	145.91	49.32	0.00	127.91
$\Psi(.), p(.)$	**2**	**170.31**	**73.73**	**0.00**	**166.31**

A4.2.7 Litoria fallax

For the single-species occupancy analysis with *Cri. signifera* included as a covariate, there were three models for which $\Delta AIC \leq 2.00$ (Table A4.2.7). The Akaike weights (w_i) for the model that did not include $sigO$ for occupancy and did not include $sigD$ for detection was approximately twice that of the next model. Because these models were nested, the simplest of the three was considered the preferred model. This was the model without $sigO$ influencing occupancy and without $sigD$ affecting detection.

Table A4.2.7: Top-ranked variable occupancy, variable detection models with combinations of habitat variables and *Crinia signifera* used to model occupancy for *Litoria fallaxi*. Listed are the number of parameters (n) AIC, ΔAIC, Akaike weights (w_i) and maximised log-likelihood ($2Log(l)$) for each of the top-ranked models.

Model	n	AIC	ΔAIC	w_i	$2Log(l)$
$\Psi(LONG + sW + rW), p(SURVEY)$	8	580.92	0.00	0.44	564.92
$\Psi(LONG + sW + rW + sigO), p(SURVEY)$	9	582.12	1.20	0.24	564.12
$\Psi(LONG + sW + rW), p(SURVEY + sigD)$	9	582.71	1.79	0.18	564.71
$\Psi(LONG + sW + rW + sigO), p(SURVEY + sigD)$	10	583.91	2.99	0.10	563.91
$\Psi(LONG + sW + rW + sigO + sigO{:}sW + sigO{:}rW), p(SURVEY + sigD)$	12	585.62	4.70	0.04	561.62
$\Psi(.), p(.)$	**2**	**765.26**	**184.34**	**0.00**	**761.26**

A4.2.8 Litoria latopalmata

For the single-species occupancy analysis with *Cri. signifera* included as a covariate, there were three models for which $\Delta AIC \leq 2.00$ (Table A4.2.8). The Akaike weights (w_i) for the model that did not include $sigO$ for occupancy and did not include $sigD$ for detection was approximately twice that of the next model. Because these models were nested, the simplest of the three was considered the preferred model. This was the model without $sigO$ influencing occupancy and without $sigD$ affecting detection.

Table A4.2.8: Top-ranked variable occupancy, variable detection models with combinations of habitat variables and *Crinia signifera* used to model occupancy for *Litoria latopalmata*. Listed are the number of parameters (n) AIC, ΔAIC, Akaike weights (w_i) and maximised log-likelihood ($2Log(l)$) for each of the top-ranked models.

Model	n	AIC	ΔAIC	w_i	$2Log(l)$
$\Psi(LONG), p(AT)$	4	394.59	0.00	0.50	386.59
$\Psi(LONG + sigO), p(AT)$	5	396.32	1.73	0.21	386.32
$\Psi(LONG), p(AT + sigD)$	5	396.32	1.74	0.21	386.33
$\Psi(LONG + sigO), p(AT + sigD)$	6	398.06	3.47	0.09	386.06
$\Psi(.), p(.)$	**2**	**506.51**	**111.92**	**0.00**	**502.51**

A4.2.9 Litoria peronii

For the single-species occupancy analysis with *Cri. signifera* included as a covariate, there were three models for which $\Delta AIC \leq 2.00$ (Table A4.2.9). The Akaike weights (w_i) for the model that did not include $sigO$ for occupancy and did not include $sigD$ for detection was approximately twice that of the next model. Because these models were nested, the simplest of the three was considered the preferred model. This was the model without $sigO$ influencing occupancy and without $sigD$ affecting detection.

Table A4.2.9: Top-ranked variable occupancy, variable detection models with combinations of habitat variables and *Crinia signifera* used to model occupancy for *Litoria peronii*. Listed are the number of parameters (n) AIC, ΔAIC, Akaike weights (w_i) and maximised log-likelihood ($2Log(l)$) for each of the top-ranked models.

Model	n	AIC	ΔAIC	w_i	$2Log(l)$
$\Psi(ripV + C), p(SUREVY)$	7	375.69	0.00	0.49	361.69
$\Psi(ripV + C), p(SUREVY + sigD)$	8	377.51	1.82	0.20	361.51
$\Psi(ripV + C + sigO), p(SUREVY)$	8	377.69	2.00	0.18	361.69
$\Psi(ripV + C + sigO), p(SUREVY + sigD)$	9	379.51	3.82	0.07	361.51
$\Psi(ripV + C + sigO + sigO{:}ripV)$, $p(SUREVY + sigD)$	10	379.79	4.10	0.06	359.79
$\Psi(.), p(.)$	**2**	**505.77**	**130.09**	**0.00**	**501.77**

A4.2.10 Litoria verreauxii

For the single-species occupancy analysis with *Cri. signifera* included as a covariate, there were three models for which $\Delta AIC \leq 2.00$ (Table A4.2.10). The Akaike weights (w_i) for the model that did not include $sigO$ for occupancy and did not include $sigD$ for detection was greater than that of the next best model. Because these models were nested, the simplest of the three was considered the preferred model. This was the model without $sigO$ influencing occupancy and without $sigD$ affecting detection.

Table A4.2.10: Top-ranked variable occupancy, variable detection models with combinations of habitat variables and *Crinia signifera* used to model occupancy for *Litoria verreauxii*. Listed are the number of parameters (n) AIC, ΔAIC, Akaike weights (w_i) and maximised log-likelihood ($2Log(l)$) for each of the top-ranked models.

Model	n	AIC	ΔAIC	w_i	$2Log(l)$
$\Psi(LAT + LONG + ALT), p(AT + H)$	7	484.04	0.00	0.44	470.04
$\Psi(LAT + LONG + ALT + sigO), p(AT + H)$	8	485.11	1.07	0.26	469.11
$\Psi(LAT + LONG + ALT), p(AT + H + sigD)$	8	486.01	1.98	0.16	470.01
$\Psi(LAT + LONG + ALT + sigO), p(AT + H + sigD)$	9	487.09	3.05	0.09	469.09
$\Psi(.), p(.)$	**2**	**527.97**	**43.93**	**0.00**	**523.97**

A4.2.11 Litoria wilcoxii

For the single-species occupancy analysis with *Cri. signifera* included as a covariate, there were three models for which $\Delta AIC \leq 2.00$ (Table A4.2.11). The Akaike weights (w_i) for the model that did not include $sigO$ for occupancy and did not include $sigD$ for detection was greater than that of the next best model. Because these models were nested, the simplest of the three was considered the preferred model. This was the model without $sigO$ influencing occupancy and without $sigD$ affecting detection.

Table A4.2.11: Top-ranked variable occupancy, variable detection models with combinations of habitat variables and *Crinia signifera* used to model occupancy for *Litoria wilcoxii*. Listed are the number of parameters (n) AIC, ΔAIC, Akaike weights (w_i) and maximised log-likelihood ($2Log(l)$) for each of the top-ranked models.

Model	n	AIC	ΔAIC	w_i	$2Log(l)$
$\Psi(LONG + ALT + sW + rW), p(AT)$	7	140.53	0.00	0.40	126.53
$\Psi(LONG + ALT + sW + rW + sigO), p(AT)$	8	141.17	0.64	0.29	125.17
$\Psi(LONG + ALT + sW + rW), p(AT + sigD)$	8	142.19	1.66	0.18	126.19
$\Psi(LONG + ALT + sW + rW + sigO), p(AT + sigD)$	9	142.83	2.30	0.13	124.83
$\Psi(.), p(.)$	**2**	**153.81**	**13.28**	**<0.01**	**149.81**

A4.2.12 Uperoleia laevigata

For the single-species occupancy analysis with *Cri. signifera* included as a covariate, there were two models for which $\Delta AIC \leq 2.00$ (Table A4.2.12). The Akaike weights

(w_i) for the model that included *sigO* for occupancy and included *sigD* for detection was more than twice that of the next model. Because these models were nested, the simplest of the three was considered the preferred model. This was the model with *sigO* influencing occupancy and with *sigD* affecting detection.

Table A4.2.12: Top-ranked variable occupancy, variable detection models with combinations of habitat variables and *Crinia signifera* used to model occupancy for *Uperoleia laevigata*. Listed are the number of parameters (*n*) *AIC, ΔAIC*, Akaike weights (w_i) and maximised log-likelihood (*2Log(l)*) for each of the top-ranked models.

Model	*n*	*AIC*	*ΔAIC*	w_i	*2Log(l)*
Ψ(sigO), p(SURVEY + sigD)	7	151.70	0.00	0.45	137.70
Ψ(.), p(SURVEY + sigD)	6	153.49	1.79	0.18	141.49
Ψ(.), p(.)	**2**	**153.81**	**2.11**	**0.16**	**149.81**
Ψ(sigO), p(SURVEY)	6	153.97	2.26	0.15	141.97
Ψ(.), p(SURVEY)	5	155.76	4.06	0.06	145.76

A4.3 Model selection for Comparison of Occupancy for Frog Species with *Gambusia holbrooki* (Chapter 6)

Occupancy model comparison tables presented in the following results, show all models in the AIC comparisons for modelling frog species occupancy with the eastern mosquito fish (*Gambusia holbrooki*). The ΔAIC for the independent occupancy, independent detection model ($\Psi(.), p(.)$), indicates the strength of support for the inclusion of the covariates for both occupancy and detection that were included in the final model for each of the species. These values are included in the results for each species as a comparison to the preferred model where applicable. In a comparison of models, a $\Delta AIC > 2.00$, indicates strong support for one or a combination of factors included in the preferred model; the effect of *G. holbrooki* on the occupancy and detection of the frog species and the inclusion of the other habitat and environmental covariates. A description of each of the covariates used in the following models are provided in Table A4.1.

A4.3.1 Crinia parinsignifera

For the single-species occupancy analysis with *G. holbrooki* included as a covariate, there were three models for which $\Delta AIC \leq 2.00$ (Table A4.3.1). The Akaike weights (w_i) for the simplest model was greater than that of the other two more complex models. Therefore, because these models were nested, the simplest of the three was considered the preferred model. This was the model without $gamO$ influencing occupancy, and without $gamD$ affecting detection.

Table A4.3.1: Top-ranked variable occupancy, variable detection models with combinations of habitat variables and *G. holbrooki* used to model occupancy for *Crinia parinsignifera*. Listed are the number of parameters (n) AIC, ΔAIC, Akaike weights (w_i) and maximised log-likelihood ($2Log(l)$) for each of the top-ranked models.

Model	n	AIC	ΔAIC	w_i	$2Log(l)$
$\Psi(.rW + sW + LONG), p(AT + H + WS)$	8	506.26	0.00	0.39	490.26
$\Psi(.rW + sW + LONG + gamO), p(AT + H + WS)$	9	507.05	0.80	0.26	489.05
$\Psi(.rW + sW + LONG), p(AT + H + WS + gamD)$	9	508.26	2.00	0.15	490.26
$\Psi(.rW + sW + LONG + gamO), p(AT + H + WS + gamD)$	10	509.05	2.80	0.10	489.05
$\Psi(.rW + sW + LONG + gamO + gamO{:}rW + gamO{:}sW), p(AT + H + WS)$	11	509.65	3.39	0.07	487.65
$\Psi(.rW + sW + LONG + gamO + gamO{:}rW + gamO{:}sW), p(AT + H + WS + gamD)$	12	511.65	5.39	0.03	487.65
$\Psi(.), p(.)$	**2**	**528.98**	**22.72**	**0.00**	**524.98**

A4.3.2 *Crinia signifera*

For the single-species occupancy analysis with *G. holbrooki* included as a covariate, there were three models for which $\Delta AIC \leq 2.00$ (Table A4.3.2). The Akaike weights (w_i) for the simplest model was more than twice that of the other two more complex models. Therefore, because these models were nested, the simplest of the three was considered the preferred model. This was the model without $gamO$ influencing occupancy, and without $gamD$ affecting detection.

Table A4.3.2: Top-ranked variable occupancy, variable detection models with combinations of habitat variables and *G. holbrooki* used to model occupancy for *Crinia signifera*. Listed are the number of parameters (n) AIC, ΔAIC, Akaike weights (w_i) and maximised log-likelihood ($2Log(l)$) for each of the top-ranked models.

Model	n	AIC	ΔAIC	w_i	$2Log(l)$
$\Psi(LONG + ALT + emV), p(AT + H)$	7	640.38	0.00	0.48	626.38
$\Psi(LONG + ALT + emV + gamO), p(AT + H)$	8	642.22	1.84	0.19	626.22
$\Psi(LONG + ALT + emV), p(AT + H + gamD)$	8	642.38	2.00	0.18	626.38
$\Psi(LONG + ALT + emV + gamO + gamO{:}emV),$ $p(AT + H gamD)$	10	643.85	3.46	0.08	623.85
$\Psi(LONG + ALT + emV + gamO),$ $p(AT + H + gamD)$	9	644.22	3.84	0.07	626.22
$\Psi(.), p(.)$	**2**	**760.11**	**119.73**	**0.00**	**756.11**

A4.3.3 Limnodynastes dumerilii

For the single-species occupancy analysis with *G. holbrooki* included as a covariate, there were three models for which $\Delta AIC \leq 2.00$ (Table A4.3.3). The Akaike weights (w_i) for the simplest model was more than twice that of the other two more complex models. Therefore, because these models were nested, the simplest of the three was considered the preferred model. This was the model without $gamO$ influencing occupancy, and without $gamD$ affecting detection.

Table A4.3.3: Top-ranked variable occupancy, variable detection models with combinations of habitat variables and *G. holbrooki* used to model occupancy for *Limnodynastes dumerilii*. Listed are the number of parameters (n) AIC, ΔAIC, Akaike weights (w_i) and maximised log-likelihood ($2Log(l)$) for each of the top-ranked models.

Model	n	AIC	ΔAIC	w_i	$2Log(l)$
$\Psi(.), p(SURVEY)$	5	363.34	0.00	0.52	353.34
$\Psi(gamO), p(SURVEY)$	6	365.20	1.86	0.21	353.20
$\Psi(.), p(SURVEY + gamO)$	6	365.34	2.00	0.19	353.34
$\Psi(gamO), p(SURVEY + gamO)$	7	367.20	3.86	0.08	353.20
$\Psi(.), p(.)$	**2**	**426.94**	**63.60**	**0.00**	**422.94**

A4.3.4 Limnodynastes fletcheri

For the single-species occupancy analysis with *G. holbrooki* included as a covariate, there were three models for which $\Delta AIC \leq$ 2.00 (Table A4.3.4). The Akaike weights (w_i) for the simplest model was more than twice that of the other two more complex models. Therefore, because these models were nested, the simplest of the three was considered the preferred model. This was the model without $gamO$ influencing occupancy, and without $gamD$ affecting detection.

Table A4.3.4: Top-ranked variable occupancy, variable detection models with combinations of habitat variables and *G. holbrooki* used to model occupancy for *Limnodynastes fletcheri*. Listed are the number of parameters (n) AIC, ΔAIC, Akaike weights (w_i) and maximised log-likelihood ($2Log(l)$) for each of the top-ranked models.

Model	n	AIC	ΔAIC	w_i	$2Log(l)$
$\Psi(LONG), p(AT)$	4	48.28	0.00	0.53	40.28
$\Psi(LONG + gamO), p(AT)$	5	50.27	1.99	0.20	40.27
$\Psi(LONG), p(AT + gamD)$	5	50.28	2.00	0.20	40.28
$\Psi(LONG + gamO), p(AT + gamD)$	6	52.27	3.99	0.07	40.27
$\Psi(.), p(.)$	**2**	**63.01**	**14.73**	**<0.001**	**59.01**

A4.3.5 Limnodynastes peronii

For the single-species occupancy analysis with *G. holbrooki* included as a covariate, there were three models for which $\Delta AIC \leq$ 2.00 (Table A4.3.5). The Akaike weights (w_i) for the simplest model was more than twice that of the other two more complex models. Therefore, because these models were nested, the simplest of the three was considered the preferred model. This was the model without $gamO$ influencing occupancy, and without $gamD$ affecting detection.

Table A4.3.5: Top-ranked variable occupancy, variable detection models with combinations of habitat variables and *G. holbrooki* used to model occupancy for *Limnodynastes peronii*. Listed are the number of parameters (n) AIC, ΔAIC, Akaike weights (w_i) and maximised log-likelihood ($2Log(l)$) for each of the top-ranked models.

Model	n	AIC	ΔAIC	w_i	$2Log(l)$
$\Psi(sW + rW), p(AT + MI)$	6	274.26	0.00	0.52	262.26
$\Psi(sW + rW + gamO), p(AT + MI)$	7	276.19	1.94	0.20	262.19
$\Psi(sW + rW), p(AT + MI + gamD)$	7	276.26	2.00	0.19	262.26
$\Psi(sW + rW + gamO), p(AT + MI + gamD)$	8	278.19	3.94	0.07	262.19
$\Psi(sW + rW + gamO + sW{:}gamO + rW{:}gamO),$ $p(AT + MI + gamD)$	10	281.10	6.85	0.02	261.10
$\Psi(.), p(.)$	**2**	**312.04**	**37.78**	**0.00**	**308.04**

A4.3.6 Limnodynastes tasmaniensis

For the single-species occupancy analysis with *G. holbrooki* included as a covariate, there were three models for which $\Delta AIC \leq 2.00$ (Table A4.3.6). The Akaike weights (w_i) for the simplest model was greater than that of the other two more complex models. Therefore, because these models were nested, the simplest of the three was considered the preferred model. This was the model without $gamO$ influencing occupancy, and without $gamD$ affecting detection.

Table A4.3.6: Top-ranked variable occupancy, variable detection models with combinations of habitat variables and *G. holbrooki* used to model occupancy for *Limnodynastes tasmaniensis*. Listed are the number of parameters (n) AIC, ΔAIC, Akaike weights (w_i) and maximised log-likelihood ($2Log(l)$) for each of the top-ranked models.

Model	n	AIC	ΔAIC	w_i	$2Log(l)$
$\Psi(LONG + ALT + emV), p(SURVEY)$	8	494.45	0.00	0.45	478.45
$\Psi(LONG + ALT + emV + gamO), p(SURVEY)$	9	495.36	0.91	0.28	477.36
$\Psi(LONG + ALT + emV), p(SURVEY + gamD)$	9	496.45	2.00	0.16	478.45
$\Psi(LONG + ALT + emV + gamO), p(SURVEY + gamD)$	10	497.36	2.91	0.10	477.36
$\Psi(.), p(.)$	**2**	**600.51**	**106.07**	**0.00**	**596.51**

A4.3.7 *Litoria dentata*

For the single-species occupancy analysis with *G. holbrooki* included as a covariate, there were three models for which $\Delta AIC \leq$ 2.00 (Table A4.3.7). The Akaike weights (w_i) for the simplest model was more than twice that of the other two more complex models. Therefore, because these models were nested, the simplest of the three was considered the preferred model. This was the model without $gamO$ influencing occupancy, and without $gamD$ affecting detection.

Table A4.3.7: Top-ranked variable occupancy, variable detection models with combinations of habitat variables and *G. holbrooki* used to model occupancy for *Litoria dentata*. Listed are the number of parameters (n) AIC, ΔAIC, Akaike weights (w_i) and maximised log-likelihood ($2Log(l)$) for each of the top-ranked models.

Model	n	AIC	ΔAIC	w_i	$2Log(l)$
$\Psi(LONG + LAT + emV), p(AT)$	6	96.58	0.00	0.46	84.58
$\Psi(LONG + LAT + emV + gamO), p(AT)$	7	98.22	1.64	0.20	84.22
$\Psi(LONG + LAT + emV), p(AT + gamD)$	7	98.58	2.00	0.17	84.58
$\Psi(LONG + LAT + emV + gamO + gamO{:}emV), p(AT + gamD)$	9	99.78	3.20	0.09	81.78
$\Psi(LONG + LAT + emV + gamO), p(AT + gamD)$	8	100.22	3.64	0.07	84.22
$\Psi(.), p(.)$	**2**	**170.31**	**73.73**	**0.00**	**166.31**

A4.3.8 *Litoria fallax*

For the single-species occupancy analysis with *G. holbrooki* included as a covariate, there were three models for which $\Delta AIC \leq$ 2.00 (Table A4.3.8). The Akaike weights (w_i) for the simplest model was more than twice that of the other two more complex models. Therefore, because these models were nested, the simplest of the three was considered the preferred model. This was the model without $gamO$ influencing occupancy, and without $gamD$ affecting detection.

Table A4.3.8: Top-ranked variable occupancy, variable detection models with combinations of habitat variables and *G. holbrooki* used to model occupancy for *Litoria fallax*. Listed are the number of parameters (n) AIC, ΔAIC, Akaike weights (w_i) and maximised log-likelihood ($2Log(l)$) for each of the top-ranked models.

Model	n	AIC	ΔAIC	w_i	$2Log(l)$
$\Psi(LONG + sW + rW), p(SURVEY)$	8	580.92	0.00	0.51	564.92
$\Psi(LONG + sW + rW + gamO), p(SURVEY)$	9	582.74	1.81	0.21	564.74
$\Psi(LONG + sW + rW), p(SURVEY + gamD)$	9	582.92	2.00	0.19	564.92
$\Psi(LONG + sW + rW + gamO), p(SURVEY + gamD)$	10	584.74	3.81	0.08	564.74
$\Psi(LONG + sW + rW + gamO + gamO{:}sW + gamO{:}rW),$ $p(SURVEY + gamD)$	12	588.50	7.57	0.01	564.50
$\Psi(.), p(.)$	**2**	**765.26**	**184.34**	**0.00**	**761.26**

A4.3.9 Litoria latopalmata

For the single-species occupancy analysis with *G. holbrooki* included as a covariate, there were three models for which $\Delta AIC \leq 2.00$ (Table A4.3.9). The Akaike weights (w_i) for the simplest model was more than twice that of the other two more complex models. Therefore, because these models were nested, the simplest of the three was considered the preferred model. This was the model without $gamO$ influencing occupancy, and without $gamD$ affecting detection.

Table A4.3.9: Top-ranked variable occupancy, variable detection models with combinations of habitat variables and *G. holbrooki* used to model occupancy for *Litoria latopalmata*. Listed are the number of parameters (n) AIC, ΔAIC, Akaike weights (w_i) and maximised log-likelihood ($2Log(l)$) for each of the top-ranked models.

Model	n	AIC	ΔAIC	w_i	$2Log(l)$
$\Psi(LONG), p(AT)$	4	394.59	0.00	0.53	386.59
$\Psi(LONG + gamO), p(AT)$	5	396.50	1.91	0.20	386.50
$\Psi(LONG), p(AT + gamD)$	5	396.59	2.00	0.19	386.59
$\Psi(LONG + gamO), p(AT + gamD)$	6	398.50	3.91	0.07	386.50
$\Psi(.), p(.)$	**2**	**506.51**	**111.92**	**0.00**	**502.51**

A4.3.10 Litoria peronii

For the single-species occupancy analysis with *G. holbrooki* included as a covariate, there were three models for which $\Delta AIC \leq 2.00$ (Table A4.3.10). The Akaike weights (w_i) for the simplest model was more than twice that of the other two more complex models. Therefore, because these models were nested, the simplest of the three was considered the preferred model. This was the model without $gamO$ influencing occupancy, and without $gamD$ affecting detection.

Table A4.3.10: Top-ranked variable occupancy, variable detection models with combinations of habitat variables and *G. holbrooki* used to model occupancy for *Litoria peronii*. Listed are the number of parameters (n) AIC, ΔAIC, Akaike weights (w_i) and maximised log-likelihood ($2Log(l)$) for each of the top-ranked models.

Model	n	AIC	ΔAIC	w_i	$2Log(l)$
$\Psi(ripV + C), p(SURVEY)$	7	375.69	0.00	0.48	361.69
$\Psi(ripV + C + gamO), p(SURVEY)$	8	377.18	1.50	0.23	361.18
$\Psi(ripV + C), p(SURVEY + gamD)$	8	377.69	2.00	0.18	361.69
$\Psi(ripV + C) + gamO, p(SURVEY + gamD)$	9	379.18	3.50	0.08	361.18
$\Psi(ripV + C + gamO + gamO{:}ripV), p(SURVEY + gamD)$	10	381.18	5.50	0.03	361.18
$\boldsymbol{\Psi(.), p(.)}$	**2**	**505.77**	**130.09**	**0.00**	**501.77**

A4.3.11 Litoria verreauxii

For the single-species occupancy analysis with *G. holbrooki* included as a covariate, there were three models for which $\Delta AIC \leq 2.00$ (Table A4.3.11). The Akaike weights (w_i) for the simplest model was greater than that of the other two more complex models. Therefore, because these models were nested, the simplest of the three was considered the preferred model. This was the model without $gamO$ influencing occupancy, and without $gamD$ affecting detection.

Table A4.3.11: Top-ranked variable occupancy, variable detection models with combinations of habitat variables and *G. holbrooki* used to model occupancy for *Litoria verreauxii*. Listed are the number of parameters (n) AIC, ΔAIC, Akaike weights (w_i) and maximised log-likelihood ($2Log(l)$) for each of the top-ranked models.

Model	n	AIC	ΔAIC	w_i	$2Log(l)$
$\Psi(LAT + LONG + ALT), p(AT + H)$	7	484.04	0.00	0.41	470.04
$\Psi(LAT + LONG + ALT + gamO), p(AT + H)$	8	484.57	0.53	0.32	468.57
$\Psi(LAT + LONG + ALT), p(AT + H gamD)$	8	486.04	2.00	0.15	470.04
$\Psi(LAT + LONG + ALT + gamO), p(AT + H + gamD)$	9	486.57	2.53	0.12	468.57
$\boldsymbol{\Psi(.), p(.)}$	**2**	**527.97**	**43.93**	**0.00**	**523.97**

A4.3.12 Litoria wilcoxii

For the single-species occupancy analysis with *G. holbrooki* included as a covariate, there were three models for which $\Delta AIC \leq 2.00$ (Table A4.3.12). The Akaike weights (w_i) for the simplest model was greater than that of the other two more complex models. Therefore, because these models were nested, the simplest of the three was considered the preferred model. This was the model without $gamO$ influencing occupancy, and without $gamD$ affecting detection.

Table A4.3.12: Top-ranked variable occupancy, variable detection models with combinations of habitat variables and *G. holbrooki* used to model occupancy for *Litoria wilcoxii*. Listed are the number of parameters (n) AIC, ΔAIC, Akaike weights (w_i) and maximised log-likelihood ($2Log(l)$) for each of the top-ranked models.

Model	n	AIC	ΔAIC	w_i	$2Log(l)$
$\Psi(LONG + ALT + sW + rW), p(AT)$	7	140.53	0.00	0.36	126.53
$\Psi(LONG + ALT + sW + rW + gamO), p(AT)$	8	141.81	1.28	0.19	125.81
$\Psi(LONG + ALT + sW + rW + gamO + gamO{:}sW + gamO{:}rW), p(AT)$	10	142.00	1.47	0.17	122.00
$\Psi(LONG + ALT + sW + rW), p(AT + gamD)$	8	142.53	2.00	0.13	126.53
$\Psi(LONG + ALT + sW + rW + gamO), p(AT + gamD)$	9	143.81	3.28	0.07	125.81
$\Psi(LONG + ALT + sW + rW + gamO + gamO{:}sW + gamO{:}rW), p(AT + gamD)$	11	144.00	3.47	0.06	122.00
$\Psi(.), p(.)$	**2**	**153.81**	**13.28**	**<0.0001**	**149.81**

A4.3.13 Uperoleia laevigata

For the single-species occupancy analysis with *G. holbrooki* included as a covariate, there were three models for which $\Delta AIC \leq$ 2.00 (Table A4.3.13). The Akaike weights (w_i) for the model including $gamO$ and for the model which did not include $gamO$ for occupancy were approximately the same. Because these models were nested, the simplest of the three was considered the preferred model. This was the model without $gamO$ influencing occupancy, and without $gamD$ affecting detection.

Table A4.3.13: Top-ranked variable occupancy, variable detection models with combinations of habitat variables and *G. holbrooki* used to model occupancy for *Uperoleia laevigata*. Listed are the number of parameters (n) AIC, ΔAIC, Akaike weights (w_i) and maximised log-likelihood ($2Log(l)$) for each of the top-ranked models.

Model	n	AIC	ΔAIC	w_i	$2Log(l)$
$\Psi(.), p(SURVEY)$	5	427.31	0.00	0.39	417.31
$\Psi(gamO), p(SURVEY)$	6	427.61	0.30	0.34	415.61
$\Psi(.), p(SURVEY + gamD)$	6	429.31	2.00	0.14	417.31
$\Psi(gamO), p(SURVEY + gamD)$	7	429.61	2.30	0.12	415.61
$\Psi(.), p(.)$	**2**	**484.25**	**56.94**	**0.00**	**480.25**

Appendix 5

Single-season single-visit occupancy model covariates from the most parsimonious model for 13 species detected in the current study. These covariates were used to create the graphs in Chapter 5.

Table A1: Coefficient estimates and their standard errors (se) of occupancy for the most parsimonious model for 13 species found in the current study. NOTE: only 13 of the 18 detected species are presented as five species occupancy models did not converge.

Species	**Occupancy Parameter**									
	β_0	LAT	$LONG$	ALT	sW	rW	emV	$ripV$	C	F
Crinia parinsignifera	-1.16 (0.47)	–	0.26 (0.47)	–	0.83 (0.53)	-0.16 (0.53)	–	–	–	–
Crinia signifera	0.30 (0.73)	–	1.97 (0.48)	-1.08 (0.77)	–	–	1.43 (0.56)	–	–	–
Limnodynastes dumerilli	-1.21 (0.18)	–	–	–	–	–	–	–	–	–
Limnodynastes fletcheri	-5.51 (1.29)	–	-5.91 (2.34)	–	–	–	–	–	–	–
Limnodynastes peronii	-2.26 (0.75)	–	–	–	1.2 (0.81)	0.45 (0.81)	–	–	–	–
Limnodynastes tasmaniensis	-5.48 (1.08)	–	-1.48 (0.59)	4.62 (1.07)	–	–	0.81 (0.59)	–	–	–
Litoria dentata	-4.07 (0.73)	2.30 (0.67)	-1.47 (1.06)	–	–	–	0.19 (1.07)	–	–	–
Litoria fallax	-1.09 (0.46)	–	-1.04 (0.43)	–	1.46 (0.52)	0.85 (0.51)	–	–	–	–
Litoria latopalmata	-0.89 (0.21)	–	-3.25 (0.68)	–	–	–	–	–	–	–
Litoria peronii	-1.17 (0.50)	–	–	–	–	–	–	0.91 (0.70)	-0.75 (0.34)	–
Litoria verreauxii	-6.46 (1.33)	1.15 (0.43)	-0.40 (0.67)	5.28 (1.24)	–	–	–	–	–	–
Litoria wilcoxii	-0.83 (1.58)	–	-1.45 (0.78)	-3.23 (1.41)	-0.66 (1.47)	1.41 (1.13)	–	–	–	–
Uperoleia laevigata	-1.10 (0.17)	–	–	–	–	–	–	–	–	–

Table A2: Coefficient estimates and their standard errors (se) of detection for the most parsimonious model for 13 species found in the current study. NOTE: only 13 of the 18 detected species are presented as five species occupancy models did not converge.

Species	**Detection Parameter**								
	β_0	AT	H	WS	MI	$R48$	$SURVEY\ 2$	$SURVEY\ 3$	$SURVEY\ 4$
Crinia parinsignifera	-2.18 (0.68)	0.08 (0.03)	2.04 (0.99)	0.11 (0.04)	–	–	–	–	–
Crinia signifera	2.80 (0.66)	-0.23 (0.03)	2.07 (0.79)	–	–	–	–	–	–
Limnodynastes dumerilli	0.83 (0.37)	–	–	–	–	–	-0.29 (0.44)	-2.11 (0.49)	-4.64 (1.07)
Limnodynastes fletcheri	-9.79 (5.21)	0.63 (0.32)	–	–	–	–	–	–	–
Limnodynastes peronii	-3.90 (0.94)	0.23 (0.05)	–	–	-1.21 (0.46)	–	–	–	–
Limnodynastes tasmaniensis	0.67 (0.27)	–	–	–	–	–	0.52 (0.39)	-0.80 (0.36)	-3.42 (0.58)
Litoria dentata	-22.86 (12.04)	1.46 (0.76)	–	–	–	–	–	–	–
Litoria fallax	2.61 (0.46)	–	–	–	–	–	-1.81 (0.50)	-3.47 (0.51)	-5.09 (0.60)
Litoria latopalmata	-6.11 (0.90)	0.33 (0.05)	–	–	–	–	–	–	–
Litoria peronii	2.22 (0.61)	–	–	–	–	–	-2.31 (0.62)	-4.18 (0.70)	*
Litoria verreauxii	-0.56 (0.76)	-0.08 (0.03)	3.69 (1.02)	–	–	–	–	–	–
Litoria wilcoxii	-0.20 (1.21)	0.10 (0.07)	–	–	–	–	–	–	–
Uperoleia laevigata	0.95 (0.34)	–	–	–	–	–	-0.19 (0.44)	-0.79 (0.43)	-3.70 (0.68)

* NOTE: Survey 4 omitted from model as it caused convergence errors.