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SHORT COMMUNICATION

Archaic, terrestrial Hamilton's frogs (*Leiopelma hamiltoni*) display arboreal behaviours

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Abstract: New Zealand has three species of endemic amphibians in the genus *Leiopelma*, all of which are threatened with extinction. The primary threats to their persistence are mammalian predators and habitat loss, and the translocation of these frogs into restored habitat is a common method of conservation. The Maud Island frog (*Leiopelma hamiltoni*), is considered terrestrial with habitat needs centering on complex boulder-strewn habitat. However, during recent surveys of a translocated population, we found repeated use of arboreal habitat within this species. Further, trail camera observations made several months later confirm this habitat use to persist across seasons. While the function of this arboreal behaviour is unknown, it suggests Maud Island frogs use more complex, vertical habitat than previously thought, which should be considered in future conservation efforts.

Keywords: amphibian conservation, habitat use, *Leiopelma hamiltoni*, *Leiopelma pakeka*, Maud Island frog

Introduction

Amphibians represent the most globally threatened vertebrate taxa on our planet, with between 30–40 % of all amphibian species threatened with extinction (Stuart et al. 2004; Bishop et al. 2012; Scheele et al. 2019). While the reasons for these declines are complex (Collins & Storfer 2003; Beebee & Griffiths 2005; Allentoft & O'Brien 2010; Ford et al. 2020), habitat degradation and loss are recognized as main contributors to the current extinction crisis (Gallant et al. 2007; Gardner et al. 2007; Tilman et al. 2017). Accordingly, practitioners have placed an emphasis on studies that observe how species interact with their preferred habitat. A better understanding of how amphibians use their environments can lead to improved conservation outcomes. For example, more focused restoration targets can increase the likelihood of restored land being successfully repopulated by amphibian species of conservation concern (Brown 1994; Burgin & Wotherspoon 2009; Lannoo et al. 2009; Briggler & Ackerson 2012).

New Zealand has three endemic species of amphibian, all frogs within the genus *Leiopelma* (*Leiopelma archeyi*, *L. hamiltoni*, *L. hochstetteri*). Leiopelmatids are one of the most archaic lineages of frogs in the world, estimated to have diverged from other anurans roughly 200 million years ago (Roelants et al. 2007). All three species are currently classified as Threatened under both the IUCN's Red List and the New Zealand threat classification (Bishop et al. 2013; IUCN 2019). One of the terrestrial species of leiopelmatids, the Maud Island frog (*L. hamiltoni*), was extirpated from the North and South Islands of New Zealand due to habitat alteration and introduced mammalian predators (Bell 2010; Easton 2018). Currently there remain only two remnant populations of Maud Island frogs on predator-free Stephens Island (Takapourewa) in the Cook Strait and Maud Island (Te Pākeka) in the Marlborough Sounds. To increase the likelihood of species persistence, translocations were undertaken to Motuara Island and Long Island, both in Queen Charlotte Sound. The first translocation of Maud Island frogs to mainland New Zealand occurred at Zealandia Ecosanctuary (Wellington, New Zealand) in 2006 (Campbell-Hunt 2002; Lukis 2009). The Zealandia population remains the only free-roaming population of Maud Island frogs on the New Zealand mainland.

Maud Island frogs are a long-lived (43+ years; Bell & Bishop 2018) and sedentary species of frog maintaining home ranges of 26.7 ± 2.2 m^2 ($\bar{x}$ ± SE) over multiple decades (Bell & Moore 2015). Maud Island frogs are classically described as a terrestrial species observed to feed, eat, and mate, on or within rockpiles (Bell 1985; Bell & Pledger 2010; Germano & Bishop 2007; Van Winkel et al. 2018). As such, ideal restored habitat currently focuses on a complex ground environment

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free of mammalian predators (Brown 1994; Lukis 2009). For example, frog habitat restoration on Stephens Island consisted of excavating a 1.6 m deep pit, backfilling it with 15 t of rock, and then covering the pile with detritus (Brown 1994). However, on Maud Island, frogs are primarily found in the only patch of remnant old-growth forest on the island, and anecdotal observations are often made of the frogs climbing trees. The purpose of this behaviour is still unknown (Waldman 2016; Germano & Bishop 2007), but the presence of arboreal habitat is not thought to be a primary requirement for this species' persistence.

In early 2020, we undertook the first visual survey of a free-roaming Maud Island frog population at Zealandia Ecosanctuary since 2012 (Karst 2013). During this time, we observed frogs repeatedly using arboreal habitat and set up a trail camera to determine the frequency and extent of this use. Here, we (1) describe the arboreal behaviours repeatedly seen in the classically-terrestrial Maud Island frog and (2) make management recommendations in response to these new behaviours.

Methods

Study site

In 2006, 60 Maud Island frogs were translocated into Zealandia Ecosanctuary, a 252 ha predator-free restoration site in Wellington. These frogs were divided into two groups with equal sex-ratios and placed into enclosures for close monitoring of reproduction and survival. In 2012, an additional 101 Maud Island Frogs were translocated to the sanctuary and placed inside a little spotted kiwi (*Apteryx owenii*) exclusion fence surrounding one of the enclosures. The frogs within this kiwi exclusion fence are herein referred to as the free-roaming population. The area within the exclusion fence is thickly vegetated by native kawakawa trees (*Piper excelsum*) and supplejack vines (*Ripogonum scandens*) with a sloped ground covered in multiple rockpiles. Additionally, a boardwalk has been installed to minimize ground disturbance during surveys.

Visual Surveys

We conducted surveys over eight consecutive nights (27 January–3 February 2020) at Zealandia Ecosanctuary in Wellington, New Zealand, beginning all surveys after dusk (approximately 2100 hrs). During the first five nights (27 January–31 January), we focused surveys within the enclosure pens; because one enclosure is located within the kiwi exclusion fence and soft-release site, we were able to visually survey the free-roaming frog population. Surveys were performed for 2 hrs each night (approximately 2100–2300 hrs) and followed the methods outlined by Karst (2013) from the initial translocation. We walked 1 m wide transects uphill within the kiwi exclusion fence, visually scanning from ground level to 2 m off the ground for frogs. When we located a frog, we captured it by hand and marked the location with a reflective pin. We then collected morphometric data on the individual (including snout-vent length: SVL) and measured the distance from the ground to the capture location. Using the standards outlined in Bell and Pledger (2010), we considered individuals with SVLs > 40 mm to be female. The sex of frogs with SVLs < 40 mm could not be determined, and thus we regarded these as unknown (Bell 1978). Finally, we released each frog at their initial capture location.

Trail Camera Observations

In response to the frequent sightings of a Maud Island frog appearing to use an arboreal retreat, we installed a trail camera (Moltrie Products, Birmingham AL, USA). We positioned the camera at a height of 1.5 m off the forest floor and a distance of 1 m away from the trunk of the kawakawa tree from 27 July–6 August 2020. The camera was programmed to take one photograph each minute from 1700 to 0000 hours daily,

Table 1. Individual ID's, sex, snout-vent length (SVL), and perch height. Individual LH-36 was located during surveys of the nearby enclosure, and thus was not captured (NC) to minimize disturbance. However, perch height was collected.

ID (Sex)	SVL (mm)	Perch Height (m)
LH-15 (F)	46	0.67
LH-16 (F)	46	0.39
LH-17 (F)	49	0.32
LH-27 (Unknown)	37	1.02
LH-32 (F)	43	0.54
LH-36 (Unknown)	NC	1.36

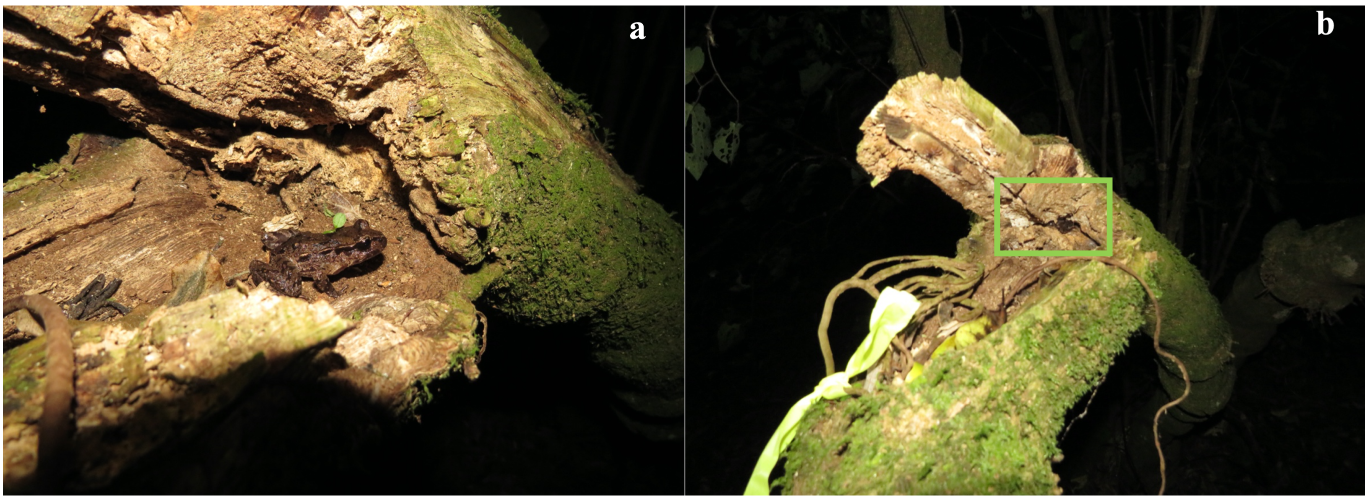

Figure 1. (a) Maud Island Frog (individual LH-27) observed in a cracked kawakawa tree 1.02 m above ground during visual surveys (see green box for LH-27 entering tree) during January–February 2020; (b) Individual LH-27 retreating into the broken tree branch.

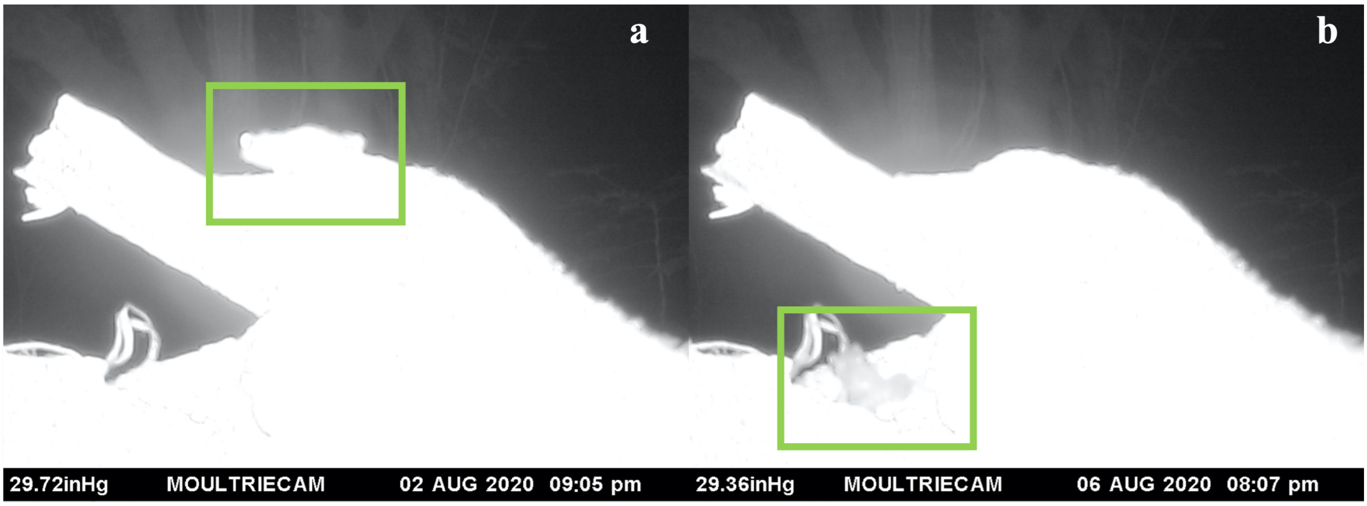

Figure 2. A Maud Island frog (*L. hamiltoni*, in green box) visualized via trail camera using the same tree as seen during visual surveys. A Maud Island frog was seen exiting and entering the tree opening on 31 July, 2 August (a), and 6 August (b).

in order to determine whether the frog often observed on this tree was using it as a refugia, or retreat site. Due to travel restrictions associated with COVID-19, our installation of the trail camera was delayed by several months after visual surveys. However, this allowed us to see whether frogs may be using this arboreal retreat across seasons.

Results

Visual Surveys

During the first five nights of visual surveys, we focused our observations on frogs within enclosures as part of Zealandia's biennial population monitoring. We did not take height measurements of Maud Island frogs sighted above ground outside of the enclosures on these nights, but we did observe frogs repeatedly climbing and emerging from the cracked trunk of a large kawakawa tree (Fig. 1). During the three nights of surveys within the kiwi-exclusion fence, we reported 35 frog encounters. Of these, six encounters occurred off the forest floor (9% of total observations); four by assumed females and two by frogs whose sex could not be determined. The heights of the various encounters ranged from 0.32–1.36 m (Table 1) and individuals were found perched on supplejack vines. During these surveys, a frog was again seen using the cracked kawakawa tree trunk as a perch throughout the night.

Trail Camera Observations

Using the trail camera, we photographed a frog emerging from the previously mentioned kawakawa trunk opening 1.02 m aboveground on three of the ten nights of observation. A frog emerged at 1904 hrs on 31 July, at 1944 hrs on 2 August, and at 1901 hrs on 6 August. We are unable to determine if this is the same frog, as the clarity of our trail camera is not detailed enough for individual pattern recognition. Regardless, a frog was repeatedly seen emerging from and spending significant amounts of time on the tree opening across multiple nights (Fig. 2). During the night of 6 August, the frog retreated to and re-emerged from the tree opening multiple times.

Discussion

New Zealand's endemic Maud Island frog (*L. hamiltoni*) has been previously described as a terrestrial species whose habitat is primarily comprised of complex rockpiles covered in leaf litter with sparse surrounding vegetation (Bell 1985; Bell & Pledger 2010; Germano & Bishop 2007; Van Winkel et al. 2018). Here we describe the use of elevated, arboreal habitat by multiple individuals over the course of several survey nights. Further, we present the first example of a Maud Island frog using an arboreal habitat as a likely refugia. These findings have direct implications for the management of this species of conservation concern. During our initial visual surveys, we located multiple Maud Island frogs using vertical tree habitat.

Of the six frogs found using arboreal habitat, four could be identified as female by SVL measurements. However, because the sex ratio of this population is unknown, we are unable to determine if there is a sex bias to this behaviour. Previous work has found Maud Island frogs off the ground and within trees (Germano & Bishop 2007; Waldman 2016), but these observations have been standalone and are often anecdotal. In other frog species, arboreal habitat use is often associated with mating behaviours (Kime et al. 2000). Calls transmitted from arboreal perches can travel farther than those made at ground level making them detectable to a greater number of potential mates (Parris 2002; Cicchino et al. 2020). However, leiopelmatid frogs lack external ears and do not produce mating calls. Regardless, the occasional use of arboreal habitat by Maud Island frogs has been postulated to function in breeding behavior as a means of pheromone signaling (Waldman 2016), though Maud Island frogs have never been observed mating or nesting in the wild and the presence of pheromone signaling in this species is yet unconfirmed (but see Lee and Waldman 2002; Waldman & Bishop 2004; Waldman 2016).

Arboreal behavior can also serve a predatory function and offers the individual access to a greater variation of preferred prey items (Stewart 1985; Mahan & Johnson 2007). Maud Island frogs primarily consume invertebrates including mites and flies (Kane 1980) and may seek higher perches for hunting. Another possible theory for this behaviour is predator avoidance. Before the introduction of invasive mammalian predators, the primary threat to New Zealand's leiopelmatid frogs were flightless ratite birds and the endemic tuatara (*Sphenodon punctatus*), both of which are ground-based visual hunters (Egeter et al. 2015). This co-evolution could have led to the development of arboreal behaviors as a means of predator avoidance. However, the relationship between native predators and Maud Island frogs still requires considerable research.

In addition to finding Maud Island frogs using vertical habitat during visual surveys, our findings are the first to record the repeated use of an arboreal habitat as a likely refugia. The significance of the continued use of the same tree cavity across not only multiple nights, but multiple seasons, suggests that arboreal habitats may be significant to the Maud Island frog. While there are still many gaps in our understanding of their yearly reproductive cycle, hormone analyses of Maud Island frogs found peak levels of testosterone, estrogen, and progesterone metabolites during the Austral winter (Germano et al. 2012). Further, testicular histology of Maud Island frogs showed significant seasonal differences and again supported a winter breeding period for this species (Germano 2010). While our initial visual surveys occurred in the Austral summer, trail camera observations occurred during the Austral winter. Thus, the presence of a yearly reproductive cycle not marked with continued periods of spermiogenesis or elevated hormone levels, in combination with the use of tree habitat across multiple seasons, suggests that arboreal behaviors in Maud Island frogs are not restricted to breeding activity.

Maud Island frogs have been classically described as terrestrial, but it must be noted that this description has largely been shaped by observations of small, relict populations isolated to large rockpiles, which may not allow frogs to select for varied habitat (Bell 1978; Newman et al. 1978; Brown 1994). Subsequently, current recommendations for the habitat requirements of Maud Island frogs suggest a complex boulder-strewn habitat with minimal vegetation. These requirements are used when constructing artificial habitat for captive and semi-captive populations, as well as release site selection for translocated populations (Brown 1994; Lukis 2009). However, the observations obtained through visual surveys and trail cameras suggest that Maud Island frogs use arboreal habitats across multiple seasons. We therefore suggest that vertical habitat be included amongst the habitat requirements for Maud Island frogs, particularly when choosing locations for reintroduction to the mainland. The exact function of this use, as refugia, hunting ground, or breeding location, is yet unknown, but its prevalence in this reintroduced population suggests it may be important for their persistence at reintroduction sites.

In combination with previous findings in other populations, the results of this study indicate that our current understanding of Maud Island frog habitat use may be insufficient. Because these frogs are both cryptic and rare, this data has been difficult to collect. Accordingly, this work adds significant evidence of habitat use that varies beyond our current understanding of this threatened amphibian. As conservation efforts like translocations and reintroductions continue to bolster Maud Island frog numbers, the selection of habitats that adequately meet the complex needs of this species will be required for successful population persistence. As such, further work investigating the full extent and purpose of habitat use across seasons and life stages is needed for Maud Island frogs. Regardless, this work sheds new light on this cryptic taxa, and we suggest that vertical habitat be considered in their ongoing management.

A Note on Taxonomy

In 1998, *L. hamiltoni* on Maud Island were formally described as *L. pakeka* using allozyme and morphometric data (Bell et al. 1998). However, in 2001, partial 12S ribosomal RNA and cytochrome b gene sequences suggested that *L. hamiltoni* and *L. pakeka* were monophyletic (Holyoake et al. 2001). This work has since been supported by microsatellite analyses, and *L. pakeka* has been synonymized with the senior synonym *L. hamiltoni* (Burns et al. 2017; Easton 2018).

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Author Contributions

JTA: conceptualization, investigation, methodology, formal analysis, writing: original draft preparation, review and editing, visualization, project administration. SKL: investigation, writing: original draft, review and editing, visualization. PJB: conceptualization, methodology, writing: review and editing, supervision, funding acquisition.

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