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Use of dead tree-fern trunks as oviposition sites by the terrestrial breeding frog *Leiopelma archeyi*

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Abstract: While most anurans lay their eggs in or near water, there is a wide diversity of species that lay their eggs on the ground, under rocks, or in burrows. For these terrestrial-breeding species, identifying the habitat requirements of oviposition sites is particularly useful for conservation and management planning, given that oviposition in anurans is strongly related to the environmental characteristics in which they live. *Leiopelma archeyi* is an endemic New Zealand frog that reproduces on moist substrates. Males brood eggs and carry larvae within retreats until metamorphosis is complete. Two previous observations (in November 2014) reported frogs attending eggs inside dead, hollow trunks of tree-ferns (ponga, *Cyathea* spp. or *Dicksonia* spp.). We examined whether these observations were random or whether ponga was a breeding resource consistently used by *L. archeyi*. We used a non-disturbance protocol and focussed on searching inside ponga systematically during three consecutive breeding seasons. This monitoring allowed us to corroborate the reproductive mode previously known for this species and confirm ponga as a recurring oviposition site for *L. archeyi*. Around 10% of the oviposition sites monitored during the parental-care period were observed with more than one adult inside. Furthermore, we selected three individual ponga known to be used as oviposition sites to mark the centre of a plot from which we measured all ponga trunks. We fitted a mixed-model logistic regression to examine whether the use of ponga as an oviposition site by *L. archeyi* was predicted by length and/or diameter at the opening of the trunk. However, neither of these trunk characteristics were useful predictors for the use of ponga as an oviposition site. Our observations raise questions about the reproductive mode of this species such as oviposition site fidelity, and interactions within a community level between two ancestral lineages (Leiopelmatidae and tree ferns).

Keywords: amphibian conservation, breeding behaviour, communal nesting, *Cyathea*, *Dicksonia*, Leiopelmatidae, natural history, non-invasive monitoring, oviposition site fidelity, parental care

Introduction

In anurans, the location where fertilisation and egg laying occur during amplexus is called an oviposition site (Duellman & Trueb 1986). There are two basic types of oviposition sites: aquatic and terrestrial, the former being representative of most anuran species (Duellman & Trueb 1986). However, anuran species with terrestrial oviposition sites and endotrophic larval development are present in many lineages from around the world, including Microhylidae species from New Guinea (Menzies 1976), *Eleutherodactylus* spp. from the Neotropics (Duellman & Trueb 1986), *Arthroleptis* spp. from sub-Saharan Africa (Wells 2007), and two of the three extant *Leiopelma* species from New Zealand (Bell 1978, 1985).

Some anuran terrestrial species use the ground beneath a log, leaves, or stones as oviposition sites, for example, the Puerto Rican frog *Eleutherodactylus coqui* lays eggs in curled dead leaves of *Cecropia* trees (Wells 2007) whereas

Cophixalus concinnus lays eggs under rocks (Hoskin 2004). Other species lay their eggs inside cavities, burrows, or small water-filled crevices in terrestrial plants, for example, *Hylophorbus rufescens* lays eggs in damp cavities close to the ground level (Menzies 1976); *Oreophryne* species use hollow aerial tubers of epiphytes (Matsui et al. 2013); and *Eleutherodactylus* species use cavities in tree ferns (Estrada & Hedges 1996). Parental care, in the form of egg attendance, has been associated with terrestrial oviposition of anuran species on wet substrates as a behaviour exhibited by the parent to improve the chances of survival for its offspring (Duellman & Trueb 1986), although this correlation of parental attendance and terrestrial reproduction varies between different taxonomic groups (Zamudio et al. 2016).

All native frogs in New Zealand belong to the genus *Leiopelma*. Based on morphological and phylogenetic studies, *Leiopelma* is considered to retain three ancestral features: the presence of nine amphicoelous vertebrae (compared to

eight in other anurans), the presence of an epipubis, and the retention of ‘true ribs’ (ossified ribs that articulate with the diapophyses of the vertebrae) (Noble 1931; Stephenson 1951; Stephenson 1952; Stephenson 1960; Roelants & Bossuyt 2005; Clarke 2007; Worthy et al. 2013). It is hypothesised that after the break-up of Pangaea, Leiopelmatidae evolved in isolation on Gondwana and eventually became isolated on Zealandia c. 80–55 Ma (Worthy & Holdaway 2002; Roelants & Bossuyt 2005).

Leiopelma archeyi is a native frog classified as “At Risk - Declining” in the New Zealand Threat Classification System (Burns et al. 2018) and ‘Critically endangered’ in the IUCN Red List of Threatened Species (IUCN/SSC Amphibian Specialist Group 2017). Furthermore, this species is a treasure for tangata whenua (the local Māori people and the interconnectedness between those people and the land; Cisternas et al. 2019). The distribution of this terrestrial frog has declined substantially from its pre-human distribution to its current isolated populations: two relict areas and one translocated site of the North Island, New Zealand (Fig. 1) (IUCN/SSC Amphibian Specialist Group 2017; Burns et al. 2018; Zoological Society of London 2018).

The reproductive mode of *L. archeyi* can be described as eggs deposited terrestrially that undergo direct development (Turbott 1942; Duellman & Trueb 1986; Haddad & Prado 2005; Crump 2015). The most common oviposition sites recorded in the literature for *L. archeyi* are under logs or flat stones (Archev 1922; Stephenson & Stephenson 1957; Bell 1978; Thurley & Bell 1994; Eggers 1998), but also references of oviposition sites at the base of crown (*Blechnum discolor*) and tree ferns (Thurley & Bell 1994), rice grass (*Microlaena acenacea*) (pers. obs.; Whareorino DOC database), and under a dead tree-fern trunk (Bell 1978). In addition, two oviposition sites inside standing dead tree-fern trunks were observed in Whareorino in November 2014 (P. Ramírez, pers. comm.).

In oviposition sites, a pair of frogs may spend more than one day together before the female lays eggs in October. The male broods the eggs for 2–3 months and carries froglets—small-tailed individuals between stages 42 when forelimbs appear and 46 when metamorphosis is completed; Gosner (1960)—on its back for another 1–2 months (Stephenson 1951; Bell 1978). No secondary sexual characteristics have been reported for *L. archeyi* other than sexual dimorphism in body length, i.e. females are larger measured as snout-vent length (SVL) (Bell 1978). However, as Germano et al. (2011) demonstrated in *L. hamiltoni*, sex recognition based on body length can be inaccurate given the marked overlap in size range measurements for both sexes.

In this study, we conducted systematic field monitoring of a natural population over three breeding periods to determine whether the anecdotal observation of two oviposition sites inside a hollowed tree fern trunk was an unusual event or a recurrent behaviour for this species. In this study, we used the term ‘ponga’ to refer to vertical, diagonal leaning, or horizontal dead trunks or stumps of tree ferns (*Cyathea* spp. or *Dicksonia* spp.) that have rotted and become entirely or partially hollow. If the frogs are regularly using ponga for oviposition, the availability of this resource may be important to assess for future habitat quality studies involving *L. archeyi*. We also investigated the relationship between the occupancy of ponga as an oviposition site and the structural characteristics of the ponga. We assumed that the structural characteristics of the ponga would influence the microhabitat conditions of temperature, humidity, and light levels available for egg and

larval development. Specifically, we measured and compared the length and the diameter at the opening of ponga used by frogs and those that were available but not used.

This study provides baseline natural history information on habitat parameters associated with *L. archeyi* oviposition sites used in natural populations. These habitat parameters can be used to assess habitat quality at potential sites for translocations, and to design *in-situ* management actions for habitat improvement or captive breeding (Bell 2010; Bishop et al. 2013). Furthermore, this study provides valuable information on egg attendance and nest-site selection in terrestrial breeding anurans.

Methods

Study area

The study area is a c. 5000 m² block within the Whareorino Conservation Area, a protected forest in the west of the Waikato region, New Zealand (Fig. 1). The vegetation of the site is characterised by the presence of *Griselinia littoralis* with *Coprosma grandifolia* in the highest stratum, together with *Beilschmiedia tawa* and *Weinmannia racemosa*. The understorey is composed mainly of tree fern species (*Cyathea* and *Dicksonia*), up to 10 m high, together with young trees of *Pseudowintera colorata* and *B. tawa*. The lower stratum is dominated by *Blechnum* spp. and several bryophytes *sensu lato*. The study site has an estimated 95% canopy cover (Cisternas 2019) and was selected because of the anecdotal observation of two ponga used as oviposition sites in November 2014 (P. Ramírez, pers. comm.) (Fig. 2).

Field monitoring of oviposition sites

Searches of oviposition sites inside dead tree-fern trunks (i.e. ponga) were conducted during the day within the study area during three breeding seasons, between October 2015 and February 2018. Once a ponga (vertical, diagonal leaning or horizontal) was found, it was checked for use by a frog, using a head-torch. To keep a sampling approach in compliance with the legal and cultural protection of this species, while ensuring the feasibility of a visual check, we limited our searches on vertical and diagonal leaning ponga to trunks shorter than 140 cm height from ground. A ponga was confirmed as an oviposition site if a frog(s) with eggs or froglets were observed inside (Table 1). We also monitored potential oviposition sites, identified as ponga with two frogs inside prior to the period when eggs first appeared (October), as we assumed that these frogs may have been in the early stages of mating behaviour. Each oviposition site was marked (by attaching a plastic label nearby) on the first encounter and checked up to three times per breeding season between October 2015 and February 2018. As oviposition sites were discovered, the number monitored increased over time (Table 1). Upon completion of this study, plastic labels, flagging tape and all other materials used were carefully removed.

Structural characteristics of ponga used as oviposition sites

To explore what (if any) structural characteristics influence the use of ponga as oviposition sites by *L. archeyi*, we used a resource-selection function framework (Muff et al. 2019). We compared the structural characteristics of the ponga locations used as oviposition sites (encoded as $y = 1$) with the structural characteristics of ponga assumed available for

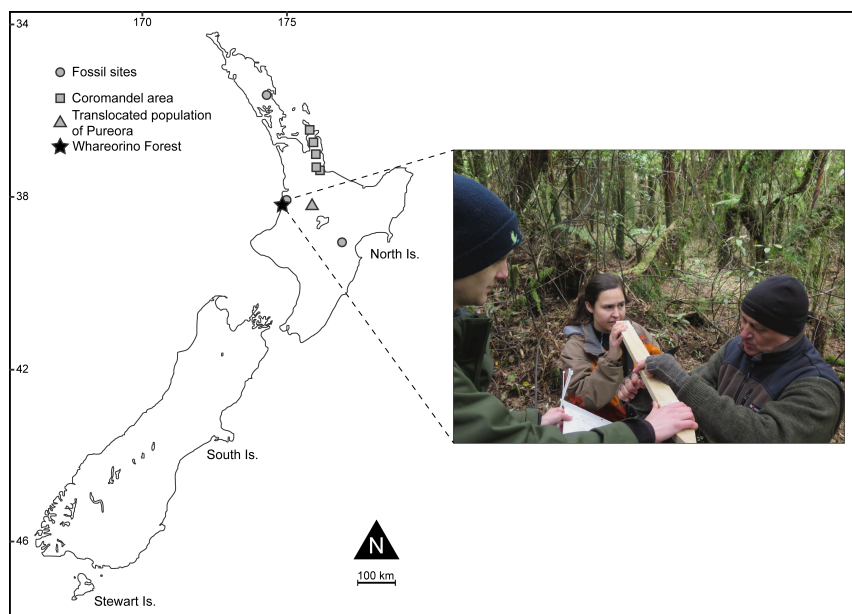


Figure 1. Map of the geographic distribution of *Leiopelma archeyi* (left). Researchers in the study area (right).



Figure 2. Natural history observations associated with breeding activity. Top: Pair of frogs in inguinal amplexus inside a punga on 15 October 2017 (Photo credit: Phil Bishop). Centre: Frog sitting over eggs on 14 November 2014 (Photo credit: Patricia Ramírez). Bottom: Larvae within stages 43–45 Gosner (1960) on a frog's back on 18 February 2018 (Photo credit: Hayley Ricardo).

the individual but not used (encoded as $y = 0$). To determine these unused locations, we haphazardly selected three plots within the study area, following the criterion that the centre point of each plot corresponded to an oviposition site known to be used repeatedly during consecutive years. The size of the plots (10×10 m) refers to a searched area that hypothetically overlap with the home range area described for this species: a few metres square (Bell 1997); c. 4 m^2 (Ramírez 2017).

Inside each plot, we systematically searched for ponga (shorter than 140 cm height) and measured the length and the diameter at the opening of each ponga found. For ponga with two openings, such as a horizontal ponga lying on the forest floor, we averaged both diameter values for the analysis. Density of ponga inside these three plots was 0.1 ponga m^{-2} (range: 0.05–0.17; SD = 0.06).

We used R interface R-INLA to run a mixed-effects logistic regression model within a Bayesian framework (Muff et al. 2019). We kept the default settings and used a random intercept $N(0, \sigma_{ID}^2)$ and fixed variance $\sigma_{ID}^2 = 10^6$. For the fixed effects (length and diameter at the opening) we used the INLA (default) priors $\beta \sim N(0, \sigma_{\beta}^2)$ with $\sigma_{\beta}^2 = 10^4$. We considered individual heterogeneity as a random effect and estimated individual-specific intercepts, and two random slopes, one for each fixed effect. We estimated posterior distributions and parameterised variances, i.e. precisions, for fixed and random effects, including posterior means and medians of the precisions. All statistical analyses were performed in program R (R Core Team 2019), and code is available in Appendix S1 in Supplementary Material.

Results

Field monitoring observations

A total of 27 ponga were monitored during this study, 17 of which were confirmed as oviposition sites on at least one of

the nine visits carried out to the study area (Appendix S2). Based on these observations, the annual reproductive pattern of *L. archeyi* was determined as individuals pairing in inguinal amplexus in October, frogs attending eggs (three to ten) from October to February and carrying froglets (two to eight) on their backs from January to February (Table 1, Appendix S2). More than one adult frog (unknown sex), as close as touching each other, was sometimes observed inside the oviposition site during egg attendance (three out of 23, 13%), and after hatching of froglets (one out of nine, 11%) (Appendix S2). Six out of the 17 ponga confirmed as oviposition sites were used repeatedly between years; five were used for two consecutive years (29%) and one was used for three consecutive years (6%) (Appendix S2).

Quantitative modelling of structural characteristics of ponga used as oviposition sites

A total of 35 ponga were measured for this analysis inside three 10×10 m plots. Five of the ponga measured were used as an oviposition site, and 30 were not. Within each plot, the proportion between ponga used as an oviposition site and available ponga varied between 10% and 20%. Preliminary descriptive results of ponga measurements are summarised in Table 2 and Appendices S3–S7. Modelling suggests that there is not enough evidence to correlate length and diameter at the opening to the use of a ponga as an oviposition site by *L. archeyi* (Table 3). Posterior mean and mode of the variance for ponga length was 0.03 and 1.6×10^{-4} , respectively; and posterior mean and mode of the variance for diameter at the opening of the ponga was 0.028 and 2.69×10^{-4} , respectively.

Discussion

Anurans present a wide variety of reproductive modes, including aquatic, partially aquatic, and terrestrial reproduction

Table 1. Field observations of ponga monitored.

Monitoring date(s)	No. of ponga monitored	No. of ponga confirmed as oviposition site	Behaviour observed associated with breeding activity
1 October 2015	3	0	Inguinal amplexus
28 November 2015	12	7	Frog over eggs
6 February 2016	13	4	Frog with froglets on its back
1 October 2016	16	0	Inguinal amplexus
2 December 2016	18	8	Frog over eggs
23 January 2017	18	5	Frog over eggs
22 May 2017	18	0	---
15-17 October 2017	25	3	Inguinal amplexus, and frog over eggs
3-4 February 2018	27	6	Frog over eggs, and frog with froglets on its back

Table 2. Summary of results from measurements of ponga included in modelling analysis.

Ponga	Length (cm)		Diameter at the opening (cm)	
	Mean	SD	Mean	SD
Used as oviposition site ($n = 5$)	76.00	33.26	6.5	2.65
Not used as oviposition site ($n = 30$)	69.38	28.12	6.64	2.38
Total	70.32	28.45	6.62	2.38

Table 3. Summary for the posterior distribution of fixed effects and variances parameterised as precisions on the use of ponga as an oviposition site by *Leiopelma archeyi*. Quant: quantiles. Kld: Kullback-Leibler Divergence.

Parameters	Mean	SD	0.025 quant	0.5 quant	0.975 quant	Mode	Kld
Fixed effects							
(Intercept)	-9.478	577.819	-1143.931	-9.494	1124.029	-9.478	7.625×10^{-11}
Length	0.383	0.696	-0.86	0.345	1.874	0.302	3.694×10^{-4}
Diameter at the opening	-0.164	0.581	-1.312	-0.164	0.977	-0.158	4.865×10^{-6}
Random slopes							
Precision for length	313.885	8577.797	0.454	15.981	1782.159	0.705	
Precision for Diameter at the opening	341.164	8596.198	0.877	20.235	1975.34	1.712	

(Duellman & Trueb 1986; Beebee 1996; Wells 2007). The reproductive mode described for *Leiopelma archeyi* is terrestrial reproduction, with parental care and oviposition sites located at the base of grasses and ferns, and under stones and logs (Archey 1922; Stephenson & Stephenson 1957; Bell 1978; Thurley & Bell 1994; Eggers 1998), in which endotrophic larvae develop until larvae with rudimentary forelimbs hatch and complete metamorphosis on the adult's back (Bell 1985; 'mode II-D-17' in Duellman & Trueb 1986; 'mode 23' in Haddad & Prado 2005; 'mode 23' in Wells 2007; 'mode 8' in Crump 2015; Bell & Bishop 2018). Here, we successfully monitored *L. archeyi* breeding behaviour inside hollowed dead tree-ferns (ponga). Despite our small sample size, we accumulated observations that support in general the reproductive mode previously described for this species (Bell 1978, 1985).

Parental care in anurans varies from relatively simple behaviours like egg attendance to more elaborate adaptations like viviparity (Smiseth et al. 2012). In this study, we confirm *L. archeyi*'s parental care in the form of dorsal brooding of eggs and in the form of larvae with forelimbs getting on to an adult's back (as in Bell 1978, 1985; Thurley & Bell 1994). In every case, froglets were ventrally touching the adult's back or legs. The ventral skin is the major site for water uptake in *L. archeyi* (Cree 1989). Furthermore, we agree with two observations made by Eggers (1998): that the number of eggs attended decreased as the size of the eggs increased and that it is commonly observed in undeveloped eggs apparently infected with fungi close to where the adult frog is doing egg attendance.

A small proportion of our parental care observations (c. 10%) correspond to situations where more than one frog was apparently involved in parental care duties. This type of observation has also recently been recorded in captivity (PJB, pers. obs.). Other observations of more than two frogs together on apparent breeding behaviour (i.e. amplexus) have been reported for *L. archeyi* in the field (Cree & Daugherty 1991) and in captivity (Bell 1978).

From the observations here reported, doubt remains as to whether all frogs observed inside one ponga were executing parental care duties (communal nesting) or if only one of them was brooding eggs or carrying froglets and the others were only sharing a retreat site. Previous observations on the use of ponga by multiple individuals as a retreat site (i.e. without evidence of breeding activity) reported the presence of up to nine adult frogs (> 35 mm SVL) under a single fallen tree-fern (A Smale, DOC, pers. comm.), and three frogs inside a ponga used as an oviposition site in the previous breeding season, during October 2017 in Pureora Forest (Cisternas

et al. 2021). Furthermore, it was not possible to determine the sex of the individuals observed on parental care duties in this study via visual inspections of oviposition sites. Stephenson and Stephenson (1957) reported that several *L. archeyi* frogs crouching over egg clusters proved to be males, although it remains unclear how they determined the sex of the breeding individuals. Whether the occurrence of male solitary brooding (Bell 1978, 1985) is combined with facultative communal nesting as occurs in other anuran species (McDiarmid & Gorzula 1989; Barreto & Andrade 1995; Giaretta & Facure 2006), warrants further research.

Site fidelity of oviposition sites in anuran species with parental care, such as *Eleutherodactylus* and microhylid species from the Americas and Papua New Guinea respectively, has been associated with the defence and repeated use of sites where the risks associated with terrestrial egg mortality (desiccation, predation, and attacks by pathogenic bacteria or fungi) are minimised (Bickford 2004; Wells 2007). We found that approximately one-third of ponga oviposition sites used during one breeding season were also used during the next breeding season. Anecdotal observations carried out after this study also confirm the repeated use between seasons of the same ponga as an oviposition site for *L. archeyi* (pers. obs.). Our data show that ponga is fragile to natural weather events and animal disturbance (e.g. feral goats scratching their horns against the ponga), which may affect the availability of this resource for repeated use as an oviposition site from one season to the next. In relation to the low level of repeated use of the same ponga during the third breeding season (2017–2018), it is possible that this difference was associated with a drought that occurred during that period which also had a negative impact on frog capture rates during the 2017 monitoring session performed by Department of Conservation staff (A Quinnell, pers. comm.). November 2017 was the sixth warmest November on record for New Zealand, with temperatures well above average, particularly for Te Kuiti (central Waikato region, c. 35 km to the east of the study area), where the mean temperature was 1.5 °C warmer than normal (NIWA Taihoro Nukurangi 2017).

The resources and conditions present in an area that produce occupancy by a given organism are called habitat (Hall et al. 1997). Often the resources present in the oviposition sites described for *L. archeyi* are surroundings of a moisture-conserving mixture protected from light (Stephenson & Stephenson 1957). Considering ponga as a resource used by *L. archeyi* for oviposition, we failed to show what conditions (structural characteristics) of ponga determine occupancy in part due to methodological issues related to the study design

applied. Previous breeding observations of *L. archeyi* suggested that even a small amount of disturbance is enough to cause the oviposition site to be abandoned (R Gibson, Auckland Zoo, pers. comm.; Cisternas 2019), and this is also true for other amphibian terrestrial breeders (Breitenbach 1982). Thus, there were clearly limits to measuring any structural characteristic inside the hollow ponga used as oviposition sites, such as depth and presence of double chambers (Cisternas 2019), in order to keep a non-invasive study protocol. Further studies could attempt to measure these characteristics during late autumn (April to June) because *L. archeyi* activity declines during winter and other periods of cold temperatures (Bell et al. 1985), and in our study most of the monitored oviposition sites were empty during that period.

Our observations contribute to understanding the natural history and breeding behaviour of this threatened terrestrial anuran. Along with *Sechelophryne gardineri* (Nussbaum & Wu 2007), they are the only known reports of oviposition sites inside hollow tree-ferns. The systematic field observations carried out on consecutive breeding seasons allowed us to confirm the consecutive use of the same ponga for oviposition and parental care duties in *L. archeyi*. Furthermore, both *Leiopelma* frogs (Carr et al. 2015; Feng et al. 2017) and tree-fern species of Dicksoniaceae (Noben et al. 2017) and Cyatheaceae (Korall & Pryer 2014) have been part of the New Zealand biota for a long time, suggesting that the community associations between the ancestral lineages investigated in this study can also be considered ancestral. This study contributed to increasing knowledge of ancestral lineages that are of utmost importance to understanding the evolution of parental care diversity in anurans (Furness & Capellini 2019).

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Additional Information and Declarations

Conflicts of interest: The authors disclose no conflicts of interest.

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Ethics: Work with frogs was conducted under permission from the University of Otago Animal Ethics Committee (AEC 60/2015) and from the Department of Conservation (40696-FAU).

Data and code availability: The data from this article are available upon request to the authors. Code is available in Appendix S1.

Author contributions: All authors worked on the conceptualisation of the project, with JC and LJE developing the methods. All authors contributed to the investigation and JC lead analysis and writing with LJE supporting the writing, editing and project administration.

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Supplementary material

Additional supporting information may be found in the supplementary material file for this article:

Appendix S1. R code used for INLA analysis. See article webpage on NZES website for code.

Appendix S2. Field database observations.

Appendix S3: Histogram of predictive variable length of ponga.

Appendix S4: Histogram of predictive variable diameter at the opening of ponga.

Appendix S5: Length of ponga as a predictor of oviposition site.

Appendix S6: Diameter at the opening of ponga as a predictor of oviposition site.

Appendix S7: Relationship between predictor variables.

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