



## Colour variation and behaviour of the cryptic New Zealand frog *Leiopelma archeyi*

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**Abstract:** Understanding the ecology of cryptic species is essential for designing effective monitoring and conservation strategies. *Leiopelma archeyi* is a native New Zealand frog with cryptic colouration, patterning, and behaviour. Our study examined dorsal colour variation and climbing behaviour in this species. Our first aim was to investigate if *L. archeyi* demonstrates colour crypsis by background-matching. Secondly, we determined if green pigmentation is lost as frogs age by comparing frog body size (a proxy for age) with the percentage of green on their dorsal surface. Finally, to better understand frog climbing behaviour, we examined which factors influenced the height above ground that frogs were found at. The study was conducted in Wharekairauponga New Zealand between 2017 and 2021. Visual nocturnal surveys were undertaken in 112 survey plots where frogs were captured, photographed, and measured. Unexpectedly, *L. archeyi* tended to not show background-matching between their substrate and the colour of their dorsum. Among other possible explanations, this trend might suggest their disruptive colouring is enough to camouflage them in their visually complex habitat, or the trend might be related to observer bias. Larger *L. archeyi* individuals had less green on their dorsal surface compared to smaller ones suggesting colour change with increasing age does occur in *L. archeyi*. This could reduce the longer-term reliability of photographs to identify individuals. Larger *L. archeyi* were also found at greater heights off the ground compared to smaller individuals, a pattern which, among other possible reasons, could be due to reduced biological constraints (e.g. risk of predation or desiccation) for larger frogs. Finally, *L. archeyi* climbed to greater heights off the ground at cooler temperatures and climbing behaviour was uncommon in the summer months. Improving our understanding of *L. archeyi*'s behaviour and ecology is an essential component of successfully conserving this endangered species.

**Keywords:** anuran, arboreal, camouflage, climbing, colouration, Leiopelmatidae, monitoring, photo ID

### Introduction

Understanding the ecology of cryptic species is essential for designing effective monitoring and conservation strategies, but gathering this knowledge is often challenging (Baling et al. 2016). Camouflage can occur in many ways, from visual crypsis which often involves disruptive colouration (Price et al. 2019), to behavioural crypsis that means individuals are less visible or detectable (Reaney & Whiting 2003). New Zealand's native frogs (*Leiopelma* spp.) are sit-and-wait predators and have cryptic colouration, patterning, and behaviour (Bell 1978). Crypsis is important for *Leiopelma* spp., not only for hunting, but also for predator avoidance. Some of the natural predators of *Leiopelma* spp. were likely owls, weka (*Gallirallus australis*) and tuatara (*Sphenodon punctatus*), all of which use sight to hunt (Newman 1977; Worthy & Holdaway 1994; Ramirez 2017). Conversely, introduced predators, such as pigs (*Sus* spp.), rats (*Rattus* spp.), and mice (*Mus musculus*), hunt by smell, which renders the freeze tactic a less effective defense (Ramirez 2017). As a consequence, *Leiopelma* spp. are under threat, with *L. hamiltoni* being reduced to living on pest free off-shore islands (Holyoake et al. 2001; Longson et al. 2017).

Unlike other frogs, leiopelmatids have only limited vocal capability, meaning acoustic signals cannot be used to monitor or detect them. Therefore, although artificial refuges have shown some potential for detecting and monitoring leiopelmatids (Wakelin et al. 2003), their current monitoring mainly relies on visual surveys. As such surveys are prone to observer bias (Crossland et al. 2005; Haigh 2007), understanding which factors may influence detectability of leiopelmatids by humans in visual surveys is important. In our study, we examine two such factors, colour crypsis, and vertical habitat use, for *Leiopelma archeyi* (Archey's frog).

*Leiopelma archeyi* is one of three Leiopelmatid species, representing an evolutionarily distinct lineage of amphibians endemic to New Zealand. *L. archeyi* demonstrates highly variable colouration and patterning on their dorsal surface, with colouration ranging from almost entirely brown to almost entirely green, with all combinations in between (Bell 1994; Thurley & Bell 1994; Bradfield 2004). These colourations and patterns may be a form of predator avoidance (Stevens et al. 2006) and patterns are considered unique enough to identify individuals using photo identification (Bradfield 2004). Understanding how colouration might vary as an individual

ages also has important implications for various aspects of the ecology of this species (e.g. predation risk, conspicuousness to mates). However, it is still unknown whether the highly variable colouration of *L. archeyi* can change with age (Bradfield 2004), as observed in other frog species such as *Oreophryne ezra* (Bulbert et al. 2018) and *Elachistocleis haroi* (Bueno-Vallafañe et al. 2020). For example, in *E. haroi* yellow spots and their intensity vary with body length in post-metamorphic individuals, with specific expansion on the gular, side, and chest area as individuals age (Bueno-Vallafañe et al. 2020). The role of colouration in sexual selection and additionally its significance for predation risk are discussed as mechanisms that might drive these ontogenetic colour changes in *E. haroi* (Bueno-Vallafañe et al. 2020).

Early research on *L. archeyi* noted that within populations the ratio of green to brown frogs tends to be uneven (Bell 1978). Subsequently, Thurley and Bell (1994) reported that frogs with “some green dorsal patterning” were found more often in or on vegetation, whereas “predominantly brown” individuals were equally distributed between vegetation and rocky substrates or logs. Since most of the native predators of leiopelmatids, such as owls, weka, and tuatara hunt by sight (Newman 1977; Worthy & Holdaway 1994; Ramirez 2017), frog camouflage might have been an effective defence adaptation against these native predators. Nevertheless, Thurley and Bell (1994) cautioned that additional research is needed to test this adaptation hypothesis more thoroughly.

*Leiopelma archeyi* is found in damp native forests typically at altitudes between 400–1000 m a.s.l. (Bell 1978). Currently, the species’ known populations are restricted to the Coromandel Forest Park (including Wharekirauponga south of the Coromandel Peninsula) and Whareorino Forest in the North Island of New Zealand where they occasionally occur sympatrically with *L. hochstetteri* (Bell 1989; Bell 1994; Bishop et al. 2013; Burns et al. 2018), plus a translocated population in Pureora Forest Park, Waikato (Cisternas 2019). *Leiopelma archeyi* is predominantly nocturnal (Bell 1978; Cree 1989) and previous studies have observed notable increases in their likelihood of emergence from underground refuge sites during wet and humid weather (Bell 1978; Cree 1989; Hotham 2019). *Leiopelma archeyi* have also been previously observed to be effective climbers and found to emerge on vegetation more often than other *Leiopelma* species (Stephenson & Stephenson 1957; Bell 1978; Cree 1989; Ramirez 2017), although the factors that influence their climbing behaviour remain unknown.

Against this scientific background, our study had two aims. Firstly, to understand what factors influence colour variation in *L. archeyi*, we examined how the percentage of green colouration on the dorsal surface varied with respect to biotic (frog size) and abiotic (background colour, season) factors. Specifically, if *L. archeyi* demonstrates colour crypsis by background-matching, we expected the colour of *L. archeyi* would match with the colour of the substrate they were found on. Secondly, if ontogenetic changes influence patterns of frog colouration, we expected that the percentage of green on the dorsal surface of frogs would vary with their body size (a proxy for age). We also examined seasonal differences in colouration and expected that if colouration was linked to seasonal factors, such as courtship or mating behaviour, we may expect colour variation to vary across a year.

Second, to better understand frog climbing behaviour, we examined what factors influenced the height above ground that frogs were found at. We asked whether body size (as a proxy for age) could influence climbing behaviour, expecting that

smaller frogs might be less likely to climb to minimise their predation risk (Ramirez 2017). To understand if climbing behaviour relates to activity levels, we also examined whether the height above ground that frogs were found varied with body temperature, the time of night or between seasons. We expected that if climbing behaviour simply reflects activity levels, frogs will be found at higher distances above ground in warmer temperatures and/or seasons, or at later times in the night.

## Methods

### Study area and frog survey sites

Frog surveys were carried out in Wharekirauponga (hereafter abbreviated as WKP) in the southern Coromandel Forest Park, North Island, New Zealand, for the purpose of fauna assessments prior to explorative mining activities. WKP is public conservation land administered by the Department of Conservation (DOC). The Coromandel area was disturbed by mining exploration and deforestation for kauri logging from the 1800s to the mid-1900s (Napier et al. 2009; Hotham 2019). Today, the WKP valley largely consists of naturally regenerated native forest. Some exotic plant species including wilding pine (*Pinus contorta*) and inkweed (*Phytolacca octandra*) have been noted in more recently disturbed areas (Boffa Miskell Ltd 2019). The terrain in WKP consists of undulating hills and frog survey sites were located on both ridges and in gullies throughout the area. The highest and lowest points in the catchment are 665 m and 20 m above sea level (Boffa Miskell Ltd 2019). During 2017–2021, the township closest to WKP (Waihi; c. 9.6 km from WKP; 134 m a.s.l.) received an annual rainfall of 1380–2390 mm. This is likely to be an underestimate of rainfall in WKP due to its higher elevation and location along the Coromandel Ranges.

Frog surveys were undertaken as part of an ecological assessment for a mining company wanting to explore for gold. Survey sites were selected based on their suitability for gold exploration. Sites that could not be cleared for gold mining exploration (for reasons such as containing significant tree species as defined by DOC, or trees with a diameter at breast height of 50 cm) were not surveyed for frogs. This exclusion might have introduced some bias to the surveys, but this limitation was unavoidable in the current study. The microhabitat at the surveyed sites typically consisted of a diverse and dense understory with habitat complexity which provides refuge opportunities for frogs. Frog surveys were carried out between February 2017 and May 2021, during austral spring, summer, and autumn (October to May), to ensure the breeding (November), brooding (December), and non-breeding (March) seasons (Bell 1978) were represented. A total of 112 sites (20 × 20 m) were surveyed in the study. Each site was surveyed up to three times in total. The intervals between individual surveys varied due to the dependency on specific weather conditions (i.e. wet and humid weather); consequently, some sites were re-surveyed on consecutive nights whereas others had up to 6 months between surveys. Between February and December 2017, each site was surveyed on three different nights with suitable weather conditions (minimum temperature of 12 degrees Celsius and wet or moist conditions), or until five or more frogs had been found in the site prior to the final survey (whichever happened first). From January 2018 onwards, each site was surveyed in its entirety on three occasions (even if more than five frogs were found in total).



## Frog surveys

Surveys began approximately 1 hour after sunset and continued until sunrise. Surveyors were equipped with Lenser light-emitting diode (LED) head-torches (model MH3 or SE05) and an optional LED hand-held torch (model P7). At the start of each survey, weather conditions (precipitation, humidity, and temperature) were measured with a Kestrel 3000 Pocket Weather Meter device (Kestrel Meters, Philadelphia, USA). During each survey, a team of three surveyors systematically searched the site (20 × 20 m) walking side by side. Surveys detected both emerged frogs as well as frogs that were in refuge sites by looking under leaf litter and vegetation (from ground level to 2 m above ground). Care was taken not to disturb refuge sites and fragile habitat.

When a frog was found, it was hand captured using a new pair of disposable gloves for each new frog to avoid potentially spreading disease to the animal (Haigh et al. 2007). Frogs were handled for no more than 10 minutes to avoid stressing the animals or raising their body temperature (Lunghi et al. 2016). Each caught frog was placed in a clean plastic bag (Bell 1994) and its dorsal and ventral sides were photographed using an Olympus Tg-6 Tough camera (Olympus Ltd, Notting Hill, Australia). Snout-to-vent length (SVL in mm; distance from the tip of the snout to the end of the urostyle; Bell et al. 2004) was measured using digital callipers (Jobmate digital calliper, model number J701-2702). Body temperature (°C) was recorded within one minute of capture and measured with an infrared digital thermometer (Digitech QM-7218). The substrate type (e.g. the plant species or leaf litter present directly under the frog), and the estimated height above ground (cm) where the frog was found was recorded.

## Photo processing

Photos of each frog were processed manually and each was assigned a ‘percentage of green’ (estimated by eye in increments of 5%) based on the amount of its dorsal surface that was green (Fig. 1). The percentage of green assignment process was blindly repeated for half of the photos to account for learning errors. Frogs were excluded from the analysis if a photo was not taken or if the photo quality was poor (i.e. blurry, over-exposed, or accuracy in assigning the percentage of green from a photo debatable;  $n = 57$ ). The substrate the

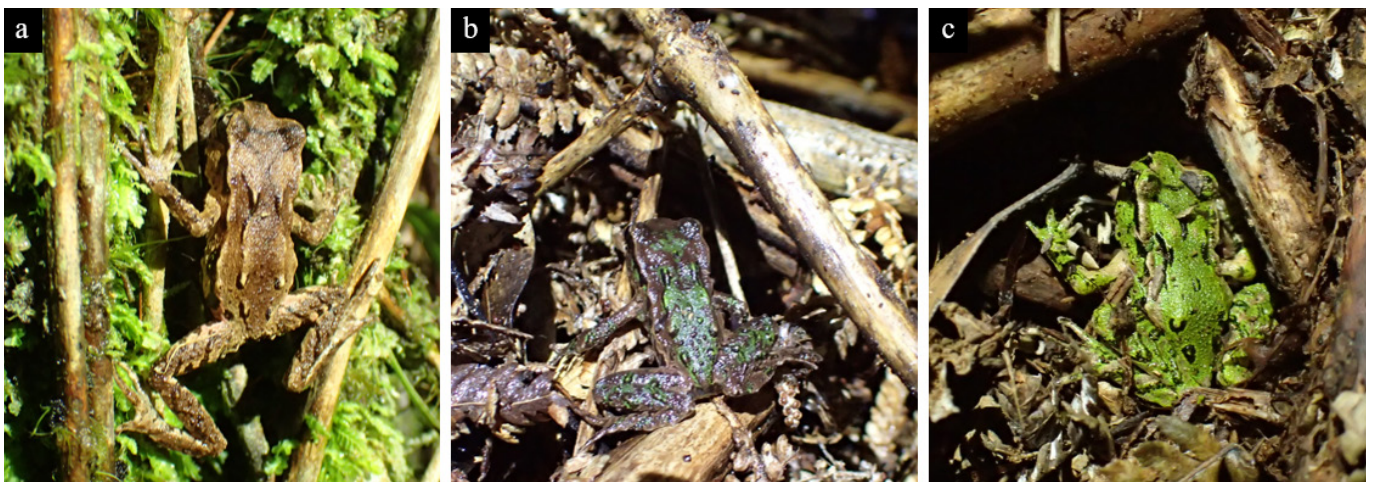
frog had been found on at the time of capture (according to written descriptions in the surveyors’ field notes) was assigned to two categories, “green” or “brown”. If a frog was found on leaf litter, the substrate category was classified as brown. If a plant species was specified, the substrate colour assigned was generally green (unless further information provided, for example “dead fronds”, resulted in an assignment to brown). When the substrate category could not be clearly identified (e.g. tree ferns contain both green and brown foliage, and it was unclear which part of the plant the frog was on), the observations were excluded from the analysis ( $n = 71$ ).

## Data analysis

Over the entire study period, 652 frogs were found in Wharekairauponga in 250 surveys. Prior to analysis, any frogs recorded as a recapture in the dataset were removed ( $n = 32$ ), to avoid counting the same individual more than once. All data were analysed in R version R 4.0.5 (2021-03-31) (R core team 2021).

First, to understand what factors influenced colour variation of frogs, a linear mixed-effects regression was used. The percentage of green (of the frog dorsum) was the response variable, and substrate colour (green or brown), body size (measured as SVL, mm), and season (autumn, spring, or summer) were included as fixed effects. Site and survey year were included as random effects. Error variances were equal across groups of the predictor variables (Levene’s test), thus no transformation of the data was required. The marginal (fixed effects only) and conditional (fixed and random effects)  $R^2$  was calculated using the *r.squaredGLMM* function in the package MuMIn (Barton 2022). Four hundred and fifty observations were included in this analysis after the omission of observations where the substrate or frog colour was not recorded, or frog body size was not recorded. Both substrate and frog colour were recorded for 500 frogs, and frog colour was recorded for 533 frogs.

To determine what factors influenced the height above ground that a frog was found, a second linear mixed-effects regression was used. In this regression model, height above ground (where the frog was found) was the response variable, and frog body temperature at the time of capture (scaled and centered), frog size (measured as SVL in mm, scaled and



**Figure 1.** Examples of *Leiolopelma archeyi* individuals that were classified as (a) 0%, (b) 50%, and (c) 100% green. Photos taken by Boffa Miskell staff.

centered), season (autumn, spring, or summer), and the time of night (in minutes, relative to 5pm) were included as fixed effects. To test for a potential non-linear relationship between temperature and height above ground, a quadratic term for body temperature was also included in the model. Site and survey year were included as random effects. Following exclusion of missing observations for body temperature, height above ground or SVL, sample size for this analysis was 282. Height above ground was recorded for 364 frogs.

## Results

### Frog colouration and background matching

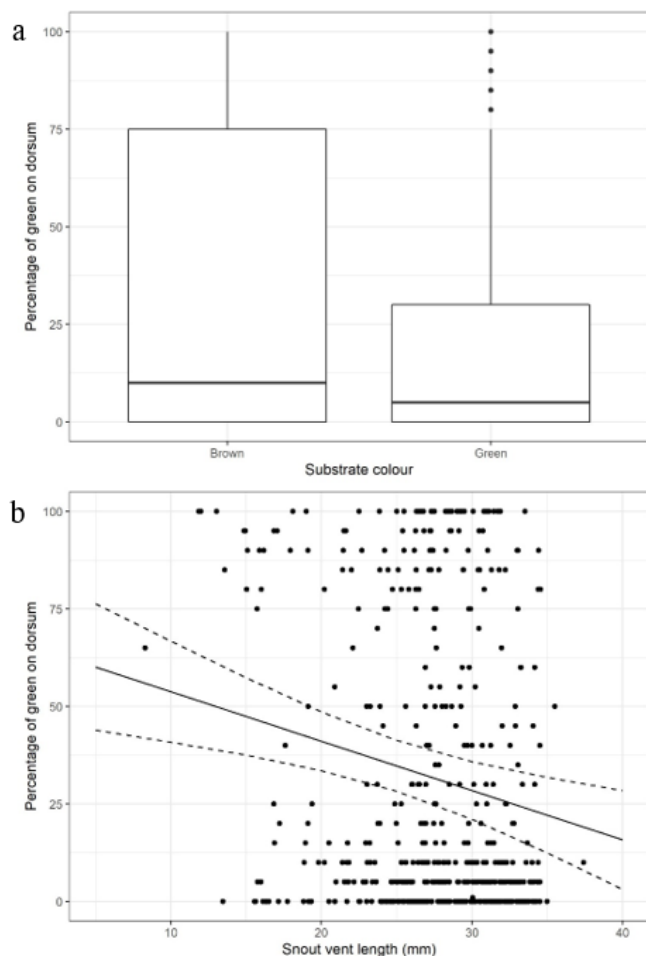
Frog colouration information was available for 533 individual frogs. The average percentage of green on the dorsal surface of these frogs was 28.3% (range 0–100%). Most frogs had more brown than green on their dorsum (72.6%,  $n = 387$ ), with 24.7% of frogs ( $n = 132$ ) having more green than brown on their dorsum. The remaining 2.7% ( $n = 14$ ) had equal amounts of green and brown. One individual had yellow pigment on its dorsum, and two frogs had pink pigmentation

on their limbs. A total of 178 (of 500) frogs were found on green substrates and 322 frogs on brown substrates. For 33 frogs, no information was available regarding the colour of the substrate they were found on. Frogs on brown substrates appeared to have a higher mean percentage of green on their dorsum than frogs on green substrates (Fig. 2a); however, the difference was not significant ( $\chi^2 = 2.05$ ,  $df = 1$ ,  $P = 0.152$ ).

The average size of *L. archeyi* (measured as SVL) captured was 27.7 mm (range 8.8–37.4 mm). Larger frogs had a lower percentage of green on their dorsum than smaller frogs (Fig. 2b). This negative linear relationship was significant ( $\chi^2 = 11.43$ ,  $df = 1$ ,  $P < 0.001$ ). Season had no significant effect on the percentage of green recorded on the frog dorsum ( $\chi^2 = 0.03$ ,  $df = 2$ ,  $P = 0.99$ ). Overall, the model explaining frog colouration had a relatively small  $R^2$  (marginal  $R^2 = 0.037$ ; conditional  $R^2 = 0.067$ ), suggesting there was a substantial amount of unexplained variation.

### Frog climbing behaviour

In this data set, 43.1% of frogs were found more than 1 cm off the ground ( $n = 157$ ) (height above ground information was available for 364 frogs in total). The average height above the ground they were found at was 21.9 cm (range 0–200 cm). The height above ground where frogs were found was significantly related to their body size (SVL) ( $\chi^2 = 17.14$ ,  $df = 1$ ,  $P < 0.001$ ), with larger frogs (SVL about 23 mm or more) found in a wider range of vertical habitats than smaller frogs (Fig. 3a). Body temperature had a marginally significant effect on the height above ground frogs were found ( $\chi^2 = 2.94$ ,  $df = 1$ ,  $P = 0.087$ ). As frog temperature increased, the height above ground that frogs were found tended to decrease (Fig. 3b). The quadratic term of temperature was not significant ( $\chi^2 = 0.26$ ,  $df = 1$ ,  $P = 0.609$ ). In addition, there was a marginal effect of season on the height above ground that frogs were found ( $\chi^2 = 4.89$ ,  $df = 2$ ,  $P = 0.087$ ), with frogs almost exclusively found at ground level in the summer compared with autumn and spring (Fig. 3c). There was no significant effect of the time of night on the height above ground that frogs were found ( $\chi^2 = 0.251$ ,  $df = 1$ ,  $P = 0.616$ ). Overall, the model for frog height had a moderate  $R^2$ , with the conditional  $R^2$  being substantially higher (0.478) than the marginal  $R^2$  (0.100), suggesting that the random effects of site and year explained a reasonable amount of the variation in frog height.

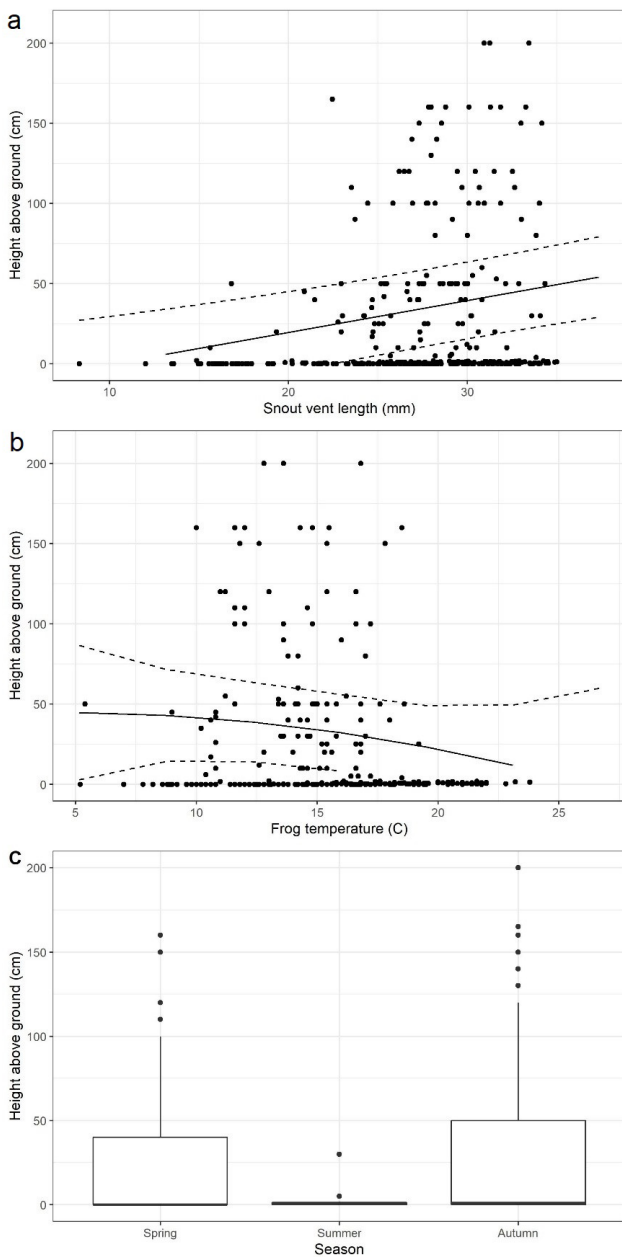


**Figure 2.** (a) Percentage of green on each individual *Leiopelma archeyi* frog on substrates classified as brown or green in Wharekairauponga, New Zealand. (b) Percentage of green on the frog dorsum in relation to the size of each frog (snout-to-vent length, SVL, in mm). The regression line (percentage green =  $66.57 - 1.26 \times \text{SVL}$ ) is shown with 95% confidence intervals (dashed lines).

## Discussion

In our study, *L. archeyi* displayed substantial variation in dorsal colouration (as a percentage of green). This colouration varied with the substrate the frogs were found on, and with the size of the frog. Surprisingly, frogs tended to not match their substrate colour, which may highlight the effect of colour contrast on their detectability, perhaps because a stronger colour contrast with the substrate made it easier for observers to detect the frogs. The percentage of green on the frogs' dorsal surface decreased linearly in larger individuals, which may reflect an effect of age on greenness. Frogs were regularly found above ground, with larger individuals (over 23 mm SVL) being found higher above ground than smaller frogs. The height above ground where frogs were detected varied the most at moderate frog body temperatures (10–19°C). Overall, our study demonstrates that colouration and height above ground could influence detectability of *L. archeyi* frogs by human observers, with some biases relating to how detectability may





**Figure 3.** (a) Relationship between the body size (snout-to-vent, mm) of each *Leiopelma archeyi* frog and the height above ground it was found (in cm) in Wharekirauponga, New Zealand. The regression line is shown (height =  $38.63 + 19.27 \times \text{SVL}$  (scaled)), with 95% confidence intervals. (b) The relationship between the body temperature (in °C) of each frog at time of capture and the height above the ground it was found (in cm). The regression line is shown (height =  $38.63 - 15.59 \times \text{temperature}$  (scaled)), with 95% confidence intervals. (c) Boxplot showing the height above ground that frogs were found in spring, summer, and autumn.

change with frog body size or height above ground. Thus, the study fills an important gap in our understanding of the ecology of *L. archeyi*.

### **Leiopelma archeyi** colouration and background matching

*Leiopelma archeyi* individuals found on brown substrates had a slightly higher percentage of green on their dorsum than frogs found on green substrates, although this difference was

not significant. At first glance, this trend disagrees with the hypothesis that frogs seek substrates that they colour match with in order to camouflage. Nevertheless, it seems unlikely that there would be no ecological benefit to camouflaging for *L. archeyi*, particularly from native predators who hunt by sight, e.g. ruru (*Ninox novaeseelandiae*), tuatara, and the extinct laughing owl (*Ninox albifacies*) (Newman 1977; Worthy & Holdaway 1994; Ramirez 2017). Further, given *L. archeyi* is a sit-and-wait predator, effective camouflage is essential. Consequently, our finding does not rule out the use of camouflage in *L. archeyi* for several reasons. First, variation in environmental colours may be sufficient to provide suitable camouflage habitat for the variety of dorsal colours observed in *L. archeyi*. The habitat which *L. archeyi* occupy is visually busy, which is likely to provide effective camouflage for this species with disruptive colouration and patterning. Second, as *L. archeyi* has mainly nocturnal emergence (Bell 1978) and our study was conducted at night, colour matching may not be as essential to camouflage success at night due to the low light conditions (Norris & Lowe 1964), except perhaps to avoid predation by owls. Thus, our results might have been different had the study been conducted during daylight hours. Third, more important than colour matching could be the frogs' disruptive patterning concealing the true outline of their bodies (Thurley 1996). Fourth, single-point observations of frogs do not necessarily demonstrate their choosing similarly coloured substrates, but could also represent coincidental occurrence on a particular background colour at the time of observation (e.g. a frog moving from point A to B happened to be observed on brown substrate).

A fifth potential explanation for this unexpected result is that frogs on backgrounds that did not match their dorsal surface were easier to detect visually, and therefore were more likely to be found in the surveys. The effect of colour or pattern mismatch on detectability by humans has been demonstrated in other studies (e.g. Karpestam et al. 2013; Nokelainen et al. 2019). For example, crabs were more difficult to detect by researchers when placed on visually more complex backgrounds (Nokelainen et al. 2019). This interpretation would suggest there may be a bias towards finding frogs that are sitting on contrasting backgrounds. However, our analysis suggests this bias may be relatively minor because we only found a non-significant trend rather than a clear significant difference. Finally, frog and substrate colourations were not measured in a rigorous manner that eliminated subjective human observer perception of colour; thus, this second type of observer bias might have played a role, as well.

In our study, larger frogs (based on their SVL) tended to have less green on their dorsal surface than smaller frogs (in a linear negative relationship). Assuming body size corresponds to age in Leiopelmatid frogs (Whitaker & Alspach 1999), this result suggests that older frogs tend to be less green than younger frogs. While we cannot determine if larger individuals (i.e. likely older frogs) lost green as they aged, or never had green pigment to begin with, our findings are consistent with work by Thurley (1996) who reported that larger *L. archeyi* had a higher proportion of brown colouring on their dorsal surface. A possible reason for green colour loss in adult *L. archeyi* could be to improve survival as adults by being less conspicuous as brown colouration is typically less prominent in a damp forest. Ontogenetic colour change has also been reported in other anurans such as *Elachistocleis haroi* (Bueno-Vallafañe et al. 2020), six species in the *Gastrotheca* genus (Carvajal-Endara et al. 2019), and *Oreophryne ezra* (Bulbert et al. 2018). In the

example of *Elachistocleis haroi*, it is thought colour change improved sexual display and enabled predator avoidance through colour crypsis (Bueno-Vallafañe et al. 2020).

Colour or pattern changes in *L. archeyi* with increasing size/age may have important conservation implications. It was previously thought colour patterns on *L. archeyi* remained unchanged over its lifespan (Stephenson & Stephenson 1957). More recent discussions around possible colour changes in *L. archeyi* suggested that if such changes are occurring in some individuals, they are gradual (Bradfield 2004; Murray 2010). For example, a small change to a black dorsal pattern of an individual *L. archeyi* that coincided with the growth of the frog between captures was reported by Easton (2020). Our own finding that larger *L. archeyi* individuals had less green on their dorsal surface compared to smaller frogs adds to this ongoing discussion around potential colour loss or pattern changes in *L. archeyi*. If colour or patterning of *L. archeyi* do indeed change over the lifespan of an individual, this has implications for the reliability of photo ID to identify individuals. In the short term, this method is likely to still be an effective way to identify individuals, whereas in the longer term that reliability might decrease because *L. archeyi* is a long-lived species and has been reported to live for over 35 years (Bell et al. 2020).

#### Climbing behaviour of *Leiopelma archeyi*

Larger *L. archeyi* individuals (i.e. over 23 mm SVL) were found utilising a greater range of vertical habitat compared to that of smaller frogs in our study. Types of vertical habitat utilised by larger frogs include various species of tree fern, tree species, and kiekie (*Freycinetia banksii*). There are at least four possible explanations for this apparent partitioning of vertical habitat. First, larger (and likely older) frogs may be less sensitive to predation than smaller frogs due to their less conspicuous colouration or increased experience in being camouflaged (Formanowicz et al 1981; Toledo 2007; Székely et al. 2020). The habitat off the ground is further from refuge sites such as tree hollows or burrows under the ground (Haigh et al. 2007), and thus carries with it a greater risk of exposure to some frog predators. Smaller frogs may be more vulnerable to predators, and therefore reduce their predation risk by remaining on the ground where habitat complexity is greater than that of exposed tree trunks. Second, smaller frogs may be more prone to desiccation when they are higher above the ground (Spotila 1972; Jaeger 1978). Smaller frogs have a larger surface area to volume ratio than larger frogs, thus climbing and consequent exposure to a drier environment may be more detrimental for smaller frogs (Stewart 1985) as maintaining hydration (or re-hydrating in a timely manner) is vital for their survival (Cree 1989). A similar relationship between frog age/size and climbing behaviour has been found in *Eleutherodactylus coqui*, an arboreal frog in Puerto Rico (Steward 1985). Juvenile *E. coqui* were reported to remain on the ground near retreat sites, whereas adults climbed to the canopy during the night (Steward 1985). Third, larger frogs might have been more easily detectable at heights above ground by human observers than smaller frogs, causing a third type of observer bias in our data.

In our study, the height climbed above ground was highest for frogs that had a body temperature between 10 and 19°C, with some frogs found up to 2 m above ground (note this was the height limit of the searches, so frogs could have occurred above this height). Climbing behaviour appeared to decline above 19°C when frogs were mainly recorded on the ground.

This response suggests climbing behaviour could be associated with body temperature or moisture regulation (Jaeger 1978). Thus, there could be an optimal body temperature range for climbing (or general frog activity), or a need to be on the ground when at warm or cool temperatures, depending on the humidity. As frogs are ectothermic (Valenzuela-Sánchez et al. 2015), warmer temperatures should result in a higher metabolic rate, and thus potentially more climbing behaviour; however, this was observed only up to a threshold. There may be more airflow higher off the ground, which only a well-hydrated frog at the optimal temperature can cope with, compared to a frog with lower hydration status who cannot afford further water loss. Further, if frog climbing behaviour can be regarded as a proxy of general activity rates, then our results suggest that *L. archeyi* activity is highest at body temperatures between 10 and 19°C. Due to the correlation between warmer temperature with higher humidity in moist environments, we must also be cautious when interpreting the influence of body temperature alone.

We also observed a pattern where frogs were almost exclusively found on/near the ground during the summer months, whereas they climbed more often in autumn or spring (which is thought to be the mating season; Bell 1978). One possibility is that this pattern might be related to breeding or mate seeking (i.e. communication or courtship; Wells 1977). It is thought *Leiopelma hamiltoni* communicate through chemical signalling (Lee & Waldman 2002; Waldman & Bishop 2004; Waldman 2016), a behaviour which is also seen in other amphibians (Woodley 2014). Chemical cues may be more easily dispersed above the ground, thus *L. archeyi* could be climbing for the purpose of mate seeking. Possible sexual activity has been observed in the closely related *L. hamiltoni* where two individuals were found in close contact resembling amplexus 3 m above the ground on a perch (Waldman 2016). An alternative possibility could be for the purpose of foraging, as larger individuals may have access to different foraging opportunities above the ground. *Leiopelma archeyi* are sit-and-wait predators and perhaps have better success with catching flying insects when they are above ground level (Shaw et al. 2012).

#### Conclusions

In our study, *L. archeyi* frogs displayed cryptic colouration patterns that changed with increasing body size (although with a small effect size). Further, the frogs occupied a range of vertical habitats, and their tendency to climb was associated with their body size, as well as with body temperature and seasonal effects. Cryptic colouration and colour matching behaviour may play a role in the visual detection of individuals during frog monitoring surveys, although there are several potential explanations for our finding that *L. archeyi* frogs tended to not show background-matching between their substrate and the colour of their dorsum. We did not investigate detection rates but this would be an interesting avenue to investigate in future research because if observers were biased towards detecting larger individuals or those who contrast with their background, this could mislead future community estimates. Further, the effectiveness of photo ID for *L. archeyi* needs to be determined, and one way to do this would be to examine historical photo records for similar colour loss trends as in our study.

Regarding vertical habitat use of *L. archeyi*, because

frogs were found in the whole range of searched habitat (up to 2 m), there could have easily been additional frogs higher than 2 m above ground that were missed in the current study. Identifying the factors that influence where frogs are found will improve our understanding of the effectiveness of current monitoring protocols, and aid future conservation planning. Therefore, we propose that vertical habitat is searched thoroughly up to heights of more than 2 m above ground when conducting future surveys for *L. archeyi*, to investigate potential arboreal behaviour. Improving our understanding of *L. archeyi* behaviour and ecology is an essential component of successfully conserving this endangered species, and efforts should continue towards expanding this knowledge.

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## Additional Information and Declarations

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**Ethics:** Collection permits were issued by the Department of Conservation to undertake this work.

**Data availability:** The data and code from this article are available from the authors.

**Author contributions:** JP contributed to data collection, analysed the data and wrote the manuscript. SG and CM provided advice on the statistical analysis and contributed to writing and editing the manuscript.

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