Reproductive biology of Hawaiian lava crickets

Aarcha Thadi [*], Justa Heinen-Kay, John T. Rotenberry, Marlene Zuk

Department of Ecology, Evolution & Behavior, University of Minnesota, MN, United States

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ABSTRACT

Insects have spread across diverse ecological niches, including extreme environments requiring specialized traits for survival. However, little is understood about the reproductive traits required to facilitate persistence in such environments. Here, we report on the reproductive biology of two species of endemic Hawaiian lava crickets (*Caconemobius fori* and *Caconemobius anahulu*) that inhabit barren lava flows on the Big Island. We examine traits that reflect investment into reproduction for both male and female lava crickets and compare them to the non-extremophile Allard's ground cricket (*Allonemobius allardi*) in the same sub-family. Lava cricket females possessed fewer, but much larger eggs than ground crickets, while males do not provide the costly nuptial gifts that are characteristic of the Nemobiinae subfamily. Lava crickets also have longer ovipositors relative to their body length than related *Caconemobius* species that occupy cave habitats on the Hawaiian islands. The differences in reproduction we report reveal how these little-known cricket species may increase survival of their offspring in the resource-deprived conditions of their hot, dry environments.

Introduction

Insects occupy almost all terrestrial ecological niches and can be found in several environments that are considered extreme - i.e., outside the physiological tolerance ranges of most organisms (Grant et al., 2017; Rothschild and Mancinelli, 2001). Insects have evolved in ways that allow them to survive these harsh environments. For example, freeze-tolerance has evolved multiple times, allowing insects to survive extremely cold temperatures (Sinclair et al., 2003). Likewise, adaptations altering hemolymph physiology and homeostasis allow numerous aquatic insects to survive in extremely acidic conditions (pH ~3–4 for the lesser waterboatman, *Corixa punctata* and the chalk-fronted corporal, *Libellula julia*; Morris, 1989; Rockwood & Coler, 1991). Both survival and reproduction are governed by physiological adaptations. Research on insect life in extreme environments has predominantly focused on physiological adaptations that pertain to survival (Birrell et al., 2020; Burtscher et al., 2018; Cloudsley-Thompson, 1988; Grant et al., 2017; Rothschild and Mancinelli, 2001), leaving reproductive traits relatively understudied, though a few papers have shown a reduction in the length of the reproductive life-stage of insects inhabiting these environments (Zhang et al., 2015; Zhang et al., 2013; Zhao et al., 2014). Uncovering the differences in reproductive physiology that insects in extreme environments possess will enable us to ascertain explanations for how survival is possible in these areas.

The aftermath of a volcanic eruption creates one of the most extreme environments on Earth – large expanses of bare rock completely devoid of macroscopic life (Fig 1, left). It can be challenging for organisms to re-establish life on the newly formed and completely barren lava landscape (Aplet et al., 1998; Kitayama et al., 1995; Mueller-Dombois and Boehmer, 2013; Smith and Fretwell, 1974). Perhaps surprisingly, the first macroscopic colonists in volcanic regions around the world are often arthropods, rather than plants or lichens (Ashmole et al., 1992; Elizalde, 2014; Howarth, 1979; Howarth, 1987; New et al., 1997). Endemic lava crickets in the Hawaiian Islands ('ūhini nēnē pele in Hawaiian) in the genus *Caconemobius* (Fig 1, right) (Orthoptera: Trigonidiidae, subfamily Nemobiinae) are believed to be the first multicellular colonizer of barren lava fields (Howarth and Mull, 1992; Otte, 1994). Lava crickets have increased desiccation resistance and are only active on the surface at night (Ahearn and Howarth, 1982), presumably to cope with the dry climate and daytime surface temperatures over 50 °C. Prior to the establishment of vegetation on a lava flow, the crickets subsist predominantly on wind-borne detritus (Howarth, 1979). When first described, lava crickets were believed to always be the first colonizers of barren lava flows (Howarth and Mull, 1992; Otte, 1994). More recent work has shown that lava crickets are not always found on new flows, but are able to persist on still-sparsely vegetated flows of up to 220 years old (Heinen-Kay et al., 2021), demonstrating that we still have much more to understand about what enables the persistence of

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these crickets. While the physiological traits that enable survival in this challenging environment have received some prior research attention (Ahearn and Howarth, 1982; Howarth, 1979; Howarth, 1987), the behaviors and reproductive traits involved in lava cricket reproduction remain unknown.

Lava crickets face challenges to reproduction distinct from other cricket species in their family. To begin with, lava crickets are wingless, a common adaptation seen in island insects (Howarth and Mull, 1992; Leihy and Chown, 2020; Wagner and Liebherr, 1992). This reduces their capacity for dispersal to search for mates and further prevents them from attracting conspecifics through stridulation, the way most crickets do. Once they find mates, lava crickets must invest resources into successful reproduction. Lava crickets are in the ground cricket subfamily Nemobiinae (Orthoptera: Trigonidiidae). In this family, females of some species chew on specialized tibial spurs of males during mating (Fedorka and Mousseau, 2002; Fulton, 1931; Mays, 1971). By performing this spur chewing behaviour, females can obtain hemolymph of up to 8% of the male's body mass in a single mating (Fedorka and Mousseau, 2002), allowing for increased allocation of resources to offspring and increasing her reproductive output (DiRienzo and Marshall, 2013). This behaviour may occur numerous times during the cricket's lifetime as females do not discriminate between chewed and intact spurs (Fedorka and Mousseau, 2002; Piascik et al., 2010). For lava crickets, however, providing this nuptial gift may be difficult in the hot, dry, environment of the lava flows where conserving body fluid is imperative. After mating, females must ensure that they are allocating sufficient resources to offspring (which can be instrumental in determining offspring survival; Roff 1993 and references therein), so they are well-equipped for the infrequent nutrient availability of their habitat. Finally, ground crickets tend to oviposit deep in soil to ensure that their eggs can hatch prior to drying out (Masaki, 1979; Tauber et al., 1986). In a rocky, barren area, with potentially little availability of soil and dry conditions, modifications to ovipositor length may be required to ensure egg survival.

Here, we describe aspects of the reproductive biology of these two lava flow-inhabiting *Caconemobius* species for the first time, focusing on two species: *Caconemobius fori* and *Caconemobius anahulu*. By studying these species, we aim to (a) determine whether they possess the ability to perform the spur-chewing nuptial gift giving behavior and (b) investigate aspects of lava cricket females' reproduction that may translate into improved survival in the extreme environment of the lava flows. We sampled these two species by collecting them in different habitats, *C. fori* in a comparatively wetter, higher elevation site in Hawai'i Volcanoes National Park, *C. anahulu* in the drier, hotter low-elevation region of Kona (for more habitat details see (Heinen-Kay et al., 2021)). We compared our findings in the lava crickets with

another nemobiine, Allard's ground cricket (*Allonemobius allardi*), commonly found in dry, well drained woodlands, upland fields and slopes, lawns, roadsides, and grassy sand areas (Alexander and Thomas, 1959; Tennis, 1983; Vickery and Kevan, 1985; Bland, 2003; Himmelman, 2009) across its range in central and eastern North America. We provide this comparison to provide context for our measurements of lava crickets, comparing them to a non-extreme temperate-dwelling species that is representative of typical Nemobiinae species.

First, we examined lava cricket males for the specialized nuptial gift-giving tibial spur. We predict that males will not possess this spur, as costs of providing a hemolymph-based nuptial gift are high in this environment. Next, we describe the number and size of eggs found in wild-caught females and calculate an estimate of reproductive output, by multiplying the number of eggs found with the volumes of these eggs and scaling this by body size. Theory suggests that, when allocating more resources to offspring increases their survival, females should produce fewer, larger offspring when resources are limited (Fox and Czesak, 2000; Smith and Fretwell, 1974). However, an alternative strategy of increasing offspring number and reducing allocation to individual offspring is seen, albeit predominantly in plants (Dani and Kodandaramaiah, 2017). We wanted to see if lava crickets, like other insects, would reduce egg number and increase egg size relative to Allard's ground cricket females, given the low food availability and harsh climate of the lava. Third, we compare ovipositor lengths relative to body size of the lava crickets with those of the closest related species (*Caconemobius varius, Caconemobius uuku, Caconemobius howarthi, Caconemobius albus, Caconemobius paralbus*) that are cave-adapted (Otte, 1994), as well as the non-extreme Allard's ground cricket, to gain insight into adaptations to ensure egg-hatching in lava crickets. As cave-dwelling crickets experience higher humidity levels than lava-dwelling species, we expect that if the lava crickets are placing their eggs deep in cracks within the lava to prevent drying out, they should have longer ovipositors than the cave-dwellers relative to body length.

Methods

Field sampling

We collected two species of lava crickets (*C. fori* and *C. anahulu*) from unvegetated lava flows on the Big Island of Hawai'i. *Caconemobius anahulu* were collected from the Hualālai flows (~220 years old) in Kona during August 2021. *Caconemobius fori* were collected from various sites in Hawai'i Volcanoes National Park (Mauna Ulu flows which were ~45 years old, Alanui and Mulawai a Pele flows were both ~50 years old) during August 2021 and August 2022. We determined these locations

Fig. 1. (left) Alanui lava cricket collection site, 52-year old unvegetated 'a'a. (right) Female *Caconemobius fori*, photo credits: John Rotenberry (left), Geoffrey Miller (right).

through previous sampling visits during 2019 (Heinen-Kay et al., 2021).

We used live traps to capture *Caconemobius* spp. Our method of live-trapping followed Heinen-Kay et al. (Heinen-Kay et al., 2021). Briefly, we sliced off the top of plastic water bottles (500 mL to 2 L), inserted the inverted top into the bottle's body, and secured it with tape, thus creating a funnel that led into the bottle's body. We baited the body of the bottle with Lee Kum Kee™ shrimp paste on crumpled paper. We inserted the traps into cracks in the lava, oriented such that lava crickets could walk or fall into them. We left these traps overnight and checked their contents the next morning. We transferred live crickets to portable terraria with structure and minimal food, and preserved dead crickets in 70% alcohol while in the field. Upon return to the University of Minnesota, we kept these dead crickets at 4°C and later dissected them. We collected *Allonemobius allardi* live, by hand, on the St Paul campus of the University of Minnesota during August and September of 2021 and 2022. These crickets were stored in the same way as the lava crickets prior to dissection, to eliminate the effects of storage method on egg size.

Female egg measurements and ovipositor lengths

We dissected adult females, identified by the presence of an ovipositor, and removed eggs from the abdominal cavity, recording the total number of eggs found. We measured eggs rather than entire ovary mass as orthopteran reproductive tissue does not have ovaries that are separate from eggs – the eggs arise from ovarioles that are part of the gonad tissue mass (Snodgrass, 1993). We measured the length and width of up to 10 intact eggs to the nearest 0.01 mm using digital calipers, then calculated egg volumes using the formula for an ellipsoid ($\frac{2}{3}\pi \times \left(\frac{width}{2}\right)^2 \times length$). For some individuals, we were unable to obtain measurements for 10 eggs if they did not contain enough eggs or the eggs had lost their shape during preservation. In these cases, we measured any intact eggs that were available. To account for variation in body size, we recorded female pronotum length to the nearest 0.01 mm. Finally, we recorded ovipositor lengths from the tip of the ovipositor to its base on the body of the cricket to the nearest 0.01 mm.

Male tibial spur

To determine if the males had the specialized spur used in nuptial gift-giving, we observed legs of male crickets (sample size: *C. fori* = 32; *C. anahulu* = 10; Allard's ground cricket = 30) under a simple dissecting microscope at 25x magnification. We recorded the presence or absence of the specialized spur, as well as whether the spur present in that position was broken or intact. In Nemobiinae species that perform this nuptial gift-giving behavior, a broken spur indicates at least a single mating (Mays, 1971). We identified the specialized spur by its rigid, short, teardrop shape, in comparison to the longer, floppy, bristle-covered spur typically seen on tibia of both sexes (Fig. 3) (Fedorka and Mousseau, 2002; Fulton, 1931; Mays, 1971). We photographed representative samples with the help of staff of University of Minnesota Imaging Centre, using reflectance microscopy (Nikon A1si).

Statistical analysis

We performed statistical analyses in R (v4.1.3; R Core Team, 2021). To perform species comparisons between egg volumes, reproductive output (estimated by multiplying egg number and egg volume) and ovipositor lengths, we fit linear models using the "lm" function with "Species" as a predictor variable and "Pronotum Length" as a covariate to control for body size variation. To investigate species differences in egg numbers, we used a Poisson generalised linear model using the "glm" function in the lme4 package (v 1.1.32, Bates et al., 2015), with the same structure as the models above. We used the 'relevel' function to change the model's reference level to perform comparisons between the various species. As the identity of the researcher that made the measurements did not influence the variables we were interested in, we did not include it as a covariate in analyses.

Results

Investment into eggs in lava crickets

The species differed significantly in the number of eggs in their body cavity, with Allard's ground cricket having significantly more eggs than both *C. fori* (reference level = Allard's ground cricket; est. ± SE = $-2.3286 \pm 0.; z = -20.827, p < 0.001$) and *C. anahulu* (est. ± SE = $-2.4763 \pm 0.1256; z = -19.711, p < 0.001$) females (Fig. 2, left). The two lava cricket species did not differ in the number of eggs they possessed (reference level = *C. anahulu;* est. ± SE = $0.1477 \pm 0.1603; z = 0.921, p = 0.357$) (Fig. 2A). There was a significant effect of the pronotum length on egg number, with females that had larger pronotums tending to lay more eggs (est. ± SE = $0.8656 \pm 0.1797; z = 4.817, p < 0.001$).

There was a significant effect of species on egg, with both lava cricket species having significantly larger eggs than Allard's ground cricket (reference level = Allard's ground cricket; *C. fori:* est. ± SE = $0.275 \pm 0.0267; t = 10.287, p < 0.001$; *C. anahulu:* est. ± SE = $0.32324 \pm 0.03819; t = 8.465, p < 0.001$) (Fig. 2B). However, the two lava cricket species did not have different egg volumes (reference level = *C. anahulu;* est. ± SE = $-0.04824 \pm 0.04165; t = -1.158, p = 0.252$). There was no effect of the pronotum length on egg volumes (est. ± SE = $-0.01284 \pm 0.057; t = -0.225, p = 8.23$).

Finally, when comparing reproductive output, there was a significant effect of species on reproductive output with both lava cricket species having significantly reduced reproductive output than Allard's ground cricket (reference level = Allard's ground cricket; *C. fori:* est. ± SE = $-8.207 \pm 1.367; t = -6.002, p < 0.001$; *C. anahulu:* est. ± SE = $-10.377 \pm 1.953; t = -5.312, p < 0.001$) (Fig. 2C). However, the two lava cricket species did not differ in their reproductive output (reference level = *C. anahulu;* est. ± SE = $2.170 \pm 2.131; t = 1.018, p = 0.3131$). There was a significant effect of the pronotum length on reproductive output with females that had larger pronotum widths having higher reproductive outputs (est. ± SE = $5.858 \pm 2.915; t = 2.01, p = 0.495$).

Lack of a specialized tibial spur for lava crickets

We did not observe specialized tibial spurs on any of the lava cricket males that we sampled (*C. fori* = 32; *C. anahulu* = 10) (Fig. 3). However, all 30 Allard's ground cricket had the specialized spur on both legs. For the lava cricket males, the tibial spur was structurally similar to other spurs on its legs and resembled in both shape and size the unspecialized spurs that female ground crickets possessed in this position.

Ovipositor lengths in lava crickets compared to cave crickets

Allard's ground cricket had overall longer ovipositors relative to body size compared to either lava cricket species (reference level = Allard's ground cricket; *C. fori:* est. ± SE = $-1.9067 \pm 0.1365; t = -13.967, p < 0.001$; *C. anahulu:* est. ± SE = $-1.6708 \pm 0.1795; t = -9.309, p < 0.001$) (Fig 4A). However, the two lava cricket species did not differ in their ovipositor lengths (reference level = *C. anahulu;* est. ± SE = $-0.2359 \pm 0.1749; t = -1.349, p = 0.181$). There was a significant effect of the pronotum length on ovipositor length, with females that had higher pronotum lengths having higher ovipositor lengths (est. ± SE = $1.2481 \pm 0.2849; t = 4.381, p < 0.001$).

Compared to the cave *Caconemobius* species, lava crickets had longer ovipositors relative to body size (Fig. 4B).

Discussion

We report, for the first time, aspects of lava cricket reproductive biology that likely reflect adaptations that enable persistence in the
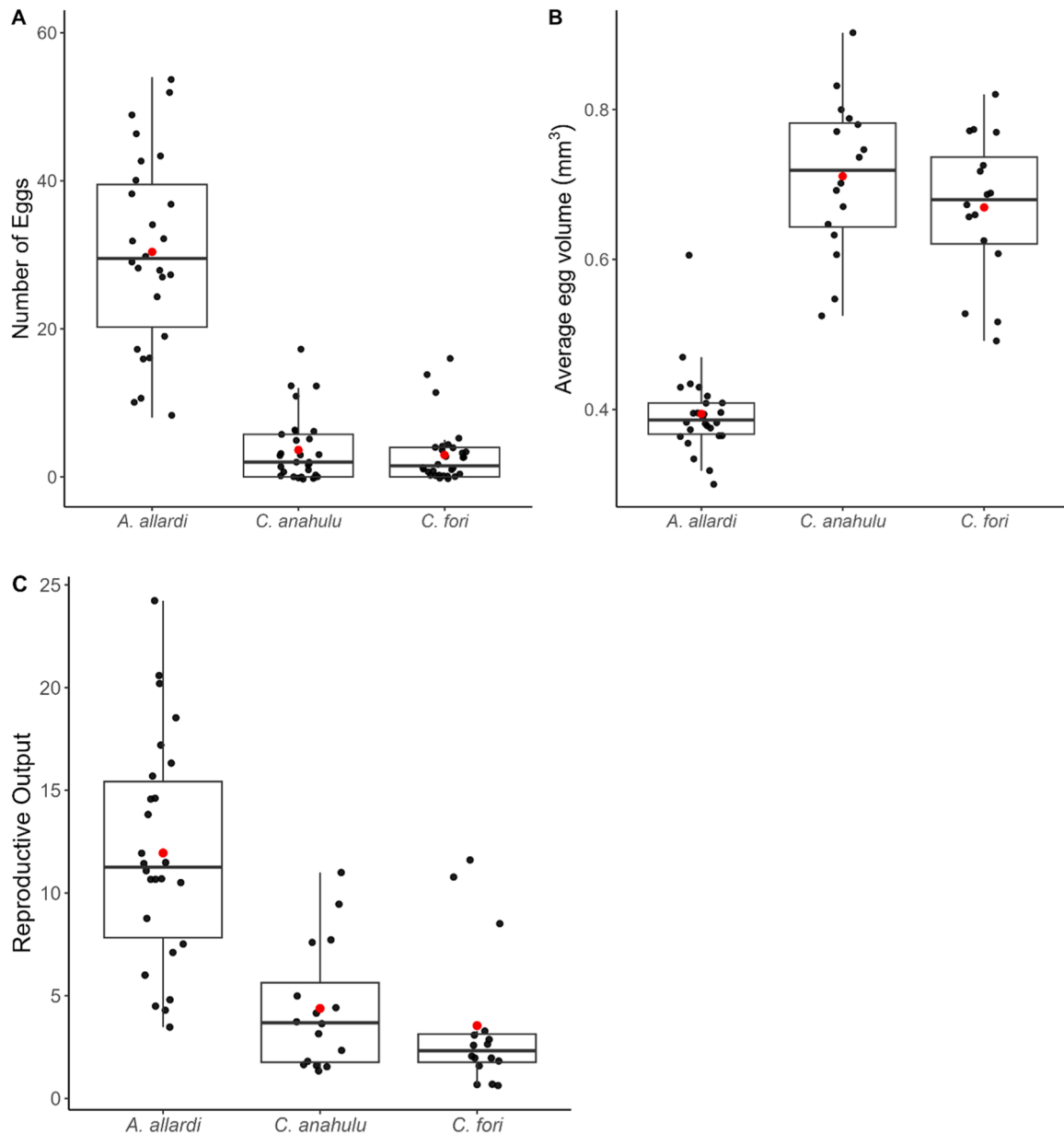
Fig. 2. . (A) Number of eggs found in the reproductive cavity of female Allard's ground cricket (Allonemobius allardi), and the two lava cricket species, *Caconemobius anahulu* and *Caconemobius fori* and (B) the average volume of measured eggs. (C) Estimated reproductive output of the dissected females, calculated by multiplying the number of eggs with egg volumes calculated. Center lines show the medians; red circles represent means; box limits indicate the 25th and 75th percentiles; whiskers extend 1.5 times the interquartile range from the 25th and 75th percentiles. Both *Caconemobius* species had fewer, larger eggs than Allard's ground cricket.

extreme environment of the barren lava flows of Hawai'i. Perhaps most notably, lava crickets possess fewer, larger eggs than the related Allard's ground cricket females (Fig. 2), and overall have lower reproductive output as supported by theory and experimental work (Dani and Kodandaramaiah, 2017; Fox and Czesak, 2000; Smith and Fretwell, 1974). Our results support previous speculation that lava crickets may be severely nutrient limited. Overall, we see reduced reproductive output for lava crickets while controlling for body size via pronotum length, which agrees with previous work showing that reproduction reduces for insects in extreme environments (Zhang et al., 2015; Zhang et al., 2013; Zhao et al., 2014). Our data on egg size and number reflect a snapshot of female fecundity in the field as all crickets were field caught, but we are unable to capture total lifetime egg production, as we were unable to control for age and variation in resource acquisition prior to capture. Rearing individuals in a common lab environment may help control for differences in developmental environments and genetic

variation that may influence our data.

As we predicted, lava cricket males did not possess the specialized spur for nuptial gift-giving found in other members of the Nemobiinae sub-family (Fig 3). In a hot climate and with unreliable food availability, there would be a high cost associated with providing a nuptial gift of up to 8% of the male's hemolymph, or any nuptial gift at all (Fedorka and Mousseau, 2002; Fulton, 1931; Mays, 1971). In such a dry environment, there may be a high benefit to receiving a nuptial gift. In the vast landscape of the barren lava fields, while males and females are found in equal proportions (personal observation, all authors), which may mean that crickets are able to find multiple mates during their lifetimes. However, orthopterans are typically income breeders that lay eggs in clutches once sufficient resources are accumulated (Branson, 2008). Given that lava crickets lay very few eggs, it is possible that they may lay few separate clutches or even a single clutch. If this is the case, it may mean that the crickets mate very few times, or may just mate singly,
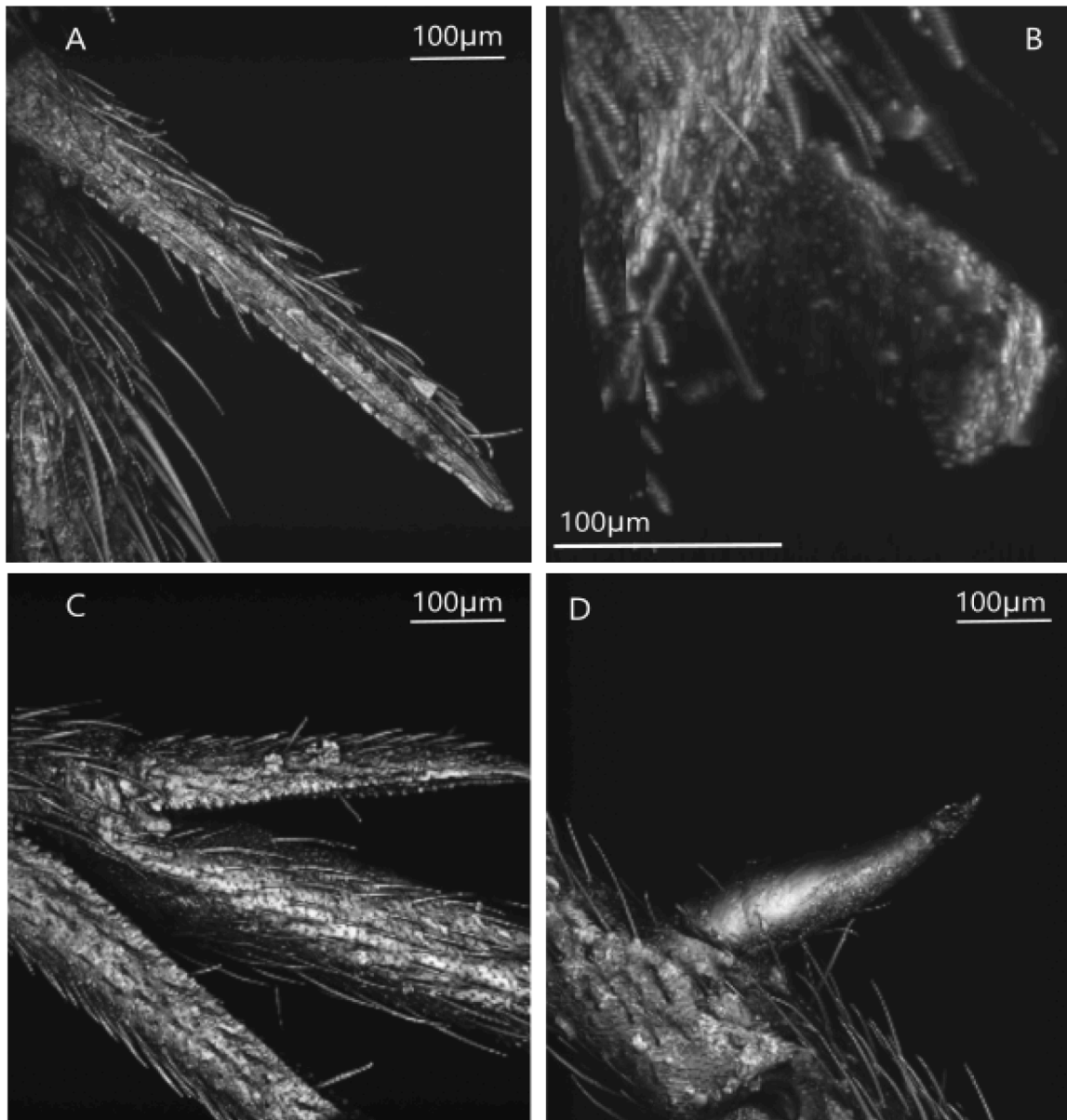
Fig. 3. Tibial spur images taken using reflectance confocal microscopy of (A) female Allard's ground cricket *(Allonemobius allardi*, B) mated male Allard's ground cricket, (C) male lava cricket *(Caconemobius anahulu*, D) unmated male Allard's ground cricket.

which may be linked to why the male crickets lack a specialized spur for nuptial gift-giving.

The absence of a nuptial gift in lava crickets brings into question whether there are alternative ways through which males in these species provide direct benefits for offspring survival. Some possible strategies of costly male investment into reproduction can be speculated upon based on mating behaviors seen in other closely related species. For example, in some Nemobiines, females consume the spermatophore after allowing sperm to drain into her reproductive tract (Fulton, 1931), obtaining nutrients. Mating behaviors of lava crickets have not yet been recorded, and doing so will help to elucidate such strategies. Most male crickets invest into costly mate attraction through song production, but as lava crickets do not have wings, they may be investing into mate attraction or mate finding in other ways. Lava crickets of both sexes have extremely elongated antennae, reflecting their reliance on mechanosensory and chemosensory cues to navigate their environment (personal observation, all authors). Other wingless cave cricket species of both sexes use excreta-based cues for aggregation (Yoder et al., 2010), as do other

common cricket species (McFarlane et al., 1983; Nagel and Cade, 1983). Lava cricket mating may parallel that of the wingless Cook Strait giant weta, wherein males compete in scrambles for mates (Kelly and Gwynne, 2022; Kelly and Gwynne, 2023), and further work could explore this possibility. Sex-specificity in mate attraction cues or mate-finding may be another route through which males invest into mating, something which would be important in the complex subterranean landscapes they inhabit.

Masaki (1986) found that longer ovipositors in Nemobiines is correlated with higher likelihood of eggs drying out before hatching. Ovipositors were longer for the Allard's ground cricket than for the lava cricket species (Fig. 4, left). As Allard's ground cricket is an egg over-wintering species, longer ovipositors, along with the larger eggs laid by the lava crickets, may be advantageous to ensure that eggs do not dry up over the many months they incubate (Bradford et al., 1993). In the lab, lava cricket eggs hatched within 6 weeks (Thadi et al., unpublished data). Lava crickets possessed longer ovipositors relative to body size than congeneric cave crickets (Fig 4, right) which encounter relative
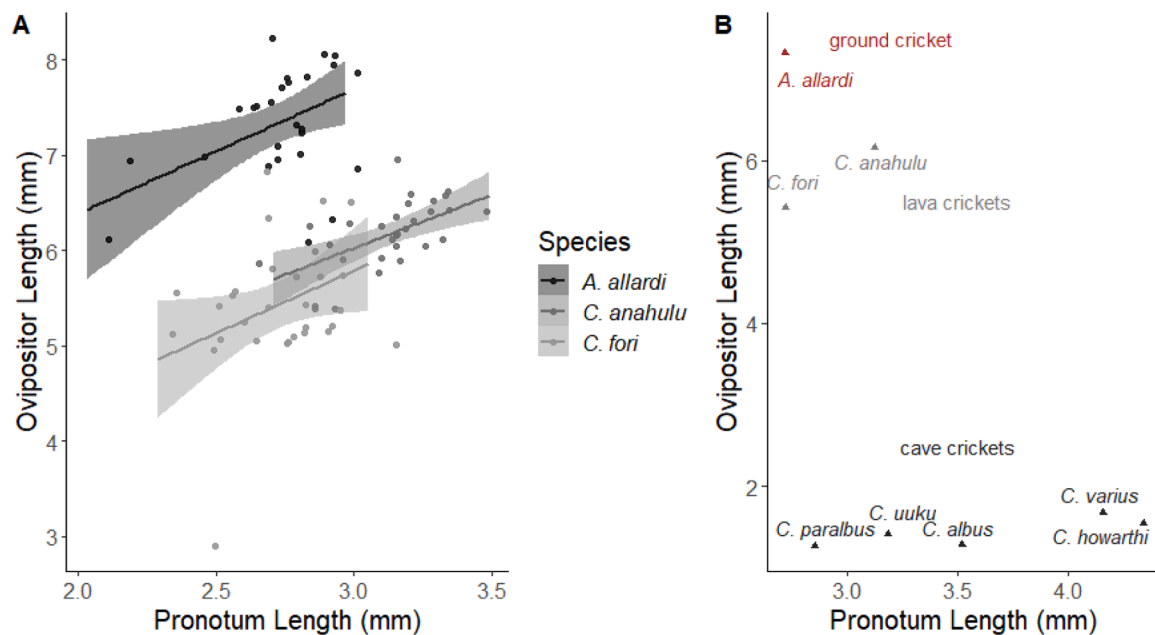
Fig. 4. . A) Relationship of ovipositor length to pronotum length for Allard's ground cricket (*Allonemobius allardi*), and two species of lava cricket (*Caconemobius anahulu* and *Caconemobius fori*), and B) mean ovipositor length plotted for these species as well as Hawaiian *Caconemobius* cave cricket species (data taken from (Otte, 1994)). Grey bands in A represent 95% confidence intervals around the linear fit for each species. Lava crickets have comparatively smaller ovipositors relative to body size compared to Allard's ground cricket, but larger than their cave-dwelling counterparts.

humidity (RH) levels of 80% and upwards (Ahearn and Howarth, 1982). It appears likely that lava crickets are laying their eggs deep into substrate in the cracks in the lava, potentially to avoid drying out at 50–80% RH (Ahearn and Howarth, 1982; Heinen-Kay et al., 2021). In the lab these crickets will lay eggs in wet cheesecloth, like other crickets, demonstrating that they are likely to be laying eggs buried within substrate.

This study has captured some of the potentially adaptive differences in reproduction between lava crickets and their relatives, that may be instrumental for persistence in this challenging habitat. Future studies may compare lava cricket life-history and behavior to other members of the *Caconemobius* genus such as the Hawaiian cave and lava tube crickets, and others in the Nemobiinae sub-family, to bridge the gap of understanding how reproductive biology alters in complex environmental conditions to facilitate survival of these understudied species. Changes to reproductive behavior, life-history allocation, physiology, or morphology are all instrumental in permitting or constraining the ability of an organism to reproduce, and understanding the extent of accommodation of such changes is instrumental in understanding life in extreme environments.

Declaration of competing interest

The authors of the manuscript "Reproductive biology of Hawaiian lava crickets" declare no conflicts of interest.

Data availability

Data, as well as the code used for analysis and to make figures are available through Dryad DOI: 10.5061/dryad.c2fqz61h2.

Author CRediT statement

AT, JHK and MZ conceptualized the study. All authors contributed equally to collecting the data. AT performed the analyses with support from the other authors. AT wrote the manuscript and all other authors provided critical feedback on the manuscript.

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