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Preference and performance of Pūrerehua Kahukura (*Vanessa gonerilla gonerilla*) on native and introduced nettles of AotearoaGreer J Sanger¹ , Janice M Lord²  and Jennifer M Jandt^{1*} ¹Otago University Zoology Department, 340 Great King Street, Dunedin North, Dunedin 9016²Otago University Botany Department, 464 Great King Street, Dunedin North, Dunedin 9016*Author for correspondence (Email: jenny.jandt@otago.ac.nz)

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Abstract: The preference-performance hypothesis suggests that female insects prefer to oviposit on the host plant that provides the highest fitness for offspring. However, introduced plants can cause ecological traps, wherein animals lay eggs on low quality (often introduced) species instead of higher quality (usually native) species. Pūrerehua kahukura | New Zealand red admiral butterfly (*Vanessa gonerilla gonerilla*) lay eggs on native and introduced nettles (*Urtica* spp.). We tested both host preference for female oviposition and host performance for development of larvae. To test preference, we used oviposition cages in which we provided adult kahukura with native *Urtica ferox*, native/introduced *U. australis* hybrid, and introduced *U. urens*. To test performance, we collected the eggs and, after hatching, provided them with one of the three nettles for their development to adulthood. Kahukura only laid on *U. ferox* ($n = 8$) and *U. australis* hybrid ($n = 2$). No butterflies laid eggs on more than one *Urtica* species, even though some individuals laid >10 eggs while in the oviposition cages. Pupal weights were significantly higher for larvae reared on *U. ferox* compared to those reared on *U. australis* hybrid and *U. urens*. Although larvae were significantly heavier when fed *U. ferox*, larvae raised on *U. australis* hybrid had higher probability of survival to adulthood and faster development rates. Kahukura oviposition preference ranking ($U. ferox \geq U. australis > U. urens$) qualitatively matched larval development ranking ($U. ferox > U. australis = U. urens$), supporting the preference-performance hypothesis for this population. If kahukura have the option to oviposit on native *Urtica* spp., our results suggest that they are unlikely to be duped into ovipositing on a lower quality host plant. While *U. urens* may act as a trap in some areas, kahukura may be able to escape that fate if native plant species are made more readily available.

Keywords: kahukura, larval performance, Nymphalidae, ongaonga, oviposition preference, preference-performance hypothesis, red admiral butterfly, *Urtica*, *Vanessa gonerilla*

Introduction

In butterflies, maternal host plant choice for oviposition is a crucial decision because it determines their offspring's larval development and survival (García-Barros & Fartmann 2009; Berteá et al. 2020). If the wrong choice is made, it could result in few or no offspring surviving until adulthood. Some species are generalists, meaning larvae can feed on many plant species, although fitness may differ between host plants. Other species are specialists, only able to survive by feeding on a particular plant species or genus (Miller & Hammond 2003; García-Barros & Fartmann 2009; Ali & Agrawal 2012). In either case, identifying appropriate host plants is important for individual survival, as the fitness of individuals on different host plant species can vary greatly.

Larval development on host plants can depend on several factors, including temperature and host plant quality (Awmack & Leather 2002; Kingsolver et al. 2006). Host plant quality affects growth rate, size, and weight, which in turn affects survival and fecundity (Haukioja & Neuvonen 1985;

Awmack & Leather 2002). However, host plants need to be more than just nutritionally suitable for larval development. Some species sequester chemicals from host plants, making larvae toxic or unpalatable to potential predators (Grosman et al. 2005; Soler et al. 2007; Bruinsma et al. 2009; Allmann & Baldwin 2010; Knerl & Bowers 2013; Gowler et al. 2015; Freedman et al. 2022).

Lepidopteran butterflies and moths locate host plants using visual and chemical cues from a distance, and tactile cues up close (Reisenman et al. 2010; Berteá et al. 2020). Upon arriving at a potential host plant, chemosensilla on the end of antennae, proboscis, legs, and ovipositor are used to detect plant cues directly (Calvert & Hanson 1983; Baur et al. 1998; Katte et al. 2022). Some Nymphalid butterflies do not use their forelegs for walking and instead use them in drumming behaviour to identify the chemical properties of host plants before ovipositing (Bell & Cardé 1984; Thiele et al. 2016; Silva et al. 2018). This is where they rapidly brush the sensilla found on the fifth tarsomere of the foretarsi against the leaves before deciding whether to oviposit (Bell & Cardé

1984; Thiele et al. 2016; Silva et al. 2018). The sensilla on the mid and hind tarsi in both sexes are used to detect sugars to aid in locating food (Silva et al. 2018). Usually, female insects prefer to oviposit on the host plant that provides the highest fitness (larval performance) for offspring; this is known as the preference-performance hypothesis (Jaenike 1978; Courtney 1981; Valladares & Lawton 1991; Clark et al. 2011). However, occasionally mistake oviposition events occur, where a female lays eggs on a low-quality plant when higher quality plants are available (e.g. in Nymphalidae, Pieridae, and Papilionidae; Straatman 1962; Berenbaum 1981; Larsson & Ekbom 1995; Davis & Cipollini 2014; Augustine & Kingsolver 2018). This may occur when high quality host plants are rare, the female sensory organs are damaged, or novel low quality introduced plants emit similar cues to high quality native plants (Larsson & Ekbom 1995). For example, swallowtails (*Papilio glaucus*, Nymphalidae) failed to reject an unsuitable introduced plant as a host, despite physical differences, because of chemical similarities (Berenbaum 1981). Often these novel plant species are phylogenetically related to the original host plant (Nair 2002).

Introduced plants can dominate a landscape, resulting in lower discovery rates of native host plants. This is a particular concern in Aotearoa as at least 53% of wild-growing vascular plants in Aotearoa are introduced species (Mooney & Cleland 2001; Diez et al. 2009; Hulme 2020). If these dominating introduced plant species lead to an increase in mistake oviposition but offer reduced quality to developing larvae, they are considered ecological traps (Scheirs et al. 2004; Digweed 2006; Gripenberg et al. 2007; Murphy 2007a, b; Davis & Cipollini 2014; Davis et al. 2015; Hale & Swearer 2016; Yoon & Read 2016; Augustine & Kingsolver 2018; Sun et al. 2020; Horstmann 2021). Introduced or novel plants can act as ecological traps by attracting ovipositing species

but then being nutrient poor, lacking chemical compounds sequestered by larvae, and/or being structurally unsuitable in that larvae cannot hide or protect themselves (Bowers 1980; Bowers & Farley 1990; Sun et al. 2020). A meta-analysis of 76 experiments found that among the 19 studies that looked at both oviposition preference and larval performance, 38% involved introduced hosts acting as true ecological traps (Yoon & Read 2016). However, host expansion to a non-lethal lower fitness host may not always lead to a long term ecological trap; if the shift is gradual in both preference and performance, insects can adapt to the novel host over time (Keeler & Chew 2008). Although larvae tend to develop best when raised on native host plants (McMahon 2007; Murphy 2007a; Keeler & Chew 2008; Davis & Cipollini 2014; Fickenscher et al. 2014; Sourakov 2015; Yoon & Read 2016; Augustine & Kingsolver 2018; Wiatrowska et al. 2018; Sun et al. 2020; Chandra & Hodge 2021), there are cases where larvae reared on closely related introduced plants can exhibit higher fitness (Uusitalo 2004; Knight et al. 2008; Karolewski et al. 2014). These introduced plants may ultimately inherit the native plant's herbivores (Colautti et al. 2004; Mlynarek 2015). For example, the native host plant of the ornate bella moth (*Utetheisa ornatrix*, Erebididae) is *Crotalaria incana*, but the moth now prefers to lay eggs on the related introduced *C. pallida*; larvae have higher survival and higher pupal weights when raised on the introduced species (Cogni 2010).

Pūrerehua kahukura | New Zealand red admiral (*Vanessa gonerilla gonerilla*, Nymphalidae) is endemic to mainland Aotearoa and completes its life cycle on nettles (*Urtica* spp., Urticaceae) (Fig. 1a). Nettles, considered by some as weeds because of their sting, are often removed from recreational, rural, and/or urban areas (Vennell 2019). The loss of host plants, as well as an increase in pesticides and introduced parasitoid wasps, has led to an anecdotal decline

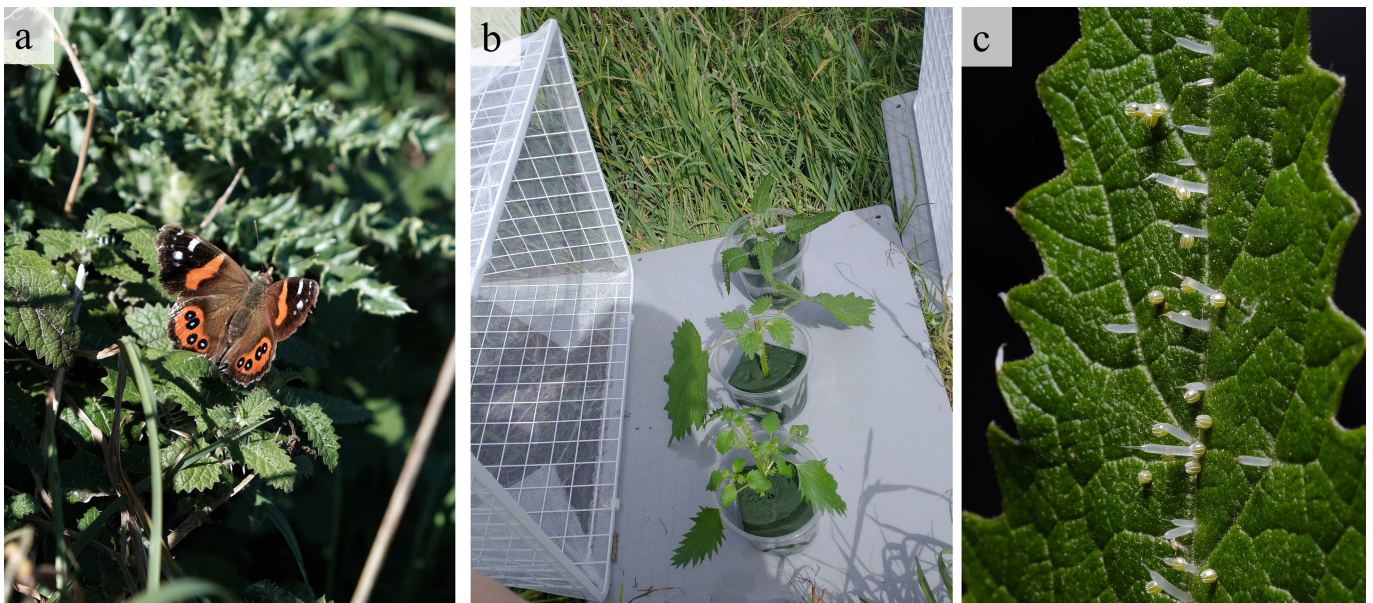


Figure 1: Oviposition cage set up and kahukura eggs. (a) Kahukura basking on wild *Urtica ferox* at the Highgrove site. (b) Three nettle species cuttings (*U. ferox*, *U. australis* hybrid, and *U. urens*), standing upright in wet florist foam which is sitting in clear plastic cups half full of water. The cuttings are inside oviposition cages with a plastic base, and a white metal basket covered in mesh is attached to the base on one side with hinges to act as a lid. A yellow piece of paper was placed under a clear small petri dish full of 25% sugar water. (c) Kahukura eggs on *U. ferox* leaves, oviposited by the first kahukura used in the experiment (18 November 2022). The butterfly oviposited 64 eggs total, many on the topside of the leaf close to or on the stinging trichomes. Images a and b by Greer Sanger, image c by Andrew Fordyce, reproduced with permission.

in kahukura in the latter part of the twentieth century (Barron 2004; Vennell 2019). Aotearoa is home to five native and three introduced nettle species, as well as native/introduced hybrids. Ongaonga/stinging tree nettle (*Urtica ferox*, Aotearoa endemic) is considered the primary host of kahukura. However, this conclusion has been based on general observations; no preference experiments have been conducted before this study to the best of our knowledge. *Vanessa g. ida* (Chatham Island subspecies) is endemic to offshore Rēkohu (Chatham Islands) and their larvae feed on *Urtica australis* (Chatham Island nettle) which is also native to some areas of southern Aotearoa (Barron 2004). Also, kahukōwhai/yellow admiral (*Vanessa itea*, Aotearoa and Australian native) and *V. atalanta* (red admiral found in North and South America, Europe, and Asia) are often observed laying eggs on introduced dwarf nettle (*Urtica urens*) (Stefanescu 2001; Hubregtse 2019).

Here we addressed whether female kahukura can discriminate and/or have an oviposition preference for native vs. native/introduced hybrid and/or introduced nettle species that are found throughout Aotearoa. We then investigated how larval development is affected when raised on these different nettles. We predicted that kahukura would prefer native *Urtica ferox* with which it has co-evolved. However, if the introduced or hybrid *Urtica* species were acting as ecological traps and/or butterflies could not discriminate among them, then oviposition rates should be evenly distributed across native and introduced nettles. Further, if introduced or hybrid *Urtica* species have the potential to act as ecological traps, then individuals raised on those species would exhibit reduced fitness compared to those raised on native *Urtica ferox*.

Methods

Nettle planting and collection

Urtica australis hybrid (likely a result of cross-pollination between *U. australis* and *U. dioica*, J. Knight pers. comm.) and *U. ferox* seeds were purchased from New Zealand Seeds (<https://nzseeds.co.nz>) and Moths and Butterflies of New Zealand Trust (<https://www.nzbutterflies.org.nz>) respectively. Seeds were sown on 6 August 2021. Initial germination of *U. australis* hybrid seeds was faster than that of *U. ferox*. On 11 October 2021, *U. australis* hybrid were transplanted into individual 7L (PB12) plastic bags with potting mix and two handfuls of sheep pellets mixed in. On 18 November 2021, *U. ferox* were transplanted into 7L pots.

Urtica urens is not available to purchase as seed. Between 11 October 2021 and 7 February 2022, we transplanted *U. urens* from urban gardens and from Invermay Agricultural Centre (Mosgiel) into PB12 pots. However, these died within a few weeks after transplanting. In February 2022, we began taking cuttings from the *U. urens* plants instead of transplanting the entire plant. Cuttings were stored in wet florist foam in a container of water. Cuttings lasted 8–12 days before wilting.

From 18 November 2021 through mid-January 2022, we collected 13–17 cm tall cuttings of *U. ferox* from sites with established wild populations (Highgrove, Long Beach, and the Pyramids; see Fig. 2 and Supplemental Table S1). By mid-January, the *U. ferox* planted from seed were large enough to be used in experiments. The *U. australis* hybrid planted from seed grew fast enough that we used those plants throughout the duration of the study. We initially wanted to test all five native and three introduced nettle species found in Aotearoa, however we were only able to get the two most common species

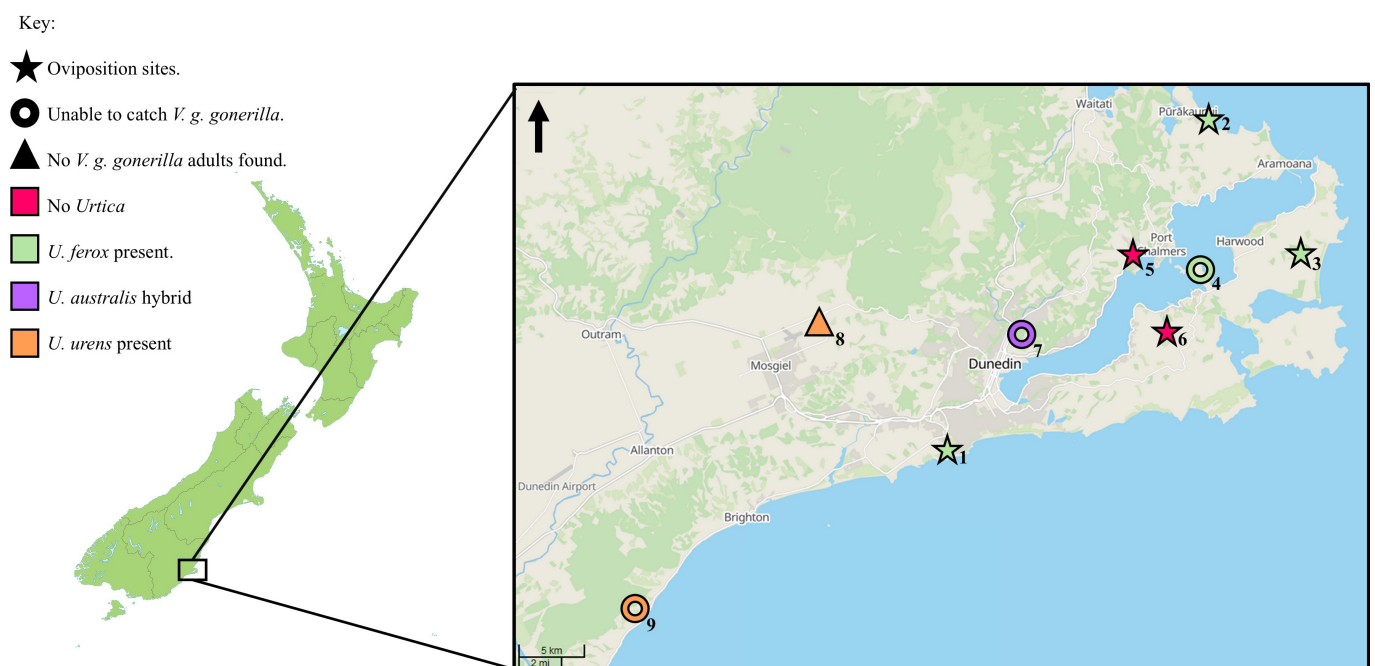


Figure 2: Map of experimental sites in Dunedin area. Sites visited for oviposition and nettle collection from 18 November 2021 to 10 April 2022. Stars represent oviposition sites, circles represent sites where we were unable to catch *Vanessa gonerilla gonerilla* but they were present, and the triangle represents a site visited frequently but where we never saw any adult *V. g. gonerilla*. The colours determine which *Urtica* species were present at each site. Numbers refer to sites in Supplementary Material S1. The black arrow points north, and the scale bar represents 5km. NZ map derived from “Transparent location map of New Zealand” by Gobeirne, licensed under CC BY SA 3.0. Dunedin map derived from “Land Information New Zealand Data Service” by Map Tiler and OpenStreetMap contributors, licensed under CC BY-SA 2.0.

(*U. ferox* and *U. urens*) and *U. australis* hybrid. A rare native, *U. aspera* was also sown but never germinated.

Locations and permissions

We used iNaturalist to determine location and time of year that both kahukura and nettle species might be found in the Ōtepoti/Dunedin region (Sanger 2023). We received permission to work at nine locations: Dunedin City Council, Yellow Eyed Penguin Trust, Portobello Marine Lab, Edward Elison, Dunedin Botanic Gardens, Larnach Castle, Sawyers Bay Ecosanctuary, and Invermay Agricultural Centre (Fig. 2; Appendix S1 in Supplementary Material).

Experiment 1: oviposition preference

Experimental set-up

From 18 November 2021 to 10 April 2022, we conducted oviposition experiments in the field. Five oviposition cages were constructed using white wire baskets (40.5 × 28.5 × 54 cm) attached to a grey acrylic plastic floor with hinges and a latch (Fig. 1b). Holes were added on the outside edge of the floor to allow tent pegs to secure the cages to the ground. Insect netting was used to cover the wire baskets so the butterflies could not escape.

Fresh nettle plants and/or cuttings were taken to the site on the day of the experiment. A cutting of similar size (c. 15 cm tall) and devoid of insects, insect damage, or eggs was taken from each nettle species and placed standing up in wet florist foam. Florist foam was kept in plastic containers half full of water to keep the foam from drying out on hot days. Each cage contained one cutting of each of the three nettle species for the butterfly to choose from. The arrangement of the nettle species inside the cage was alternated for each kahukura that was caught, so that each nettle species was equally represented in the middle or edge of the cage. A 25% sugar water was provided on one side of the cage with a yellow piece of paper underneath as a visual cue (Fig. 1b). Sugar water was stored at 4°C between oviposition experiment days and kept in an insulated bottle while in the field.

A large butterfly net was used to catch the kahukura, generally when they were resting, basking, feeding, or ovipositing. When each butterfly was extracted from the net a second person snipped a tarsus from a hind leg to ensure the same kahukura was not recaptured on another day. Tarsi were stored in individually labelled 1.5 mL micro-centrifuge tubes containing 70% ethanol for future genetics work. Only butterflies with both back legs fully intact when caught were used for experiments. The kahukura were then placed inside the oviposition cage (one per cage) near the sugar water, and the cage was then closed and secured (Fig. 1b).

Experiments were conducted, on average, for two days each week due to weather limitations and field assistant availability. Dates and times varied based on permissions and success of finding and catching kahukura. Experiments began between 10 a.m. and 11 a.m. and could last until 6 p.m. Butterflies were caught during their peak activity period of 10 a.m. to 3 p.m. The sex of kahukura cannot be determined without dissection, which means it is likely that both sexes were caught; mating status was unknown. We assumed a 1:1 sex ratio, and that some females would be unable to oviposit (Barron 2004).

Data collection

An oviposition trial lasted 3–4 hours: if the butterflies were still actively exploring nettles after 3 hours they were left in

the cage for an additional hour; if the butterflies were visibly struggling (e.g. fell into the water reservoir) they were released early. During this time, we recorded the physical appearance of the butterflies (e.g. evidence of wing wear) and general behaviours. Every hour of the trial, we recorded cloud cover (estimated: clear skies, little cloud, cloudy, very cloudy), as well as temperature (°C), humidity (%), and wind speed (m s^{-1}) using a digital Kestrel weather monitor. From 9 December 2021, we also collected barometric pressure.

After the trial, butterflies were released. We then carefully inspected each of the leaves on the cuttings in the cage for eggs (Fig. 1c) and recorded the number of eggs on each nettle species.

Data analysis

When kahukura laid eggs in experiments, they laid all their eggs on only one of the plant options. Because only 10 of the kahukura oviposited during experiments, and none of them laid eggs on *U. urens*, we used a one-tailed Fisher's Exact test to compare the number of individuals that chose to oviposit on *U. ferox* versus *U. australis* hybrid. A one-tailed test was used because it was predicted that there would be a directional preference for native *U. ferox*. To see if the number of eggs that ovipositing kahukura laid varied between *U. ferox* and *U. australis* hybrid, we used multiple linear regression with a Poisson distribution, where site and nettle choice were included as factors, and the number of eggs oviposited was included as the response variable. We then ran a separate model to determine whether other environmental factors influenced the number of eggs oviposited by the laying butterflies, because the small sample size limited the number of variables we could include. We calculated the mean temperature, humidity, wind speed, and barometric pressure for each trial where oviposition occurred. Temperature was highly correlated with both humidity and wind speed, so was not included in the model. Barometric pressure was removed because it was only collected for 8 of the 10 butterflies that laid eggs during trials. We used multiple linear regression with Poisson distribution, where mean humidity and mean wind speed were included as factors, and number of eggs oviposited was included as the count response variable. We compared the model ($\text{eggs} \sim \text{mean humidity} + \text{mean wind speed}$) with each factor on its own, to see which model fit the data best. The Akaike information criterion (AIC) showed that the model best fit the data when only humidity was included ($\text{eggs} \sim \text{mean humidity}$). All analyses were run using GraphPad Prism version 9.4.1.

Experiment 2: larval performance

The *Urtica* spp. cuttings that had eggs oviposited on them in Experiment 1 were brought back to Ōtākou Whakaihū Waka | University of Otago, Te Tari Mātai Kararehe | Zoology Department, and kept at room temperature in a laboratory for 6–9 days until they hatched into first instar larvae (Appendix S2). The mean temperature in the laboratory while larvae developed was 19.29°C (minimum = 16.13°C, maximum = 24.14°C). The first nine larvae brought back to the laboratory prior to 27 January 2022, when temperature monitoring commenced, likely experienced similar temperatures during their initial developmental stages as the laboratory was centrally heated. The ideal range for kahukura larval development is 15–20°C (Barron 2004). Eggs were left on cuttings that were kept standing in florist foam and water in plastic cups. Eggs were checked daily for larval emergence. We used larvae from eggs from 7 of the 10 females that laid more than one egg in

Experiment 1. The sites of origin were High Grove and the Pyramids. Unused larvae were returned to the site where they were oviposited.

After hatching, larvae were placed into individual containers (17 × 17 × 8.5 cm). Each container was lined with two moist paper towels to help prevent leaf and larval desiccation. Paper towels were re-moistened at the same time as larvae were fed, and replaced as needed. Containers were covered with fine insect netting and secured with a rubber band to prevent escape. Indirect natural sunlight was provided through adjacent windows. On warm days, we opened the windows for fresh air.

Once larvae emerged, larvae from each clutch were evenly assigned an *Urtica* spp. food treatment; *U. ferox*, *U. australis* hybrid, or *U. urens*. Larvae were fed every two days. To feed the larvae, *Urtica* spp. leaves were taken from plants or from healthy cuttings. Extra *U. urens*, *U. australis* hybrid, and *U. ferox* leaves were stored at 4°C with a damp paper towel for use when fresh samples could not be collected. Refrigerated leaves were replaced every 8–12 days. All leaves used to feed larvae were firm and healthy, and all larvae were fed leaves stored for the same period of time.

Larvae were provided with an *ad lib* diet of their assigned *Urtica* spp. food treatment calibrated to larval size. First instar larvae were fed 0.10 g of leaf, and the amount of food increased by 0.10 g as the larvae grew and/or when we noticed they had finished all their food on feeding days (this occurred during later instars). When food needed to be increased for one larva, it was increased for all larvae from the same clutch to ensure *ad lib* food. Fifth instar larvae received a max of 0.60–0.80 g of leaf on feeding days. The range in leaf weight is because even in the same clutch of larvae some pupated early while others continued to grow and required more food.

Some larvae grew very slowly or stopped growing altogether at early instars, even when other larvae from the same clutch developed normally. In these few cases, the leaf was decreased for the slow growing/not growing individuals as they were receiving far more *Urtica* spp. leaf than was needed. This was necessary to avoid wasting the *Urtica* spp., as at times throughout summer *Urtica urens* died down and new patches could be difficult to locate.

For each larva, we recorded dates for egg hatching, pupation, and adult emergence, as well as death or escape where necessary. When larvae pupated, they hung from the mesh covering their container. To weigh them without destroying the pupa, we carefully removed the mesh and pupae, and weighed both on the scale. After the butterfly emerged from the pupa, the mesh was weighed without the pupa casing, and subtracted from the weight with mesh and pupa to give the weight of the pupa. Most butterflies that emerged were released at the site where they were initially oviposited. Those that could not be returned to their original site were released at the Dunedin Botanic Gardens or High Grove walkway.

In mid-January 2022 we discovered some mould in the containers (possibly due to other insects in the lab). The paper towels were changed as soon as any mould was found, the mesh covers were washed with ethanol and water, and we were careful to take them on and off the containers with the same side down. We added less water to the paper towels so they would dry out between checks, which reduced the mould. This meant that at early instar stages the small pieces of leaf were more likely to dry out by the next check if the larva did not eat it all. When this happened, the leaf weight was raised by 0.10g for all in that group so the larger leaves were less likely to dry out.

Data analysis

To test whether larval survival (as a binary yes/no variable) was affected by *Urtica* spp. food groups, we used a 2 × 3 Chi-square test. We also used a Kaplan-Meier Survival Analysis with a log-rank (Mantle-Cox) test. This was followed by three pairwise tests to compare the survival curves two at a time, to see which food groups were significantly different. Because of multiple comparisons, the significance threshold of the *p* value was adjusted using the Bonferroni-corrected α value method: $\alpha = 0.05/3 = 0.017$. To see if the mould issue influenced larval survival, we ran a Chi-square test comparing the number that survived until butterfly emergence (yes/no) with and without mould. Analyses were conducted in GraphPad Prism v. 9.4.1.

Only those larvae that survived and emerged as adults were included in analyses of developmental times. To see if there were any patterns in development times from larva to pupa, pupa to butterfly, and larva to butterfly, we used Kruskal-Wallis tests in GraphPad Prism v. 9.4.1. To determine if *Urtica* spp. food groups affected pupal weights, we used a linear mixed model using R version 4.2.0, and the nlme package (R Core Team 2022; RStudio Team 2022; Pinheiro et al. 2023), where mother (clutch) was included as a random effect.

Results

Experiment 1: oviposition preference

The peak period for catching kahukura was from December 2021 to mid-January 2022, with a second smaller and shorter peak from late February 2022 to early March 2022. A total of 47 kahukura adults of unknown sex were caught, 10 of which laid eggs in the experiments (Appendix S3). One kahukura was recaptured and was immediately released. The behaviour of the first kahukura in the oviposition cage was observed for c. 1 hr. For c. 20min, she fluttered between all three of the nettle species, brushing her front vestigial bristled prothoracic limbs against each nettle cutting's leaves; this is referred to as “drumming behaviour” (Bell & Cardé 1984). She then stopped visiting the *U. urens* but continued to visit both the *U. australis* hybrid and *U. ferox* until she started ovipositing her eggs on *U. ferox*. She oviposited a total of 62 eggs on *U. ferox* only, across the whole cutting (Fig. 1c).

Although the difference was not significant, of those females that laid eggs during the experiment, more kahukura laid eggs on *U. ferox* ($n = 8$) than on *U. australis* hybrid nettle ($n = 2$) (Fisher's Exact: $p = 0.055$; Fig. 3a). None of the butterflies laid eggs on *U. urens* (Fig. 3a). There was no difference in the number of eggs each laid on *U. ferox* vs. *U. australis* hybrid ($Z = 1.082$, $p = 0.279$; Fig. 3b). The number of eggs laid varied across sites; those collected from High Grove laid more eggs than those collected at the Pyramids ($Z = 6.205$, $p = < 0.001$; Appendix S3). Females laid fewer eggs when relative humidity was higher ($Z = 4.625$ $p = < 0.001$; Fig. 3c).

Experiment 2: larval performance

Eggs from the same clutch hatched at the same time, 6–9 days after oviposition (mean ± SE = 7 ± 0.365, median = 6.5). We assigned 28 larvae to each of the three treatment groups, splitting eggs from each clutch evenly across treatments. A few early instar larvae escaped; therefore, we collected development data on 79 larvae total ($n = 28$ on *U. ferox*, $n = 26$ on *U. australis* hybrid, and $n = 25$ on *U. urens*; Appendix S4).

Kahukura were most likely to survive to adulthood when

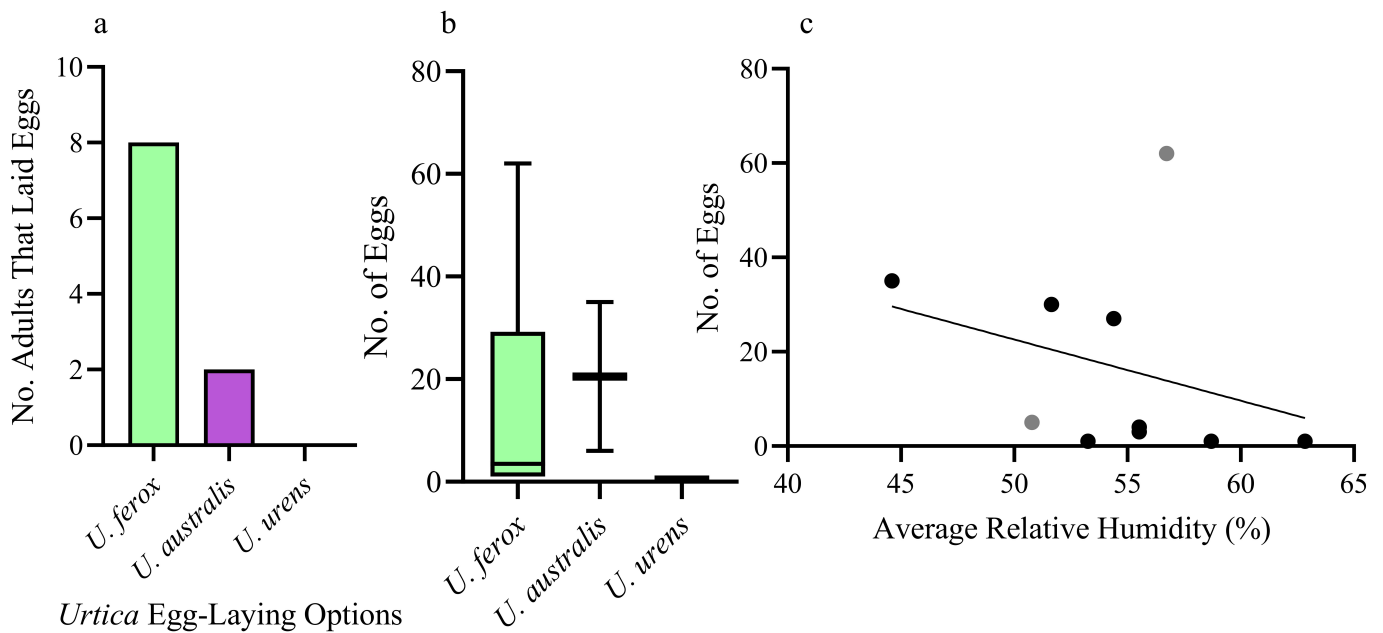


Figure 3: Kahukura oviposition choice preference. (a) The number of kahukura adults (of 47 that were caught and placed in an oviposition experiment) that oviposited eggs on *Urtica ferox* ($n = 8$), *Urtica australis* hybrid ($n = 2$), and *Urtica urens* ($n = 0$). (b) Number of eggs kahukura oviposited per nettle species. Kahukura did not oviposit any eggs on the *Urtica urens*. The black line in the boxes indicates the median number of eggs laid on each of the nettle groups. The box extends from the 25th to the 75th percentiles, the lower whisker represents the minimum value, and the upper whisker represents the maximum value. *U. ferox*: $n = 129$, *U. australis*: $n = 42$, *U. urens*: $n = 0$. (c) Relative humidity effect on the number of eggs kahukura oviposited. Black data points are from kahukura at the Pyramids site, and grey data points are from the High Grove site. The line shows the negative relationship between the number of eggs oviposited with increasing relative humidity (%). The line is fitted with a simple linear regression ($R^2 = 0.09$). $n = 10$ ovipositing females.

fed the *U. australis* hybrid ($n = 13$, 50%), compared to *U. ferox* ($n = 5$, 18%) and *U. urens* ($n = 4$, 16%) ($\chi^2_2 = 9.49$, $p = 0.009$). Moreover, the survival curves varied across larvae fed on the different diets ($\chi^2_2 = 6.05$, $n = 79$, $p = 0.049$; Fig. 4b). After applying the Bonferroni adjusted p value (0.017), kahukura larvae raised on *U. australis* hybrid had moderately higher survival than *U. ferox* ($\chi^2_1 = 5.44$, $p = 0.019$), or *U. urens*, ($\chi^2_1 = 4.69$, $p = 0.030$). There was no difference between survival curves of *U. ferox* and *U. urens* ($\chi^2_1 = 0.004$, $p = 0.953$). There was no difference in the number of survivors exposed ($n = 15$) or not exposed ($n = 7$) to mould ($\chi^2_1 = 2.909$, $p = 0.088$).

Larvae raised on *U. ferox* formed pupae that were heavier (0.472 ± 0.049 g) than those reared on *U. urens* (0.315 ± 0.021 g; $t_{16} = 2.46$, $p = 0.025$), and those reared on *U. australis* hybrid (0.341 ± 0.220 g; $t_{16} = 3.04$, $p = 0.008$; Fig. 4a). There was no difference in the mean pupal weights between *U. australis* hybrid and *U. urens* raised larvae ($t_{16} = -0.55$, $p = 0.590$; Fig. 4a).

The number of days between stages of larval development across the different nettle species were all statistically non-significant. However, larvae were marginally faster to reach pupation when raised on *U. australis* hybrid (median = 31 days; 95% CI 31–35 days) and slowest when raised on *U. urens* (median = 36.5 days; 95% CI 33–43 days; $H_2 = 5.25$, $d = 0.17$, $p = 0.071$; Fig. 4c). Larvae raised on *U. urens* had slightly longer pupation (median = 18.5 days; 95% CI 14–19) before butterfly emergence than *U. ferox* (median = 15 days; 95% CI 14–16) and *U. australis* (median = 14 days; 95% CI 14–16), with pupation times being similar for the

latter two ($H_2 = 4.55$, $d = 0.13$, $p = 0.102$; Fig. 4d). The time from larval emergence to butterfly emergence was shortest for larvae raised on *U. australis* hybrid (median = 47 days; 95% CI 45–51), while those raised on *U. urens* typically took the longest (median = 55 days; 95% CI 47–62) ($H_2 = 4.99$, $d = 0.16$, $p = 0.076$; Fig. 4e).

Discussion

We explored the extent to which introduced nettle species in Aotearoa act as ecological traps to the endemic kahukura | NZ red admiral butterfly (*Vanessa gonerilla gonerilla*). Adult females showed an oviposition preference for native *Urtica* spp. and larvae exhibited increased weight gain when fed native ongaonga (*Urtica ferox*). Interestingly, larval survival was highest and development to adulthood was fastest when raised on a native *U. australis* hybrid (likely *U. australis* \times introduced *U. dioica*) rather than on native *U. ferox* or introduced *U. urens*. We ranked the nettle species for kahukura oviposition preference (*U. ferox* \geq *U. australis* $>$ *U. urens*) which qualitatively matches the larval development ranking (*U. ferox* $>$ *U. australis* = *U. urens*), supporting the preference-performance hypothesis for this population of kahukura. Kahukura had lowest survival on *U. urens*, but because some larvae survived, this species may act as a possible back-up for kahukura where preferred nettle species are unavailable. Alternatively, the effect of *U. urens* on larval performance suggests that introduced nettles may act as ecological traps

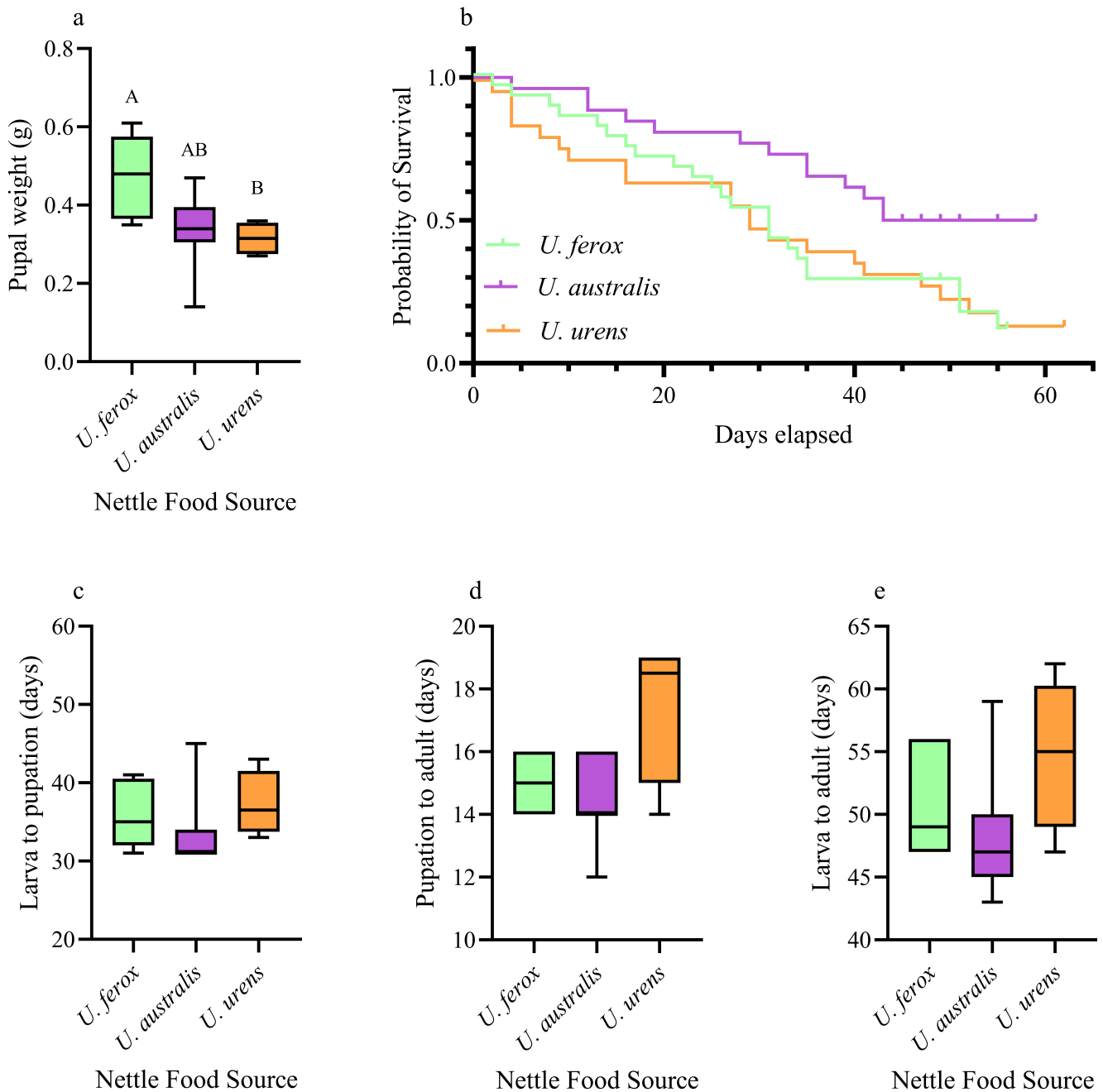


Figure 4: Kahukura larval development. (a) Results showing kahukura pupal weights. The weight of pupae in grams in relation to *Urtica* spp. food groups: *Urtica ferox*, *Urtica australis* hybrid, and *Urtica urens*. Letters above the box plots (A, AB, B) indicate which are significantly different from one another. Only survivors are included. *Urtica ferox*: $n = 5$, *U. australis* hybrid: $n = 13$, *U. urens*: $n = 4$, total: $n = 22$. (b) The probability of survival decreased more quickly for larvae raised on *Urtica ferox* and *Urtica urens* compared to those raised on *Urtica australis* hybrid. Larval diet is indicated by colour: *U. ferox* ($n = 28$) = green; *U. australis* hybrid ($n = 26$) = purple, *U. urens* ($n = 25$) = orange. (c) Days from larval emergence to pupation of kahukura on different host plant species (d) Days from pupation to butterfly emergence. (e) Days from larval emergence to butterfly emergence.

for kahukura in the absence of native nettle species. However, we found no evidence that the population of kahukura used in this study are currently experiencing an ecological trap from introduced nettle. The majority preferred to oviposit on native *U. ferox* which naturally occurs in the area, and none chose to oviposit on introduced *U. urens*.

Three criteria need to be met for an introduced plant to be

considered an ecological trap: (1) equal or higher preference for the introduced host plant over the co-evolved species, (2) individual fitness differs between two or more host plants, (3) fitness is reduced when raised on the introduced (preferred) host plant compared to other available host plants (Robertson & Hutto 2006; Horstmann 2021). When cues are too similar to differentiate among suitable host plants, an ecological trap can

emerge, resulting in population decline or extinction of the host species (Yoon & Read 2016; Singer & Parmesan 2018; Steward & Boggs 2020). For example, *Pieris virginiensis* show a late seasonal preference for introduced *Alliaria petiolata* over their native host *Cardamine diphylla*, possibly because the native plant begins to senesce earlier in the season than the introduced host (Davis & Cipollini 2014; Augustine & Kingsolver 2018). All larvae that were fed only the introduced plant died before reaching pupation, evidence of a late-season ecological trap. While we did find evidence that fitness (pupal weight and survival rate) was reduced when larvae were reared on the introduced *U. urens*, the adults did not lay eggs on *U. urens*, suggesting kahukura can distinguish *U. urens* from native *U. ferox* and native/introduced *U. australis* hybrid. With the mixed results of higher pupation on *U. ferox* and higher survival on *U. australis* hybrid, we suggest these two species are relatively equal in host quality and do not cause an ecological trap. Mixed larval performance is uncommon but does occur. For example, feeding on introduced *Plantago lanceolata* resulted in slower development rates for *Anartia jatophae* (white peacock) and *Euphydryas editha* (Edith's checkerspot), but these species had higher adult weights and higher survival respectively than when reared on their traditional host plants (Knerl & Bowers 2013; Singer & Parmesan 2018). More research would be required to determine how pupal weight can be used to predict adult kahukura fitness.

As observed in our study, many Lepidopteran spp. prefer to oviposit on native host plants rather than introduced plants (White et al. 2008; Cogni 2010; Fortuna et al. 2013; Yoon & Read 2016 and references therein; Chandra & Hodge 2021). The endemic Fijian swallowtail butterfly (*Papilio schmelzi*) shows strong preference for ovipositing, and larvae gain more weight, on the native host plant limeberry (*Micromelum minutum*), over introduced mandarin orange (*Citrus reticulata*) (Chandra & Hodge 2021). These strong correlations between oviposition preference and larval performance support the preference-performance hypothesis (Jaenike 1978; Courtney 1981; Valladares & Lawton 1991; Clark et al. 2011).

A factor that could affect host plant suitability is the susceptibility of the nettles to parasites or predators (Fortuna et al. 2013; Karolewski et al. 2014). Natural enemies of kahukura eggs and larvae on *U. ferox* can lead to >80% mortality in some populations (*Telenomus* sp.: 57–66% egg mortality; *Pteromalus puparum*: 3.6–27.1% pupal mortality; *Echthromorpha intricatioria*: 61–82.1% mortality; Barron 2004). Because larvae in this study were raised in controlled lab conditions, we could not compare susceptibility to parasites or predators across the different nettle species. Volatile infochemicals can be released by plants when they have been attacked by herbivores, which may attract predators and/or parasitoids of the herbivores feeding on the plant (Amo et al. 2013; Volf 2018). It is possible that parasitism rates may be lower on the introduced plant *U. urens* if the parasitoids do not have strong associations between their prey and these plants (Karolewski et al. 2014). As the parasitoids of kahukura are introduced species, this may not be the case, and they may have a stronger association between their prey and the introduced nettle (Barron 2004). Adult female kahukura lay eggs on any part of the nettle, but they are mostly found on the top of a leaf, often near the stinging hairs (Fig. 1c; Han Kelvin and Sanger unpub. data). *Urtica* species differ in the intensity of sting, with *U. ferox* delivering the most painful and dangerous chemical concoction (Pilgrim 1959; Clark 1993; Hammond-Tooke et al. 2007; Kittow 2013; Xie et al. 2022). The sting

from *U. australis* hybrid and *U. urens* is mild in comparison, so these species may provide less protection for larvae.

Host suitability can also be affected by the size and structure of the whole plant and individual leaves, which vary between *Urtica* species. Because we used plant cuttings of similar size for oviposition and measured leaves for feeding in our study, plant height and leaf size did not influence our results. Fender's blue butterfly (*Icaricia icariodes fenderi*) prefers native *Lupinus oreganus* over introduced *Arrenatherum elatius* (Severns 2008). However, when the introduced plant is cut to the same height as the native species, the preference changes to favour the introduced plant (Severns 2008). Kahukura larvae also use silk to wrap leaves around themselves like a tent while feeding and pupating (Barron 2004). *Urtica urens* has much smaller leaves than *U. ferox* and *U. australis* hybrid, which may make larvae more at risk of attack, as they may struggle (or fail) to build tents large enough to hide in. The introduced nettle is also short lived, so the food source might not last long enough for the larvae, resulting in the need to search for another plant, also putting them at risk. The toxicity level of nettles, size of the leaves, nutritional value and evolutionary time spent with the different nettle species may all contribute to kahukura choosing the native nettles over the introduced nettle. We were also unable to grow the introduced nettle in the same way as the other two species, so this may have played a role. However, at the start of the experiment, when our cultivated *U. ferox* was too small for cuttings, we used wild *U. ferox* cuttings, and the butterflies still preferred *U. ferox*.

Oviposition behaviour is likely affected by traits of the individual butterfly and abiotic conditions. Fecundity is determined during larval development. The quality of the host plant affects larval growth rate, size at pupation, and, ultimately, adult weight. In many Lepidoptera species, larger females have higher fecundity and adult survival during overwintering (Richerson et al. 1978; Haukioja & Neuvonen 1985; Barah & Sengupta 1991; Smith 2002; Calvo & Molina 2005). We were unable to determine the achieved adult fecundity or survival, as we released adults soon after emergence. The weights of adult butterflies were not measured as adult butterfly weight is correlated with pupal weight, and therefore potential fecundity can be inferred by pupal weight (Awmack & Leather 2002; Tammaru et al. 2002). It is likely that larvae raised on *U. ferox* will have higher adult fecundity and survival than those raised on other species, as they were larger (Awmack & Leather 2002; Tammaru et al. 2002). Increasing relative humidity had a negative effect on how many eggs were laid in the oviposition experiment. Excessive humidity also decreases fecundity in the codling moth *Cydia pomonella* (Howell 1981). Additional research under laboratory conditions could investigate this further to determine the ideal humidity level for kahukura fecundity.

It may be that our sample size was too small, our research areas too restricted, or the different nettle growing conditions used might explain why no kahukura chose to lay eggs on the introduced *U. urens*. There are anecdotal accounts of kahukura ovipositing on *U. urens* and other introduced species in an area devoid of native nettle species (J.M. Lord, pers. obs.). This highlights the importance of sampling across multiple populations when studying a complex behavioural trait such as oviposition preference (Keeler & Chew 2008; Forister et al. 2013). We argue that when kahukura have the option to lay eggs on native or introduced nettle, they will choose the native species. This is further supported by our observation of the butterflies during the oviposition experiment. Individuals

would use the time inside the cages to explore all of the nettle species, using tactile chemosensory cues to identify the plants. None of the butterflies laid eggs on more than one plant species; the first individual we tested laid 63 eggs, all on one cutting of *U. ferox*.

Future research could examine the abundance of kahukura eggs, larvae, pupae, and parasitisation rates on each of the nettle species in the wild. The rate at which kahukura encounter the different *Urtica* species across the country could also help shed light on where they are most at risk of mistake oviposition events. There is strong evidence that invasive plants reduce Lepidoptera species richness and abundance (Yoon & Read 2016). Burghardt et al. (2010) found a reduction in specialist larval abundance on introduced plants even when they were closely related to their native host plants. Additional research could compare preference and performance of kahukura across populations with different nettle species compositions. Although kahukura do not prefer *U. urens*, if many mistake oviposition events occur in the wild due to relative plant abundance or other reasons, this could have a significant effect on the population. Widespread oviposition on *U. urens* has the potential to reduce kahukura survival and adult weight, which could in turn affect adult fecundity, further reducing abundance (Tammaru & Haukioja 1996; Tammaru et al. 2002; Calvo & Molina 2005; Burghardt et al. 2010).

Here we found that while the introduced host nettle species, *Urtica urens*, has the potential to act as an ecological trap for kahukura | NZ red admiral butterflies (*Vanessa gonerilla gonerilla*), if females have access to ongaonga/endemic stinging tree nettle (*U. ferox*), or native/introduced *U. australis* hybrid they are unlikely to be negatively affected. Our results support the preference-performance hypothesis: kahukura adults prefer to lay eggs and larvae perform better when fed on native *U. ferox* and native/introduced *U. australis* hybrid. However, where perennial, slow-growing *U. ferox* has been eradicated, often due to their severely stinging trichomes, preferred kahukura habitat declines and subsequent disturbance favours annual, fast-growing *U. urens*. Although larvae have lower pupal weight when reared on this species rather than native species, they can still survive to adulthood; however, lower larval, and therefore adult, sizes could have longer term effects on fecundity. So, while *U. urens* may act as a trap in some areas, kahukura may still be able to escape that fate if native plant species are allowed to grow and spread. Larvae reared on *U. australis* hybrid had high survival rates, so *U. australis* could be an important host plant where *U. ferox* is not found or allowed to be planted. Additionally, *U. australis* hybrid grows faster than *U. ferox* and is less aversive. More data is needed concerning kahukura preference for, and performance on, other native nettle species, as well as oviposition preferences and the potential for ecological traps affecting native *V. g. ida* and kahukōwhai (*V. itea*).

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Additional information and declarations

Conflicts of interest: the authors declare no conflicts of interest.

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Ethics: Field and lab protocols were designed to cause the lowest impact on wild kahukura populations, with all butterflies released back to the wild. Permission was granted prior to access by all private landowners, trusts, and agencies. Approval was granted by Ngāi Tahu Research Consultation Committee of Ōtākou Whakaihū Waka.

Data availability: The datasets generated or analysed during the current study are available from the corresponding author upon reasonable request.

Author contributions: JML conceived the idea, GJS, JML, and JMJ designed the methods, GJS carried out data collection, analysis, and wrote the manuscript draft, and all authors contributed to review and editing.

References

- Ali JG, Agrawal AA 2012. Specialist versus generalist insect herbivores and plant defense. *Trends in Plant Science* 17(5): 293–302.
- Allmann S, Baldwin IT 2010. Insects betray themselves in nature to predators by rapid isomerization of green leaf volatiles. *Science* 329(5995): 1075–1078.
- Amo L, Jansen JJ, van Dam NM, Dicke M, Visser ME 2013. Birds exploit herbivore-induced plant volatiles to locate herbivorous prey. *Ecology Letters* 16(11): 1348–1355.
- Augustine KE, Kingsolver JG 2018. Biogeography and phenology of oviposition preference and larval performance of *Pieris virginiensis* butterflies on native and invasive host plants. *Biological Invasions* 20(2): 413–422.
- Awmack CS, Leather SR 2002. Host plant quality and fecundity in herbivorous insects. *Annual Review of Entomology* 47(1): 817–844.
- Barah A, Sengupta A 1991. Correlation and regression studies between pupal weight and fecundity of muga silkworm *Antheraea assama* Westwood (Lepidoptera: Saturniidae) on four different foodplants. *Acta Physiologica Hungarica* 78(3): 261–264.
- Barron MC 2004. Population ecology of the red admiral butterfly (*Bassaris gonerilla*) and the effects of non-target parasitism by *Pteromalus puparum*. Unpublished PhD thesis, Lincoln University, Christchurch, New Zealand.
- Baur R, Haribal M, Renwick JAA, Städler E 1998. Contact chemoreception related to host selection and oviposition behaviour in the monarch butterfly, *Danaus plexippus*. *Physiological Entomology* 23(1): 7–19.
- Bell WJ, Cardé RT 1984. *Chemical Ecology of Insects*. London, Chapman and Hall. 523 p.
- Berenbaum M 1981. An oviposition “mistake” by *Papilio glaucus* (Pilionidae). *Journal of the Lepidopterists' Society* 35(1): 75.

- Berteaux CM, Casacci LP, Bonelli S, Zampollo A, Barbero F 2020. Chemical, physiological and molecular responses of host plants to Lepidopteran egg-laying. *Frontiers in Plant Science* 10: 1768.
- Bowers MD 1980. Unpalatability as a defense strategy of *Euphydryas phaeton* (Lepidoptera: Nymphalidae). *Evolution*: 586–600.
- Bowers MD, Farley S 1990. The behaviour of grey jays, *Perisoreus canadensis*, towards palatable and unpalatable Lepidoptera. *Animal Behaviour* 39(4): 699–705.
- Bruinsma M, Posthumus MA, Mumm R, Mueller MJ, van Loon JJ, Dicke M 2009. Jasmonic acid-induced volatiles of *Brassica oleracea* attract parasitoids: effects of time and dose, and comparison with induction by herbivores. *Journal of Experimental Botany* 60(9): 2575–2587.
- Burghardt KT, Tallamy DW, Philips C, Shropshire KJ 2010. Non-native plants reduce abundance, richness, and host specialization in lepidopteran communities. *Ecosphere* 1(5): 1–22.
- Calvert WH, Hanson FE 1983. The role of sensory structures and preoviposition behavior in oviposition by the patch butterfly, *Chlosyne lacinia*. *Entomologia Experimentalis et Applicata* 33(2): 179–187.
- Calvo D, Molina JM 2005. Fecundity–body size relationship and other reproductive aspects of *Streblote panda* (Lepidoptera: Lasiocampidae). *Annals of the Entomological Society of America* 98(2): 191–196.
- Chandra V, Hodge S 2021. Fijian swallowtail butterfly *Papilio schmeltzi* (Papilionidae: Lepidoptera) shows clear preference–performance relationships on both native and exotic host plants. *Austral Entomology* 60(1): 225–233.
- Clark F 1993. Tree nettle (*Urtica ferox*) poisoning. *New Zealand Medical Journal* 106: 234–234.
- Clark KE, Hartley SE, Johnson SN 2011. Does mother know best? The preference–performance hypothesis and parent–offspring conflict in aboveground–belowground herbivore life cycles. *Ecological Entomology* 36(2): 117–124.
- Cogni R 2010. Resistance to plant invasion? A native specialist herbivore shows preference for and higher fitness on an introduced host. *Biotropica* 42(2): 188–193.
- Colautti RI, Ricciardi A, Grigorovich IA, MacIsaac HJ 2004. Is invasion success explained by the enemy release hypothesis? *Ecology Letters* 7(8): 721–733.
- Courtney SP 1981. Coevolution of pierid butterflies and their cruciferous foodplants. *Oecologia* 51(1): 91–96.
- Davis SL, Cipollini D 2014. Do mothers always know best? Oviposition mistakes and resulting larval failure of *Pieris virginiensis* on *Alliaria petiolata*, a novel, toxic host. *Biological Invasions* 16(9): 1941–1950.
- Davis SL, Frisch T, Bjarnholt N, Cipollini D 2015. How does garlic mustard lure and kill the West Virginia white butterfly? *Journal of Chemical Ecology* 41(10): 948–955.
- Diez JM, Williams PA, Randall RP, Sullivan JJ, Hulme PE, Duncan RP 2009. Learning from failures: testing broad taxonomic hypotheses about plant naturalization. *Ecology Letters* 12(11): 1174–1183.
- Digweed SC 2006. Oviposition preference and larval performance in the exotic birch-leafmining sawfly *Profenusa thomsoni*. *Entomologia Experimentalis et Applicata* 120(1): 41–49.
- Fickenscher J, Litvaitis J, Lee T, Johnson P 2014. Insect responses to invasive shrubs: implications to managing thicket habitats in the northeastern United States. *Forest Ecology and Management* 322: 127–135.
- Forister M, Scholl C, Jahner J, Wilson J, Fordyce J, Gompert Z, Narala D, Alex Buerkle C, Nice C 2013. Specificity, rank preference, and the colonization of a non-native host plant by the Melissa blue butterfly. *Oecologia* 172(1): 177–188.
- Fortuna TM, Woelke JB, Hordijk CA, Jansen JJ, van Dam NM, Vet LE, Harvey JA 2013. A tritrophic approach to the preference–performance hypothesis involving an exotic and a native plant. *Biological Invasions* 15(11): 2387–2401.
- Freedman MG, Choquette S-L, Ramírez SR, Strauss SY, Hunter MD, Vannette RL 2022. Population-specific patterns of toxin sequestration in monarch butterflies from around the world. *bioRxiv* [Preprint]. <https://doi.org/10.1101/2021.10.15.464593> (accessed 29/07/2024).
- García-Barros E, Fartmann T 2009. Butterfly oviposition: sites, behaviour and modes. In: Settele J, Shreeve T, Konvička M, van Dick H (eds) *Ecology of butterflies in Europe*. Cambridge, Cambridge University Press. Pp. 29–42.
- Gowler CD, Leon KE, Hunter MD, de Roode JC 2015. Secondary defense chemicals in milkweed reduce parasite infection in monarch butterflies, *Danaus plexippus*. *Journal of Chemical Ecology* 41(6): 520–523.
- Gripenberg S, Morriën E, Cudmore A, Salminen J-P, Roslin T 2007. Resource selection by female moths in a heterogeneous environment: what is a poor girl to do? *Journal of Animal Ecology* 76(5): 854–865.
- Grosman AH, Van Breemen M, Holtz A, Pallini A, Rugama AM, Pengel H, Venzon M, Zanuncio JC, Sabelis MW, Janssen A 2005. Searching behaviour of an omnivorous predator for novel and native host plants of its herbivores: a study on arthropod colonization of eucalyptus in Brazil. *Entomologia Experimentalis et Applicata* 116(2): 135–142.
- Hale R, Swearer SE 2016. Ecological traps: current evidence and future directions. *Proceedings of the Royal Society B: Biological Sciences* 283(1824): 20152647.
- Hammond-Tooke GD, Taylor P, Punchihewa S, Beasley M 2007. *Urtica ferox* neuropathy. *Muscle & Nerve* 35(6): 804–807.
- Haukioja E, Neuvonen S 1985. The relationship between size and reproductive potential in male and female *Epirrita autumnata* (Lep., Geometridae). *Ecological Entomology* 10(3): 267–270.
- Horstmann S 2021. Ecological traps in bees and butterflies. Unpublished introductory essay, Swedish University of Agricultural Sciences, Uppsala, Sweden.
- Howell JF 1981. Codling moth: the effect of adult diet on longevity, fecundity, fertility, and mating. *Journal of Economic Entomology* 74(1): 13–18.
- Hubregtse V 2019. Problems for the yellow admiral butterfly '*Vanessa itea*' at Notting Hill, Victoria. *The Victorian Naturalist* 136(3): 117–121.
- Hulme PE 2020. Plant invasions in New Zealand: global lessons in prevention, eradication and control. *Biological Invasions* 22(5): 1539–1562.
- Jaenike J 1978. On optimal oviposition behavior in phytophagous insects. *Theoretical Population Biology* 14(3): 350–356.
- Karolewski P, Jagodzinski AM, Giertych MJ, Lukowski A, Baraniak E, Oleksyn J 2014. Invasive *Prunus serotina*—a new host for *Yponomeuta evonymellus* (Lepidoptera: Yponomeutidae)? *European Journal of Entomology* 111(2): 227.
- Katte T, Shimoda S, Kobayashi T, Wada-Katsumata A, Nishida R, Ohshima I, Ono H 2022. Oviposition stimulants

- underlying different preferences between host races in the leaf-mining moth *Acrocercops transecta* (Lepidoptera: Gracillariidae). *Scientific Reports* 12(1): 14498.
- Keeler MS, Chew FS 2008. Escaping an evolutionary trap: preference and performance of a native insect on an exotic invasive host. *Oecologia* 156(3): 559–568.
- Kingsolver JG, Shlichta JG, Ragland GJ, Massie KR 2006. Thermal reaction norms for caterpillar growth depend on diet. *Evolutionary Ecology Research* 8(4): 703–715.
- Kittow NC 2013. A case of canine poisoning with New Zealand tree nettle (ongaonga, *Urtica ferox*). *New Zealand Veterinary Journal* 61(1): 60–62.
- Knerl A, Bowers MD 2013. Incorporation of an introduced weed into the diet of a native butterfly: consequences for preference, performance and chemical defense. *Journal of Chemical Ecology* 39(10): 1313–1321.
- Knight KS, Oleksyn J, Jagodzinski AM, Reich PB, Kasprovicz M 2008. Overstorey tree species regulate colonization by native and exotic plants: a source of positive relationships between understorey diversity and invisibility. *Diversity and Distributions* 14(4): 666–675.
- Larsson S, Ekbom B 1995. Oviposition mistakes in herbivorous insects: confusion or a step towards a new host plant? *Oikos* 72(1): 155–160.
- McMahon SD 2007. Preference and performance of the wild indigo duskywing (*Erynnis baptisiae*) on its native host yellow wild indigo (*Baptisia tinctoria*) and on the introduced plant crown vetch (*Securigera varia*). Unpublished PhD thesis, Eastern Michigan University, Michigan, United States of America.
- Miller JC, Hammond PC 2003. Lepidoptera of the Pacific Northwest: Caterpillars and Adults. Morgantown, Forest Health Technology Enterprise Team, US Department of Agriculture. 324 p.
- Mlynarek JJ 2015. Testing the enemy release hypothesis in a native insect species with an expanding range. *PeerJ* 3: e1415.
- Mooney HA, Cleland EE 2001. The evolutionary impact of invasive species. *Proceedings of the National Academy of Sciences* 98(10): 5446–5451.
- Murphy SM 2007a. The effect of host plant on larval survivorship of the Alaskan swallowtail butterfly (*Papilio machaon alaska*). *Entomologia Experimentalis et Applicata* 122(2): 109–115.
- Murphy SM 2007b. Inconsistent use of host plants by the Alaskan swallowtail butterfly: adult preference experiments suggest labile oviposition strategy. *Ecological Entomology* 32(2): 143–152.
- Nair PV 2002. Oviposition mistakes in butterflies. *Zoo's Print Journal* 17(1): 689.
- Pilgrim R 1959. Some properties of the sting of the New Zealand nettle, *Urtica ferox*. *Proceedings of the Royal Society of London. Series B. Biological Sciences* 151(942): 48–56.
- Pinheiro J, Bates D, DebRoy S, Sarkar D, Team RC 2023. nlme: linear and nonlinear mixed effects models. Version 3.1-157. <https://CRAN.R-project.org/package=nlme>.
- R Core Team 2022. R: a language and environment for statistical computing. Version 4.2.1. Vienna, Austria, R Foundation for statistical computing. <https://www.R-project.org/>.
- Reisenman CE, Riffell JA, Bernays EA, Hildebrand JG 2010. Antagonistic effects of floral scent in an insect–plant interaction. *Proceedings of the Royal Society B: Biological Sciences* 277(1692): 2371–2379.
- Richerson JV, Cameron EA, White DE, Walsh M 1978. Egg parameters as a measure of population quality of the gypsy moth, *Lymantria dispar*. *Annals of the Entomological Society of America* 71(1): 60–64.
- Robertson BA, Hutto RL 2006. A framework for understanding ecological traps and an evaluation of existing evidence. *Ecology* 87(5): 1075–1085.
- RStudio Team 2022. RStudio: integrated development environment for R. Version 2022.7.1+554. <http://www.rstudio.com/>.
- Sanger GJ 2023. The preference and performance of *Vanessa gonerilla* on native and introduced nettles of NZ. Unpublished masters thesis, University of Otago, Dunedin, New Zealand.
- Scheirs J, Zoebisch TG, Schuster DJ, De Bruyn L 2004. Optimal foraging shapes host preference of a polyphagous leafminer. *Ecological Entomology* 29(3): 375–379.
- Severns PM 2008. Exotic grass invasion impacts fitness of an endangered prairie butterfly, *Icaricia icarioides fenderi*. *Journal of Insect Conservation* 12(6): 651–661.
- Silva DS, Barp EA, Kucharski LCR, Moreira GRP 2018. Sensing the plant surface prior to feeding and oviposition: differences in external ultrastructure and function among tarsi of *Heliconius erato*. *Neotropical Entomol* 47(1): 85–95.
- Singer MC, Parmesan C 2018. Lethal trap created by adaptive evolutionary response to an exotic resource. *Nature* 557(7704): 238–241.
- Smith RJ 2002. Effect of larval body size on overwinter survival and emerging adult size in the burying beetle, *Nicrophorus investigator*. *Canadian Journal of Zoology* 80(9): 1588–1593.
- Soler R, Harvey JA, Kamp AF, Vet LE, Van der Putten WH, Van Dam NM, Stuefer JF, Gols R, Hordijk CA, Martijn Bezemer T 2007. Root herbivores influence the behaviour of an aboveground parasitoid through changes in plant-volatile signals. *Oikos* 116(3): 367–376.
- Sourakov A 2015. You are what you eat: native versus exotic *Crotalaria* species (Fabaceae) as host plants of the ornate bella moth, *Utetheisa ornatrix* (Lepidoptera: Erebidae: Arctiinae). *Journal of Natural History* 49(39–40): 2397–2415.
- Stefanescu C 2001. The nature of migration in the red admiral butterfly *Vanessa atalanta*: evidence from the population ecology in its southern range. *Ecological Entomology* 26(5): 525–536.
- Steward RA, Boggs CL 2020. Experience may outweigh cue similarity in maintaining a persistent host-plant-based evolutionary trap. *Ecological Monographs* 90(3): e01412.
- Stratman R 1962. Notes on certain Lepidoptera ovipositing on plants which are toxic to their larvae. *Journal of the Lepidopterists' Society* 16(2): 99–103.
- Sun KK, Yu WS, Jiang JJ, Richards C, Siemann E, Ma J, Li B, Ju RT 2020. Mismatches between the resources for adult herbivores and their offspring suggest invasive *Spartina alterniflora* is an ecological trap. *Journal of Ecology* 108(2): 719–732.
- Tamaru T, Haukioja E 1996. Capital breeders and income breeders among Lepidoptera: consequences to population dynamics. *Oikos* 77(3): 561–564.
- Tamaru T, Esperk T, Castellanos I 2002. No evidence for costs of being large in females of *Orgyia* spp. (Lepidoptera, Lymantriidae): larger is always better. *Oecologia* 133(3): 430–438.
- Thiele SC, Rodrigues D, Moreira GR 2016. Oviposition

- in *Heliconius erato* (Lepidoptera, Nymphalidae): how essential is drumming behavior for host-plant selection? *Journal of Insect Behavior* 29(3): 283–300.
- Uusitalo M 2004. European bird cherry (*Prunus padus* L.) a biodiverse wild plant for horticulture. Jokioinen, Finland, MTT Agricultural Research. 85 p.
- Valladares G, Lawton JH 1991. Host-plant selection in the holly leaf-miner: does mother know best? *Journal of Animal Ecology* 60(1): 227–240.
- Vennell R 2019. The history and use of New Zealand's native plants: the meaning of trees. Auckland, New Zealand, Harper Collins Publishers. 256 p.
- Volf M 2018. Differential response of herbivores to plant defence. In: Merillon J-M, Ramawat KG eds. Co-evolution of secondary metabolites. Cham, Springer International Publishing. Pp. 77–100.
- White EM, Sims NM, Clarke AR 2008. Test of the enemy release hypothesis: the native magpie moth prefers a native fireweed (*Senecio pinnatifolius*) to its introduced congener (*S. madagascariensis*). *Austral Ecology* 33(1): 110–116.
- Wiatrowska B, Łukowski A, Karolewski P, Danielewicz W 2018. Invasive *Spiraea tomentosa*: a new host for monophagous *Earias clorana*? *Arthropod-Plant Interactions* 12(3): 423–434.
- Xie J, Robinson SD, Gilding EK, Jami S, Deuis JR, Rehm FBH, Yap K, Ragnarsson L, Chan LY, Hamilton BR, Harvey PJ, Craik DJ, Vetter I, Durek T 2022. Neurotoxic and cytotoxic peptides underlie the painful stings of the tree nettle *Urtica ferox*. *Journal of Biological Chemistry* 298(8): 102218.
- Yoon Sa, Read Q 2016. Consequences of exotic host use: impacts on Lepidoptera and a test of the ecological trap hypothesis. *Oecologia* 181(4): 985–996.

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Supplementary Material

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Appendix S1. Supplemental tables and table legends

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