Notes on the distribution, ecology, and life history of *Maotoweta virescens* (Orthoptera, Rhaphidophoridae, Macropathinae) and a comparison of two survey methods

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Abstract

When described in 2014, *Maotoweta virescens* was believed to be one of New Zealand's rarest cave wētā (Rhaphidophoridae). Here, we present new information about the distribution, ecology, and life history of the species. *M. virescens* has now been recorded from indigenous forest sites throughout the length of the western South Island, where it can occur in relatively high abundance. *M. virescens* shows a close association with arboreal mosses, particularly *Weymouthia mollis*, roosting within them during the day and feeding on them at night. The wētā has also been documented feeding on lichens and dead insects. The species is hypothesized to have a lifecycle of approximately one year, closely linked to season. Eggs are thought to hatch out relatively quickly after being laid in summer and early autumn, with the species overwintering as nymphs and maturing the following late spring through to early-autumn. Further work is required to fully understand its biology. A comparison was made between active night searching and vegetation beating as two different methods for the detection and monitoring of *M. virescens*. Beating of *W. mollis* and other suitable *M. virescens* microhabitats was found to be significantly more effective than night searching. Our results show that *M. virescens* is widespread and can occur at relatively high densities within South Island temperate forests, with the species' perceived rarity to date largely owing to a lack of survey effort and the past use of ineffective sampling methods.

Keywords

Introduction

Orthopteroid insects belonging to the family Rhaphidophoridae are found throughout most temperate regions of the world (Hubbell and Norton 1978). Rhaphidophorids are commonly referred to as cave crickets, camel crickets, or sand-treader crickets in various parts of the world. Many rhaphidophorid species are entirely confined to caves, while many others are typically closely associated with other cavities such as tree hollows, burrows, or leaf litter, sheltering within them during the day and emerging at night to feed (Ingrisch and Rentz 2009).

Within New Zealand (NZ), rhaphidophorids are commonly known as cave wētā. The name 'wētā' is also used for New Zealand Orthoptera in the family Anostostomatidae, including the tree wētā (*Hemideina* spp.) and giant wētā (*Deinacrida* spp.), which are often viewed as national icons. However, the more secretive cave wētā are relatively poorly known. The NZ cave wētā fauna is diverse relative to the country's land area. The 71 known species (Trewick et al. 2016) equate to 8.6% of the world's rhaphidophorid species (Cigliano et al. 2022). Little is known about the ecology and biology of most cave wētā. Previous studies within NZ have focused on cave dwelling species (Richards 1954, 1961, 1962, 1965, 1966, Fea and Holwell 2018), but little has been published on species found in other habitats, such as forests. More recent taxonomic studies have added to our knowledge of the ecology and biology of NZ's cave wētā (e.g., Cook et al. 2010, Johns and Cook 2014, Fitness et al. 2018, Hegg et al. 2019, 2022), but further studies are needed.

None of NZ's cave wētā have yet been assessed for the IUCN Red List (IUCN 2022). However, Trewick et al. (2016) evaluated all 71 species of cave wētā known at that time (56 described, 15 tag named taxa) using the New Zealand Threat Classification System (NZTCS), which assesses a species' risk of extinction based on estimates of population size and trend criteria (Townsend et al. 2008). At that time, 25 cave wētā species were classified as At Risk or Data Deficient (Trewick et al. 2016). The category Data Deficient indicates that there is insufficient information on the population size and trend of a species to properly assess its threat status. Improving our understanding of the distribution, ecology, and biology of Data Deficient species is essential to assigning an appropriate threat classification and enabling effective conservation measures where they are needed.

Despite its distinctive green coloration, which distinguishes it from almost all other NZ cave wētā species, *Maotoweta virescens* Johns & Cook, 2014 escaped scientific attention until recently. At

the time of its description, *M. virescens*, commonly called the moss wētā, was believed to be one of the rarest species of cave wētā in New Zealand as it was known from only seven specimens (Johns and Cook 2014). Five of the seven were collected from the Takitimu Mountains in Southland in 2006, while the remaining two were collected more than 60 years earlier, one each from Fiordland and northwest Nelson (Johns and Cook 2014). The apparent rarity of the species meant that little information existed in relation to its distribution, ecology, and biology and therefore its population size or trend (Johns and Cook 2014), and consequently, the species was classified as Data Deficient within the NZTCS when first assessed (Trewick et al. 2016).

To improve our knowledge of rare or poorly known species such as *M. virescens*, survey methods must be designed to maximize the chance of reliably detecting the target species when it is present (Schori et al. 2020). The use of ineffective survey methods can negatively influence our understanding of species ecology and rarity (Gaston 1994). Forest-dwelling cave wētā are nocturnal (Richards 1961) and so spotlighting desirable habitat at night has traditionally been the main method of detection (e.g., Johns and Cook 2014, Hegg et al. 2019). However, spotlighting has been found to be relatively unsuccessful for the cryptic *M. virescens*, with Johns and Cook (2014) reporting a detection rate of one wētā for every 192 minutes of searching. To resolve this, we attempted to identify the most suitable method for detecting and possibly monitoring *M. virescens* during targeted surveys for Data Deficient invertebrates in the Southland Region.

The objectives of the current study were as follows: (1) to improve our understanding of the distribution, ecology, and life history of *M. virescens*, (2) to identify the most suitable means of detecting and/or monitoring *M. virescens*, and (3) to recommend an appropriate threat classification for *M. virescens* to help determine whether conservation action is required for its protection. The findings from this study may have relevance to other species of forest-dwelling Rhaphidophoridae.

Methods

Field surveys.—Surveys for *M. virescens* were undertaken at 20 South Island sites from January–June 2021 (Table 1). These surveys were part of a wider Department of Conservation (DOC)-led project (Tweed and Wakelin 2021) intended to increase knowledge on the distribution and relative abundance of invertebrate species from the Southland region of NZ classified as Data Deficient within the NZTCS.

Surveys were conducted in a range of habitat types, including mixed temperate forest, open beech forest, subalpine shrubland, and alpine grasslands. However, most surveys were conducted within mixed temperate forest or open beech forest. These are the characteristic forest types of the higher and lower rainfall regions of NZ's South Island, respectively (Table 1).

In the South Island, the canopy of mixed temperate forest comprises a variable mixture of tree species including several species of Podocarpaceae (podocarps), Nothofagaceae (southern beeches), and Myrtaceae (myrtles), among others (Wardle 1991).

Table 1. Locations surveyed for *Maotoweta virescens* during this study arranged from north to south. Site name area codes follow Crosby et al. (1998): FD = Fiordland, OL = Otago Lakes, SI = Stewart Island, SL = Southland, WD = Westland. Annual average rainfall values were extracted from Ministry for the Environment (2015). Survey type codes are as follows: P/A = presence/absence survey (i.e., beating and/or night searches used for detection but not timed); TNS = timed night search; TBS = timed beating survey (during daylight). The total duration for each timed survey is given in minutes.

Site name	Habitat	Average annual rainfall (mm)	Survey date(s)	Latitude (°), Longitude (°)	Survey type	*M. virescens* detected	No. specimens collected
Karangarua Valley, WD	Mixed temperate forest	8,374	08/06/21	-43.707, 169.867	P/A (day + night)	Yes	2
Martins Bay, WD	Mixed temperate forest	5,644	22–23/02/21, 26/02/21	-44.342, 168.009	P/A (day + night)	Yes	6
Hokuri Creek, WD	Mixed temperate forest	6,211	25/02/21	-44.409, 168.059	TBS (225 mins)	Yes	17
George Sound, FD	Mixed temperate forest	7,884	03/02/21	-44.985, 167.438	P/A (day + night)	Yes	2
Henry Pass, FD	Alpine grassland, subalpine shrubland	8,383	01–02/02/21	-45.010, 167.498	P/A (day only)	No	NA
Caswell Sound, FD	Mixed temperate forest	7,386	04/02/21	-45.047, 167.307	TNS (100 mins), TBS (70 mins)	Yes	8
Lake Marchant, FD	Mixed temperate forest	7,386	05/02/21	-45.056, 167.317	P/A (day only)	Yes	1
Junction Burn, FD	Mixed temperate forest	6,306	09–11/02/21	-45.151, 167.498	P/A (day + night)	Yes	4
Lake Mistletoe, OL	Open beech forest	1,311	12/02/21	-45.201, 167.824		No	NA
Hanging Valley Track, Doubtful Sound, FD	Mixed temperate forest	7,782	01/03/21	-45.471, 167.143	TNS (180 mins), TBS (95 mins)	Yes	12
Old Doubtful Track, Doubtful Sound, FD	Mixed temperate forest	7,782	02/03/21	-45.479, 167.171	TBS (90 mins)	Yes	4
Wilmot Pass, FD	Mixed temperate forest and subalpine scrub	7,009	04/03/21	-45.512, 167.197	P/A (day only)	Yes	1
Princhester Creek, Takitimu Mountains, SL	Open beech forest	1,096	06/03/21	-45.600, 167.956	TBS (105 mins)	Yes	1
Grebe Valley, FD	Mixed temperate forest	4,019	26/01/21	-45.659, 167.344	P/A (day only)	Yes	1
Borland Saddle, FD	Open beech forest, alpine grassland	2,278	25/01/21	-45.747, 167.382	P/A (day only)	No	NA
Borland Lodge, FD	Open beech forest	1,318	24/01/21	-45.780, 167.533	P/A (day + night)	No	NA
Rakeahua Valley, SI	Mixed temperate forest	1,751	08–11/03/21	-46.982, 167.881	P/A (day + night)	No	NA
Ulva Island, SI	Mixed temperate forest	1,401	13/03/21	-46.892, 168.099	P/A (day only)	No	NA
Fern Gully, SI	Mixed temperate forest	1,387	14/03/21	-46.929, 168.130	P/A (day only)	No	NA
McLean Falls, SL	Mixed temperate forest	1,339	15/03/21	-46.572, 169.347	TBS (20 mins)	Yes	2

The presence and/or dominance of each of the canopy species varies geographically. The understories are typically dominated by broadleaved trees, shrubs, and ferns. Most surfaces are covered in thick layers of mosses, such as *Weymouthia mollis* (Hedw.) Broth., as well as numerous liverworts and lichens (Fig. 1A). These forests are typical of much of the western South Island, Fiordland, and the Catlins regions (Wardle 1991). The forests of Stewart Island are similar in composition but lack the southern beeches (Wardle 1991). Although numerous subclassifications can be designated (e.g., podocarp-broadleaf, beech-podocarp, etc.), here mixed temperate forest is used to refer collectively to the relatively high-rainfall forests, which are typically more diverse than the open beech forests described below.

The beech forest habitats surveyed were dominated by one or more of the southern beeches, with a relatively open, low-diversity understory comprised largely of divaricating shrubs (Fig. 1B). These open beech forests are typical of the forests of drier areas to the east of the Southern Alps (Wardle 1991). Mosses, lichens, and liverworts were also abundant, though the species composition differed, with a general lack of the hanging mosses seen in the mixed temperate forests.

Surveys for *M. virescens* were undertaken by a) visual spotlight searches at night, and b) beating of understory vegetation during the day. Notes were recorded on the habitat in which each wētā was detected, including the plants on which they were observed, the structure of the surrounding forest, and the elevation. Some wētā encountered at each location were collected for morphological analysis.

Comparison of survey methodologies.—In addition to the presence-absence surveys noted above, timed night searches and daytime beating searches were undertaken at a subset of sites.

Night searches. Timed night searches were undertaken at two Fiordland locations: Caswell Sound and Doubtful Sound (Table 1). Searches involved walking through suitable *M. virescens* habitat and scanning vegetation, particularly hanging and climbing mosses, with head torches. Any *M. virescens* encountered were recorded along with details of location, time of detection, the vegetation they were detected on, weather conditions, and any other notable information. The number of surveyors and the survey duration were recorded to calculate search effort. Night searches occurred between 21:00–23:00 NZDT hours, though the total length of the survey varied. Data on night searches from the type locality of Princhester Creek in the Takitimu Mountains were also extracted from Johns and Cook (2014).

Beating. We used daytime beating as the primary method for detecting *M. virescens* during this study. Preliminary work indicated that *M. virescens* might roost within mosses during the day, so we opted to use daytime beating as a sampling method. The traditional beating method for sampling invertebrates from vegetation uses a flat or slightly convex beating tray. Here, beating for *M. virescens* was undertaken using an entomological net (38 cm diameter) instead of a flat tray, as it ensured wētā were not able to jump away before being recorded. Wētā specimens were primarily collected off the inside walls of the net, although some smaller nymphs were found among the debris in the bottom of the net.

Timed beating surveys were conducted following the same methodology as timed night surveys and were conducted at six locations (Table 1). Hanging and climbing mosses were targeted for beating over an entomological net, as described above. The start and end times of the survey were recorded to allow for calculation of the search effort. Beating surveys typically occurred between 10:00 and 19:00 NZDT hours, although the length of the survey varied between sites.

Fig. 1. Forest types surveyed during this study. **A.** Typical mixed temperate forest photographed at Hokuri Creek in the lower Hollyford Valley, FD (note the extensive covering of *Weymouthia mollis* and other mosses and liverworts on the trunks and limbs of most trees and shrubs, as well as the forest floor); **B.** Typical open beech forest photographed within the Takitimu Mountains, SL (photo credit: N Harbison-Price).

Statistical analysis.—A Wilcoxon rank-sum test was used to compare the mean search time per *M. virescens* specimen observed for night searching and beating surveys. Analysis was conducted using the wilcox.test() function of the statistical software R (R Core Team 2021). Data were plotted using the package ggplot2 (Wickham 2016).

Additional distribution records.—The curators of NZ's largest entomological collections were contacted to determine whether they held any *M. virescens* specimens: New Zealand Arthropod Collection (NZAC), Auckland Museum (AMNZ), Te Papa (MONZ), Canterbury Museum (CMNZ), Lincoln University Entomology Research Collection (LUNZ), and Otago Museum (OMNZ). A single specimen was reported from the AMNZ collection, while CMNZ holds those specimens reported by Johns and Cook (2014). No other specimens were reported. Records were also obtained from T Jewell (pers. comm.), R Morris (pers. comm.), and from iNaturalist (2022).

Distribution and environmental variables.—All available records of *M. virescens* were plotted using QGIS v3.16.0. The elevation of each record was assessed using NZTopo50 map series. Values for the annual rainfall at the detection locations were extracted from the Ministry for the Environment's annual average rainfall data (Ministry for the Environment 2015). Area codes used throughout represent biogeographical regions identified by Crosby et al. (1998) and are routinely used when documenting the collection localities of invertebrate specimens within NZ.

Observations of captive wētā.—A total of five adult female and two adult male *M. virescens* were kept in captivity for up to one month to observe their behavior and diet. The incidentally biased sex ratio among captive specimens available meant that up to four females were kept together with a single male. Wētā were kept in a plastic tank lined with paper towel. The tank was misted once per day to keep it moist. Twigs were placed in the tank for the wētā to climb and roost on. Mosses (*Weymouthia mollis (Hedw.) Broth.*, Orthotrichaceae sp.), lichens (*Cladonia ?confusa* R. Sant., *?Lobaria* sp., *Pseudocyphellaria* sp., *Yarrumia ?colensoi* (C.Bab.) D.J.Galloway), liverworts (*?Trichocolea ?mollissima* (Hook.f. & Taylor) Gottsche, *?Lepicolea* sp.), and the leaves of some vascular plants (*Coprosma rhamnoides* A.Cunn., *Metrosideros* sp., *Fuscospora* sp., *Weinmannia racemosa* (L.f.) Pillon et H.C.Hopkins) were collected from the same localities as the wētā and placed within the tank. Insect carcasses were also offered to the captive wētā in the form of freshly caught hoverflies (*Melanostoma fasciatum* (Macquart, 1850) (Diptera, Syrphidae), which were swept from rank grass and killed by freezing.

Behavioral observations were made opportunistically both during the day and at night, and given the small sample size available, no attempt was made to undertake a full quantitative analysis of behavior. At night, the wētā were observed using a red light, as this is known to cause less disturbance to cave wētā than white or yellow lights (Butts 1983). The relative locations of individuals within the tank, whether they were feeding, and interactions between individuals were all recorded. Lichens and hoverfly bodies were inspected for signs of feeding each morning.

Morphological characteristics.—Both nymphs and adults were collected to study the growth and development of *M. virescens*. A total of 10 adults and 51 nymphs were collected from various locations during the surveys. Specimens were preserved in 70% ethanol and have been deposited within the Phoenix Collection housed at Massey University, Palmerston North, NZ. The length of the hind femur, hind tibiae, body, and ovipositor for the females were measured using digital calipers for all collected specimens. The presence or absence of an ovipositor was used to sex the specimens, which may have led to some early instar female nymphs being falsely identified as males. Due to this uncertainty, no statistical comparison was made between the body sizes of male and female nymphs. Morphology measurements were plotted using the package ggplot2 (Wickham 2016) within the statistical software R (R Core Team 2021).

Results

Distribution.—*Maotoweta virescens* has now been recorded throughout the length of the South Island of NZ, with most records occurring to the west of the Southern Alps (Fig. 2). Records extend from the Cobb Valley (NN) in the northwest to McLean Falls in the Catlins Conservation Park (SL) in the southeast (Fig. 2). The
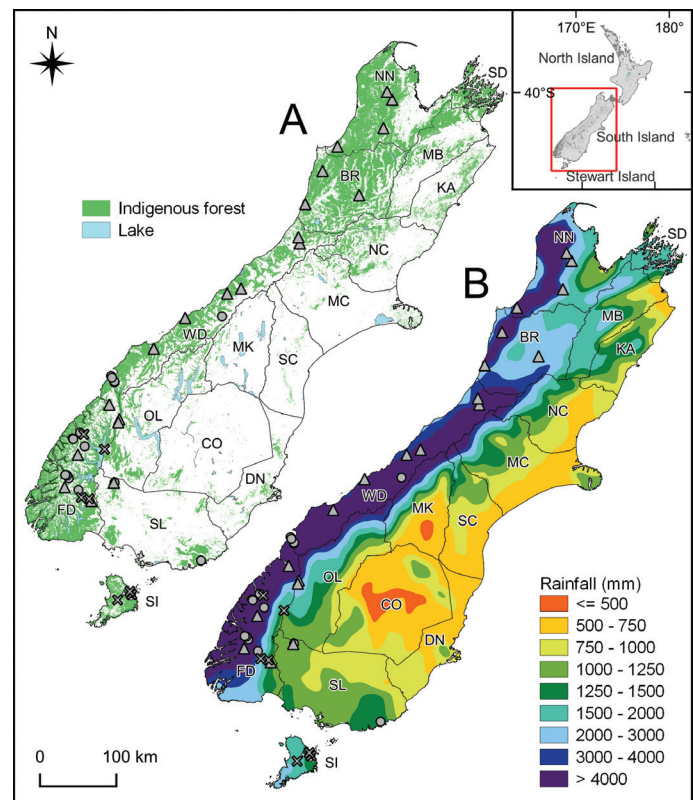

Fig. 2. Known records of *Maotoweta virescens*. **A.** Records overlain on the current extent of indigenous forest; **B.** Records overlain on mean annual rainfall. Circles represent records of *M. virescens* obtained during this study, triangles are confirmed records from other sources, and crosses indicate sites surveyed during this survey at which *M. virescens* was not detected. The extent of indigenous forest was taken from Landcare Research (2020). Rainfall data is from the Ministry for the Environment (2015) Area codes and boundaries follow Crosby et al. (1998).

latter record (-46.57157, 169.34744) marks the only confirmation of the species from the east coast of the South Island, extending the known range by 150 km eastwards, with the nearest known population occurring in the Takitimu Mountains, SL. *Maotoweta virescens* was detected at most sites surveyed during this study, with the exceptions of Borland Lodge (FD), Borland Saddle (FD), Henry Pass (FD), and Lake Mistletoe (OL) (Fig. 2, Table 1). *Maotoweta virescens* was also not detected on Stewart Island despite extensive searching (Fig. 2, Table 1).

Habitat.—*Maotoweta virescens* is now known from a wide elevation range, having been recorded from sea level at Caswell Sound, FD during this study, and at altitudes of up to 1,200 masl at Mt Arthur, NN, in the earlier study of Johns and Cook (2014). The species appears to be strongly associated with moderate-to-high rainfall forests with all records occurring in areas averaging 1,096–8,374 mm per year (Fig. 2). Princhester Creek in the Takitimu Mountains, SL, and the Karangarua Valley, WD, represent the lowest and highest precipitation sites, respectively.

Records from this study and additional distribution records indicate that *M. virescens* is primarily associated with mature forest habitats (Fig. 2). It has been recorded from both mixed temperate forests and beech forests but was not detected in the subalpine shrublands or grasslands surveyed during this study.
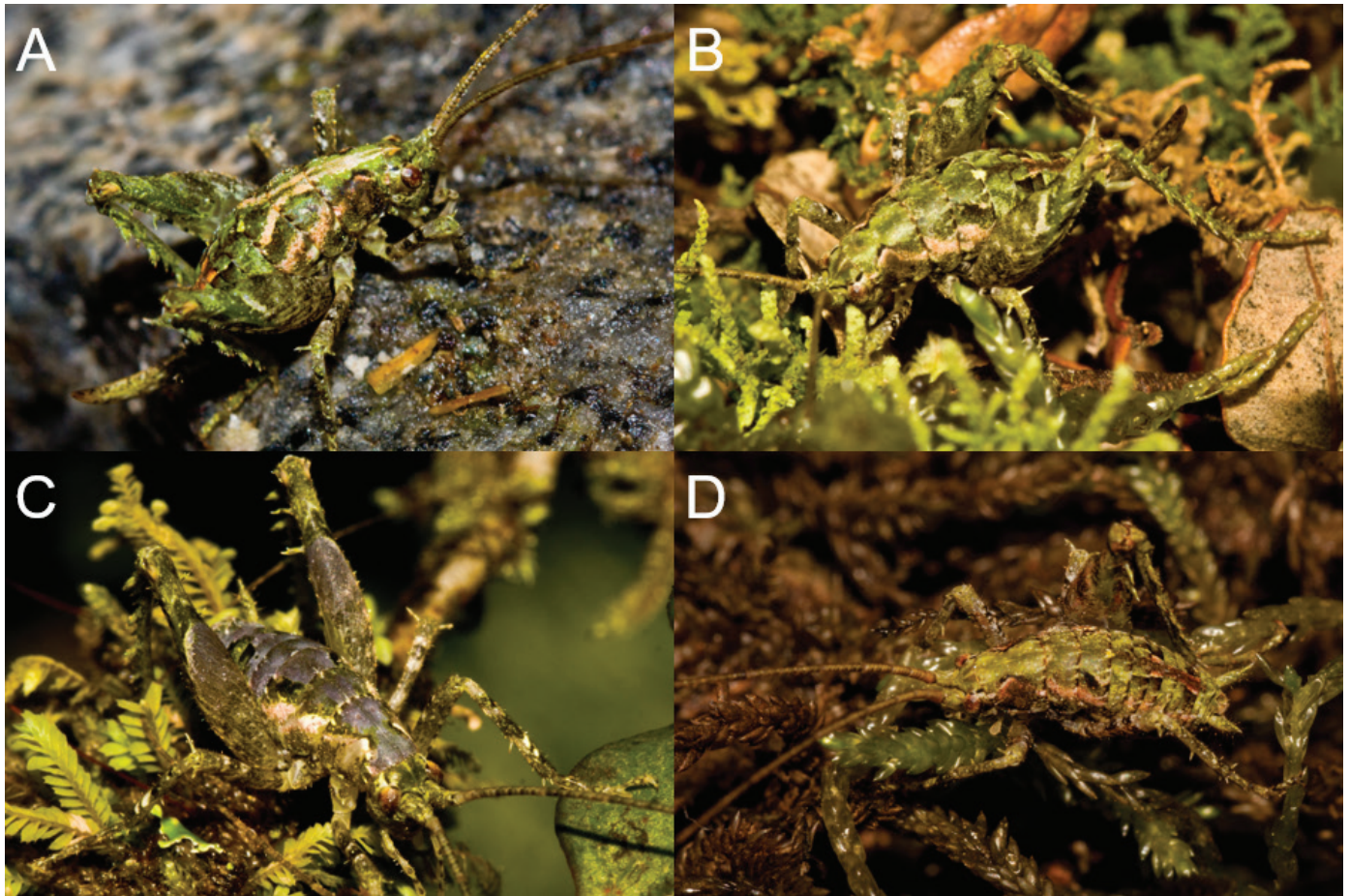
Fig. 3. Photos of adult *Maotoweta virescens*. **A.** Female from Milford Sound, FD; **B.** Female from Lake Gunn, FD; **C.** Male from Milford Sound, FD; **D.** Male from Runanga, WD. Photo credit: Tony Jewell (www.flickr.com/photos/rocknvole/).

Maotoweta virescens was detected in all mixed temperate forest locations surveyed in Fiordland, Westland, and the Catlins (Table 1, Fig. 2). Within this forest type, both nymphs and adults were found to be particularly closely associated with arboreal moss and liverwort communities. Most *M. virescens* detected within this forest type were beaten from the hanging moss *Weymouthia mollis*, though some were also beaten from other moss species, lichens, and leafy liverworts (Marchantiophyta: Jungermanniopsida), while others detected at night were found climbing tree trunks. The plant species on which the moss was growing seemed to have little influence on the presence or absence of *M. virescens,* as individuals were beaten from moss growing on a diverse range of trees, shrubs, and tree ferns, as well as dead trees and limbs. Fig. 3 shows photos of live specimens in their natural habitat.

Maotoweta virescens was also found within open beech forest. A single nymph was beaten from a *Coprosma rhamnoides* shrub in the forest understory at Princhester Creek in the Takitimu Mountains, SL, the type locality for *M. virescens*. This shrub had a thin layer of an unidentified species of moss on its stem. Although mats of mosses and liverworts were present on most tree trunks, the open beech forest habitat lacked the curtains of hanging moss characteristic of *M. virescens* habitat within the mixed temperate forests surveyed. *Maotoweta virescens* was not detected from open beech forest searched near Borland Lodge, FD, or at Lake Mistletoe, OL; however, the species has been confirmed from Monowai Flats, ~1 km from the site surveyed at Borland Lodge (T Jewell pers. comm.; Fig. 2).

Although no adults of any other cave wētā species were encountered while beating moss for *M. virescens*, the nymphs of other species were occasionally caught, including *Talitropsis chopardi* (Karny, 1937) and *Notoplectron brewsterense* (Richards, 1972). Several species of cave wētā were also routinely encountered on the trunks of trees or on the forest floor during night searches for *M virescens*, including *Miotopus richardsae* Fitness, Morgan-Richards, Hegg & Trewick, 2018, *Talitropsis sedilloti* Bolívar, 1882, and several *Isoplectron* species.

Morphological characteristics.—Based on body measurements and the development of female genitalia, all specimens collected appeared to be either adults or early-instar nymphs (Fig. 4). Only a single late-instar nymph was observed during the surveys: a penultimate instar female that underwent its final molt in captivity less than 24 hours after capture and was therefore measured as an adult (depicted in Fig. 5H).

The lengths of the bodies (2.3–5.1 mm), hind femur (2.1–4.2 mm), and hind tibia (2.2–4.5 mm) of the nymphs measured (n = 51) displayed an almost continuous range, with no discrete size classes evident that could be used to separate instars. The two nymphs collected from the Karangarua Valley, WD, had marginally longer hind tibiae and femora than any other early-instar nymphs measured, but their body sizes overlapped with those of the other collected nymphs (Fig. 4A, B). The female nymph from Karangarua also had a longer ovipositor than all other female nymphs (Fig. 4C).
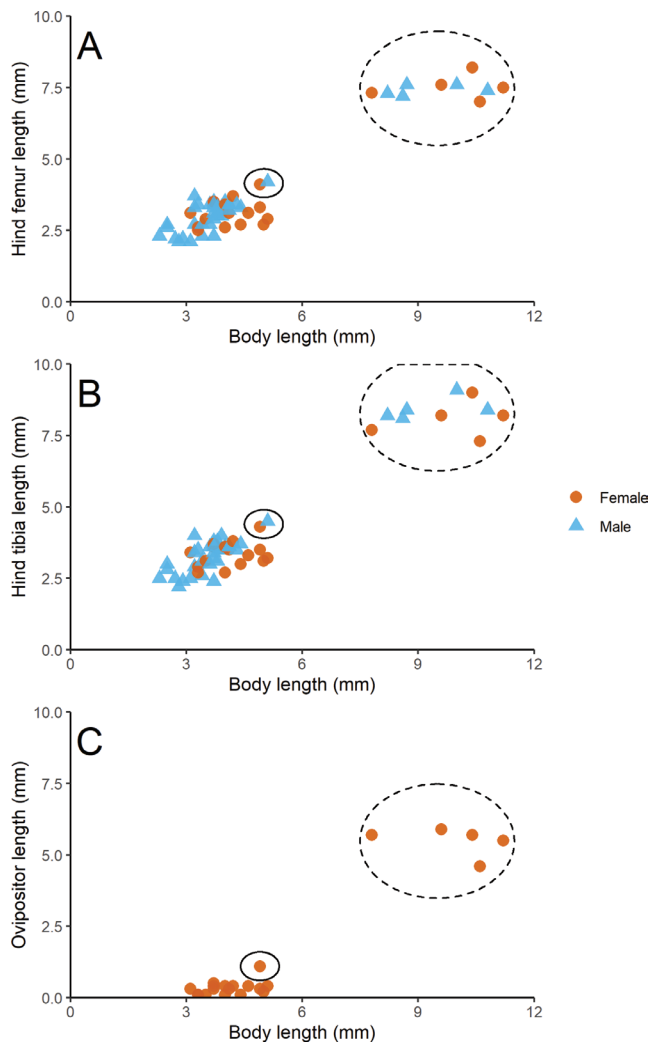
Fig. 4. Hind femur (**A**), hind tibia (**B**), and ovipositor (**C**) length of *Maotoweta virescens* specimens collected in this study plotted against body length. The observations within the solid oval on each plot are the specimens collected from the Karangarua Valley, WD, in June; those within the dashed oval are adult specimens collected during this study; those not circled are other early-instar nymphs collected during this study.

Among adult specimens (n = 10), the length of the body, hind femur, and hind tibia ranged from 8.6–10.8 mm, 7.2–7.6 mm, and 8.1–9.1 mm, respectively, for males (n = 5), and from 7.8–11.2 mm, 7.0–8.2 mm, and 7.3–9.0 mm for females (n = 5). Ovipositor length ranged from 4.6–5.9 mm.

Color variation.—The coloration of *M. virescens* was found to be highly variable (Fig. 5), but all color morphs observed to date resemble the habitat of mosses, liverworts, and lichens in which the wētā lives (Figs 3, 5, 6). Individuals of distinctly different color morphs were found cohabiting on several occasions. Fig. 5 shows some of the color and pattern variations noted during this study, although the full range of variation is even greater than depicted here (also see Fig. 3 for further examples).

Behavioral observations.—In captivity, *M. virescens* was found to be entirely nocturnal. During the day, the wētā would roost on twigs, camouflaged among clumps of moss. When at rest, the wētā would fold their antenna beneath their body and then fold them again, approximately beneath the mesocoxa, so that the tips lay flat along the branch on which they were sitting (i.e., they were folded into a collapsed S-shape when viewed laterally; Fig. 6). Individuals were observed roosting both separately and near one or more other wētā. In the field, the number of wētā beaten from a clump of moss containing *M. virescens* varied between one and five individuals. Nymphs and adults were usually detected separately, although on some occasions, nymphs were beaten from the same clumps of moss as adults.

At night, captive *M. virescens* would roam around their enclosure, climbing along twigs as well as the walls and ceiling of the enclosure. Roaming wētā waved their antenna in front of them constantly, stopping only when they encountered a food source. When two individuals met each other, they would pause briefly, inspect each other with their antenna, and then move around one another, continuing their path. No aggression was observed between individuals. Captive individuals that died overnight were removed the following day. No feeding damage was observed on any of the dead wētā.

No mating was observed in captivity or in the field, but males and females were found in proximity on numerous occasions. Oviposition was also not observed but the swollen abdomen of a female caught at Martins Bay (26 February 2021) suggested at least some females were gravid at the time the surveys were conducted.

A single captive wētā was observed undergoing ecdysis from the penultimate instar to an adult on the 04 March 2021. The female (depicted pre-molt in Fig. 5H) clung to the underside of a twig with its head facing downwards. At the final stages of the process, the wētā hung from its exuviae, attached only by the tips of its antenna and ovipositor, which were the last structures to be withdrawn. The entire process took approximately 30 minutes. The pigmentation of the female was somewhat paler following ecdysis, although this darkened quickly. The patterning of the individual remained unchanged.

Diet.—*Maotoweta virescens* were observed feeding on the moss *Weymouthia mollis* in the field during night searches. *Weymouthia mollis* was actively fed on by captive *M. virescens* but appeared to lose its palatability as it dried out. Some feeding was observed on a second moss offered (Orthotrichaceae sp.) but not for sustained periods, suggesting it was not a preferred food source.

Captive wētā actively fed on the foliose lichens offered, particularly *Yarrumia ?colensoi*. The wētā ate holes through the middle of the sheets of *Yarrumia* but were only observed feeding on the edges of *Pseudocyphellaria* and *?Lobaria* lichens. No feeding was observed on the fruticose *Cladonia confusa*. No browsing was observed on either the liverworts or the leaves of any of the vascular plants offered.

All insect carcasses offered to the captive wētā were consumed on the first night; however, several captive wētā that died overnight were not fed on by others prior to their removal the following day.

Comparison of survey methodologies.—The mean search time per *M. virescens* specimen detected using beating was significantly lower than that of active night searching (Wilcoxon's test, *p* = 0.038, Fig. 7). When searching suitable habitat, *M. virescens* was encountered on average once every 28.1 minutes while beating and every 157.3 minutes while active night searching (Fig. 7). For beating, this dropped to one individual every 12.7 minutes if the Princhester Creek survey (105 minutes per individual) was excluded. Princhester Creek was the only open beech forest habitat included in the timed surveys, with the remaining sites all being mixed temperate forest (see Table 1).
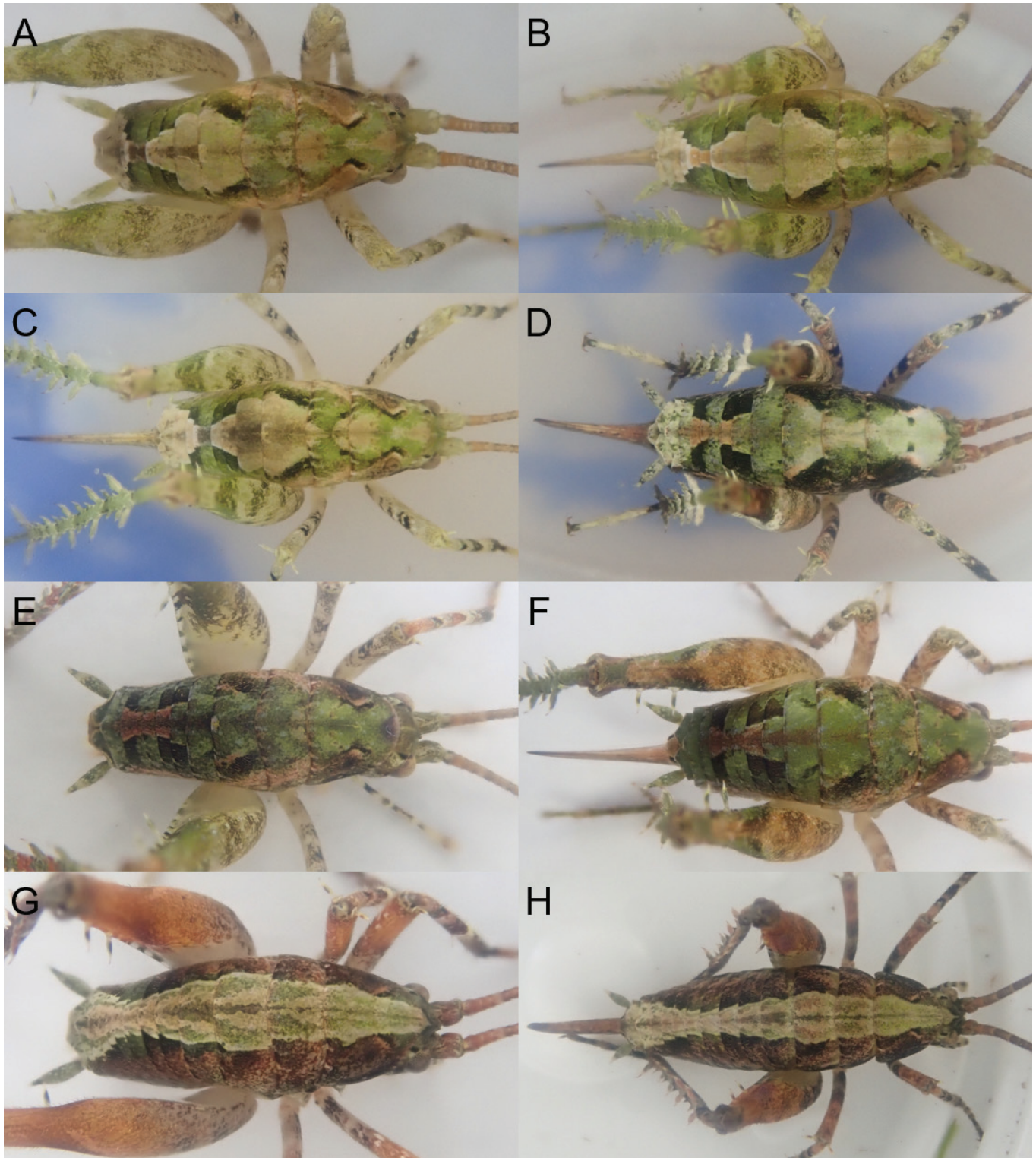
Fig. 5. Examples of phenotypic variation displayed by *Maotoweta virescens*. **A.** Male, Martins Bay, WD; **B.** Female, Martins Bay, WD; **C.** Female, Doubtful Sound, FD; **D.** Female, Wilmot Pass, FD; **E.** Male, Martins Bay, WD; **F.** Female, Martins Bay, WD; **G.** Male, Hokuri Creek, WD; **H.** Penultimate instar female, Doubtful Sound, FD. Note: images are not to scale. Body length of all individuals was between 7.8 mm (**H**) and 11.2 mm (**B**).

Discussion

This study has shown that *M. virescens* is widely distributed throughout NZ's South Island. Current records suggest that the species is most closely associated with the mixed temperate forests of the western and southern South Island. However, records from the Takitimu Mountains, SL (Johns and Cook 2014, R Morris pers. comm., and this study) and Monowai Flats, SL (T Jewell pers. comm.) indicate that the species is also capable of inhabiting open beech forest habitat. Given that the species has been detected

across a wide latitudinal and elevational range, as well as from several different forest ecotypes, it seems likely that the species will be recorded from other locations in the South Island following further survey efforts. We did not detect *M. virescens* on Stewart Island during this study, but given that ours was the first targeted search effort for the species on the island, more survey effort is needed. Several other cave wētā species are known from both the South Island and Stewart Island, including *Talitropsis sedilloti* (Michel et al. 2008) and *Miotopus richardsae* (Fitness et al. 2018). Similarly, although the species has not yet been recorded from the North Island, its presence cannot be discounted, as several of NZ's cave wētā species are known to inhabit both the North and South Islands, including both species mentioned above. Suitable forest habitat for *M. virescens*, including *Weymouthia mollis*, is present on both Stewart Island and the North Island.

Although some species of Rhaphidophoridae are known to be closely associated with plants (e.g., the North American species *Gammarotettix bilobatus* (Thomas, 1872) (Stidham 2005)), most described NZ cave wētā species are typically cavity dwellers, sheltering in locations such as caves, tree cavities, or under and among debris on the ground, coming out only at night to feed (Richards 1962, 1966, Hegg et al. 2019). *Maotoweta virescens* may be unique among the described cave wētā species within NZ and globally, as it appears to spend most, if not all, of its life cycle within arboreal mosses and lichens. The cryptic coloration of the species further supports its moss-dwelling specialization, as it undoubtedly functions to conceal *M. virescens* from native visual predators, such as insectivorous birds, while roosting within mosses during the day and possibly from nocturnal predators such as ruru/morepork (*Ninox novaeseelandiae*) while foraging at night. The diversity of color morphs (see Fig. 5) suggests that *M. virescens* may have evolved to inhabit and blend into a wide range of different micro-habitats. The cavity-dwelling behavior of most other NZ cave wētā during the day means they have less need for such cryptic coloration and may explain why most are various shades of brown and gray. The antennal folding behavior and exaggerated hind tibia spines of *M. virescens* (see Johns and Cook (2014) for morphological description) further enhance the camouflage of this species. The double-folding of the antenna possibly serves to conceal the species further among its moss habitat by reducing its overall length while also protecting them from damage. Tettigonids that rely on plant mimicry are also known to conceal their antennae, with different species displaying methods such as folding them along their bodies, laying them flat along twigs, or in some cases deliberately extending them in unusual positions to mimic the plants among which they are hidden (Nickle and Castner 1995). The spines on the hind tibia of *M. virescens* (clearly visible in Fig. 5C, D) closely resemble the phyllids of the mosses within which they live. Evidence for the effectiveness of this adaptation is shown by the presence of similar spines in the unrelated *Pleioplectron crystallae* Hegg, Morgan-Richards & Trewick, 2019, a ground dwelling species of NZ cave wētā known to be a moss specialist (Hegg et al. 2019). Many tettigoniids also possess anatomical and coloration adaptations to mimic mosses and lichens (e.g., *Lichenodraculus matti* Braun, 2011), traits that Nickle and Castner (1995) suggest evolved primarily to protect the insects against diurnal predators. Further use of beating as a method to search for cave wētā may reveal currently unknown species with similar habits, both within NZ and in other parts of the world.

Mosses, lichens, and dead insects were documented here as part of the diet of *M. virescens* and are also known to be consumed by other cave wētā species (Richards 1962, Butts 1983). However,
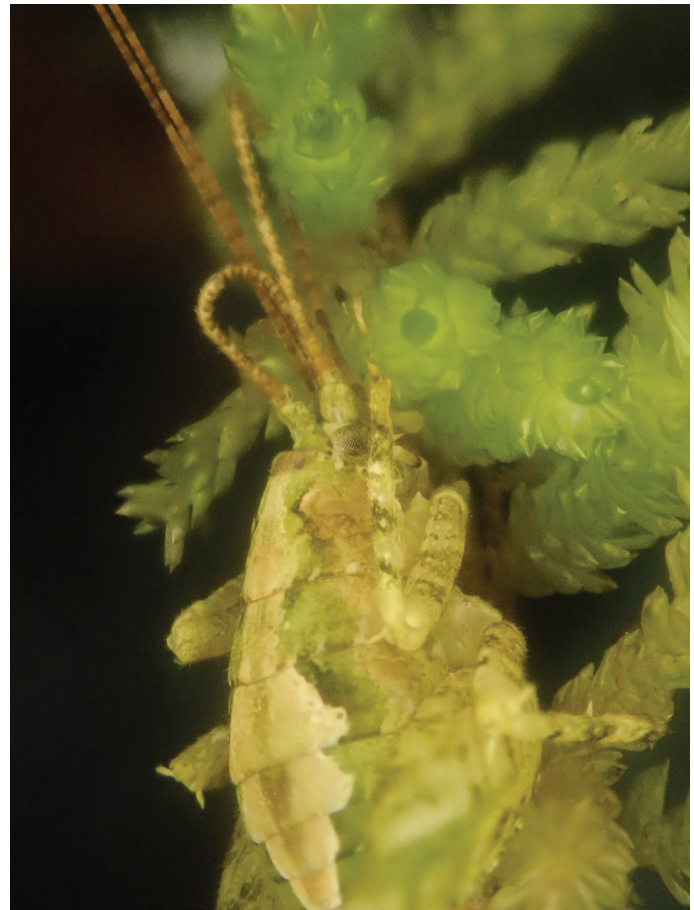

Fig. 6. Adult female *Maotoweta virescens* exhibiting the double antennal folding behavior displayed by this species when roosting within their moss habitat during the day.

M. virescens was not observed feeding on vascular plants, even though ferns and angiosperms are a major dietary component of other cave wētā such as *Insulanoplectron spinosum* Richards, 1970b (Butts 1983), *Macropathus filifer* Walker, 1869 (Richards 1954), *Pachyrhamma waitomoensis* Richards, 1958 (Richards 1962), and *Pallidoplectron turneri* Richards, 1958 (Richards 1962). Apparent diet specialization on moss and lichen has been documented for the ground-dwelling *P. crystallae* (Hegg et al. 2019), and the same may be the case for *M. virescens*, although they are likely to be opportunistic feeders given that they were documented feeding on dead insects in this study. Further work is required to understand the full dietary range of *M. virescens*.

Rearing NZ cave wētā species from eggs and/or nymphs to adulthood has been found to be challenging (Richards 1961, Butts 1983) and was not attempted here. However, based on our observations and knowledge of other cave wētā species, we suggest several hypotheses about the life history of the species for future testing. Adult *M. virescens* have been recorded from December to March, and as one of the females collected here was observed undergoing its final molt in early March, it appears maturation can occur from at least early summer to early autumn. Although it was not observed during this study, mating has been observed in both December (Johns and Cook 2014) and in March (https://inaturalist.nz/observations/21440116). Oviposition therefore likely occurs throughout summer into early autumn, and eggs may be laid in the rotting wood of trees, as has been observed for the other arbo-
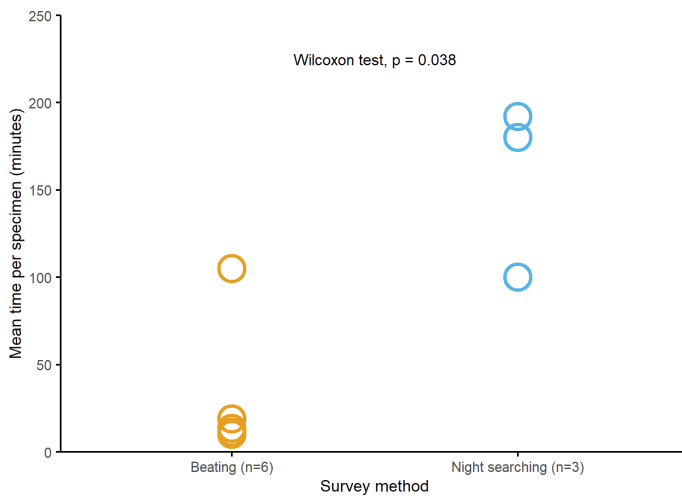
Fig. 7. Mean number of minutes searched per *Maotoweta virescens* individual detected during timed beating and active night searching surveys. The results of the Wilcoxon rank sum test are given.

real cave wētā including *Isoplectron armatum* (e.g., https://inaturalist.nz/observations/91211038) and *Talitropsis sedilloti* (e.g., https://inaturalist.nz/observations/2693757).

Among Orthopteran families such as Tettigoniidae (Hartley and Warne 1972) and Anostostomatidae (Stringer 2001), the duration of the egg stage is known to be highly variable between species and sometimes within species or even egg clutches. Similarly, the eggs of some species undergo notable diapause while others do not (Hartley and Warne 1972). Relatively little is known about the duration of the egg stage in Rhaphidophoridae, with estimates varying greatly between species, ranging from one week to four months for the North American *Daihinibaenetes giganteus* Tinkham, 1962 (Weissmann 1997) and up to eleven to twelve months for the Australian *Pallidotettix nullarborensis* Richards, 1968 (Richards 1970a). As such, one theory is that the eggs of *M. virescens* may overwinter and hatch relatively synchronously the following spring, with adults maturing approximately one year later. A seasonal lifecycle with a prolonged egg stage has been documented for the much larger *Pachyrhamma waitomoensis* with the egg stage lasting six to seven months (Richards 1961). *Pallidotettix nullarborensis* also has a prolonged egg stage, which Richards (1970a) proposed was likely to ensure eggs hatched during optimal climatic conditions.

An alternative to the above theory is that *M. virescens* has a short egg development period. This would mean that egg hatching occurs relatively quickly after mating and oviposition in summer/autumn. Nymphs would then overwinter in their early- to mid-instars before reaching maturity the following year in late spring to early autumn. Similar seasonal lifecycles have been documented for other rhaphidophorids including *Pachyrhamma edwardsii* (Scudder, 1869) from NZ (Richards 1961) and *Hadenoecus subterraneus* (Scudder, 1861) from North America (Hubbell and Norton 1978). Conversely, in *P. turneri*, instars of all ages can be found cohabiting with adults at any given time of year, suggesting an aseasonal lifecycle (Richards 1961). De Pasquale et al. (1995) found that *Dolichopoda* spp. exhibit aseasonal or seasonal development depending on whether they occupied natural or artificial cave sites, respectively, suggesting that the trait may be flexible for at least some rhaphidophorid species. For *M. virescens*, a univoltine cycle with reasonably strong seasonal synchrony in egg hatching is supported in the current study by the detection of only young nymphs and adults between January and March (mid to late summer). If

M. virescens displayed an aseasonal lifecycle, it would be expected that nymphs of all ages would have been recorded during the present study, similar to what Richards (1961) observed for *P. turneri*. Although based on evidence of only a single specimen, the relatively long ovipositor of the female nymph collected in June (winter) from the Karangarua Valley compared to all other measured nymphs further supports this, as ovipositor length is known to be one of the best indicators of nymphal development among NZ cave wētā (Richards 1961). Further sampling effort is required across all months and seasons to confirm this proposed theory.

The lack of mid-instar nymphs observed during this study may alternatively be explained by an ontogenetic niche shift in *M. virescens*. For example, *M. virescens* may move up higher into the forest canopy during the mid-instar phases of its lifecycle. Cherrill and Brown (1992) documented ontogenetic shifts in microhabitat preference in the bush cricket *Decticus verrucivorus* (Linnaeus, 1758). Within the Rhaphidophoridae, ontogenetic niche shifts have been documented for *Hadenoecus subterraneus*, which only begins to leave its cave habitat to forage at night once it reaches the fifth instar (Hubbell and Norton 1978). Interestingly, *Dolichopoda* spp. also display variation in feeding habits and diet with age; however, it is the subadults that differ from other life stages as they tend to feed outside of caves while adults and early-instar nymphs feed almost exclusively on resources within the cave (de Pasquale et al. 1995).

As has been found for other cave wētā species (e.g., Richards 1961, Butts 1983), the sizes of *M. virescens* nymphs measured here did not fall into discrete size classes corresponding to instar. The number of instars for other rhaphidophorids varies between, and possibly within, species and sexes (Hubbell and Norton 1978). For example, *Pachyrhamma edwardsii* has ten nymphal instars in the male and nine in the female (Richards 1961), while *Insulanoplectron spinosum* has nine in the male and ten in the female (Butts 1983). Because no mid- to late-instar nymphs were found, we are not able to give an accurate estimate of the number of nymphal instars for males or females of *M. virescens*. Clearly, further work is required to fully understand the life history of *M. virescens* and to test the various theories posed here.

When Johns and Cook (2014) described *M. virescens*, they believed it to be one of NZ's rarest cave wētā species. The authors presumably based this assumption on the difficulties that they encountered detecting the species while undertaking targeted night searching in the Takitimu Mountains, as well as the relative absence of *M. virescens* specimens within NZ's entomological collections. However, prior to the current study, no large-scale survey had ever been conducted for *M. virescens* specifically. The evidence presented here suggests that *M. virescens* may not be rare. By compiling all known records, as well as conducting targeted surveys using an ecologically appropriate method (i.e., beating), *M. virescens* has been shown to be geographically widespread within temperate South Island forest habitat and, in some cases, relatively abundant. Although beating can be an effective means of collecting some arboreal Orthoptera (Sperber et al. 2021), including the arboreal Nearctic rhaphidophorid *Gammarotettix bilobatus* (Stidham 2005), it has not typically been employed as a collecting method for NZ cave wētā (e.g., Johns and Cook 2014, Hegg et al. 2019, 2022). Our findings suggest that active night searching, the traditional method of cave wētā detection, is less effective for the detection of *M. virescens* than beating in mixed temperate forest, likely explaining why the species has not been detected regularly in the past. This may explain why the first two known specimens of the species were detected by the late Dr. R. R. Forster (see Johns

and Cook 2014), an esteemed arachnologist who routinely employed beating to target spiders. Future studies of rhaphidophorid diversity should consider employing foliage and moss beating as part of their collection methods.

Within the open beech forest habitat of Princhester Creek in the Takitimu Mountains, beating proved only marginally more effective at detecting *M. virescens* than night searching. This result may indicate that open beech forest represents sub-optimal habitat for *M. virescens*, meaning densities are naturally low. It could also reflect the relative lack of hanging mosses within this habitat type, which made beating more difficult. Habitat structure is known to affect the efficacy of some Orthopteran survey methods, including sweeping (Gardiner et al. 2005), hand collection (Bailey et al. 2003), and pitfall trapping (Schirmel et al. 2010). Targeted surveys employing both beating and night searching may be required to fully understand the relative abundance, ecology, and distribution of *M. virescens*. It should be noted that the results of the beating and active night searching surveys presented in this study are a preliminary comparison in locations already confirmed as suitable *M. virescens* habitat and are based on relatively small sample sizes. It is likely that the total amount of survey time taken to detect the species will vary from those documented here, particularly in surveying sites in which the species occurs at naturally low densities, as may be the case for open beech forest.

The field work reported here was completed as part of a wider project to investigate the distribution of Data Deficient invertebrates in southern NZ (Tweed and Wakelin 2021). Such work is essential for many of NZ's cave wētā species, as well as numerous other poorly known invertebrates, as a prerequisite to enable effective threat classification and to inform whether conservation management is required. This study has greatly improved our knowledge of the cave wētā *M. virescens* and provided a more effective method to detect the species. The evidence presented indicates that the wētā has a much wider distribution than previously thought, indicating a reassessment of the species threat status was required. The evidence presented was assessed by the NZTCS panel and contributed to the reclassification of the species as Not Threatened (Trewick et al. 2022).

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