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RESEARCH ARTICLE

New Zealand ground wētā (Anostostomatidae: *Hemiandrus*): descriptions of two species with notes on their biology

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Although the New Zealand ground wētā (Anostostomatidae: *Hemiandrus*) are widespread and abundant, little has been described of their ecology and behaviour. Within the genus several lineages have evolved with ovipositors that are unusually short for this orthopteran family. Some species with this derived morphological character also exhibit maternal care of eggs and offspring. Two new species are described here, *Hemiandrus maia* sp. nov. and *Hemiandrus electra* sp. nov. Although morphologically similar with medium length ovipositors, they are not sister taxa and live at opposite ends of South Island, New Zealand. The behaviour of *Hemiandrus maia* sp. nov. was studied using burrow door re-construction as a key to activity patterns. Observations at night and burrow excavation during the day were used to identify features of their behaviour. Maternal care of both eggs and nymphs was observed. *Hemiandrus maia* sp. nov. were shown to eat fruit, invertebrates and seeds without discrimination.

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Keywords: *Hemiandrus*; maternal care; behaviour; Anostostomatidae; Orthoptera; wētā; diet

Introduction

Wētā (Insecta: Orthoptera: Anostostomatidae) are an important and prominent group in New Zealand ecology (Brockie 1992). The family in New Zealand comprises three main lineages, tree (*Hemideina* White, 1846) and giant (*Deinacrida* White, 1842) wētā, tusked wētā (*Anisoura* Ander, 1938, *Motuweta* Johns, 1997) and ground wētā (*Hemiandrus* Ander, 1938) (Johns 1997; Trewick & Morgan-Richards 2004, 2005). Together, they comprise some 60 species that occupy diverse habitats from lowland forest to the alpine zone. Among them, the ground wētā are the most speciose but also the most poorly characterized and in need of most taxonomic and ecological work. Johns (1997) estimated that there might be as many as 40 undescribed species but there are nine described to date (Johns 1997; Johns 2001; Jewell 2007). In addition an estimated 10 undescribed species of *Hemiandrus* are endemic to Australia (Johns 1997), although molecular data indicate that these may not be monophyletic with the New Zealand *Hemiandrus* (Pratt et al. 2008).

New Zealand *Hemiandrus* ground wētā are found in lowland forest, riverbeds, alpine herb fields and suburban gardens but all share the characteristic of occupying holes in the ground as daytime refuges. They emerge at night to forage and mate, usually sealing the entrance of their burrow during the day with a soil plug. Although some are relatively large (30 mm) and abundant (e.g. Brockie 1992), daytime concealment below ground and nocturnal activity render ground wētā difficult to observe. This probably explains why so little is known of *Hemiandrus*

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ecology. All species of ground wētā are nocturnal and some, perhaps all, are predominantly predatory (Cary 1983). Many species climb trees at night but others are more commonly encountered on the ground and on low vegetation (Brockie 1992; Wahid 1978; BL Taylor Smith, M Morgan-Richards, SA Trewick pers. obs.). Some ecological research has been undertaken on *Hemiandrus maculifrons* (Walker, 1869) (Cary 1983), *Hemiandrus subantarcticus* (Salmon, 1950) (Butts 1983), *Hemiandrus* 'peninsularis'/'horomaka' (Wahid 1978) and *Hemiandrus pallitarsis* (Walker, 1869) (Gwynne 2002, 2004, 2005; Chappell et al. 2012).

Most Anostostomatidae females lay eggs into the soil using a long slender ovipositor; however, ovipositor length differs markedly among species of New Zealand *Hemiandrus*. Some species have a very small ovipositor that is scarcely visible. The species lacking an obvious ovipositor were at one time taxonomically distinguished as *Hemiandrus* from *Zealandosandrus* (Salmon, 1950) with fully developed ovipositors, but later synonymized (Johns 1997, 2001). A long ovipositor is common in *Hemiandrus* and other members of the family and can be considered the ancestral condition. Reduction in ovipositor length has therefore been inferred as having occurred at least three times in the New Zealand *Hemiandrus* (Pratt et al. 2008). Of the seven putative species with extremely short ovipositors (Johns 2001), six are narrow endemics (Chappell et al. 2012). Two species, *Hemiandrus maia* sp. nov. and *Hemiandrus electra* sp. nov. are very similar in appearance, but we can infer from molecular phylogenetic evidence that their medium length ovipositors are independently derived (Pratt et al. 2008).

Females of the widespread North Island species *Hemiandrus pallitarsis*, which lacks an obvious ovipositor, deposit about 50 eggs in their own burrows, where females remain with eggs and nymphs during winter and spring (Gwynne 2004; SA Trewick pers. obs.). Adult female *H. pallitarsis* are unusual in that they possess a distinctive forked structure on the sixth abdominal sternite (Gwynne 2002) that is involved in transfer of a nuptial gift during mating (Gwynne 2005). In species with long ovipositors, such as *Hemiandrus focalis* (Hutton, 1897), and in other anostostomatids (e.g. Angulo 2001; Stringer 2001), females deposit eggs into soil or moss when active outside their burrows (M Morgan-Richards pers. obs.), and there is no evidence that they have any further involvement with their offspring.

Materials and methods

Taxonomic methods

All specimens were preserved in 95% ethanol and are part of the Phoenix Lab insect collection at Massey University, Palmerston North. All ground wētā in this collection have a unique accession number with the prefix GW. Specimens were examined using an Olympus SZX7 Zoom Stereomicroscope with an attached SC100 digital camera. Body length (length from frons to distal margin of ninth abdominal tergite), head width (width of widest part of head), pronotum length (width of widest part of pronotum) and femur length measurements were made using digital callipers. Photographs of male terminalia were captured using the Olympus Image Analysis Software, which was also used to measure ovipositor length and pronotum width. Images of whole specimens were captured using a Canon EOS 40D digital camera.

Abbreviations

GW, ground wētā in the Phoenix Lab collection (Massey University, Palmerston North); MONZ, Museum of New Zealand Te Papa Tongarewa; BL, body length is the length of the insect excluding the ovipositor and other appendages; MP3, third segment of the maxillary palps; MP4, fourth segment of the maxillary palps; MP5, fifth segment of the maxillary palps; T1, first abdominal tergite; T2, second abdominal tergite; T3, third abdominal tergite; T8, eigth abdominal tergite; T9, ninth abdominal tergite; T10, tenth abdominal tergite. Area codes for recording

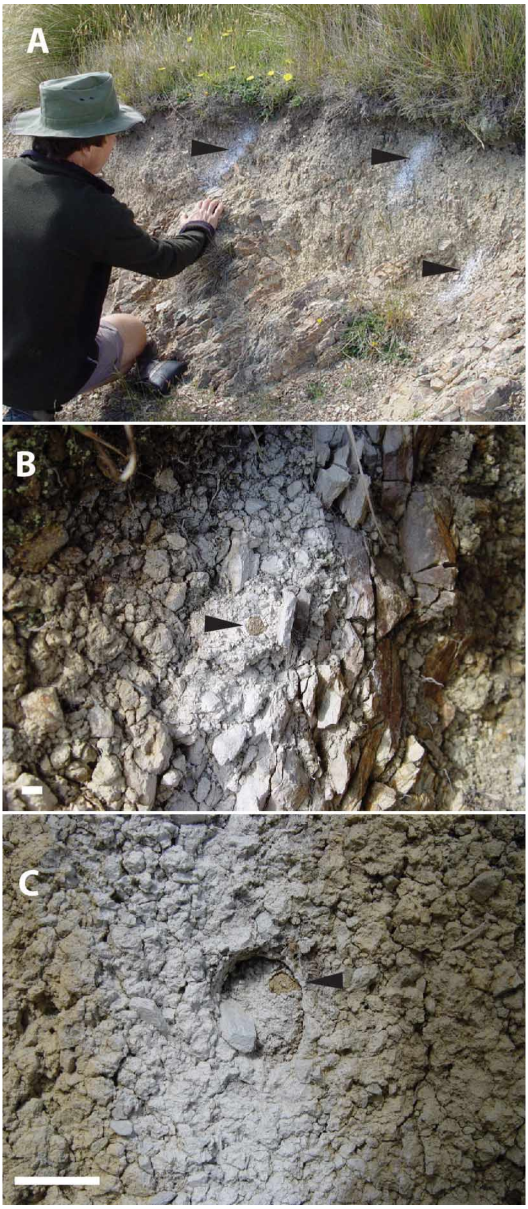

Figure 1 Burrow door reconstruction used to monitor the activity of the New Zealand ground wētā, *Hemiandrus maia* sp. nov. The entrances of burrows were identified and their soil doors were lightly sprayed with white paint. On subsequent days the door of each burrow was examined. Wētā leave their burrow during the night by breaking up the soil plug at the burrow entrance, and on returning to their burrow they rebuild the door using the surrounding soil. **A,** Cutting with three marked burrow entrances of the ground wētā *H. maia* sp. nov. at Kurinui, North Otago indicated by black arrows. **B,** The soil plug (burrow door) after reconstruction is visible against the white paint. **C,** Small circular reconstructions within the burrow door reveal activity of ground wētā nymphs. Scale bar = 10 mm.

specimen localities (Crosby et al. 1976): NN, Nelson; BR, Buller; DN, Dunedin; SL, Southland.

Activity patterns

Detailed observations of *H. maia* sp. nov. were made on a large (750 ha) private land block in the Kurinui Creek catchment, North Otago, New Zealand. The study site is at 482 m above sea level, 45°21′56.2″S, 170°43′02.2″E. At Kurinui, *H. maia* sp. nov. is sympatric with a long-ovipositor ground wētā, *Hemiandrus* 'timaru' (Johns 2001), and both are abundant. Here, we report on observations carried out 24–27 December 2007, 31 December 2009 to 01 January 2010 and 22–23 January 2013.

Night observations were made immediately after dark (22.30 h) in summer. Investigators cautiously searched open ground, forest floor and vegetation to head height by torchlight. Ground wētā observed were captured by hand, sexed and identified, see species description below.

During the day, the entrances of 75 ground wētā burrows were identified on a north-facing cutting and their soil doors were lightly marked with quick-drying white aerosol paint (Fig. 1). Each burrow door was uniquely identified. On the following day and on three subsequent days the door of each burrow was examined. Wētā leave their burrow during the night by breaking up the soil plug at the burrow entrance, and on returning to their burrow they rebuild the door using the surrounding soil. Newly constructed doors were therefore clearly visible as brown against the surrounding white paint (see Figs 1B, 1C). If the door had been reconstructed overnight then this was recorded and the burrow entrance again sprayed with paint. After 3 days of observation, nine of the monitored burrows were excavated, along with a further 11 unmonitored burrows.

Food choice experiment

Eighteen food choice arenas were set up at dusk (21.45 h) at the base of a different earth bank in which *Hemiandrus* had made burrows (Fig. 2A). Each arena was separated by about 2 m on a transect following the base of the earth bank. This spacing was appropriate for the density of wētā indicated by observations made previously. Each 60×60-mm arena was provisioned with three food items held in place with metal pins: 5 mm^3 fresh apricot; whole *Calliphora* sp. fly (previously killed by freezing); 8–12 grains of oatmeal. Apricot was used because this fruit is known to be eaten by wild *Hemiandrus* in orchards (Wahid 1978). *Hemiandrus* have been observed feeding on Diptera in the field so flies were caught on location, killed by freezing and then thawed before placement. Oatmeal was chosen as a surrogate for seed-like plant carbohydrate potentially available to ground wētā and known to be attractive to them (Johns 2001). The food items were arranged as points of a triangle within each arena. Observations were made between 23.00 h and 00.15 h following provisioning. Arenas were checked repeatedly, but each individual animal observed eating was recorded once only to ensure independence, and only when all three foods were available.

Population size estimation

We marked all the ground wētā we could see in a specified area at a particular time. We did this for *H. maia* sp. nov. at Kurinui within an area of approximately 400 m^2, and for *H. electra* sp. nov. at Awaroa (Golden Bay, Tasman District) within an area of approximately 380 m^2. The following night, we counted all the ground wētā in the same area, at the same time, and recorded how many had been marked from the previous night. We estimated population size using the Lincoln–Peterson estimator (Peterson 1896; Lincoln 1930) with the Chapman modification,

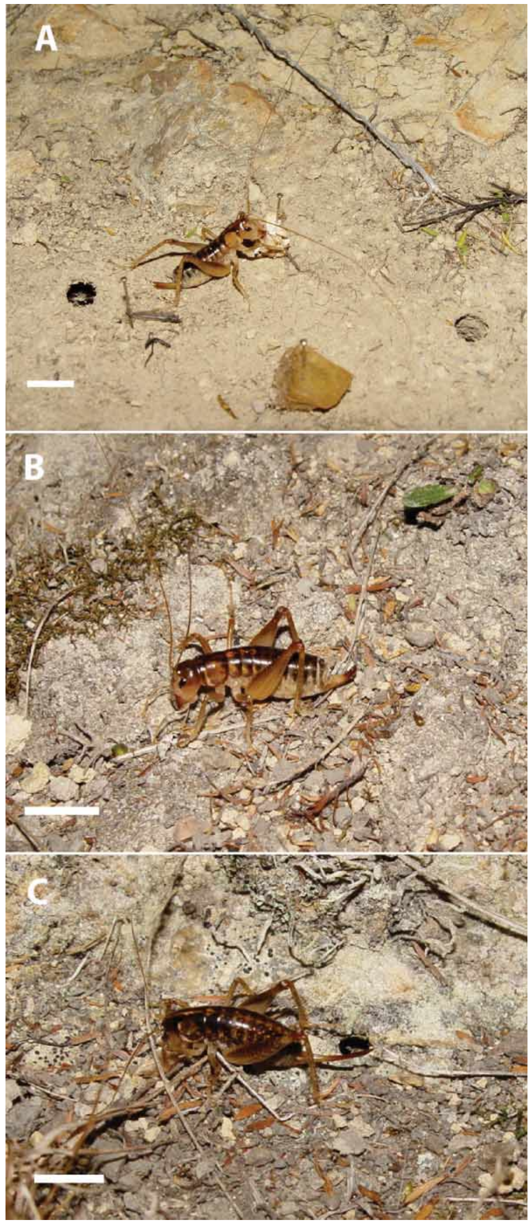

Figure 2 Food choice arenas were set up at the base of an earth bank, the habitat of New Zealand ground wētā, *Hemiandrus maia* sp. nov., at Kurinui, North Otago. Also pictured is a female of the sympatric *Hemiandrus* 'timaru', which is easily distinguished from *H. maia* sp. nov. by its long ovipositor. **A,** Food-choice arena with ground wētā feeding on oats, fly already consumed. **B,** Adult female *H. maia* sp. nov. **C,** Adult female *H.* 'timaru'. Scale bar = 10 mm.

which reduces the bias associated with small population sizes (Chapman 1951), using the following equation:

$$N = \frac{(M+1)(C+1)}{R+1} - 1,$$

where N = Estimate of total population size, M = Total number of animals captured and marked on the first visit, C = Total number of animals captured on the second visit and R = Number of animals captured on the first visit that were then recaptured on the second visit.

Species description: *Hemiandrus maia* sp. nov.
A combination of morphological structures provided useful diagnostic characters for *Hemiandrus* (Fig. 3).

Class: **Insecta**
Order: **Orthoptera**
Suborder: **Ensifera**
Superfamily: **Tettigoniodea**
Family: **Anostostomatidae** Saussure, 1859
Genus: ***Hemiandrus*** Ander, 1938.
Type species: *Hemiandrus furcifer* Ander, 1938

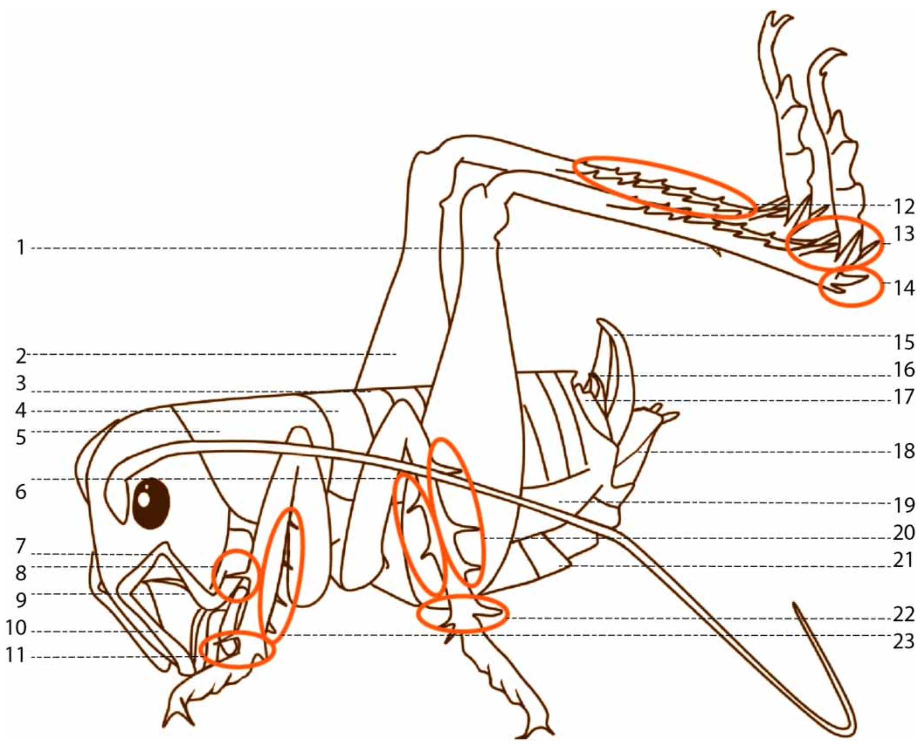

Figure 3 External morphological characters useful in the identification of *Hemiandrus* species. 1. Hind tibia: inferior articulated spines. 2. Hind femur: retrolateral surface. 3. Metanotum. 4. Mesonotum. 5. Pronotum. 6. Mid tibia: superior prolateral spines. 7. MP4. 8. Fore tibia: superior prolateral spine. 9. MP3. 10. MP5. 11. Fore tibia: apical spines. 12. Hind tibia: superior fixed spines. 13. Hind tibia: subapical spines. 14. Hind tibia: apical spines. 15. Cerci. 16. Paranal processes. 17. T10 with falci. 18. Subgenital plate. 19. Pleural membrane. 20. Mid tibia: retrolateral spines. 21. Abdominal sternites. 22. Mid tibia: apical spines. 23. Fore tibia: inferior retrolateral spines.

Diagnosis

A medium-sized ground wētā found in Otago (DN, SL), New Zealand, with the following traits: MP3 bare, MP4 55% pilose, 11 to 17 antennomeres. Body colour when live is orange-brown, pronota with large lateral pale patches; fore tibiae with a single superior prolateral spine (excluding apical spine); mid tibiae with two superior prolateral spines and three superior retrolateral spines (excluding apical spines). Females have moderately short ovipositors and maternal care. Most similar to *H. electra* sp. nov., which is found in northern South Island and distinguished by male terminalia, number of tergal stridulatory pegs and body proportions (Table 1, Fig. 4).

Hemiandrus maia sp. nov. is sympatric in parts of its distribution with *H.* 'timaru', *H. focalis* and *H. maculifrons*, but is distinguishable by body size, ovipositor length, the number of mid tibial spines and MP3 pilosity (Table 2).

Etymology

From the Greek name Maia, the eldest of the Pleiades (in Greek mythology the seven daughters of Pleione and Atlas), meaning 'mother' or 'good mother'. This name is given to this species to reflect the maternal care exhibited. *Hemiandrus maia* is probably the tag-named entity *Hemiandrus* 'evansae' (Johns 2001).

Description

Adult BL: males 16.8–24.7 mm ($n = 13$), females 19.7–25.7 mm ($n = 10$) (Fig. 5).

Head. Head shiny, darker on top; labrum cream, setose; mandibles brown; scape, pedicel and antennomeres cream and light brown; antennae longer than body; flagella composed of 11–17 antennomeres; eyes black; maxillary palps cream; MP5 100% pilose, MP4 55% pilose, MP3 bare.

Thorax. Pronotum wider than long. Pronotum, mesonotum and metanotum dark brown with large pale patches either side of a narrow pale dorsal mid-line. Sternum cream and/or light brown.

Legs. Moderately long (hind femora 2.3 to 2.7 times head width); coxae and trochanters cream and/or brown; femora and tibiae cream with brown patches. Fore tibiae with cream articulated spines with brown tips arranged in asymmetrical form as follows: four apical spines; one spine positioned medially on superior prolateral angle; none on superior retrolateral angle; four along inferior prolateral angle; four along inferior retrolateral angle. Mid tibiae with cream

Table 1 Morphological characters that distinguish the New Zealand ground wētā *Hemiandrus maia* sp. nov. and *Hemiandrus electra* sp. nov.

Character	*H. maia* sp. nov.	*H. electra* sp. nov.
Length of hind femora relative to head width	2.3–2.7 times longer	2.7–3.1 times longer
Number of stridulatory pegs on T1-T3	T1: 50–70 T2: 60–80 T3: 30–60	T1: 90–120 T2: 130–170 T3:100–150
Male terminalia:		
Subgenital plate and T8-T10		
Subgenital plate	Notched posterior margin	Simple or very slightly concave posterior margin
T8	Median lobe	Simple
T9	Flattened lobe	Weakly bilobed
T10	Pale between falci	Grey between falci

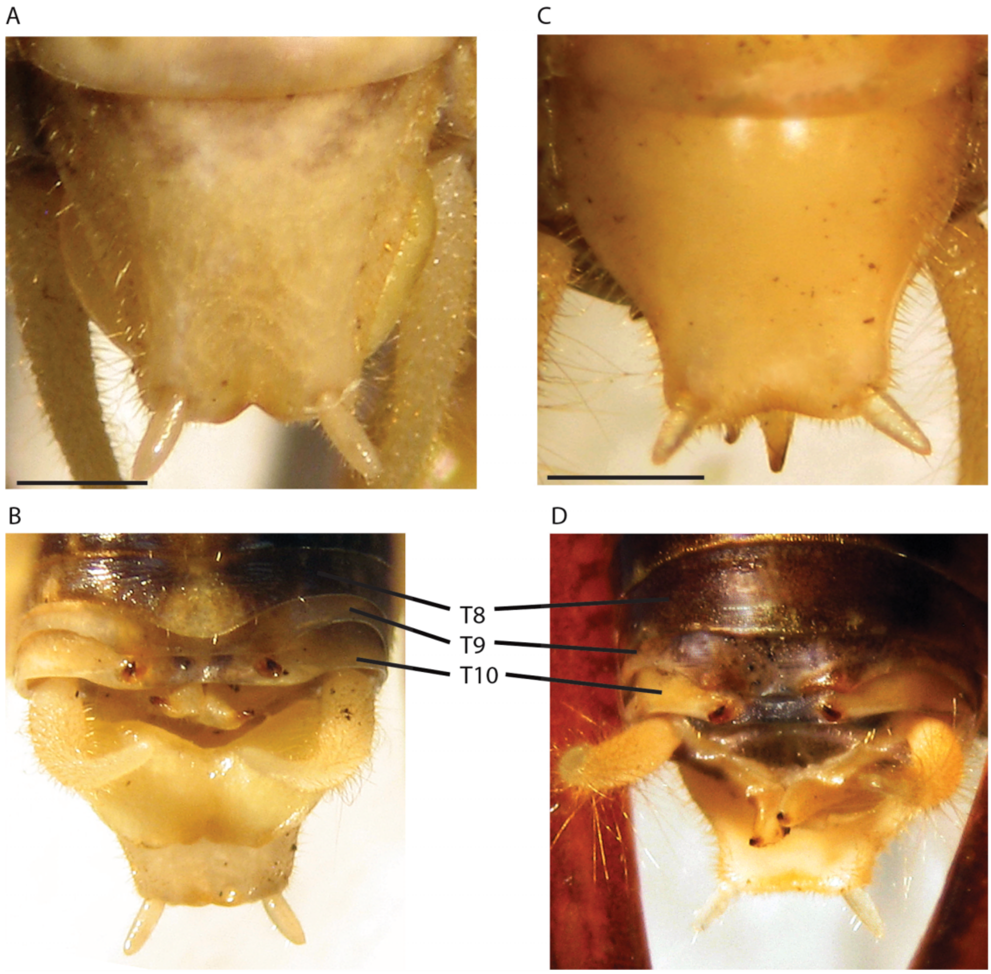

Figure 4 *Hemiandrus maia* sp. nov. adult male. **A,** Subgenital plate (ventral view). **B,** Male terminalia (dorsal view). *Hemiandrus electra* sp. nov. adult male. **C,** Subgenital plate (ventral view). **D,** Male terminalia (dorsal view). T8 dashed line, T9 dotted line, T10 solid line. Scale bar = 1 mm.

articulated spines with brown tips arranged asymmetrically as follows: four apical spines; two spines spaced along superior prolateral angle; three spines spaced along superior retrolateral angle; four spines spaced along inferior retrolateral angle; four spines spaced along inferior prolateral angle. Hind tibiae with articulated cream spines with brown tips arranged as follows: four apicals; two very large sub-apical spines on each of the superior prolateral and retrolateral angles. Seven to nine fixed spines spaced along the superior prolateral and retrolateral angles. Two to four very small articulated spines positioned along the inferior prolateral angle and zero to two on the inferior retrolateral angle. Hind femora with a patch of 5–40 stridulatory pegs on the retrolateral surface. Tarsi cream, setose, four-segmented, first segment with foot-pad divided into two, other segments with a single foot-pad.

Abdomen. Shiny brown with a pale dorsal midline and pale patches either side of the abdomen; each tergite lighter anteriorly, darker posteriorly,

Table 2 Morphological characters that distinguish the New Zealand ground wētā *Hemiandrus maia* sp. nov. from other *Hemiandrus* found within its range. Mid-tibial superior retrolateral spines excludes apical spines unlike Johns (2001).

Character	*H. maia* sp. nov.	*H.* 'timaru'	*H. focalis*	*H. maculifrons*
Body size	Medium	Small	Large	Small
(Adult head width as proxy)	4.9–6.9 mm	4.9 mm	6.8–9.6 mm	3.7–4.9 mm
	$n = 23$	$n = 2$	$n = 4$	$n = 67$
Ovipositor length	Moderately short	Long	Long	Long
Mid-tibial superior retrolateral spines	3	2	3	3
MP3 pilosity	None	None	None	Approx. 33%

sometimes giving a banded effect; sides of the abdomen dull and pilose; pleural membrane brown or cream and pilose; sternites cream but darker and more pilose towards lateral and anterior edges; T1 with 50–70 stridulatory pegs on each side; T2 with 60–80 stridulatory pegs on each side; T3 with 30–60 stridulatory pegs on each side; fourth and fifth tergites with fewer pegs; cerci cream.

Males. Cerci blunt, setose; eighth abdominal tergite T8 margin medially lobed; ninth abdominal tergite T9 margin with a flattened lobe; T10 between falci pale; subgenital plate with notched posterior margin; paranal processes long, pointed with darkened tip (Fig. 4).

Females. T9 simple; paired pits on sixth sternite; cerci long, pointed, bare tip; ovipositor moderately short: 6.5–8.6 mm ($n = 8$).

Distribution. Southeast South Island New Zealand; Otago and Southland (DN, SL) (Fig. 6A). They have been collected from the following localities: Kurinui Creek catchment, North Otago (DN) (45°21′56.2″S, 170°43′02.2″E); Caversham, Dunedin (DN) (45°53′54.5″S, 170°28′34.6″E); Portobello, Otago (DN) (45°50′22.3″S, 170°39′07.6″E); Blue Mountains (SL) (45°56′19.5″S, 169°21′13.2″E).

Type data

Holotype: Adult male (Fig. 5A): 17.1 mm collected January 2010 from Kurinui (DN) (45°21′56.2″S, 170°43′02.2″E) Hampden, North Otago, SA Trewick and M Morgan-Richards (MONZ AI.031569; GW 764). Paratype adult female (Fig. 5B): 22.6 mm, collected January 2006 from Kurinui (DN) (45°21′56.2″S, 170°43′02.2″E) Hampden, North Otago, SA Trewick and M Morgan-Richards (MONZ AI.031570; GW115).

Additional material examined

Caversham, Dunedin (DN) (GW 06A; 6B; 11; 37A; 37B; 38B); Portobello, Dunedin (DN) (GW 125, GenBank accession EU676744); Blue Mountains (SL) (GW 135; 136, GenBank accession EU676780); Kurinui, Hampden, North Otago (DN) (GW 116; 117; 118, GenBank accession EU676795; GW264; 265; 266; 405; 406; 407; 408; 503; 504; 505; 519; 520; 521; 619). These specimens are held in the Phoenix collection, Massey University.

Species description: *Hemiandrus electra* sp. nov.

Diagnosis

A medium-sized ground wētā found in Nelson, Marlborough, Tasman and West Coast (NN, BR), New Zealand, with the following traits: MP3 bare, MP4 55% pilose, 13 to 18 antennomeres. Body colour when live is red-brown, pronota with large lateral pale patches; fore tibiae with a single superior prolateral spine (excluding apical spine); mid tibiae with two superior prolateral spines and three superior retrolateral spines (excluding apical spines). Females have moderately short ovipositors. Most similar to *H. maia* sp. nov. and distin-

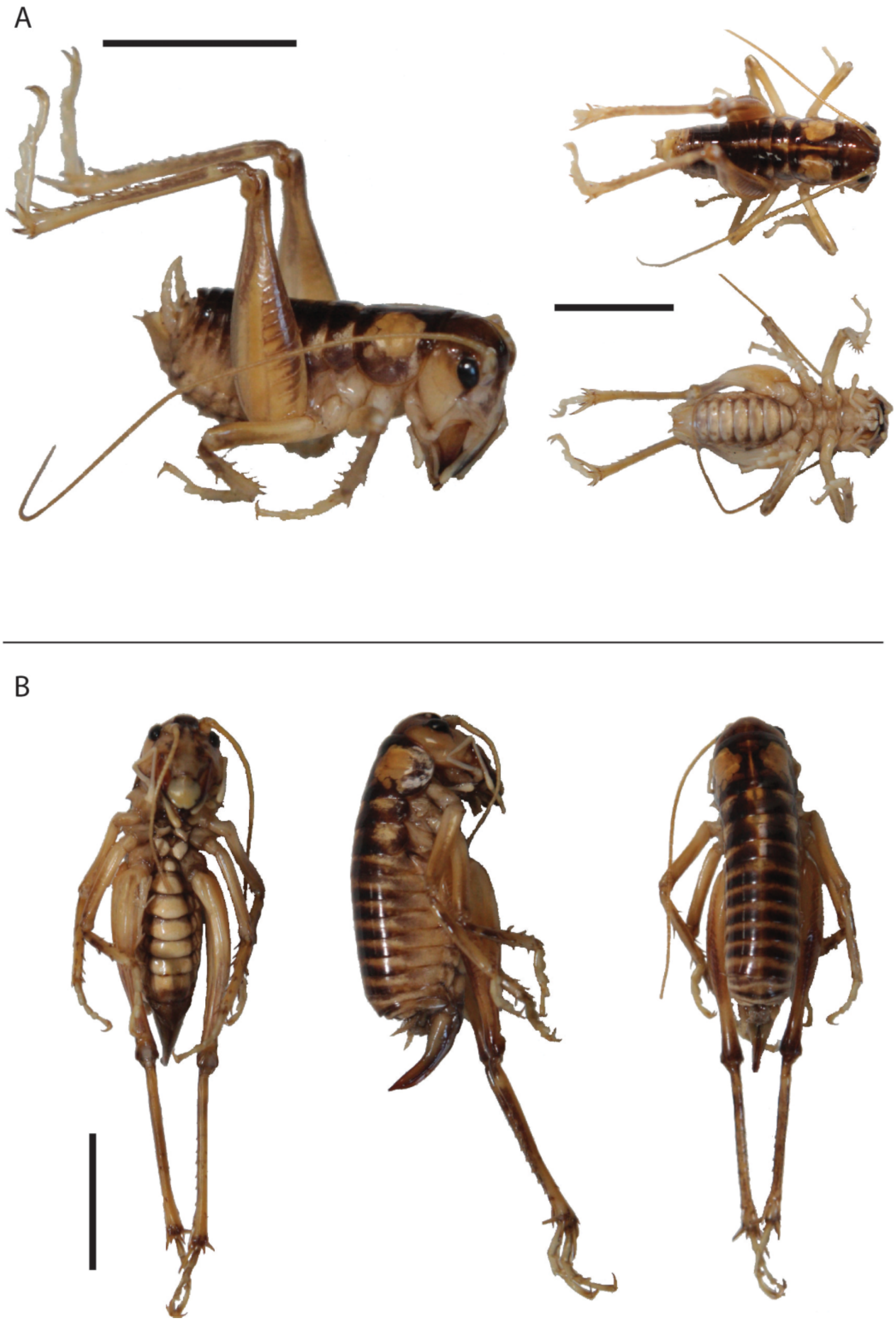

Figure 5 *Hemiandrus maia* sp. nov. **A,** Adult male. **B,** Adult female. Scale bar = 10 mm.

guished by number of tergal stridulatory pegs, male terminalia and body proportions (Table 1). *Hemiandrus electra* sp. nov. is sympatric in parts of its distribution with *Hemiandrus* 'alius', *Hemiandrus* 'disparalis', *H. maculifrons*, and possibly *Hemiandrus* 'vicinus'. *Hemiandrus electra* sp.

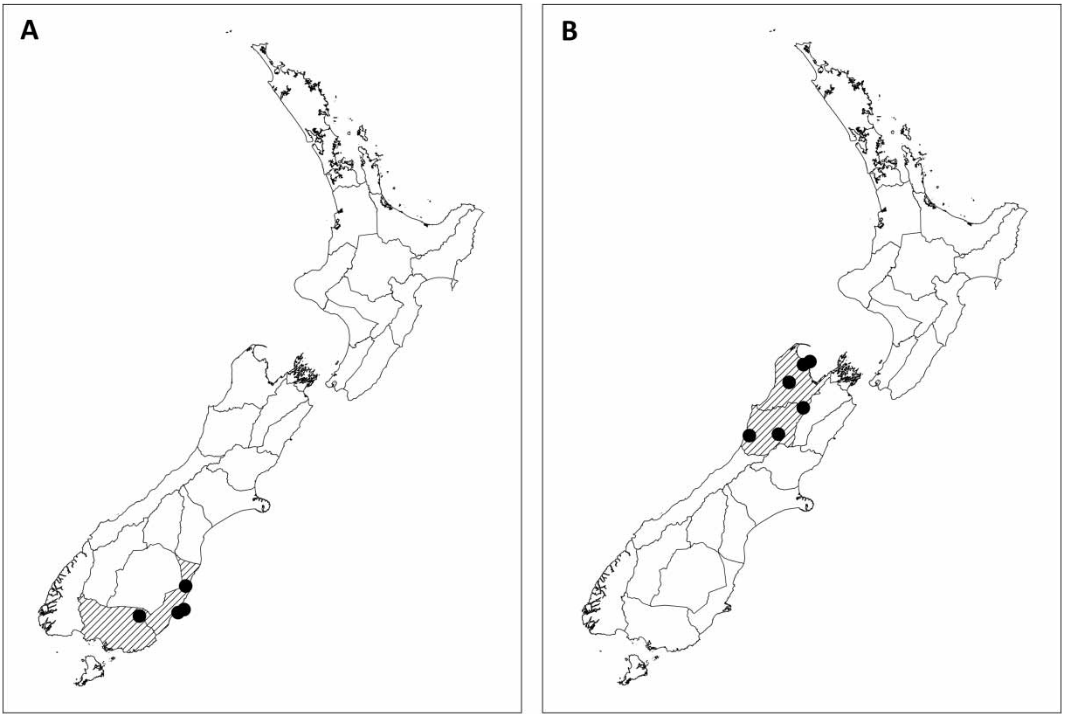

Figure 6 The distributions of two New Zealand ground wētā, showing the Crosby et al. (1976) regions in which they have been recorded. Spots indicate position of sites reported in the descriptions. **A,** *Hemiandrus maia* sp. nov. is known from southeast South Island (DN, SL). **B,** *Hemiandrus electra* sp. nov. from northwest South Island (NN, BR).

nov. can be distinguished from these species by ovipositor length, the mid-tibial spines and MP3 pilosity (Table 3).

Etymology

From the Greek name Elektra, in Greek mythology one of the seven Pleiades (daughters of Pleione and Atlas). Elektra is sister to Maia, a reference to the morphological similarity of *H. electra* sp. nov. and *H. maia* sp. nov. The name Elektra is derived from elektron meaning 'amber' and related to elektros meaning 'shining, bright', and is applied here in reference to the bright orange colour of this species. *Hemiandrus electra* sp. nov. is probably the tag-named entity *Hemiandrus* "okiwi" (Johns 2001).

Table 3 Morphological characters that distinguish the New Zealand ground wētā *Hemiandrus electra* sp. nov. from other *Hemiandrus* found within its range. Mid-tibial superior prolateral spines excludes apical spines unlike Johns (2001).

Character	*H. electra* sp. nov.	*H.* 'vicinus'	*H.* 'alius'	*H.* 'disparalis'	*H. maculifrons*
Ovipositor length	Moderately short	Short	Long	Very long	Long
Mid-tibial superior prolateral spines	2	1	2	2	2
MP3 pilosity	None	None	Approx. 30%	None	Approx. 30%

Description

Adult BL: males 14.9–21.4 mm ($n = 14$), females 18.4–24.1 mm ($n = 7$) (Fig. 7).

Head. Head shiny, darker on top; labrum cream, setose; mandibles brown; scape, pedicel and antennomeres cream and light brown; antennae longer than body; flagella composed of 13–18 antennomeres; eyes black; maxillary palps cream; MP5 100% pilose, MP4 55% pilose, MP3 bare.

Thorax. Pronotum wider than long. Pronotum, mesonotum and metanotum dark brown with large pale patches either side of a narrow pale dorsal mid-line. Sternum cream and/or light brown.

Legs. Long (hind femora 2.7 to 3.1 times head width); coxae and trochanters cream and/or brown; femora and tibiae cream with brown patches. Fore tibiae with cream articulated spines with brown tips arranged in asymmetrical form as follows: four apical spines; one spine positioned medially on superior prolateral angle; none on superior retrolateral angle; four along inferior prolateral angle; four along inferior retrolateral angle. Mid tibiae with cream articulated spines with brown tips arranged asymmetrically as follows: four apical spines; two spines spaced along superior prolateral angle; three spines spaced along superior retrolateral angle; four spines spaced along inferior retrolateral angle; four spines spaced along inferior prolateral angle. Hind tibiae with articulated cream spines with brown tips arranged as follows: four apical spines; two very large sub-apical spines on the superior prolateral and retrolateral angles. Seven to nine fixed spines spaced along the superior prolateral and retrolateral angles. Two to four very small articulated spines positioned along the inferior prolateral angle and zero or one on the inferior retrolateral angle. Hind femora with a patch of 40–70 stridulatory pegs on the retrolateral surface. Tarsi cream, setose, four-segmented, first segment with foot-pad divided into two, other segments with a single foot-pad.

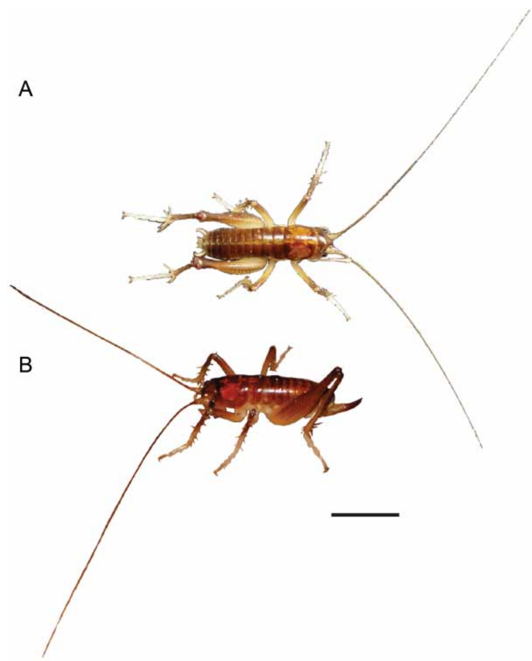

Figure 7 *Hemiandrus electra* sp. nov. **A,** Adult male. **B,** Adult female. Scale bar = 10 mm.

Abdomen. Shiny orange-brown with a pale dorsal midline; pleural membrane brown or cream and pilose; sternites cream but darker and more pilose towards lateral and anterior edges; first tergite with 90–120 stridulatory pegs on each side; T2 with 130–170 stridulatory pegs on each side; T3 with 100–150 stridulatory pegs on each side; fourth and fifth tergites with fewer stridulatory pegs; cerci cream.

Males. Cerci blunt, setose; T8 margin simple; T9 margin weakly bilobed; T10 area between falci grey; subgenital plate posterior margin simple to slightly concave; paranal processes long, pointed with darkened tip (Fig. 4).

Females. T9 simple; paired pits on sixth sternite; cerci long, pointed, bare tip; ovipositor moderately short. 6.1–6.7 mm ($n = 4$).

Distribution. Northwest South Island; Nelson, Marlborough, Tasman and West Coast (NN, BR), New Zealand (Fig. 6B). They have been collected from the following localities: Awaroa, Tasman (NN) (40°51′54.1″S, 173°01′55.4″E); St Arnaud, Tasman (BR) (41°48′06.1″S, 172° 51′00.6″E); Kahurangi National Park, Tasman (NN) (41°17′08.2″S, 172°28′16.8″E); Rameka, Tasman (NN) (40°55′35.5″S, 172°51′27.3″E); Blackball, West Coast (BR) (42°21′07.7″S, 171°22′43.5″E); Spring's Junction, West Coast (BR) (42°19′54.6″S, 172°10′20.9″E).

Type data

Holotype: Adult male (Fig. 7A): 19.3 mm, collected January 2012 from Awaroa, Tasman (NN) (40°51′54.1″S, 173°01′55.4″E), SA Trewick and M Morgan-Richards (MONZ AI.031571; GW719). Paratype adult female (Fig. 7B): 22.9 mm, collected February 2005 from Awaroa, Tasman (NN) (40°51′54.1″S, 173°01′55.4″E), SA Trewick and M Morgan-Richards (MONZ AI.031572; GW86A).

Additional material examined

Awaroa, Tasman (NN) (GW 67; 86B; 476; 477; 589; 718; 720; 721; 722; 723; 724; 791; 795); St Arnaud, Tasman (BR) (GW 43; 138, GenBank accession EU676783; GW 140; 482); Kahurangi National Park, Tasman (NN) (GW 96); Rameka, Tasman (NN) (GW 101, GenBank accession EU676741; GW 103; 107; 579; 580); Blackball, West Coast (BR) (GW 124); Spring's Junction, West Coast (BR) (GW 460). These specimens are held in the Phoenix collection, Massey University.

Results and discussion

Night observations at Kurinui, Otago

Hemiandrus maia sp. nov. (Fig. 2B) were observed in the field to feed on naturally available invertebrates (including moths, flies, bees and freshly emerged antlions). All ground wētā were observed on the ground or on vegetation < 50 cm from the ground. Two *Hemiandrus* species were observed at night, in the same area, however, no burrows of the long-ovipositor ground wētā (*H.* 'timaru') were identified (Fig. 2C). At dusk, some ground wētā removed their burrow doors and sat at the entrance. Nymphs of *H. maia* sp. nov. left burrows via small holes made within larger burrow doors (Fig. 1C).

Activity

Seventy-five ground wētā burrows were marked and observations were made of door reconstructions over 3 days, involving 225 burrow-nights in total. Sixty-six percent of all burrows showed evidence of wētā activity during one, two or three nights (Fig. 8A). Most burrow entrances were closed with a circle of new soil approximately 10 mm in diameter (Fig. 1B). On two occasions (from $n = 225$ observations) burrow entrances were not resealed during the day. This comprised one small hole, and one normal-sized entrance that was subsequently closed.

We observed that some burrows had only a small circular section (1–2 mm in diameter) of their doors reconstructed (Fig. 1C) and these burrows were scored as 'not active' as a full-grown wētā would require a larger hole for exiting the burrow. However, night observations showed that in some doors of normal size (approximately 10-mm diameter) a small hole was made and wētā nymphs left the burrow by this means. In our set of 75 marked burrows, nine had small holes made and filled during one or two nights, and three of these also had the full door reconstructed on other nights (Fig. 8A).

A third of all burrows that we marked remained inactive over all three nights. Five burrows (6.7%) were open and closed on each of the three sequential nights, 11 burrows (14.7%) were open and closed on two of the three nights and 34 burrows (45%) were opened and closed once during the three nights. Each night, between 19 (25%) and 31 (41%) of the burrows showed sign of wētā activity. These

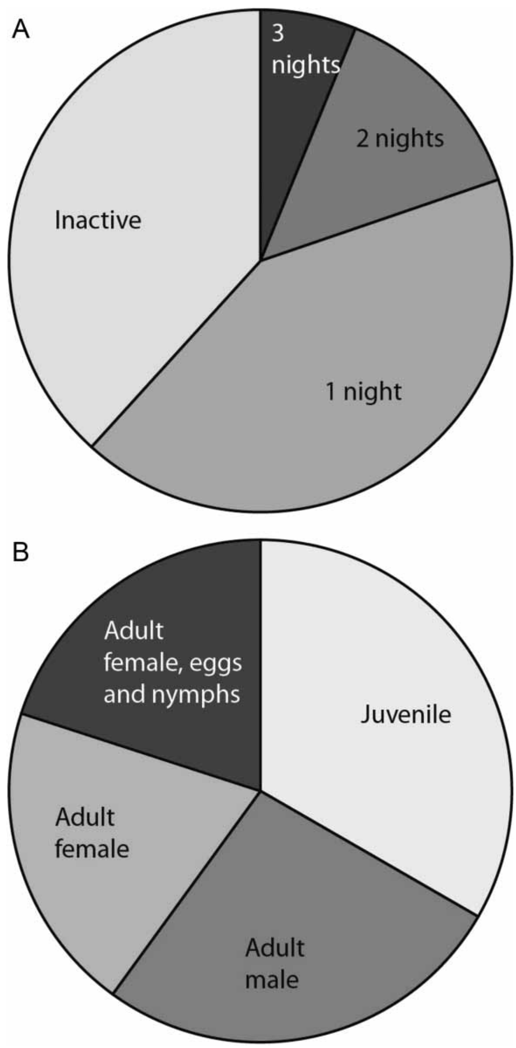

Figure 8 Activity and occupancy of burrows by the ground wētā *Hemiandrus maia* sp. nov. **A,** The proportion of wētā that were active each night as measured by burrow door reconstruction over three nights ($n = 75$ burrows), six of the burrows recorded as inactive showed evidence that ground wētā nymphs had emerged. **B,** Occupancy of burrows determined by excavation of sealed burrows ($n = 15$).

ground wētā were therefore, on average, active once every 3.17 nights during our observations.

An additional observation night was made following excavation of nine burrows and so represents a smaller sample size. The supplemented data provided these statistics: 76% of burrows showed evidence of wētā activity during one, two or three nights (never four); 24% of 67 burrows remained inactive over all four nights. Eight burrows (12%) were open and closed on three nights, 18 burrows (27%) were active on two of the four nights and 25 burrows (37%) were active once during the four nights. Each night between 17 (25%) and 29 (43%) burrows showed sign of wētā activity. These expanded data provide a similar estimate that these ground wētā were, on average, active once every 3.15 nights.

Burrow occupancy

Twenty burrows were excavated. Burrows were about 8–12 mm wide, and ranged between 25 and 205 mm in length. Most extended horizontally into the bank, but others curved gently downwards for 50–100 mm. Many open burrows that we observed were probably made or used by ground wētā, but were now unoccupied and lacked soil plugs (doors). We found dead ground wētā in two burrows without doors and three doorless burrows were empty. All 15 sealed burrows that we opened contained live ground wētā (Fig. 8B); however, four of these also had the remains of a dead ground wētā (*H. maia* sp. nov). Six burrows that showed no sign of wētā activity over three nights each contained a live ground wētā; three juveniles (two male, one unknown sex), one adult male, one adult female with eggs, one adult female with nymphs. Of the two excavated burrows that had been active twice in three nights, one contained a single adult male and the other a single adult female. One burrow, home to an adult male, had a new door on all three nights.

Of the 15 excavated burrows containing wētā (nine monitored, plus six not monitored) six contained adult females (Fig. 8B), and half these wētā had eggs and/or nymphs with them. One adult female was observed inside her burrow with 12 wētā nymphs (see Fig. 9). There were empty egg shells on the soil of the walls

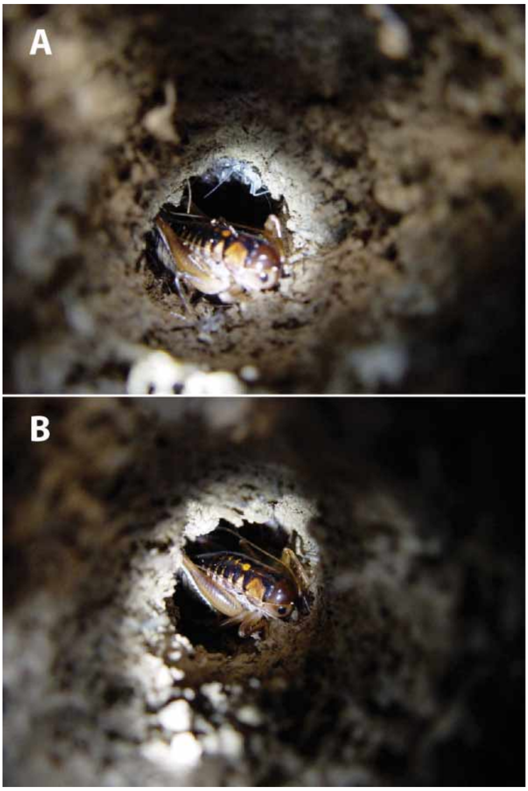

Figure 9 Female ground wētā *Hemiandrus maia* sp. nov. 'the good mother', exhibits maternal care of eggs and nymphs.

and ceiling of the burrow. On initial observation nymphs and adult all faced the burrow entrance. All excavated burrows contained the species *H. maia* sp. nov.

Feeding

Three insect taxa were observed feeding in the food-choice arenas: Rhaphidophoridae cave wētā (*Isoplectron*); Blattidae cockroaches (*Celatoblatta*); Anostostomatidae ground wētā (*Hemiandrus*). A total of 25 independent observations were made (Table 4).

Hemiandrus were seen feeding on all three of the available foods (Fig. 2A). In two instances, *Hemiandrus* individuals were observed eating oatmeal when the fly was gone, so these observations were not recorded, because consumption of the fly was not observed. Overall the cave wētā and the ground wētā ate at random, but the cockroaches showed a significant preference for the fruit ($P = 0.0009$ chi-square test). Although an important ecological association between ground wētā and fruit has been suggested (Burns 2006; but see Morgan-Richards et al. 2008), our data suggest that cockroaches might have a closer interaction with fruit than ground wētā, highlighting the limited understanding of native insect interactions with plants.

Table 4 Nocturnal insect feeding observations at food-choice arenas at Kurinui, North Otago, New Zealand. Records are independent and restricted to situations where all three foods were available.

	Oat	Fruit	Fly
Cave wētā	2	1	5
Ground wētā	5	3	2
Cockroach	0	7	0
Total	7	11	7

Population size estimation

On the first night 37 *H. maia* sp. nov. were marked at Kurinui, Otago (10 adult/subadult males; 7 adult females; 18 juveniles; 2 nymphs). On the second night, 73 wētā were observed (13 adult/subadult males; 16 adult females; 40 juveniles; 3 nymphs), of which three adult males were recaptures. We calculated population size to be 702 ± 298, with a population density of 1.8 wētā/m^2.

On the first night, 15 *H. electra* sp. nov. were marked at Awaroa, Tasman (12 adult/subadult males; 3 adult females). On the second night, 12 wētā were observed (all adult/subadult males), one of which was a recapture. We calculated population size to be 103 ± 52, with a population density of 0.3 wētā/m^2.

Conclusions

The Otago ground wētā, *H. maia* sp. nov., uses burrows during the day that are sealed with a new soil plug each time the wētā returns from nocturnal excursions. Even apparently inactive burrows contained wētā, and if we use the data from excavated burrows to extrapolate to the full set of burrows then all 75 probably contained live wētā, and about 20% might have had adult females with nymphs. We saw small holes (too small for adults to use) in nine (12%) of the burrow doors (Fig. 1C). All burrows contained *H. maia* sp. nov. *Hemiandrus* 'timaru' apparently have homes in other habitats, possibly the forest floor nearby.

During late December *H. maia* sp. nov. is, on average, active about once in every three nights. *Hemiandrus maia* sp. nov. feed on the ground where they eat invertebrates, fruit and seed contents. The females of *H. maia* sp. nov. share burrows with their eggs and nymphs. Nymphs exit and enter via small openings in the door of the burrow, even when the adult female does not emerge. Maternal care in this species has probably been independently derived, as this medium-ovipositor species is not closely related to short-ovipositor species in which this behaviour has previously been observed (Gwynne 2005). Many wētā die in their burrows, which are re-used. It is rare for a burrow entrance not to be re-sealed if a wētā is using it as a day-time hide.

Independent reduction of ovipositor length in the northern South Island wētā, *H. electra* sp. nov. might also be correlated with maternal care of eggs and nymphs. This prediction could be tested with a similar study of *H. electra* sp. nov. Sympatry with long-ovipositor species might drive selection for care of young; investigations to seek evidence of character displacement in this genus would be very rewarding.

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