

Captive-rearing of the Middle Island tusked wētā

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C.J. Winks, S.V. Fowler, and G.W. Ramsay

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Captive-rearing of the Middle Island tusked wētā

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ABSTRACT

The biology of the endangered Middle Island tusked wētā (*Motuweta isolata*) was investigated using captive-reared wētā. The project aimed to develop a reliable captive-rearing method for the Middle Island tusked wētā in order to produce sufficient numbers to enable releases to be made on islands neighbouring its sole island home—Middle Island—in the Mercury Islands, North Island, New Zealand. Micro-habitat conditions were measured in wētā habitat on Middle Island, and at a proposed release site on Double Island. Data on developmental rates, mortality, oviposition substrate preference, fecundity, and behaviour were recorded for captive Middle Island tusked wētā. Conditions leading to successful breeding in captivity were recorded. This project followed on from a previous project, which identified several factors affecting breeding success. Resulting modifications to the rearing method succeeded in reducing the mortality of juveniles and adults, and in improving oviposition success and egg hatch-rate.

Keywords: Middle Island tusked wētā, *Motuweta isolata*, captive-rearing

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1. Introduction

An investigation into aspects of the biology of the endangered Middle Island tusked wētā (*Motuweta isolata*) was carried out by Landcare Research, Mt Albert, Auckland, for the Department of Conservation (DOC), between July 1998 and June 2001. This project followed on from a previous DOC project (Winks & Ramsay 1998).

2. Background

The critically endangered Middle Island tusked wētā, *Motuweta isolata* Johns (Anostostomatidae) (Johns 1997) (Fig. 1), occurs only on Middle Island, a 13-ha island in the Mercury Islands group, located off the eastern Coromandel coast, North Island, New Zealand. The Mercury Islands group consists of seven islands, ranging from 3 to 1860 ha, plus several small unnamed stacks and islets (Fig. 2). With the exception of Great Mercury Island, which is privately owned, all islands in the group are administered by DOC as part of the Hauraki Gulf Maritime Park (Towns et al. 1990). Middle Island has a dense and diverse invertebrate and reptile fauna, and a large population of burrowing seabirds. The vegetation, although not necessarily unaltered by Polynesians, appears to

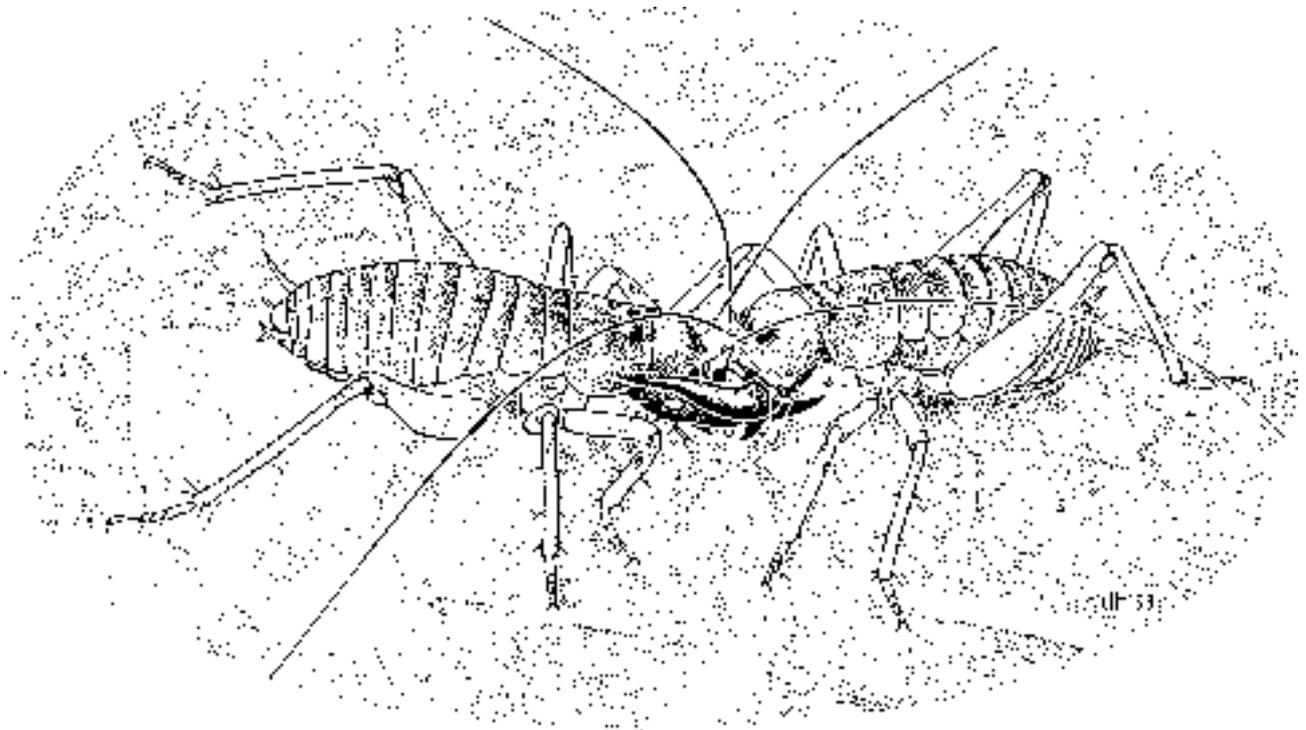


Figure 1. Adult male Middle Island tusked wētā. (Illustration by D.W. Helmore, Landcare Research.)

have been little disturbed for a considerable time. This is unusual for a northern New Zealand island. Also, there is no record of any land mammals on Middle Island (Atkinson 1964). However, the tusked wētā population probably suffers intense predation from abundant native lizards, tuatara, and giant centipedes.

Despite its large size (up to 70 mm in body length), the Middle Island tusked wētā was only discovered in 1970 (A. Whitaker pers. comm.). In captivity, males have been recorded at 28 g, and females at 37 g. However, field-measured wētā are generally smaller, with males up to 22.8 g and females up to 25.0 g (McIntyre 1998a). The thoracic shield and dorsal surfaces of the abdominal tergites are orange-red, with brown patches. The adult male has prominent tusks (outgrowths of the mandible) which curve forward and cross at the tips. The wētā are nocturnal and during the day shelter in sealed underground chambers.

Two other species of tusked wētā are known to be present in New Zealand. The Northland tusked wētā (*Hemiandrus monstrosus*) was first described in 1950 (Salmon 1950). This was re-named (synonymised) as *Anisoura nicobarica* Ander by Johns (1997). The Northland tusked wētā is much smaller than the Middle Island tusked wētā, measuring up to 21 mm in body length. The second species, the Raukumara tusked wētā, was discovered in the early 1990s and remains undescribed. It measures 30–40 mm in body length (McIntyre 1998b).

Because its entire population is confined to one small island, the Middle Island tusked wētā is extremely vulnerable. A ranking system developed to aid DOC in determining priorities for the conservation of New Zealand's threatened plants and animals placed the Middle Island tusked wētā in 'Category A' or 'Highest Priority Threatened Species' (Tisdall 1994). To minimise the threat of extinction, DOC recommended the establishment of new wētā populations on

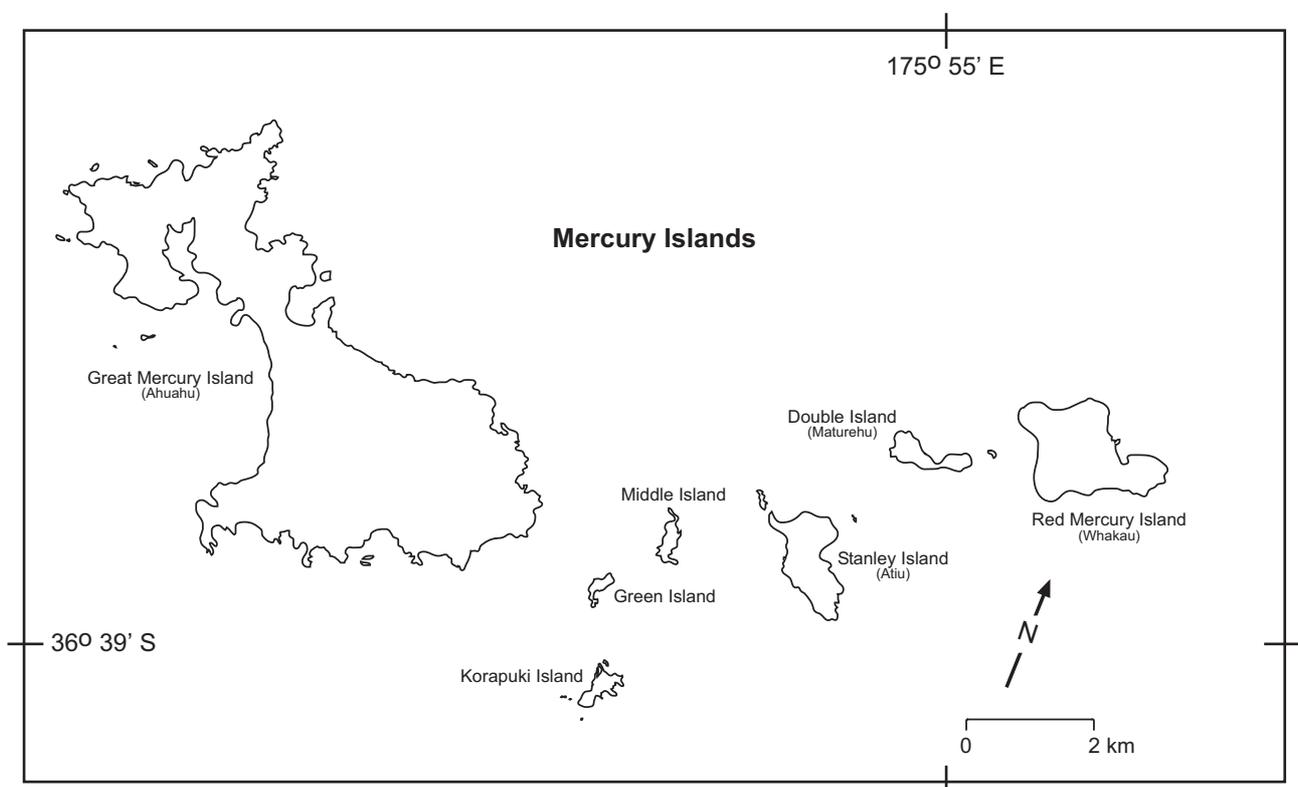


Figure 2. The Mercury Islands.

neighbouring islands. The two islands chosen for the first releases of wētā—Double Island and Red Mercury—were the subject of a successful rodent eradication programme during the early 1990s. The wētā population on Middle Island was not thought to be large enough to enable adequate numbers to be directly translocated without putting its survival on Middle Island at risk. Hence, captive breeding was necessary.

In November 1993, two juvenile female Middle Island tusked wētā were transferred from Middle Island to rearing facilities at the Mt Albert Research Centre. They were joined by an adult male in 1994. High juvenile and adult mortality, low oviposition success, and low egg hatch-rate caused difficulties during these initial attempts to rear this species (Winks & Ramsay 1998). However, important information was gained about the biology of the Middle Island tusked wētā which led to improvements in captive-rearing methods that were applied during the trials described in this report.

This report presents data and observations from trials carried out on one male and two female wētā (collected on Middle Island as juveniles during 1998) and their offspring. Data are also presented on micro-habitat conditions measured in wētā habitat on Middle Island, and at a proposed release site on Double Island.

3. Objectives

To improve captive-rearing methods of the Middle Island tusked wētā by:

- Obtaining micro-habitat data from wētā habitat on Middle Island to use as a basis for the broad simulation of field conditions in the captive-rearing facility
- Recording conditions in captivity that lead to successful breeding
- Measuring oviposition substrate preference and fecundity of female wētā
- Recording duration and mortality of all available wētā life stages
- Recording food preferences and observations of defence and aggression, burrowing, mating behaviour, oviposition, and moulting.

To improve post-release survival chances of the Middle Island tusked wētā by obtaining micro-habitat data from a proposed release site on Double Island for comparison with micro-habitat data from Middle Island.

4. Methods

4.1 MICRO-HABITAT CONDITIONS ON MIDDLE AND DOUBLE ISLANDS

In November 1994, a 'Datataker' 50 data-logger was installed in tusked wētā habitat on Middle Island, and also at a proposed release site on Double Island. The data-loggers were connected to a temperature probe, which measured air temperature at approximately 1 m above ground level, and an 'Aqua-tel+S+T' probe which measured soil temperature and soil moisture content 10 cm below ground level. A rain gauge was connected to the data-logger on Middle Island. Solar panels to keep the batteries charged were used from March 1995.

DOC staff assisted with downloading information from the data-loggers and installing new memory cards during routine visits to the islands. Data from the downloaded memory cards were transferred to a computer for analysis.

4.2 REARING CONDITIONS

4.2.1 Temperature and lighting

Rearing was carried out in a room approximately 3 m × 3 m. From mid-autumn to mid-spring, air circulation was provided by two fans drawing air in from outside the building. However, during the warmer months temperature control and air circulation were provided by an air-conditioning unit. A data-logger recorded temperature. Lighting was provided by a lamp connected to a time switch which enabled the photoperiod to be adjusted. Middle Island tusked wētā are very sensitive to light and on Middle Island they are generally not found out of their underground chambers on moonlit nights (McIntyre 1998a). Therefore, care was taken to ensure the room was completely dark when the lights were off. The temperature regime was based on temperature data obtained from Middle Island, and day lengths in the rearing room corresponded to day lengths at the latitude of Middle Island.

4.2.2 Individual rearing containers

Early-instar wētā were kept in plastic lunch boxes (22 cm × 14 cm × 9 cm). Ventilation holes, in the lid and/or sides, were covered with fine stainless steel mesh. At about fourth or fifth instar, juveniles were shifted into larger containers (35 cm × 25 cm × 15 cm). Adults and subadults were housed in containers measuring at least 60 cm × 40 cm × 35 cm. One wētā was kept per container, unless a pair were together for mating.

Moist, fine-grade vermiculite was provided to a depth of 3–5 cm in the small containers, 6–8 cm in the medium-sized containers, and 10–15 cm in the large containers. Water was added to the vermiculite when necessary to keep it moist. Sprigs of vegetation were heaped into piles inside the containers. Living conditions were kept as clean as possible by removing any mouldy food or vegetation.

4.2.3 Breeding cages

Breeding cages (100 cm × 80 cm × 60 cm) consisted of a wooden frame with stainless steel mesh covering four sides. Clear perspex panels, attached with wing nuts, covered the two smaller sides of the cages, and allowed easy access. For shelter, adult wētā were provided with a two-litre plastic ice cream container, with the lid in place and an entrance hole cut in one side. The adult wētā were content to use this as their 'chamber' and usually did not construct their own underground chamber even if suitable conditions were available. This enabled the adult wētā to be managed more easily than if they were sealed in their own underground chambers.

4.3 OVIPOSITION SUBSTRATE PREFERENCE TRIAL

Two adult female wētā (98A and 98B), collected as juveniles from Middle Island during 1998, were held individually in breeding cages. The females were allowed access to the adult male, also originating from Middle Island during 1998, at regular intervals (every 3–4 weeks, for about 2 days at a time). The females were not mated until several weeks after reaching adulthood because there was evidence that mating them too soon after this transition could be detrimental to them (Winks & Ramsay 1998).

Oviposition substrate was provided in two-litre ice cream containers with drainage holes. A 1-cm layer of fine pumice in the bottom enabled the substrate to be kept moist, but not waterlogged. Three substrates were tested: soil; a peat/pumice mix (67% peat, 33% pumice); and a soil/peat/pumice mix (50% soil, 33.5% peat, 16.5% pumice). Two randomised blocks of the three substrates were presented simultaneously to each female, making a total of six substrate containers per cage. A batch of six such substrate containers was presented to female 98A on 6 March 1999 for 26 days. This batch was then replaced by a second batch of six substrate containers to which the female was exposed for 89 days until her death on 1 July 1999.

Similarly, a batch of six substrate containers was presented to female 98B on 8 March 1999 for 24 days. This batch was then replaced by a second batch of six substrate containers to which the female was exposed for 119 days. A third batch of six substrate containers was presented to female 98B on 31 July 1999 for 6 days until her death on 6 August 1999.

After removal from the breeding cage, the substrates were carefully searched for eggs. The number of eggs per container was counted, and the eggs reinserted into the same substrate in ventilated plastic pottles. Care was taken to ensure the eggs were correctly orientated with the sharper end downward (Ramsay 1955). The substrate in the pottles was kept moist, and a thin layer of perlite (a white granular substance) was sprinkled over the surface to help identify when an egg had hatched. The pottles were checked regularly and hatchlings were removed and set up in individual containers (described above).

Data were analysed by analysis of variance using the General Linear Model procedure in SYSTAT 7. Wētā, substrate, and date, and their interactions, were included along with block as factors in the model. To ensure model assumptions

of residual normality and constant variance hold, data were square root transformed prior to analysis. Pairwise comparisons of substrate means were made using the Bonferroni method (Appendix 1).

Eggs laid by wētā 98B in her third batch of substrates (31 July 99–6 August 99) were not included in this analysis to keep the design balanced.

4.4 DURATION AND MORTALITY OF WĒTĀ LIFE STAGES

Duration and mortality of wētā life stages was recorded. Ten juveniles, of similar age (hatched 2–10 November 1999), were selected and their activity was recorded by noting whether their food or water had been disturbed. This gave an indication of the timing of ecdysis, and hence instar duration, as juveniles ceased feeding during the ‘moulting phase’ (Winks & Ramsay 1998). This method could only reliably be used for juveniles of third instar or older as younger instars ate such a small amount that it was difficult to tell whether or not they had fed. An estimate was made of the duration of each instar by measuring the time from the resumption of feeding after an inactive ‘moulting phase’ to the resumption of feeding after the subsequent inactive ‘moulting phase’.

4.5 BEHAVIOURAL OBSERVATIONS

Observations of food preferences, defence and aggression, burrowing, mating behaviour, oviposition, and moulting were recorded. Middle Island tusked wētā are nocturnal and very sensitive to light, so observations at night were made with the help of a torch covered with several layers of red cellophane. This produced a dim red glow, which generally did not appear to disturb the wētā unless the light was shone directly at them.

5. Results

5.1 MICRO-HABITAT CONDITIONS ON MIDDLE AND DOUBLE ISLANDS

A continuous run of data was recorded on both Middle Island and Double Island between January 1998 and December 2000 (Appendix 2). Additional data for January 1995 to December 1997 are recorded in Winks & Ramsay 1998.

5.1.1 Mean monthly air temperatures

Mean monthly air temperatures on Middle and Double islands were very similar (Fig. 3).

Figure 3. Mean monthly air temperatures (°C) on Middle and Double islands (1998-2000).

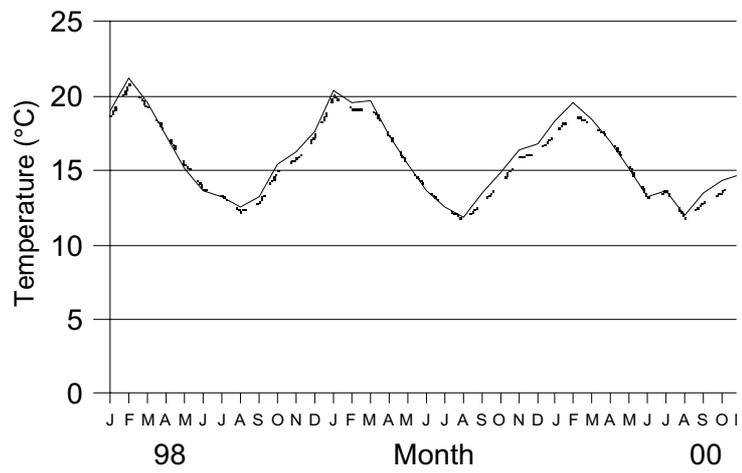


Figure 4. Mean monthly soil temperatures (°C) on Middle and Double islands (1998-2000).

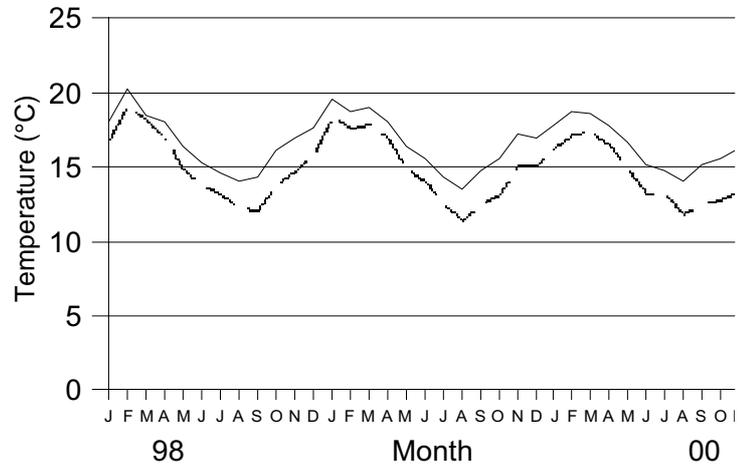
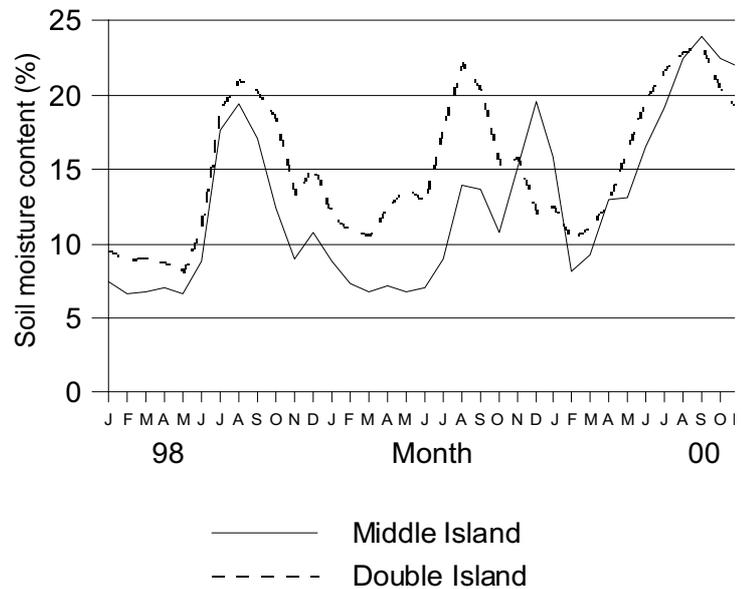


Figure 5. Mean monthly soil moisture content (%) for Middle and Double islands (1998-2000).



— Middle Island
 - - - Double Island

5.1.2 Mean monthly soil temperatures

Mean monthly soil temperature at the monitored site on Middle Island was consistently about 1-2 degrees warmer than on Double Island (Fig. 4).

5.1.3 Mean monthly soil moisture content

Mean monthly soil moisture content on Middle Island was generally lower than on Double Island (Fig. 5). There was a period of unexplained high soil moisture content readings on Middle Island during December 1999 and January 2000. The most likely explanation for this, considering some of the very high readings, is a malfunction of the data-logging equipment because rainfall during this period was not atypical (see Fig. 6).

5.1.4 Monthly rainfall on Middle Island

The mean annual rainfall on Middle Island for the period 1996-2000 was 522 mm, with a high of 650 mm for 1996, and a low of 461.6 mm for 1998. In comparison, the mean annual rainfalls for 1996-2000 at the Mt Albert Research Centre, Auckland, and at Christchurch airport were 1296 mm and 628 mm respectively. Note: Rainfall data for 1996 and 1997 (Winks & Ramsay 1998) have been included in Fig. 6 below.

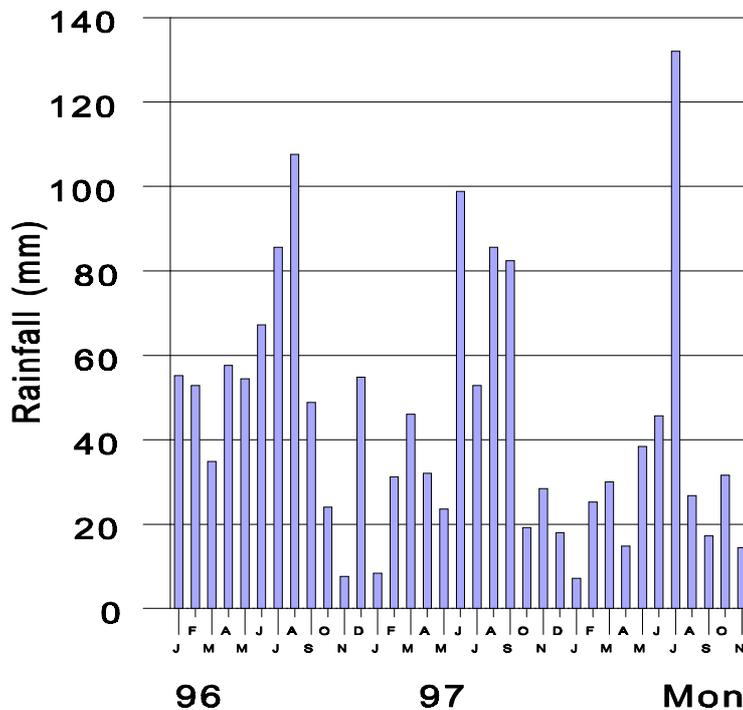
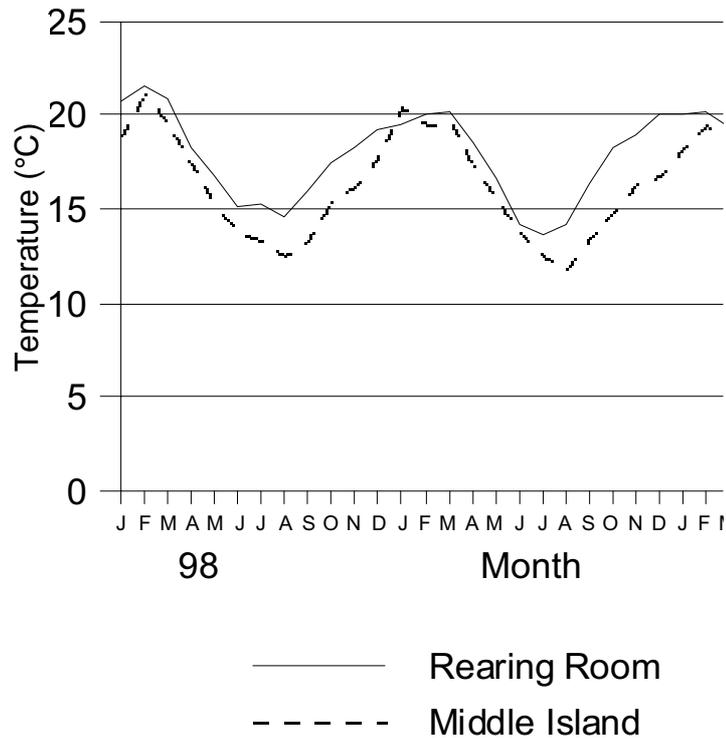


Figure 6. Monthly rainfall (mm) on Middle Island (1996-2000).

Figure 7. Mean temperatures recorded in the rearing room, and mean air temperatures recorded on Middle Island, for the period from January 1998 to December 2000.



5.2 REARING CONDITIONS

During summer and autumn, mean temperatures in the rearing room corresponded closely to air temperatures on Middle Island (Fig. 7). However, during winter and spring, temperatures were generally slightly warmer in the rearing room than on Middle Island.

5.3 OVIPOSITION SUBSTRATE PREFERENCE TRIAL

5.3.1 Substrate preference

A total of 505 eggs were recovered from the three substrates used in this trial: 310 eggs from soil; 163 from the soil/peat/pumice mix; and 32 from the peat/pumice mix. Table 1 gives the means for the three substrate types.

There was strong evidence for an effect of substrate type on oviposition for these two wētā ($P < 0.001$) (a full statistical analysis is given in Appendix 1). Pairwise comparison of substrate means (using the Bonferroni method) showed that significantly more eggs were laid in soil than in the soil/peat/pumice mix ($P < 0.05$), and that significantly more eggs were laid in the soil/peat/pumice mix than the peat/pumice mix ($P < 0.01$).

5.3.2 Number of eggs per female

Wētā 98A laid a total of 349 eggs. Of these, 274 eggs were laid over the 26-day period from 6 March 1999 to 1 April 1999, when this wētā had the opportunity to mate during one two-day period. Oviposition was observed within a day of wētā 98A being separated from the male (after mating for the first time). A

TABLE 1. MEAN NUMBER OF EGGS LAID BY WETA 98A AND WETA 98B IN THREE SUBSTRATE TYPES.

SUBSTRATE	WETA	PERIOD 1	PERIOD 2	PERIOD 3
Soil	98A	80	32.5	
	98B	20.5	22	0
Soil/peat/pumice	98A	45.5	5	
	98B	23	6	2
Peat/pumice	98A	11.5	0	
	98B	4	0	0.5

Note: Periods 1 and 2 for weta 98A were 6 Mar 99–1 Apr 99 and 2 Apr 99–1 Jul 99. Periods 1, 2 and 3 for weta 98B were 8 Mar 99–1 Apr 99, 2 Apr 99–30 Jul 99, and 31 Jul 99–6 Aug 99.

further 75 eggs were laid during April, May, and June 1999 (during this time she had the opportunity to mate several times). Wētā 98A died on 1 July 1999. An autopsy revealed 340 fully formed eggs inside this wētā, bringing the total number of eggs produced to 689.

Wētā 98B laid 156 eggs. Of these, 95 were laid over the 24-day period from 8 March 1999 to 1 April 1999, when wētā 98B had the opportunity to mate over one 2-day period. As with wētā 98A, oviposition commenced within a day of her being separated from the male (after mating for the first time). A further 56 eggs were laid by wētā 98B during April, May, June and July 1999 (during this time there was the opportunity to mate several times), and five eggs were laid during the first six days of August. Wētā 98B died on 6 August 1999. An autopsy revealed 595 fully formed eggs, bringing the total number of eggs produced to 747.

There was a significant wētā/date interaction effect ($P < 0.05$): although both wētā laid more eggs during period 1 ($P < 0.001$), wētā 98A laid a higher proportion (78.5%) of her eggs during the this period than wētā 98B (60.8%).

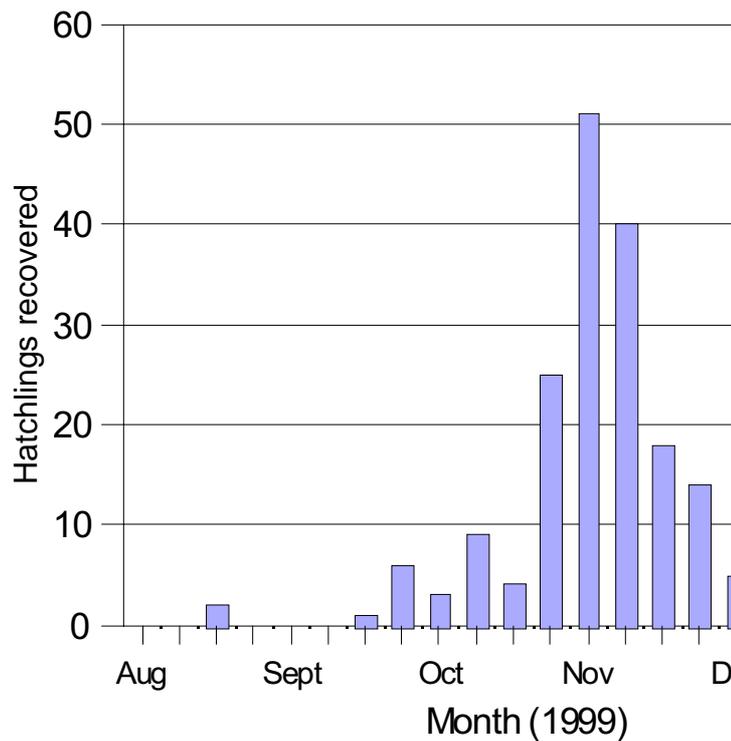
5.4 DURATION AND MORTALITY OF LIFE STAGES

5.4.1 Eggs

The eggs have an elongate oval shape and are black. Newly laid eggs are 6–7 mm in length and about 2 mm wide. As they develop, the eggs absorb water from the surrounding substrate and expand. One egg, measured close to hatching, was 7.4 mm long and 3 mm wide. The anterior pole (uppermost when laid) of the egg is rounded, and the posterior pole is slightly pointed. Hatched eggs have a characteristic exit opening, with a split in the egg chorion that extends along the upper half of one side and over the top (anterior pole) of the egg.

A total of 181 hatchling wētā (1st instar nymphs) were recovered during 1999 (Fig. 8). The first two eggs hatched in mid-August, and the third hatched in mid-September. Peak hatching occurred in early November, and the last egg hatched in late December. Eclosion (hatching) occurred at night. Exact oviposition dates were not known so precise incubation times could not be obtained. The maximum incubation time for an egg was from 262–287 days (laid by wētā 98A during period 1, and hatched on 18 December 1999). The minimum incubation

Figure 8. Time of eclosion (egg-hatch) for eggs laid during the period 6 March 1999–6 August 1999.



time for an egg was from 109–116 days (laid by wētā 98B during period 3, and hatched on 23 December 1999).

Hatching success: From a total of 505 eggs laid by both wētā, 181 hatchlings were recovered (35.8% overall hatch rate). Of these, 142 were recovered from the 349 eggs laid by 98A, (40.7% hatch rate for 98A), and 39 from the 156 eggs laid by 98B, (25% hatch rate for 98B). Overall, 78.5% of the total hatchlings originated from wētā 98A, and 21.5% from wētā 98B.

Of the 64.2% of eggs that did not hatch, 8.7% were damaged by predators, 17.0% showed fungal infection, and the remaining 38.5% had no obvious cause of death.

The egg predation was probably by the omnivorous larvae of the pasture wireworm, *Conoderus exsul* (Elateridae). Larvae were found in the soil despite checks to remove potential invertebrate predators prior to the soil being used in the trial.

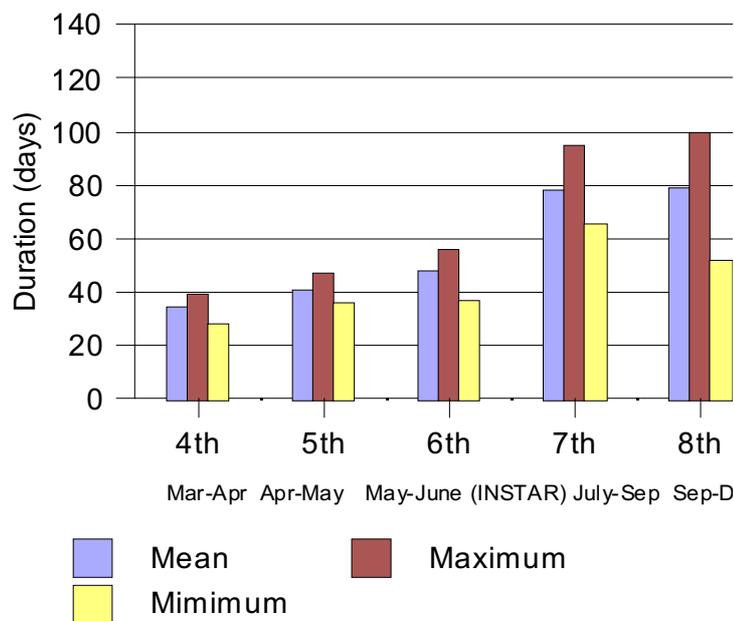
The most common fungi found infecting eggs were two species of *Paecilomyces*, which were white. A green fungus (*Myrothecium* sp.), and an orange fungus (*Volutella* sp.), were also present on some eggs. These fungi are all common soil saprophytes (E. McKenzie pers. comm.).

5.4.2 Juveniles

Developmental time: Middle Island tusked wētā pass through nine nymphal instars, with the adult being the 10th instar. Development from newly hatched nymphs to adulthood for 10 captive-reared wētā varied from 476 to 525 days, with a mean of 498 days (about 16–17 months) (Appendix 3). These 10 wētā hatched in late spring 1999, and became adults in early to mid-autumn 2001.

Feeding activity records: Regular feeding activity ceased for several weeks during the ‘moulting phase’ (Appendix 3). An estimation of duration of nymphal

Figure 9. Estimated duration of Middle Island tusked wētā nymphal instars, based on data from activity records for 10 captive-reared wētā, spring 1999 to autumn 2001.



instars (the nymphal stadia) was made from these data (Fig. 9). This increased with each successive instar, from a mean of 34.1 days for the fourth instar, to a mean of 87.8 days for the ninth (subadult) instar.

Juvenile mortality: Twelve of the 181 hatchlings recovered during 1999 died in captivity by the end of June 2001. Three died soon after hatching because of problems associated with the hatching process, which resulted in them having severely deformed legs. Four wētā died after suffering deformities during moulting, and five wētā died of unknown causes.

Sex ratio: Of the 181 hatchlings recovered during 1999, 42 were male and 133 were female, a sex ratio of 1M : 3.17F. The sex of the remaining six was not determined because they died when they were too small for their gender to be determined.

Rearing and release records: During January/February 2000, 21 early-instar wētā were sent to Ian Stringer (Massey University, Palmerston North), and 60 early-instar wētā were sent to Paul Barrett (Auckland Zoo). The remaining wētā were retained at the Mount Albert Research Centre. During May 2000, 94 juvenile (4th and 5th instar) captive-reared Middle Island tusked wētā were released on Double Island (50 wētā) and Red Mercury Island (44 wētā), in the Mercury group. A further release of 17 juvenile wētā was made on Double Island in September 2000, and 19 adult captive-reared wētā were released on Double and Red Mercury islands during Autumn 2001.

5.4.3 Adults

The duration of the adult stage (from the resumption of feeding after the final moult, to death) for the wētā used in the oviposition substrate preference trial was 173 days (5.5 months) for wētā 98A, 199 days (6.5 months) for wētā 98B, and 362 days for the male (although the male was placed in a coolroom at 10°C to prolong his life in case another adult female became available).

5.5 BEHAVIOURAL OBSERVATIONS

5.5.1 Food preferences

This species is largely carnivorous, but plant material is also eaten.

Foods eaten while in captivity:

- tropical fish flakes (Masterpet community diet flakes)
- insects (e.g. decapitated crickets, mealworm larvae and adults, and moth larvae, pupae, and adults)
- organic muesli
- leaves (e.g. *Coprosma*, *Pittosporum*, *Hebe*, *Meryta*, *Metrosideros* spp.)
- seeds (e.g. rolled oats and wheat seeds)
- berries (a wide variety)
- fruit (a wide variety)
- flowers (a wide variety).

5.5.2 Defence and aggression

Middle Island tusked wētā individuals that we studied did not display the defence behaviour commonly adopted by wētā species in the genera *Hemideina* and *Deinacrida* of raising their back legs over their back and head. When disturbed, Middle Island tusked wētā usually adopted an aggressive frontal display. Front legs were raised high off the ground, and with jaws open wide, they swayed from side to side, occasionally lunging forward. This behaviour was exhibited by both males and females of all instars. Jumping was another common defence reaction. All instars were capable of jumping, but adults in captivity rarely jumped. Defecation of foul-smelling liquid faeces was a common response to provocation. Adult males made a high-pitched rasping sound by rubbing their tusks together when threatened or disturbed. Although capable of biting, this species rarely did so when handled in captivity. Males and females, placed together for mating for a few days at a time, shared a cage without evidence of aggressive behaviour.

5.5.3 Burrowing

Males and females of all instars constructed individual shallow chambers, just beneath the ground surface, in which to shelter. They usually returned to these chambers after nocturnal foraging. Front legs were used to scoop and pass the substrate beneath the body so that it could be eventually kicked away by the hind legs. Once a hole was large enough, the wētā would turn around inside and continue shaping the chamber walls. The substrate was chewed, and apparently mixed with saliva, then plastered onto the walls of the chamber using jaws, palps, and front legs to produce a smooth finish. Once the chamber was completed, the entrance was sealed with a plug of substrate mixed with saliva. Whenever a wētā returned to its chamber after foraging at night, the entrance was resealed.

5.5.4 Mating behaviour

Pre-mating activity was observed above ground. The male and female slowly moved around and touched each other with their antennae and palps. Copulation generally occurred in the underground chambers (or the ice cream container ‘chambers’

provided for them), although copulation was also observed above ground. Both the male and female remained upright, facing in the same direction, with the female above the male. They were observed to stay in that position for long periods, but separated quickly when disturbed. There was no evidence of any stridulatory signals involved in mating activity.

5.5.5 Oviposition

Females were observed to oviposit in soft moist soil at night. Each egg-laying female would select a suitable site by exploring the ground thoroughly with her palps and antennae. She would then raise her body and depress her ovipositor so that it pointed vertically downwards, and then thrust it into the substrate. She would then remain still except for rhythmic pulsations of her abdomen every 2–3 seconds. After several minutes her abdomen would pulsate more quickly and her body would appear to tense and shudder. She would then withdraw the ovipositor and move several centimetres away before examining the ground again with her palps and antennae and repeating the exercise.

5.5.6 Moulting

Moulting occurred in the underground chamber. Occasionally, chambers were constructed against the clear plastic container sides, thus providing a clear view of the occupant. Each wētā moulted lying on its back with its legs tucked in. During moulting, which took several hours, it remained still, apart from occasional gentle movements that occurred while it tried to free itself from the old cuticle. The newly moulted wētā was pale, but darkened to normal colouration after a day or so. The shed cuticle (exuviae) was eaten soon after moulting.

Wētā occasionally became deformed during moulting, and limbs were especially susceptible to moulting problems. A severely deformed limb often resulted in the death of the individual, possibly from infection. Regeneration of broken antennae throughout several moults was observed on a number of occasions.

6. Discussion and conclusions

6.1 MICRO-HABITAT CONDITIONS ON MIDDLE AND DOUBLE ISLANDS

Prime concerns when evaluating the habitat of a potential wētā release site are food availability (see Section 6.4.1), and the temperature and moisture regime. Mean monthly air temperatures on Middle and Double islands were consistently very similar to each other. However, the mean monthly soil temperature on Middle Island was consistently warmer (by approximately 1–2°C) than on Double Island. This difference in soil temperature could be related to the positions of the data-loggers on the two islands. The data-logger on Middle Island was positioned high up on the eastern side of the gently sloping ‘Central Plateau’ (where Middle Island tusked wētā had previously been located), and the forest canopy above was not particularly dense. This may have allowed some

warming from the sun at times during the day. The surrounding vegetation would have provided some shelter from the wind. However, the data-logger on Double Island was positioned on the shady southern side of a slope, with a dense forest canopy above (the proposed site of a possible wētā release at the time the data-loggers were set up).

The soil on Middle Island was generally drier than Double Island (at the data-logger locations), and this may be related to the positions of the loggers as explained above. However, the litter on the forest floor of Double Island was, in general, deeper than that on Middle Island (McIntyre 1994), and this may have helped to maintain soil moisture during dry periods. Also, the high density of burrowing seabirds on Middle Island would help keep the soil there free-draining.

McIntyre (1998b) suggested that although the Middle Island tusked wētā survives in an unusually dry environment, it may, nevertheless, be more adapted to wetter conditions. The discovery that the smaller but similar Raukumara tusked wētā is often found under rocks in stream beds provides a point of comparison, and it is possible that the Middle Island tusked wētā may be 'marooned' in an environment that is suboptimal, and perhaps even marginal, for its survival.

Environmental data indicate that Double Island should be suitable for releases of captive-reared Middle Island tusked wētā.

6.2 OVIPOSITION SUBSTRATE PREFERENCE TRIAL

Although the effect of substrate type on oviposition was significant, the limited nature of the trial (only two females) means that substrate preferences should be investigated further. The effect of date (age of the wētā) on oviposition was also significant, and this should also be further investigated.

6.3 DURATION AND MORTALITY OF LIFE STAGES

6.3.1 Eggs

Egg development times: Incubation times ranged from a maximum of 262–287 days (about 9 months) for an egg that was laid in early autumn, to a minimum of 109–116 days (just over 3.5 months) for an egg laid in late winter. For previous studies with this species the range was from a minimum of 53–71 days (early autumn to late autumn) to a maximum of 220–272 days (late autumn to summer)(Winks & Ramsay 1998).

Development times recorded for the eggs of other wētā species are quite variable, and there are some indications that the eggs of some wētā species have a weak diapause (period of suspended development). Eggs of *Deinacrida rugosa* kept outside during winter hatched sooner when brought into the laboratory than those kept continuously in the laboratory (Ramsay 1955). Mahoenui giant wētā eggs generally hatch after about 10 months if exposed to cold winter temperatures (Richards 1994). However, one batch of eggs, laid in December 1992, hatched 24–26 months later. These were kept inside a warm house, and they hatched after being placed outside for several weeks during

winter, suggesting that a diapause was broken by exposure to cold (Domett 1996). However, another batch of Mahoenui giant wētā eggs kept at a constant 18°C hatched after about 7.5 months (Richards 1994).

The incubation periods for *D. heteracantha* and *D. fallai* was about 5 months (141 and 147 days respectively) (Richards 1973). However, in the same study Richards (1973) found some eggs of *D. heteracantha* had an incubation period of 228–258 days, which suggested a possible winter diapause, or possibly that they just experienced a slowed development due to the cold. Cary (1981) found the egg incubation period of *Zealandrosandrus gracilis* was variable (12–18 months under laboratory conditions) and he suggested that low temperatures are probably required to trigger development.

Egg mortality and hatch-rate: The 35.8% hatch-rate of eggs laid by the two female Middle Island tusked wētā (98A and 98B) in 1999 is an improvement on the 23.5% previously recorded (Winks & Ramsay 1998), and it is comparable with that of captive-reared *D. heteracantha* (36%) and *D. fallai* (23%) (Richards 1973). However, further improvements in hatch-rate may be possible, as a hatch-rate of about 40% was recorded for one batch of 300 captive-reared Mahoenui giant wētā eggs by Richards (1994), and a hatch-rate of 100% was recorded for a batch of 104 eggs from captive-reared Mahoenui giant wētā after the eggs spent between 24 and 26 months in the soil (Dommet 1996).

The reasons why some eggs did not hatch were obvious: predation (8.7% of all eggs) and fungal infection (17% of all eggs). McIntyre (1998b) reported that many of the Raukumara tusked wētā eggs laid in captivity at Victoria University had been ‘chewed’, probably by soil invertebrates in the leaf litter. Egg predation could possibly be reduced by checking the soil used for oviposition more thoroughly for potential predators, and by removing the eggs soon after oviposition and incubating them in a predator-free medium such as vermiculite or perlite.

Fungal infection is probably more difficult to overcome, unless the female wētā could be induced to lay eggs in a sterile substrate such as vermiculite (eggs laid in soil may still be contaminated by potential pathogens even if they are transferred to a sterile medium). Heat treatment of soil (in an autoclave) was tried (C.J. Winks pers. obs.) but it led to a proliferation of fungus throughout the soil. The ‘cooked’ organic material probably provided an ideal medium for airborne fungal spores to develop in the absence of fungus-feeding organisms. However, our work on soil sterilisation was limited and soil sterilisation techniques should be further investigated.

Most unhatched eggs (38.5% of total eggs) showed no obvious reason for not hatching. It is possible that these eggs were infertile or had suffered some undetectable damage or trauma that proved fatal. Our method of removing the eggs from the substrate in which they were laid and reinserting them into substrate in smaller pottles effectively eliminated the problem of losing hatchlings after hatching (which can be a problem if the eggs are left to hatch in a large cage (Winks & Ramsay 1998)), but may have resulted in undetected minute damage to some eggs.

6.3.2 Juveniles

Developmental time: The developmental period from hatching to adulthood of 16–17 months that we recorded is similar to that previously recorded for this species (mean 17.8 months, range 15.5–22 months) (Winks & Ramsay 1998). Juveniles that hatched in late May 1994 averaged 20 months to develop to adults, while those that hatched in December 1994 averaged 16.3 months to develop. This corresponds to developmental times recorded for *D. heteracantha*, where individuals that hatch in spring may become adult 14 months later and pass through only one winter, whereas others that hatch in autumn pass through two winters and become adult 21 months later (Richards 1973).

In our study, successive nymphal instars increased in duration. Part of this increase (e.g. for instars 5, 6 and 7) could be due to a slower metabolism in cooler weather, as has also been shown with captive *D. fallai* and *D. heteracantha* (Richards 1973), and Mahoenui giant wētā (Richards 1994). However, the instar with longest duration (the ninth or subadult instar), occurred during summer and early autumn.

Juvenile mortality: The 6.6% mortality rate of our juveniles compares favourably with other wētā species reared in captivity: 89.9% for *D. fallai* (Richards 1973), 82.7 % for *D. heteracantha* (Richards 1973), and 80% for Mahoenui giant wētā (Richards 1994). Failure to successfully separate from the exuviae during ecdysis (moulting) is a common cause of death recorded for captive-reared wētā (Stringer & Cary 2001). This also occasionally occurs when the first instar moults from the pronymph during hatching. Damage to a limb (e.g. from a moulting problem) often resulted in the eventual death of the individual, probably from infection (C.J. Winks pers. obs.). Cannibalism, often of moulting wētā, can be a significant cause of mortality for wētā kept together in captivity, but this did not occur with the juvenile Middle Island tusked wētā that we raised as they were reared individually. Other causes of mortality recorded for captive-reared wētā include fungal diseases, and high susceptibility of early instars to low humidity. Our captive-reared juveniles spent most of their time in chambers they had constructed in moist vermiculite, so low humidity outside their chambers may not have been a problem for them. Wētā can also be infested with mites but these probably do not kill the insect (Stringer & Cary 2001).

Sex ratio: The skewed female sex ratio (1M : 3.17F) of the juveniles we raised contrasts with the close to 1M : 1F ratio of males and females (total: 239) recorded from 10 expeditions to Middle Island (McIntyre 1998a).

6.3.3 Adults

Adult females kept in captivity lived for an average of 6 months after their final moult, and adult males lived for an average of 10 months after their final moult. These data incorporate findings from the previous study on this species (Winks & Ramsay 1998) and are based on records for a total of 14 females and 8 males. This is comparable to the estimated life expectancies of this species in the wild on Middle Island (M. McIntyre pers. comm.).

6.4 BEHAVIOURAL OBSERVATIONS

6.4.1 Food preferences

Middle Island tusked wētā appear to be primarily carnivorous. New Zealand wētā species are generally omnivorous, but range from being primarily carnivorous, e.g. *Zealandrosandrus gracilis* (Cary 1981), to being primarily vegetarian, e.g. *D. heteracantha* and *D. fallai* (Richards 1973). The bulk of the diet of the primarily carnivorous species is made up of a wide variety of invertebrates. However, two species of wētā endemic to Snares Island, *Z. subantarcticus* Salmon, and *Insulanoplectron spinosum* Richards, are known to feed on dead seabirds, as well as on invertebrates and plants (Butts 1983). These wētā feed on the muscles and feathers of the birds, as well as the associated fly larvae and pupae, ticks, lice, and other scavenging and decomposing organisms. Dead seabirds are common on Middle Island, and could form part of the diet of the Middle Island tusked wētā, but we have no data on this at present.

Dietary requirements are important when deciding on suitable release sites for captive-reared wētā. In the wild, much of the diet of the Middle Island tusked wētā would probably consist of litter invertebrates. Litter samples taken from Middle and Double islands show that litter depth is greater on Double Island than Middle Island, and litter invertebrates are much more abundant on Double Island (McIntyre 1994). This may relate to much lower seabird numbers on Double Island—10% or less of that on Middle Island—combined with the fact that predation on the litter inhabitants has been greatly reduced since rats were removed from Double Island. Middle Island, in contrast, has a suite of invertebrate-eating reptiles, as well as more abundant spiders and giant centipedes, but a minimal humus layer on the forest floor. This would suggest that Double Island would be capable of providing the dietary requirements for a considerable population of Middle Island tusked wētā.

6.4.2 Defence and aggression

Conflicts between males have been recorded (M. McIntyre pers. comm.) but the individuals we kept in captivity were kept separate except when males and females were together for mating. Males and females, placed together for mating for a few days at a time, shared a cage without evidence of aggressive behaviour. However, it was found in the earlier study that if males and females were kept together for longer periods (e.g. several weeks) there was evidence to suggest aggressive interactions, and several females died (Winks & Ramsay 1998). An autopsy of one female showed that it had a hole in its side, possibly caused by a tusk or mandible, which probably caused its death. The hole was the approximate diameter of a male wētā tusk and was surrounded internally by extensive melanisation indicating a large wound response. Large numbers of coccal bacteria were present in the haemolymph. The conclusion was that the wētā had been pierced by the tusk of a male and died from septicaemia (P. Wigley pers. comm.).

6.4.3 Burrowing

The burrowing behaviour recorded for our captive-reared Middle Island tusked wētā is very similar to that exhibited by the ground wētā, *Hemiandrus similis*

Ander (Barrett & Ramsay 1991). Both species have plentiful spines on their tibiae, which are strategically placed and effective for soil moving.

6.4.4 Mating behaviour

Although Middle Island tusked wētā are capable of stridulation when disturbed, there is no evidence from our study, or previous studies of wild or captive wētā, that these sounds are used in courtship behaviour. Studies on a similar South African species, *Libanasidus vittatus* (Kirby), concluded that their excrement contains chemical information that enables the gender of the emitter to be identified (Bateman & Toms 1998). Adult individuals preferred the scent of the opposite sex, while juveniles avoided the scent of conspecifics (which are known to be cannibalistic). Adult male *L. vittatus* mate-guard vigorously and aggressively, and the strong scent may well have a role in advertising and defending their 'residency' to other mate-searching males. Female *L. vittatus* are also aggressive, and may use their scent for territorial purposes, as well as to attract males.

As with the Middle Island tusked wētā, there is no evidence of stridulation in the courtship behaviour of wētā in the genus *Deinacrida* (giant wētā). Male Mahoenui giant wētā follow or chase females (Richards 1994), and female *D. rugosa* produce a musky odour (Ramsay 1955), suggesting that chemical communication may play a role in courtship. In contrast, stridulation seems to be the principle means of communication for the arboreal Wellington tree wētā, *Hemideina crassidens* (Blanchard) (Ordish 1992). Stridulation is supplemented at close quarters by use of both the mandibles and palps. Pheromones contained in faecal pellets may act as navigational guides for Wellington tree wētā returning to their retreats.

6.4.5 Oviposition

The oviposition behaviour we recorded for Middle Island tusked wētā is similar to that reported for a number of other wētā species, including *Deinacrida heteracantha*, *D. fallai*, *D. rugosa*, *Hemideina crassidens*, *Zealandosandrus gracilis*, and *Z. subantarcticus* (Stringer 2001). Captive-reared Middle Island tusked wētā, in this and previous studies, laid eggs from autumn through to early spring (Winks & Ramsay 1998). These observations concur with those of wild Middle Island tusked wētā on Middle Island (McIntyre 1998a).

6.4.6 Moulting

Regular feeding activity of Middle Island tusked wētā kept in captivity ceased for a period of several weeks during each 'moulting phase'. The maximum length of time recorded for a wētā in this non-feeding state was 70 days for a juvenile moulting during winter (Winks & Ramsay 1998). It presumably remained sealed in its burrow throughout this time as there was no sign that anything was disturbed in its cage. Richards (1994) reported that Mahoenui giant wētā do not eat from 4 to 14 days before moulting.

Wētā will regenerate parts of their limbs and antennae if the damage is followed by a sufficient number of moults. Regenerated limbs generally do not reach the size of their undamaged counterparts, but antennae regenerate readily, and may reach their full length after only a few moults (Ramsay 1955, 1964; Richards 1973; Barrett & Ramsay 1991).

7. Recommendations

- At least one population of Middle Island tusked wētā should be maintained in captivity, until the establishment of the wētā on Red Mercury or Double islands is confirmed.
- Further releases of captive-reared Middle Island tusked wētā should be made on both Red Mercury and Double islands.
- Wētā of suitable age should be transferred from Middle Island to captive-rearing facilities to add to the genetic variety of the captive wētā population.
- The captive-rearing method should be developed and improved by:
 - Mating females at a range of times after they become adult to gain information on how long it takes adult females to become receptive.
 - Investigating how many eggs can be fertilised per mating to gain information on how often wētā should be paired for mating, and the optimal length of time to leave a pair together.
 - Continuing to investigate oviposition substrate preference.
 - Investigating the effect of temperature on egg development.
 - Investigating soil sterilisation methods to reduce the problem of egg predation and fungal infection.
 - Trialing media such as vermiculite and perlite for egg incubation (after the eggs have been removed from the substrate in which they were laid) to reduce losses due to predation/pathogens.

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Appendix 1

STATISTICAL ANALYSIS OF THE OVIPOSITION SUBSTRATE PREFERENCE TRIAL

TABLE A1.1 ANALYSIS OF VARIANCE USING THE GENERAL LINEAR MODEL
PROCEDURE IN SYSTAT 7.

SOURCE	SUM OF SQUARES	d.f.	MEAN SQUARE	F-RATIO	P
Substrate	87.953	2	43.976	33.062	<0.001
Date	37.532	1	37.532	28.217	<0.001
Wētā	0.116	1	0.661	0.088	0.773
Block	2.130	1	2.130	1.601	0.232
Date*wētā	9.914	1	9.914	7.453	0.020
Substrate*wētā	3.616	2	1.808	1.359	0.297
Substrate*date	3.784	2	1.892	1.423	0.282
Wētā*date*substrate	0.951	2	0.476	0.357	0.707
Error	14.631	11	1.330		

TABLE A1.2 PAIRWISE COMPARISONS OF SUBSTRATE MEANS USING THE
BONFERRONI METHOD, USING MODEL MEAN SQUARE ERROR OF 1.330 WITH 11 d.f.

	MATRIX OF PAIRWISE MEAN DIFFERENCES			BONFERRONI ADJUSTMENT MATRIX OF PAIRWISE COMPARISON PROBABILITIES		
	1	2	3	1	2	3
1	0.0			1.000		
2	-1.858	0.0		0.024	1.000	
3	-4.658	-2.799	0.0	0.000	0.002	1.000

Appendix 2

MICRO-HABITAT CONDITIONS ON MIDDLE AND DOUBLE ISLANDS

TABLE A2.1 MONTHLY AIR TEMPERATURES (°C) ON MIDDLE ISLAND AND (IN PARENTHESES) DOUBLE ISLAND (1998).

1998	MEAN	MAX.	MEAN MAX.	MIN.	MEAN MIN.
January	19.0 (18.7)	25.9 (25.5)	23.0 (21.9)	10.0 (11.5)	16.5 (16.9)
February	21.2 (20.8)	27.0 (26.0)	25.2 (23.6)	14.1 (14.4)	18.9 (19.1)
March	19.5 (19.3)	24.8 (22.6)	22.9 (21.0)	14.9 (15.7)	17.4 (18.0)
April	17.4 (17.5)	23.0 (21.1)	20.1 (18.7)	12.8 (13.8)	15.7 (16.4)
May	15.2 (15.4)	19.6 (18.6)	18.0 (16.6)	9.2 (10.9)	13.8 (14.4)
June	13.7 (13.8)	18.4 (17.8)	15.8 (14.9)	8.4 (9.6)	12.3 (12.7)
July	13.3 (13.4)	17.9 (17.0)	15.6 (14.4)	9.2 (9.7)	11.9 (12.4)
August	12.5 (12.3)	18.3 (15.8)	15.5 (13.5)	7.3 (8.2)	10.8 (11.3)
September	13.3 (13.0)	19.6 (17.1)	17.0 (14.5)	7.9 (9.1)	11.2 (11.8)
October	15.4 (15.0)	22.7 (18.5)	18.9 (16.9)	11.2 (11.3)	13.4 (13.8)
November	16.2 (15.8)	23.5 (20.7)	20.6 (17.9)	12.3 (12.8)	14.0 (14.4)
December	17.7 (17.4)	25.3 (23.4)	21.5 (19.8)	11.8 (12.3)	15.3 (15.9)

TABLE A2.2 MONTHLY AIR TEMPERATURES (°C) ON MIDDLE ISLAND AND (IN PARENTHESES) DOUBLE ISLAND (1999).

1999	MEAN	MAX.	MEAN MAX.	MIN.	MEAN MIN.
January	20.4 (20.1)	27.6 (25.1)	24.3 (22.6)	16.5 (16.9)	18.2 (18.6)
February	19.5 (19.2)	25.4 (22.6)	22.8 (20.9)	15.7 (16.4)	17.6 (17.8)
March	19.7 (19.3)	25.2 (22.0)	23.2 (20.8)	15.0 (16.2)	17.7 (18.0)
April	17.3 (17.3)	24.2 (21.3)	20.2 (18.3)	10.8 (12.0)	15.9 (16.2)
May	15.5 (15.3)	21.4 (19.0)	18.3 (16.4)	8.9 (10.3)	14.0 (14.4)
June	13.7 (13.8)	18.5 (18.3)	16.0 (14.9)	8.0 (9.9)	12.0 (12.7)
July	12.5 (12.6)	17.9 (16.9)	15.6 (13.6)	7.8 (8.9)	10.9 (11.6)
August	11.9 (11.7)	18.9 (14.8)	15.0 (12.9)	7.1 (8.3)	10.0 (10.6)
September	13.5 (13.0)	20.1 (16.8)	17.2 (14.6)	7.9 (8.9)	11.5 (11.8)
October	14.9 (14.2)	21.0 (17.7)	18.8 (16.0)	8.2 (9.5)	12.7 (12.9)
November	16.4 (16.0)	21.9 (19.6)	19.7 (17.7)	10.5 (11.3)	14.3 (14.7)
December	16.8 (16.3)	24.4 (21.2)	21.0 (18.4)	10.8 (11.1)	14.3 (14.8)

TABLE A2.3 MONTHLY AIR TEMPERATURES (°C) ON MIDDLE ISLAND AND (IN PARENTHESES) DOUBLE ISLAND (2000).

2000	MEAN	MAX.	MEAN MAX.	MIN.	MEAN MIN.
January	18.3 (17.6)	24.5 (23.2)	22.2 (19.7)	13.2 (13.7)	16.1 (16.1)
February	19.5 (18.7)	26.6 (23.1)	24.3 (20.7)	14.6 (15.6)	16.8 (17.2)
March	18.5 (18.2)	26.7 (23.1)	22.3 (19.9)	12.4 (13.6)	16.4 (17.0)
April	17.0 (17.1)	22.8 (20.5)	20.2 (18.4)	10.7 (13.8)	15.3 (16.0)
May	15.2 (15.3)	20.6 (18.8)	18.0 (16.4)	11.0 (11.9)	13.9 (14.3)
June	13.2 (13.2)	17.4 (16.5)	15.4 (14.0)	7.3 (8.7)	11.7 (12.3)
July	13.6 (13.6)	18.0 (15.8)	15.3 (14.3)	10.2 (11.0)	12.5 (12.9)
August	12.0 (11.8)	17.5 (15.7)	15.0 (13)	7.5 (7.2)	10.2 (10.6)
September	13.5 (13)	20.2 (17.3)	17.4 (14.4)	7.0 (8.9)	11.4 (12.0)
October	14.4 (13.6)	20.6 (18.0)	18.7 (15.5)	7.3 (7.9)	11.9 (12.2)
November	14.8 (14.4)	20.9 (18.8)	18.5 (16.3)	11.2 (11.8)	12.6 (13.0)
December	17.6 (16.8)	26.4 (22.4)	21.9 (19.3)	10.9 (12.7)	15.3 (15.3)

TABLE A2.4 MONTHLY SOIL TEMPERATURES (°C) AT 10 cm DEPTH ON MIDDLE ISLAND AND (IN PARENTHESES) DOUBLE ISLAND (1998).

1998	MEAN	MAX.	MEAN MAX.	MIN.	MEAN MIN.
January	18.0 (16.9)	19.8 (19.2)	18.2 (17.2)	16.4 (14.8)	17.7 (16.5)
February	20.2 (19.1)	21.0 (20.3)	20.4 (19.3)	18.3 (17.0)	19.9 (18.9)
March	18.5 (18.2)	19.8 (19.5)	18.9 (18.4)	17.2 (16.9)	18.1 (17.8)
April	18.1 (16.9)	19.2 (18.4)	18.3 (17.1)	17.0 (15.4)	17.8 (16.5)
May	16.4 (14.9)	18.0 (17.2)	16.7 (15.2)	14.9 (13.0)	16.2 (14.6)
June	15.3 (13.8)	16.9 (15.9)	15.5 (14.1)	14.0 (12.2)	15.0 (13.4)
July	14.6 (13.2)	15.9 (14.8)	14.8 (13.5)	14.0 (12.2)	14.4 (13.0)
August	14.0 (12.3)	15.3 (14.1)	14.2 (12.5)	12.4 (10.0)	13.8 (12.0)
September	14.4 (12.2)	16.0 (14.2)	14.6 (12.4)	13.3 (11.1)	14.2 (11.9)
October	16.1 (13.9)	17.5 (15.5)	16.3 (14.2)	15.1 (12.5)	15.8 (13.6)
November	16.9 (14.7)	17.9 (16.2)	17.1 (14.9)	15.6 (13.7)	16.6 (14.3)
December	17.6 (16.0)	19.7 (18.7)	17.8 (16.4)	15.0 (13.7)	17.2 (15.7)

TABLE A2.5 MONTHLY SOIL TEMPERATURES (°C) AT 10 cm DEPTH ON MIDDLE ISLAND AND (IN PARENTHESES) DOUBLE ISLAND (1999).

1999	MEAN	MAX.	MEAN MAX.	MIN.	MEAN MIN.
January	19.5 (18.4)	21.7 (20.5)	19.8 (18.6)	17.5 (16.7)	19.2 (18.0)
February	18.7 (17.7)	20.2 (19.3)	18.9 (17.8)	17.7 (16.9)	18.4 (17.4)
March	19.0 (17.9)	19.9 (19.0)	19.3 (18.1)	17.9 (16.5)	18.8 (17.7)
April	18.0 (16.9)	20.1 (19.5)	18.2 (17.1)	15.8 (14.7)	17.7 (16.7)
May	16.4 (14.9)	18.1 (16.7)	16.6 (15.1)	14.7 (12.7)	16.2 (14.6)
June	15.6 (14.0)	17.6 (16.2)	15.8 (14.2)	13.6 (11.8)	15.5 (13.8)
July	14.4 (12.5)	16.0 (14.3)	14.6 (12.7)	12.7 (10.8)	14.2 (12.3)
August	13.5 (11.5)	14.6 (13.1)	13.7 (11.7)	12.6 (10.6)	13.3 (11.3)
September	14.8 (12.6)	15.8 (13.9)	14.9 (12.8)	13.7 (11.3)	14.5 (12.4)
October	15.6 (13.3)	16.7 (15.0)	15.8 (13.5)	14.0 (11.7)	15.3 (13.0)
November	17.2 (15.2)	18.2 (16.9)	17.4 (15.4)	16.3 (13.5)	17.0 (15.0)
December	17.0 (15.2)	18.0 (16.7)	17.3 (15.4)	16.2 (14.1)	16.8 (14.9)

TABLE A2.6 MONTHLY SOIL TEMPERATURES (°C) AT 10 cm DEPTH ON MIDDLE ISLAND AND (IN PARENTHESES) DOUBLE ISLAND (2000).

2000	MEAN	MAX.	MEAN MAX.	MIN.	MEAN MIN.
January	17.8 (16.3)	19.4 (18.6)	17.9 (16.6)	16.4 (14.5)	17.6 (16.0)
February	18.7 (17.2)	19.5 (18.4)	18.9 (17.4)	17.5 (16.0)	18.5 (17.0)
March	18.6 (17.3)	19.7 (18.5)	18.8 (17.5)	17.3 (15.5)	18.4 (17.0)
April	17.8 (16.6)	18.9 (17.9)	17.9 (16.8)	15.9 (15.4)	17.6 (16.4)
May	16.7 (14.9)	18.0 (16.8)	16.8 (15.1)	15.8 (13.4)	16.5 (14.7)
June	15.2 (13.3)	16.6 (15.1)	15.4 (13.5)	13.6 (11.3)	15.0 (13.1)
July	14.7 (13.2)	15.8 (14.3)	14.9 (13.4)	13.4 (12.3)	14.6 (13.0)
August	14.1 (11.9)	15.4 (13.6)	14.2 (12.1)	13.2 (11.0)	13.9 (11.7)
September	15.2 (12.5)	16.2 (14.0)	15.3 (12.7)	14.5 (11.1)	15.0 (12.3)
October	15.6 (12.8)	17.1 (14.2)	15.8 (13.0)	14.0 (10.9)	15.4 (12.5)
November	16.2 (13.5)	17.8 (15.1)	16.4 (13.7)	14.4 (12.5)	15.9 (13.3)
December	17.3 (15.4)	18.8 (17.1)	17.5 (15.6)	16.2 (13.4)	16.6 (14.7)

TABLE A2.7 MONTHLY SOIL MOISTURE CONTENT (%) FOR MIDDLE ISLAND AND (IN PARENTHESES) DOUBLE ISLAND; AND RAINFALL (mm) FOR MIDDLE ISLAND (1998).

1998	MEAN %	MAX. %	MEAN MAX. %	MIN. %	MEAN MIN. %	RAINFALL (mm)
January	7.4 (9.5)	9.3 (11.9)	7.5 (9.6)	6.6 (8.8)	7.3 (9.4)	7.2
February	6.6 (9.0)	8.2 (13.7)	6.7 (9.3)	6.1 (8.2)	6.4 (8.7)	25.2
March	6.8 (9.1)	8.7 (11.3)	6.9 (9.3)	6.2 (8.2)	6.7 (8.9)	30
April	7.0 (8.8)	8.2 (11.5)	7.1 (8.9)	6.3 (8.1)	6.9 (8.7)	14.8
May	6.7 (8.1)	7.5 (9.6)	6.8 (8.3)	6.1 (7.6)	6.6 (8)	38.4
June	8.9 (11.5)	12.4 (16.4)	9.0 (12)	6.9 (8.2)	8.7 (11.2)	45.6
July	17.6 (19.1)	25.1 (22.9)	18.3 (19.7)	12.3 (14.4)	17 (18.7)	132
August	19.4 (21.1)	20.3 (23.9)	19.5 (21.5)	17.9 (18.8)	19.3 (20.7)	26.8
September	17.1 (20.2)	19.6 (22.5)	17.2 (20.5)	13.8 (17.9)	16.9 (20.0)	17.2
October	12.4 (18.5)	16.8 (25.0)	12.6 (19.2)	10.0 (14.4)	12.2 (18.0)	31.6
November	9.0 (13.4)	10.7 (18.6)	9.2 (13.8)	7.5 (10.6)	8.9 (13.1)	14.4
December	10.7 (15.3)	14.9 (19.9)	11.0 (15.8)	7.5 (10.6)	10.4 (14.7)	78.4

TABLE A2.8 MONTHLY SOIL MOISTURE CONTENT (%) FOR MIDDLE ISLAND AND (IN PARENTHESES) DOUBLE ISLAND; AND RAINFALL (mm) FOR MIDDLE ISLAND (1999).

1999	MEAN %	MAX. %	MEAN MAX. %	MIN. %	MEAN MIN. %	RAINFALL (mm)
January	8.8 (11.9)	11.2 (13.4)	8.9 (12.0)	7.6 (11.1)	8.6 (11.8)	55.2
February	7.3 (10.9)	8.8 (12.8)	7.4 (11.0)	6.3 (9.9)	7.2 (10.8)	38.4
March	6.8 (10.6)	7.1 (11.9)	6.9 (10.7)	6.5 (10.0)	6.8 (10.5)	18
April	7.2 (12.6)	9.3 (16.6)	7.3 (13.0)	6.5 (10.2)	7.1 (12.3)	34
May	6.8 (13.8)	7.2 (17.3)	6.8 (14.0)	6.5 (11.9)	6.7 (13.6)	4.0
June	7.1 (12.8)	10.3 (17.6)	7.2 (13.2)	6.5 (11.4)	7.0 (12.4)	50.8
July	9.0 (18.1)	10.8 (24.3)	9.2 (18.6)	8.0 (14.2)	8.9 (17.7)	26.8
August	13.9 (22.2)	17.7 (25.7)	14.0 (22.7)	9.3 (18.6)	13.6 (21.9)	50.0
September	13.7 (20.4)	17.2 (24.9)	14.0 (20.8)	11.5 (17.7)	13.5 (20.0)	36.4
October	10.8 (15.4)	13.5 (18.5)	11.0 (15.7)	9.7 (13.4)	10.6 (15.0)	40.8
November	15.2 (15.8)	20.1 (22.8)	15.6 (16.3)	10.1 (12.1)	14.9 (15.5)	65.2
December	19.6 (12.2)	30.7 (15.7)	20.9 (12.6)	13.3 (10.5)	18.7 (12)	64.4

TABLE A2.9 MONTHLY SOIL MOISTURE CONTENT (%) FOR MIDDLE ISLAND AND (IN PARENTHESES) DOUBLE ISLAND; AND RAINFALL (mm) FOR MIDDLE ISLAND (2000).

2000	MEAN %	MAX. %	MEAN MAX. %	MIN. %	MEAN MIN. %	RAINFALL (mm)
January	15.9 (12.6)	22.4 (16.3)	16.3 (12.9)	9.9 (11.5)	15.6 (12.4)	20.4
February	8.1 (10.3)	9.9 (11.5)	8.2 (10.4)	7.2 (9.6)	8.0 (10.2)	19.2
March	9.3 (11.2)	11.4 (13.2)	9.4 (11.4)	7.1 (9.4)	9.1 (11.0)	71.6
April	12.9 (13.0)	18.6 (18.3)	13.3 (13.3)	8.5 (11.1)	12.6 (12.8)	95.6
May	13.1 (16.6)	17.1 (18.2)	13.2 (16.7)	10.5 (15.5)	13.0 (16.5)	10.8
June	16.6 (19.8)	19.4 (25.0)	16.8 (20.2)	10.0 (15.5)	16.3 (19.6)	46
July	19.1 (21.8)	22.6 (26.1)	19.5 (22.4)	14.6 (17.5)	18.8 (21.5)	60.8
August	22.4 (23.0)	24.9 (26.0)	22.7 (23.4)	20.3 (21.3)	22.1 (22.8)	61.6
September	23.9 (23.3)	27.4 (27.0)	24.0 (23.6)	22.3 (20.9)	23.6 (23.0)	31.2
October	22.4 (20.4)	27.0 (26.5)	22.7 (20.7)	18.9 (16.7)	22.1 (20.0)	24.8
November	21.9 (18.9)	25.2 (24.2)	22.2 (19.5)	18.6 (15.0)	21.5 (18.6)	32.0
December	20.6 (18.9)	23.7 (23.9)	20.8 (19.5)	18.6 (14.8)	20.4 (18.6)	12.8

