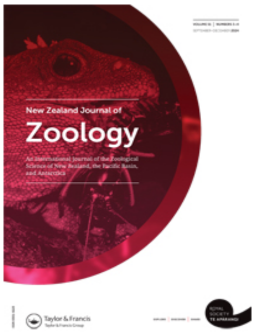

New Zealand Journal of Zoology

ISSN: (Print) (Online) Journal homepage: www.tandfonline.com/journals/tnzz20

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To cite this article: William D. Brockelsby, Colin M. Miskelly, Travis R. Glare & Maria A. Minor (20 Sep 2023): The number of larval instars in the flax weevil (*Anagotus fairburni*) (Coleoptera: Curculionidae), New Zealand Journal of Zoology, DOI: 10.1080/03014223.2023.2251898

To link to this article: https://doi.org/10.1080/03014223.2023.2251898

NEW ZEALAND JOURNAL OF ZOOLOGY
https://doi.org/10.1080/03014223.2023.2251898

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RESEARCH ARTICLE

The number of larval instars in the flax weevil (*Anagotus fairburni*) (Coleoptera: Curculionidae)

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ABSTRACT
The flax weevil *Anagotus fairburni* is a large flightless beetle, that is one of the members of the endemic insect 'megafauna' of New Zealand. It is a protected species that currently persists only on predator-free islands or in remote and difficult to access alpine areas. Little is documented about the ecology of the flax weevil. In this study we estimated the number of instars in the *A. fairburni* life cycle by measuring the head capsule widths of larvae collected in the field on Mana Island Scientific Reserve. We used kernel density function estimates to predict average head-capsule widths and the number of larval instars. We then used Brooks-Dyar's law on the head capsule width data and analysed Brooks and Crosby indexes to refine the estimated number of instars based on imperfect data. Results from sampling of 86 larvae suggested four instar groupings, but further analysis based on Brooks-Dyar's law found that *A. fairburni* likely passes through 6 or 7 larval stages prior to pupation, with some uncertainty for smaller instars. Our method provides new data on ecology of an endemic species and provides a framework for further work on similar endangered species where data is imperfect or difficult to gather.

ARTICLE HISTORY
Received 10 February 2023
Accepted 22 August 2023

HANDLING EDITOR
Rob Cruickshank

KEYWORDS
Development; larval stages; Brooks-Dyar; soil insect; invertebrate conservation

Introduction

With adults measuring just over 2 cm long, the flax weevil *Anagotus fairburni* (Brookes 1932) (Curculionidae: Aterpini) is a large flightless beetle that is one of the many extant members of the weevil 'megafauna' of New Zealand (Figure 1). The flax weevil is one of the few insect species that is fully protected under the Wildlife Act 1953 (Miskelly 2014), and is dependent on flax plants (*Phormium* spp.) for its survival during all stages of its life cycle; the adult beetles feed on flax leaves, while larvae develop underground, feeding on and within flax rhizomes (Gourlay 1931). Due to predation by introduced mammals, populations of flax weevil persist only on predator-free islands or in alpine

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Figure 1. An adult flax weevil *Anagotus fairburni*, Pororangi/Mt Stokes, Marlborough Sounds, New Zealand, 2018.

areas, which can be remote and difficult to access for research purposes (Gibbs 2009; Towns 2009).

A small population of *A. fairburni* was translocated to Te Mana o Kupe ki Aotearoa (Mana Island Scientific Reserve), an action recommended as part of the Mana Island Ecological Restoration Plan (Miskelly 1999). The translocated weevils were gathered from Te Pākeka/Maud Island Scientific Reserve and were moved in two batches, the first in 2004 (80 adult weevils) and the second in 2006 (a further 70 adult weevils). In both 2004 and 2006, weevils were released at the same location near the southern end of Mana Island (Department of Conservation 2006). Mana Island proved an ideal habitat for these weevils; in less than 10 years they had proliferated beyond what had been seen before in any other translocated population, greatly outnumbered their original source population on Te Pākeka/Maud Island. The population increased to the point they caused the collapse of flax plants near the weevil release site on Mana Island (Miskelly 2013). There is a concern that widespread loss of flax habitat might seriously impact the goldstripe gecko, *Woodworthia chrysosiretica* (Robb, 1980) on the island, and possibly lead to a substantial population decline. Mana Island is the stronghold for this gecko (Flannagan 2000; Miskelly 2023). Concerns were also raised for native birds on Mana Island which use flax nectar and seeds, such as tui, *Prosthemadera novaeseelandiae* (Gmelin, 1788), korimako *Anthornis melanura* (Sparrman, 1786) and yellow-crowned kakariki, *Cyanoramphus auriceps* (Kuhl, 1820).

Very little is documented about the ecology of the flax weevil; what little is known comes from captive weevils raised in the 1930s when the species was first discovered (Gourlay 1931). Originally described as *Phaeophanus fairburni*, this beetle was found on a track on Rangitoto ki te Tonga/D'Urville Island by Miss R. F. B. Huffam of

Richmond, Nelson, in January 1931. Two days later Ernie Fairburn (an amateur entomologist from Whangarei) figured out the host association, finding the weevil on a flax plant, and together with Edwin Gourlay, they collected several specimens which formed the basis for the original description (Brookes 1932). Gourlay's original account of the discovery of the weevil in 1931 is also one of the only detailed published records of the life history the weevil. Gourlay (1931) described the 'injurious effects' of weevil on the flax of D'Urville Island and documented his observations of the 100+ captive weevils that he took back to the Cawthron Institute in Nelson. He described their nocturnal feeding habits, provided descriptions of the egg, larval, and pupal stages, as well as observations on their preferred oviposition sites.

Gourlay (1931) provided a description (but not measurements) for the first instar larva of the flax weevil, gave average body length measurements for the largest larval instar (19 mm) and the pupa (16 mm), but made no estimate for the number of larval stages that the species may have.

Understanding the life history of an insect is essential for forecasting future abundances and for developing successful control programs. In the flax weevil, the number of larval instars and the mean head capsule widths for instars are not known, which makes instar determination in the field difficult. Knowing instar ratios in the larval population could be used for predicting future population size, and for control strategies, as larvae may be a more vulnerable life stage than adults.

We investigated how many instars the weevil goes through before becoming an adult, by excavating larvae from the bases of flax plants, measuring their head capsule widths, and applying the Brooks-Dyar rule. Based on previous work on large New Zealand weevils (McBurney 1976; Schops 1998), we had expected 5–6 instars in *A. fairburni.*

The Brooks-Dyar rule, also known as Dyar's rule (Crosby 1973) states that the sclerotised parts of an insect follow a linear geometric growth pattern during development (Brooks 1886; Dyar 1890). There is a wealth of literature generated across a range of insect taxa that have used this rule to develop a deeper understanding of their life history (Hawking and New 1996; Ahmad and Nabi 2012; Ramaiah 2018; Ferreira-Keppler et al. 2019; Kondur and Şimşek 2021). This rule is particularly useful when data is difficult to gather or incomplete, as the theory enables inferences from imperfect data (Skuhrovec et al. 2019). Not all species conform perfectly to the Brooks-Dyar rule (Elmes 2001; Lackmann 2018); however, it is widely used in entomology and other related sciences. While the gold standard for instar determination is to use morphology and chaetotaxy (May 1977; May 1993; Gosik et al. 2016), working with protected animals in nature reserves places limitations on what can be done. It is also difficult to use fine morphology in field conditions, as we wanted a comparatively simple measurement that non-specialist workers could use in the field.

Methods

Sampling of larvae

Sampling was carried out at the southern end of Mana Island in September 2019. *Anagotus fairburni* larvae were extracted from twelve flax plants by uprooting and lifting whole rosettes of heavily damaged flax and methodically searching the roots, rhizome, and the bases of leaves for larvae burrowing into the plant tissue. We first uprooted a rosette, then searched the root, and then searched each flax fan by peeling off one leaf at a time. Heavily damaged flax plants were targeted both for convenience (as flax heavily damaged by weevils is severely weakened and easy to excavate, in comparison to healthy plants) and to yield large numbers of larvae.

Identification of the larvae was based on the description provided by Gourlay (1931), with the number of larvae found on each flax plant recorded. For large larvae, head capsule widths were measured in the field using electronic field callipers accurate to 0.1 mm, and larvae were returned to the soil at the base of flax plants. Three head capsule widths measurements were taken using the callipers for each 'large' larva and an average generated from those three measurements was recorded. The small larvae were preserved in 70% ethanol and transported to Massey University, Palmerston North. They were then measured (using a dissecting microscope imaging system with the Olympus CellSens software) and the head capsule widths recorded to the nearest 0.01 mm.

Data analysis

Data analysis followed the methods described by Sukovata (2019). All analysis was done in R Studio 3.6.1, using the packages: *stats*, *ggplot2*, and *nlstools*. Following Sukovata's (2019) methodology, we used the collected head capsule data to generate histograms and visually review the data to hypothesise expected peaks of the various instar sizes present in our samples. After reviewing the histogram, we then followed approach 2 in Sukovata (2019), using the data to generate a kernel density estimate (KDE) function (Sukovata 2019, p. 3). While a variety of kernel functions exist, we used the normal (Gaussian) distribution function, where the KDE peaks correspond to the means of head capsule width in instars. Multiple bandwidth values were compared, with final values chosen for goodness of fit. KDE analysis was undertaken using the density function from the *stats* package.

After fitting the KDE with appropriate bin widths, the KDE peaks were used to generate the mean head capsule size of each detected larval instar. This mean value was then used as a starting value to fit a non-linear squares (NLS) model to head data using the *nlstools* package. The NLS fits a Gaussian curve to each instar KDE peak, producing estimates of mean and standard deviation for the head sizes in all instars. Finally, the resulting estimates of mean head width for each instar were plotted, with linear and ln regression fitted to test for the overall adherence to the Brooks-Dyar rule.

In order to confirm the accuracy of our results, we calculated Brooks-Dyar ratios and corresponding Crosby growth ratios for each of detected instars (Brooks 1886; Dyar 1890; Crosby 1973). We used the following equations to generate these ratios (Chen 2021):

$$\text{Crosby's index} = \frac{b_n - b_n - 1}{b_n - 1}$$

$$\text{Brook's index} = \frac{X_n}{X_n - 1}$$

where X_n is the mean measurement for (n instar) larvae, $X_n - 1$ is the mean measurement for ($n - 1$ instar) larvae, b_n denotes Brooks' index of (n instar) larvae, and $b_n - 1$ denotes Brooks' index of ($n - 1$ instar) larvae.

Results

In total, 86 larvae were collected and measured. No pupae were found during this research, though subsequently one pupa was found by volunteer Angela Wilson on 18 October 2020. A range of larvae sizes were found in most flax plants (Figure 2).

Visual inspection of the data suggested three or four instar groupings, although the continuous range of values made separation between groups less clear (Figure 3).

Figure 2. A range of *Anagotus fairburni* larval instars collected from the base of a single flax plant on Mana Island in 2019.

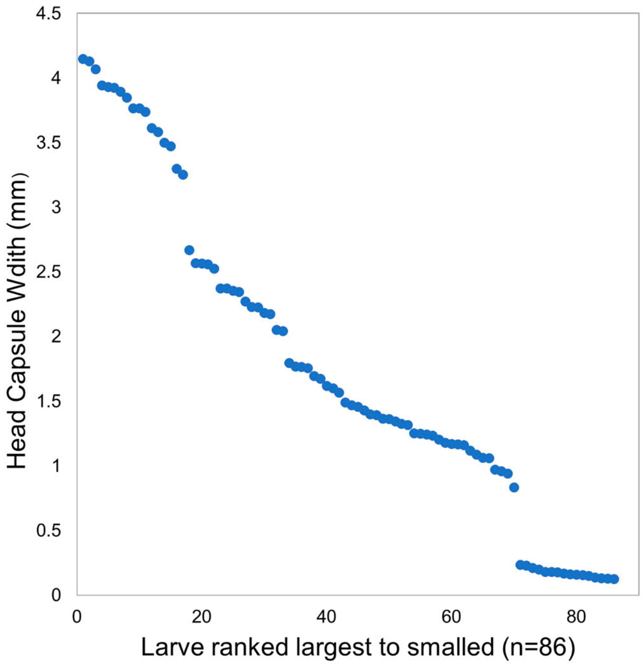

Figure 3. Head capsule width data for 86 *Anagotus fairburni* larvae collected on Mana Island in 2019. Note the almost continuous range of head capsule width measurements.

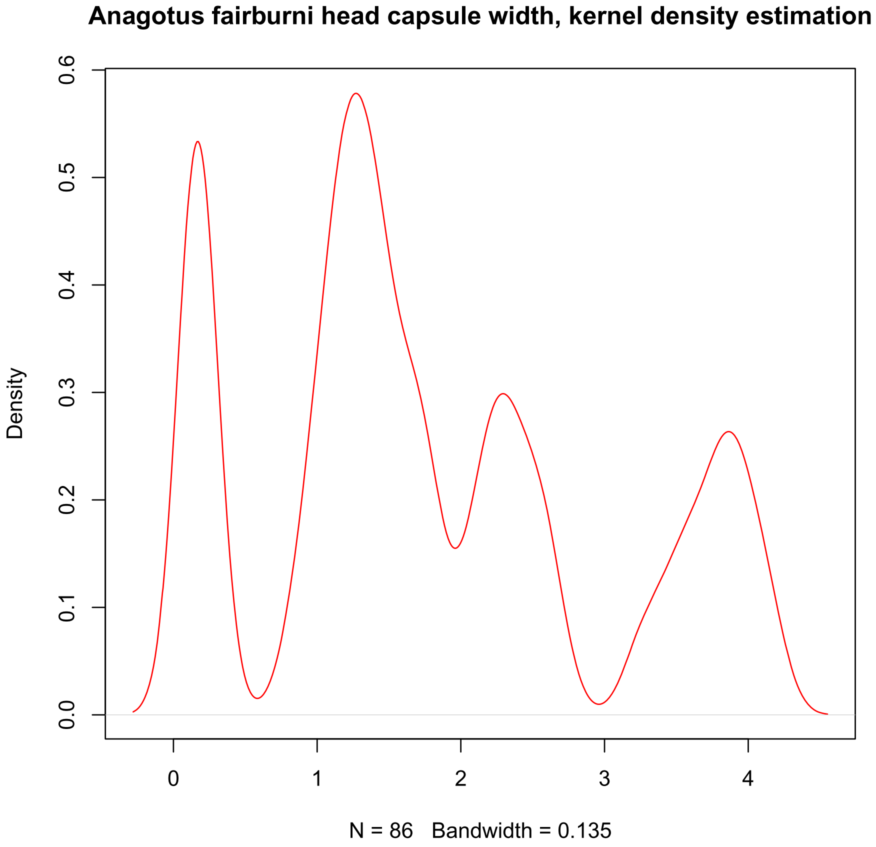

Figure 4. Kernel density estimates (KDE) of *Anagotus fairburni* larvae head capsule widths, Mana Island data, *n* = 86, bandwidth set at 0.135. X axis values in mm.

Using KDE function, four main peaks were identified (Figure 4), which were used to generate values for the most likely head capsule width for each of the corresponding four instars (in a Gaussian model, the maximum probability coincides with the mean value). The means for peak 1 and peak 4 were then used to fit a Gaussian NLS model. However, peak 2 and peak 3 were not well separated and the NLS models for these peaks would not converge; these peaks were manually fitted using Gaussian with sigma values derived from NLS and the means derived from the KDE function. As expected, there was some overlap between size ranges of instars (Figure 5).

From the data collected on Mana Island, there appears to be at least four larval instars in *Anagotus fairburni*. Data and derived parameters are presented in Table 1.

Table 1. Estimated mean head capsule widths of Anagotus fairburni larval instars predicted from KDE peaks, and corresponding Brooks-Dyar and Crosby growth ratios; Mana Island, 2019, *n* = 86.

Larval Instar	Most likely head capsule width (mm)	Brooks-Dyar ratio	Crosby growth ratio
1	0.173		
2	1.270	7.32	
3	2.292	1.80	−0.75
4	3.861	1.68	−0.06

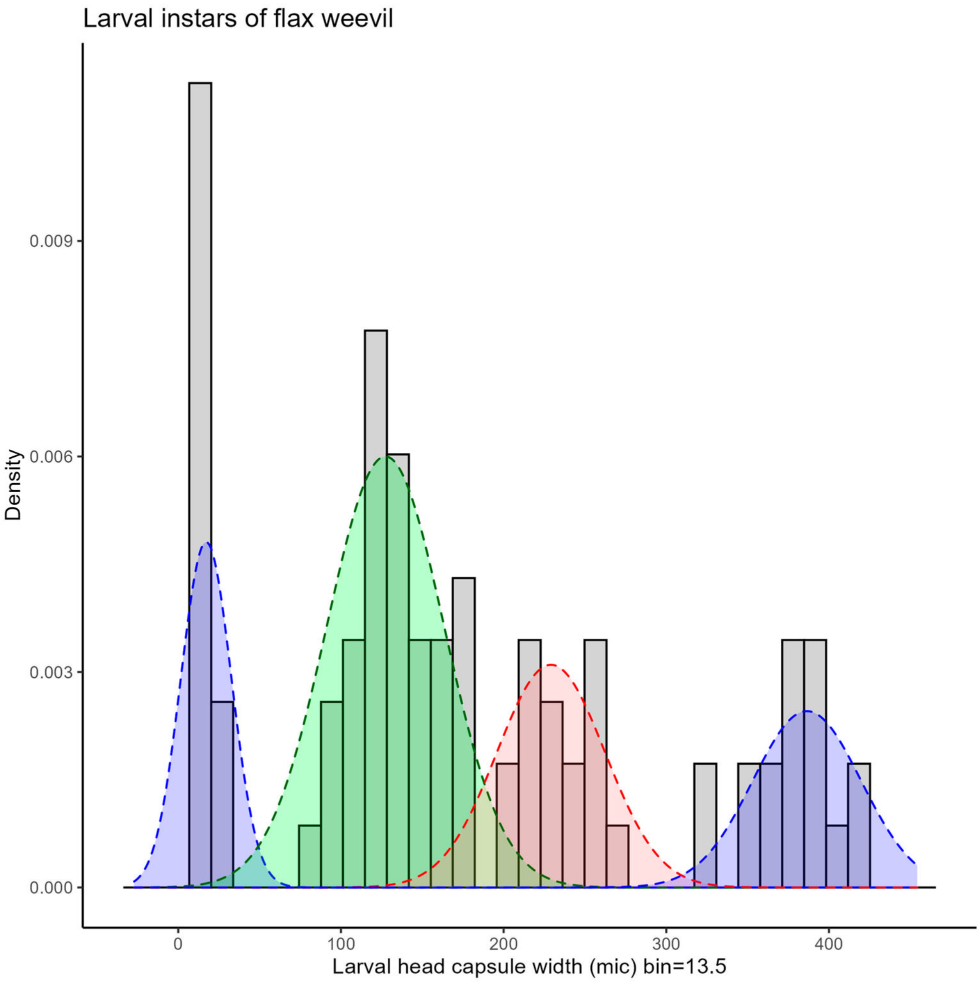

Figure 5. The hypothesised *Anagotus fairburni* larval instars, with head capsule width peaks plotted using Gaussian models. X axis values in 10^{-5} m.

Prior to beginning of this work, our hypothesis was that there would be five or six instars, as found in other large weevils such as *Hadramphus spinipennis* Broun, 1911 (Schops 1998) and the congeneric weevil *Anagotus helmsi*, Sharp, 1882, which was thought to have 'probably five instars' (McBurney 1976). This suggested that either *A. fairburni* has an unusually low number of larval instars, or that not all instars were present or could be detected in our samples.

Table 2. Estimated instars for the flax weevil *Anagotus fairburni* projected from largest to smallest based on the observed mean head capsule width for the largest instar and the mean observed Brooks-Dyar's ratio of 1.74.

Larval Instar head capsule width (mm)	1	2	3	4	5	6	7
Estimated	0.139	0.242	0.421	0.733	1.275	2.220	3.861
Observed	Minimum 0.125, mean 0.173		–	–	1.270	2.292	3.861

A Brooks-Dyar ratio is expected to be consistent between instars (Sukovata 2019). The results for instars 2/3 and 3/4 in Table 1 are consistent with this expectation. However, for instars 1/2 the Brooks-Dyar ratio of 7.32 suggests it is highly likely that at least one instar was missed. The same shows up clearly with the Crosby's growth ratio of −0.75; when the absolute value of Crosby's growth ratio is greater than 0.1, it indicates that the instar groupings do not match the Brooks-Dyar rule and that the instar stages hypothesised are not correct.

Sukovata (2019) recommended plotting the log natural values of head capsule widths for instars and checking the linear regression equations, stating that the ln-transformed means of the head capsule widths should be as close to a straight line as possible (i.e. $R^2 > 0.99$). When this was done for our data for the hypothesised four instars, the regression line was not within these bounds. However, when the first data point was removed, the remaining instars conformed to the rule (Figure 6).

Given that the data for three larger instar sizes showed conformity with the Brooks-Dyar and Crosby's ratios and met the assumptions of linearity when ln-transformed, we are confident that they are correct estimates for head capsule widths of older flax weevil larvae on Mana Island. Armed with these data, we then predicted the likely number of smaller instars and their head capsule width sizes by starting from the largest instar and extrapolating to smaller instars using the Brooks-Dyar ratio of 1.74 (average of the two values from Table 1). This approach suggests the existence of six or seven instars, before coming within the size range of our smallest observed larvae (Table 2).

Discussion

Based on previous work on New Zealand weevils (McBurney 1976; Bennett 1987; Schops 1998), we had expected 5–6 instars in *A. fairburni*. However, much larger numbers of instars occur in some weevils from the same tribe as *Anagotus* (Aterpini). The raspberry

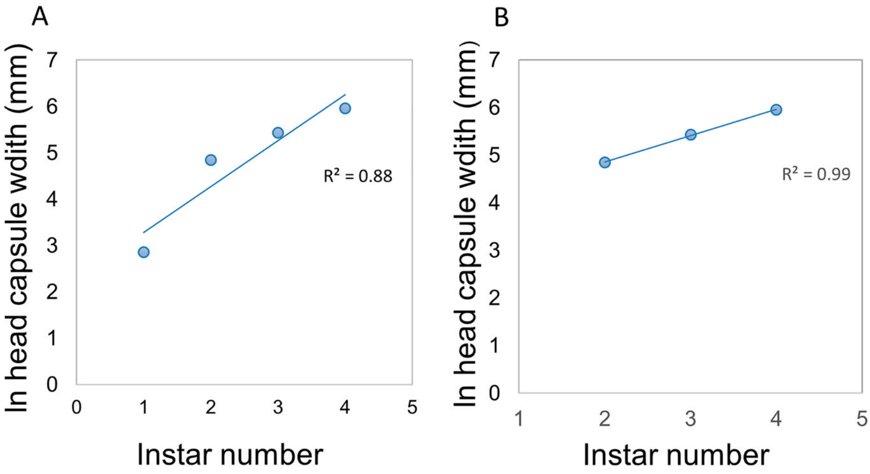

Figure 6. Fitting the ln-transformed head capsule width measurements to the linear regression for flax weevils (*Anagotus fairburni*) found on Mana Island, 2019. **A**, hypothesised four instars, **B**, for three instars with the first data point removed.

weevil *Aegorhinus superciliosus* (Guérin-Méneville, 1830) is a horticultural pest in southern Chile, and so has been well studied (Parra et al. 2009). When raised in a lab on an alternate host plant (*Daucus carota*) *A. superciliosus* went through 14 instars with very low Brooks-Dyar ratios (<1.2 on average) (Aguilera and Rebolledo 2001). Their results show that numerous instar stages are possible in this tribe of weevils.

Our sampling effort took place during one visit to the island, rather than a sustained effort over time, which may have impacted on our observed results. Access to Mana Island Scientific Reserve is limited and *A. fairburni* is a protected species, which inhibited our ability to sample more comprehensively. It is possible that the lifecycle of larvae in the soil is longer than a year, and that the laying time is spread across several months, resulting in overlapping cohorts of larvae from different generations in the soil. This overlap and a lack of regular sampling may have led to us to missing instars in our dataset and affected our results. Overlapping generations are not uncommon in larvae of beetles; examples from New Zealand include the endemic brentid *Lasiorhynchus barbicornis* (Fabricius, 1775) which spend 2 years in dead wood before emerging as adults, and large bodied sand scarabs in the genus *Pericoptus* which spend 3-5years completing their entire lifecycle (Painting and Holwell 2014; Logan 2019).

Intraspecific variation in weevil larvae size may also have affected our ability to categorise instars. Goldson et al. (2008) found that larvae of the Argentine stem weevil *Listronotus bonariensis* (Kuschel, 1955) sorted into different size cohorts reflecting different generations and seasons, something the authors hypothesised may have been due to differing environmental conditions. However, within each generation and season the larval instars mostly conformed to Brooks-Dyar rule (with ratios close to 1.4) and overall, there were only four larval instars (Goldson et al. 2008). Sexual dimorphism in weevils can also affect larval head capsule widths, particularly in later instars, as shown in the pea leaf weevil *Sitona lineatus* (Linnaeus, 1758) (see Hamon et al. 1984). This may be a factor in *A. fairburni,* as there is some evidence that females are slightly larger than males (Willaim David Brockelsby, unpublished data).

Based on data and analyses presented here, it is likely that the flax weevil (*A. fairburni*) has six or seven instars. Larger sample sizes for smaller larvae, and more accurate measurements, including morphological and chaetotaxy analysis, would help to confirm our hypothesised number of instars. A separate trial underway on Mana Island using marked weevils within a fenced enclosure/exclosure is investigating the duration of the larval life stage, and how long adults live after emergence. When combined with these longevity data, the ability to accurately assign an instar stage to any individual larva specimen collected would allow researchers to make more accurate predictions of flax weevil phenology based on larval head capsule size.

Acknowledgements

Thanks to the Friends of Mana Island for their support of all the flax weevil fieldwork, including boat trips to and from the island, supply of materials, and the teams of volunteers who set up and monitored the flax weevil study sites. Department of Conservation Kapiti Wellington and Ngāti Toa supported and approved work on the island; special thanks to rangers Nick Fisentzidis, Genevieve Spargo and Brent Tandy for their help. Mark Anderson's assistance with the collection of larvae and data on the island was greatly appreciated. Reviewers' feedback greatly improved the focus and accuracy of the manuscript.

Disclosure statement

No potential conflict of interest was reported by the author(s).

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