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Lefort M, Boyer S, Vereijssen J, Sprague R, Glare TR, Worner SP. 2015. Preference of a native beetle for “exoticism,” characteristics that contribute to invasive success of *Costelytra zealandica* (Scarabaeidae: Melolonthinae) PeerJ 3:e1454 <https://doi.org/10.7717/peerj.1454>

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14 **A native beetle fond of exotic plants. Characteristics that**  
15 **contribute to invasive success in *Costelytra zealandica***  
16 **(Scarabaeidae: Melolonthinae).**  
17

18  
19 **Abstract**

20 Widespread replacement of native ecosystems by productive land sometimes  
21 results in the outbreak of a native species. In New Zealand, the introduction of  
22 exotic pastoral plants has resulted in the diet alteration of the native coleopteran  
23 species, *Costelytra zealandica* (White) (Scarabaeidae) such that this insect has  
24 reached the status of pest. In contrast, *C. brunneum* (Broun), a close congeneric  
25 species, has not developed such a relationship with these ‘new’ host plants. This  
26 study investigated the feeding preferences and fitness performance of these two  
27 closely related scarab beetles to increase fundamental knowledge about the  
28 mechanisms responsible for the development of invasive characteristics in native  
29 insects. To this end the feeding preferences of larvae of both *Costelytra* species  
30 were investigated under controlled conditions and the survival and larval growth  
31 of the invasive species *C. zealandica* were compared on native and exotic host  
32 plants. *Costelytra zealandica*, when sampled from exotic pastures, was unable to  
33 fully utilise its ancestral native host and showed better performance on exotic  
34 plants. In contrast, *C. zealandica* sampled from native grasslands did not perform  
35 significantly better on either host and showed similar feeding preferences to *C.*  
36 *brunneum*. This study suggests the possibility of strong intra-specific variation, in  
37 the ability of *C. zealandica* to exploit native or exotic plants, supporting the

38 hypothesis that such ability underpins the existence of distinct host-races in this  
39 species.

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42 **Key words:** invasive species, native invader, plant-insect interactions, feeding  
43 preferences, New Zealand

44

45 **Suggested running head**

46 *A native beetle fond of exotic plants*

47

48

## 48 **Introduction**

49 By widely replacing native ecosystems with more economically productive land, modern  
50 intensive agriculture has often been regarded by ecologists as a driver for substantial  
51 biodiversity loss (Robinson & Sutherland 2002, Tilman *et al.* 2002, Foley *et al.* 2005).

52 Although detrimental for numerous species, anthropogenic modifications creating ‘new’  
53 ecological conditions appear to be beneficial under certain circumstances for some  
54 species of the native pool. For instance, it is acknowledged that the high diversity of  
55 phytophagous insects partially depends upon evolutionary processes that occur through  
56 the action of factors affecting their diet breadth (Gaete-Eastman *et al.* 2004), such as the  
57 appearance of a new host plant. Hence, the ecological repercussions of anthropogenic-  
58 driven modification(s) on native ecosystems are worth investigating to enhance  
59 understanding of the insect invasion process. In addition, the comparison of native and  
60 invasive congeners is recognised as a useful approach for identifying characteristics that  
61 promote invasiveness (Munoz & Ackerman 2011), even more so, as in this study, when  
62 the ‘invasive congener’ is native itself.

63 In New Zealand, the introduction of exotic pastoral plants has resulted in alteration of the  
64 diet of the native coleopteran *Costelytra zealandica* (White) (Scarabaeidae), resulting in  
65 the larvae of this endemic insect to feed intensively on the roots of ryegrass and white  
66 clover and being ranked as a major economic pest (Pottinger, 1975; Richards *et al.*,  
67 1997). Interestingly and in contrast, *C. brunneum* (Broun), a close congeneric species, is  
68 not often found in ryegrass and white clover pastures and remains mostly distributed in  
69 native habitats (Given, 1966; Lefort *et al.*, 2012, 2013). Both *Costelytra* species are  
70 considered as univoltine organisms (Atkinson & Slay 1994) with three larval stages,

71 although it is not uncommon to come across individuals that follow a two-year life cycle  
72 in the highest and coldest environments of the southern locations of New Zealand, such  
73 as Otago and Southland (Stewart 1972, Kain 1975). These two species are sympatric and  
74 share similar native hosts, mainly comprising tussock species (Poaceae) commonly found  
75 in New Zealand native grasslands (Given, 1966; Lefort *et al.*, 2012, 2013).

76 The present study aimed to investigate the feeding preferences and fitness response of  
77 these two coleopteran species, to provide new insights into the mechanisms underpinning  
78 the invasion process in *C. zealandica* and ultimately in phytophagous insects in general.  
79 The first objective of this study was to perform choice tests where the larvae of both  
80 *Costelytra* species were given the choice between a native and an exotic host plant. The  
81 second objective was to compare survival and larval growth of two populations of the  
82 invasive species *C. zealandica* when exposed to these host plants.

83

## 84 **Material and methods**

### 85 **Insect sampling and plant material**

86 Newly hatched third instar larva, as the most damaging life stage of the invasive species  
87 *C. zealandica* and the most intensively feeding life stage in *Costelytra* spp. in general,  
88 were used in perform the experiments. Because no protocol exists to produce *Costelytra*  
89 spp. offspring under laboratory conditions and all attempts to do so have failed, the best  
90 second option was to work with field collected insects. A total of four sampling sites in  
91 New Zealand's South island were used to collect second instar larvae of *Costelytra* spp.,  
92 Lincoln (43°64'04''S 172°47'82''E) and Hororata (43°32'17''S 171°57'16''E), sites A  
93 and B, and Cass (43°02'10''S 171°45'40''E) and Castle Hill (43°12'20''S 171°42'16''E),

94 as sites C and D (Figure 1). Extensive taxonomic assessments of the plants present on  
95 each site were not performed. However, the two highly dominant groups of plants present  
96 on sites A and B were exotic ryegrass (*Lolium* spp.) and clover (*Trifolium* spp.), while  
97 sites C and D were dominated by native tussock (e.g. *Poa cita*) (visually estimated over  
98 80% incidence) with no white clover (*Trifolium repens*) being present. In the two latter  
99 sites, larvae of both species were collected under large patches of native vegetation.  
100 These patches were distant enough from exotic vegetation, to ensure that no -or minimal-  
101 contact with exotic plants had occurred prior to experiments, given the very low mobility  
102 of the earliest larval stages in *Costelytra* spp.

103 Initially, the larvae were placed individually into ice tray compartments with a piece of  
104 carrot as food at 15°C ambient temperature for four days to test for the endemic amber  
105 disease according to the protocol of Jackson *et al.* (1993). Healthy larvae were identified  
106 to the species level based on the non-invasive methodologies developed by Lefort *et al.*  
107 (2012, 2013).

108 *Trifolium repens* (white clover) was grown in a glasshouse (Lincoln University, New  
109 Zealand) from seeds (PGG Wrightson Seeds Ltd, Christchurch, New Zealand) in 200 ml  
110 of potting mix comprising 60% peat and 40% sterilized pumice stones. Young plants of  
111 the native *Poa cita* (silver tussock) were purchased from a native plant nursery in  
112 Christchurch, New Zealand. Each plant was carefully transferred from its original pot to a  
113 200 ml pot, filled with potting mix as described above, and was allowed to grow for 2  
114 months prior to the feeding experiment.

115

116 ***Costelytra* spp. feeding preferences – native vs exotic host choice test**

117 The feeding preference of *C. zealandica* and *C. brunneum* larvae were tested using a  
118 three choice olfactometer with native or exotic hosts. The olfactometer comprised of  
119 three extended arms, each 120 mm in length and 40 mm in diameter, filled with gamma-  
120 irradiated soil (Schering-Plough Animal Health, Wellington, New Zealand) and a 40 x 40  
121 mm central exposure chamber. The larvae were introduced through an aperture in the  
122 central chamber. A pot containing either no plant (control pot), white clover, or silver  
123 tussock was connected at the end of each arm. Third instar larvae of *C. zealandica*  
124 collected from sites B (population B from exotic pasture, n=35) and C (population C  
125 from native grasslands, n=35) and *C. brunneum* from collection site D (population D  
126 from native grasslands, n=35) were used for this experiment. For each population, the  
127 bioassay was replicated seven times, with five new larvae inserted together in the central  
128 exposure chamber. After 24 hours, pots were disconnected from the olfactometer device,  
129 emptied of their content and larvae were counted. Between each trial, all components of  
130 the olfactometer were washed thoroughly with warm water and left to soak in clean water  
131 overnight, finally being left to air-dry on a clean counter and reassembled. Results were  
132 analyzed by Chi-squared test using R software (R Development Core Team, 2009). The  
133 significance of the choice of a plant (i.e. white clover or silver tussock) versus no plant  
134 (control) and no choice was first tested. In the event that a plant was chosen, the  
135 significance of the plant choice itself was also tested, in other words, post hoc follow-up  
136 testing was performed on white clover versus silver tussock.

137

138 ***Costelytra zealandica* fitness response on different host plants**



139 Newly moulted third instar larvae of *C. zealandica* collected from sites A (from exotic  
140 pasture, n=64) and C (from native grasslands, n=47) were randomly allocated to the two  
141 different host plant treatments (white clover and silver tussock). Each larva was kept  
142 individually in a 35 ml plastic container containing 50g of gamma-irradiated soil (as  
143 above) and was fed *ad libitum* with roots of white clover or silver tussock. Containers  
144 were randomly arranged on plastic trays and kept in an incubator at 15°C.

145 The experiment was conducted over 15 weeks, which is representative of an average  
146 length of the third instar stage of *C. zealandica*, after which all larvae were assessed for  
147 survival. At the commencement of the experiment and after the first six weeks of  
148 treatment, which corresponded to the most intensive weeks of feeding for the third instar  
149 life stage of this species, the weight of each larva was recorded. Statistical analyses to  
150 determine the effect of host plant diet on larval survival were carried out using a Chi-  
151 squared test. Average larval growth was analyzed by Welch Two Sample t-test for each  
152 population, after exclusion of larvae that died before the end of the sixth week. All  
153 statistical analyses were conducted using R software (R Development Core Team, 2009).

154

## 155 **Results**

### 156 ***Costelytra* spp. feeding preferences – native vs exotic host choice test**

157 In the choice test, only *C. zealandica* collected from exotic pastures (population B)  
158 showed a preference for the exotic white clover ( $\chi^2 = 7.88$ ,  $df = 1$ ,  $p < 0.01$ ) (Figure 2). In  
159 contrast, *C. zealandica* collected from native grassland (population C) and *C. brunneum*,  
160 did not show a preference for either plant species (Figure 2).

161

162 ***Costelytra zealandica* - larval survival and growth on exotic clover or native tussock**  
163 In contrast to the larvae from native grasslands (population C), the larvae collected from  
164 exotic pastures (population A) displayed significantly higher survival rates when fed on  
165 clover (33.3% survival) compared with larvae fed on native silver tussock (5.5%  
166 survival) ( $\chi^2 = 4.43$ ,  $df = 1$ ,  $p < 0.05$ ) (Figure 3).

167

168 No treatment effect on larval growth was detected for the population from native  
169 grasslands (population C) ( $t = -1.84$ ,  $df = 13.19$ ,  $p = 0.089$ ), while the larvae from exotic  
170 pastures (population A) gained significantly more weight when fed on clover for 6 weeks  
171 compared to when they were fed on native tussock ( $t = -3.38$ ,  $df = 40.08$ ,  $p = 0.0016$ )  
172 (Figure 4).

173

## 174 **Discussion**

175 This study investigated variations in feeding preferences and fitness response to various  
176 hosts in *C. zealandica*. The results corroborate the existence of a strong intra-specific  
177 variation of the diet breadth of this pest species (Lefort *et al.* 2014). This study also  
178 demonstrated similarities between the feeding preferences of a population of *C.*  
179 *zealandica* collected from an isolated native habitat with those of the congeneric non-pest  
180 species *C. brunneum*. The overall results of this study have provided new insight into the  
181 mechanism(s) underpinning the invasion of *C. zealandica* into improved pastures  
182 throughout New Zealand.

183 Overall fitness, as measured by survival and growth, of *C. zealandica* collected from  
184 exotic pastures was higher on the exotic host plant, white clover. Inheritance and

185 maternal effects on host choice (Mousseau & Dingle 1991, Mousseau & Fox, 1998),  
186 where offspring display high fitness performance (Fox 2006) and similar host preferences  
187 to their mother (Craig et al. 2001), is a possible explanation. Similarly, another maternal  
188 effect coined the ‘mother knows best principle’, which suggests that females tend to  
189 oviposit on host plant(s) that can potentially increase their offspring survival (Scheirs *et*  
190 *al.* 2000, Mayhew 2001), can also be a possible explanation although no evidence toward  
191 this principle has been observed in *C. zealandica* adult beetles (Kelsey 1968, Radcliffe &  
192 Payne, 1969, Kain 1975).

193 These effects are supported by the results of the choice test, where population A,  
194 comprising the pest species *C. zealandica*, collected from exotic pasture plants on which  
195 they were likely to have been feeding for several generations, chose exotic clover as the  
196 preferred host plant. In contrast, the population of *C. zealandica* collected from their  
197 native range did not show any preference in the choice tests and did not perform better on  
198 either host. The first observation negates the hypothesis of inheritance and maternal effect  
199 on host choice mentioned earlier, since based on this principle, this population would  
200 have been expected to prefer its native host (i.e. silver tussock) and have better fitness  
201 performance on this plant compared with the exotic host (i.e. white clover). Unlike silver  
202 tussock, white clover is a legume, which may partly explain the differences in larval  
203 weight gain observed in the *C. zealandica* population collected from exotic pastures.  
204 Indeed, because of their bacterial symbiosis resulting in an ability to fix nitrogen  
205 (Awmack & Leather 2002), the nutritional value of this family of plants is likely to be  
206 higher than that of grasses, such as silver tussock, used as the alternative host in this  
207 study. However, this alternative hypothesis does not explain the response of the other *C.*

208 *zealandica* population studied, which in this case would have been expected to show  
209 increased weight gain on clover as well.

210 Based on similar survival rates observed in the two populations of *C. zealandica* used in  
211 this study, and because the population collected from native grassland was presumably  
212 isolated enough to have not fed on exotic host plants prior to the experiment, it appears  
213 that the successful exploitation of an exotic plant by this species is likely a pre-existing  
214 ability. Diegisser *et al.* (2009) and Ding & Blossey (2009) suggested that some form of  
215 pre-adaptation was required for the exploitation of a novel host plant. The similarity of  
216 host choice, observed between *C. zealandica* collected from native grassland and the non-  
217 pest species *C. brunneum*, along with the current difference in exploitation of exotic  
218 pastoral plants by the two species supports the hypothesis of some degree of pre-  
219 adaptation or phenotypic plasticity in *C. zealandica*. The defence mechanisms employed  
220 by the different host plants and their effect on the fitness of the insect species studied is  
221 an interesting question. In a recent review about phytophagous insects and plant defences,  
222 Ali and Agrawal (2012) reaffirmed that generalist insects do not master, and in this sense  
223 do not totally overcome their host defences, but possess 'general mechanisms' to tolerate  
224 an array of those defences. It is possible to observe variations in this tolerance,  
225 particularly when the host-range utilised by the insect species is highly diversified and,  
226 consequently, when the family of plants have differential evolutionary histories that may  
227 have result in slight variations in their defence mechanisms. Here, *C. zealandica* may  
228 have been, in terms of fitness, less affected by the defences of white clover compared to  
229 those of the other hosts or, conversely and as recently shown by Lefort *et al.* (2015), may  
230 also have benefited from the defences of their host. The latter phenomenon has been

231 observed several times in recent insect-host interaction studies, where the defences of the  
232 hosts were artificially triggered and the resulting fitness response of the insects studied  
233 unexpectedly enhanced (e.g. Pierre *et al.* 2012, Robert *et al.* 2012).

234 The results of this study support the pre-existence of characteristics that may have  
235 contributed to the invasion success of the New Zealand native scarab *C. zealandica*, into  
236 exotic pastures throughout New Zealand in contrast to its native congener, *C. brunneum*  
237 that maintains small populations in native grasslands. Additionally, the differences in  
238 feeding preferences between different populations of the pest species *C. zealandica*, seem  
239 to confirm recent evidence (Lefort *et al.* 2014) of the existence of distinct host-races in  
240 this species. With regards to cryptic species, many studies have highlighted the  
241 importance of correct species identification for the accomplishment of successful  
242 biological control (e.g. Rosen 1986, Paterson 1991, Silva-Brandão *et al.* 2013). Similarly,  
243 we believe that the delineation of host-races in pest species could have vital implications  
244 in term of pest control management and strategies. For instance, caution should be taken  
245 before denominating a species as a single entity by employing terms such as “pest  
246 species” or “invasive species”, and care must be taken during insect sampling and  
247 identification, particularly when performing bioassays for which the outcome may vary  
248 depending on the host-race used.

249

249 **Acknowledgments**

250 The authors would like to thank Richard Townsend and St Andrew's College of  
251 Christchurch for granting access to the different insect collection sites.

252

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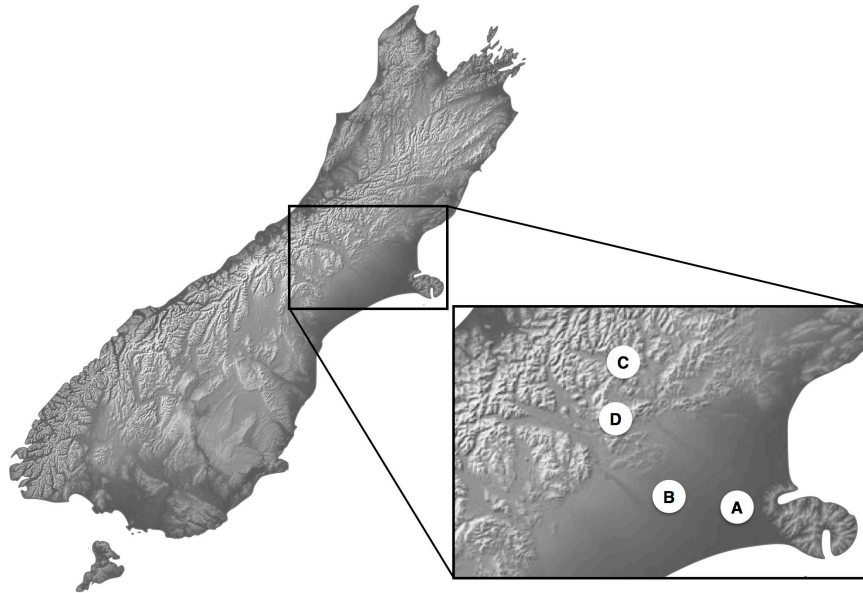
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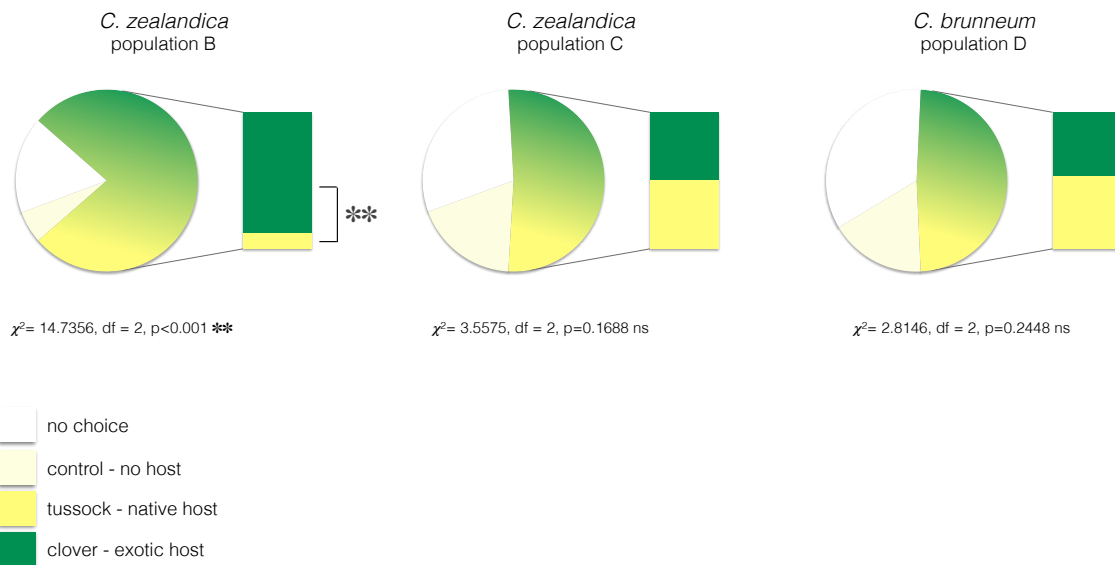
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## Figures and legends



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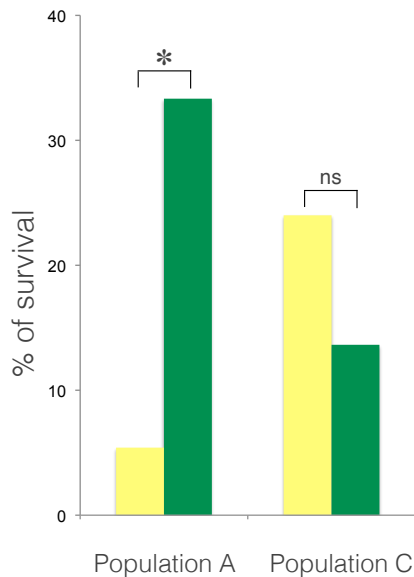
**Figure 1.** Location map for *Costelytra zealandica* and *C. brunneum* sample sites.



330

331 **Figure 2.** Plant choice of larvae of three populations of *Costelytra* in a three-arm olfactometer. With  
332 choices of (a), *C. zealandica* population B (collected from exotic pastures), (b) *C. zealandica* population C  
333 (collected from native tussock grassland) and (c) *C. brunneum* population D (collected from native tussock  
334 grassland). \*\* indicates  $p < 0.01$  and ns indicates  $p > 0.05$ .

335



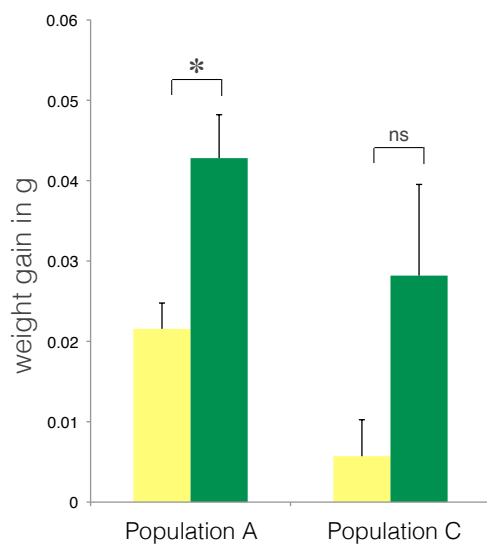
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337 **Figure 3.** Percentage of larval survival of *Costelytra zealandica* from site A (collected from exotic

338 pasture) and site C (collected from native tussock grassland) after 15 weeks of feeding on tussock (yellow

339 bars) and white clover (green bars) host plants. \* indicates  $p < 0.05$  and ns indicates  $p > 0.05$ .

340



341

342 **Figure 4.** Average weight gain of larvae of *Costelytra zealandica* from site A (collected from exotic

343 pasture) and site C (collected from native tussock grassland) after 6 weeks of feeding on tussock (yellow

344 bars) and clover (green bars) host plants. Vertical bars represent SE. Pairwise comparisons were performed

345 using Welch Two Sample t-test. \* indicates  $p < 0.05$  and ns indicates  $p > 0.05$ .