

Counter-intuitive developmental plasticity induced by host quality

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Adaptation to different hosts plays a central role in the evolution of specialization and speciation in phytophagous insects and parasites, and our ability to experimentally rank hosts by their quality is critical to research to understand these processes. Here we provide a counter-intuitive example in which growth is faster on poor quality hosts. The leaf beetles *Oreina elongata* and *Oreina cacaliae* share their host plant with the rust *Uromyces cacaliae*. Larvae reared on infected *Adenostyles alliariae* show reduced growth rate, reduced maximum weight and longer development time. However, they normally respond adaptively to the rust's mid-season arrival. When switched during development from healthy to infected leaves, larvae accelerate growth and reduce development time, but pupate at lower body weight. In this novel plant–insect–fungus interaction, infection forms the cue to trade off life-history traits in order to complete development within the brief alpine summer. It represents a novel mode of developmental plasticity, which is likely to be found in other host–parasite systems whenever host quality deteriorates due to multiple infection or ageing. This phenotypic plasticity would modify competition after co-infection and the mutual selection imposed by hosts and parasites, and creates a paradoxical negative correlation between growth rate and environmental quality.

Keywords: phenotypic plasticity; life-history traits; growth rate; trade-off; Chrysomelidae; rust fungus

1. INTRODUCTION

Not all food is equal. For phytophagous insects, plants differ in quality as a source of food, both when comparing species and at the intraspecific level (Jaenike 1990). The variation is typically manifested as differences in the rate of mass gain on different hosts, with reduced growth on poor quality hosts. This effect on growth allows food quality to be defined from the point of view of the organism, and our ability to rank hosts in this way plays a critical role in research on the evolution of specialization, host-race formation and speciation in insects and parasites (Jaenike 1990; Norton & Carpenter 1998; Dres & Mallet 2002; Hendry *et al.* 2007).

There is, however, another possible reaction to low-quality food. Many species do not grow at their maximum rate under normal conditions. This is despite the theoretical advantages of a shortened juvenile period and increased adult body size, and is thought to be a result of the developmental costs of rapid growth (Stearns 1992; Arendt 1997; Metcalfe & Monaghan 2001). Whatever the reason, this restraint allows phenotypic plasticity in the form of accelerated growth in response to environmental cues such as photoperiod, enabling larvae to complete development after a delay or when produced late in the season (Nylin & Gotthard 1998; Metcalfe & Monaghan 2001). Food quality provides another potential cue for plasticity. In many parasites, parasitoids and phytophagous insects, the ovipositing female chooses the only food source available to larvae at the host, plant or patch level. Escape from deteriorating conditions is impossible, and exposure of larvae to poor-quality food

owing to co-infection or host ageing can indicate that their circumstances will only get worse from that point onwards. An adaptive response may therefore be to accelerate growth, producing a counter-intuitive negative relationship between food quality and growth rate.

Here we report exactly this behaviour in two species of alpine leaf beetle in response to rust attack of their host plant. The beetles *Oreina elongata* and *Oreina cacaliae* share their host plant, *Adenostyles alliariae*, with the rust fungus *Uromyces cacaliae*. The life cycles of all four species are tightly bound in their high-altitude alpine environments, where they have only two to three months each year when the habitat is free of snow. Rust infection of the host plant reduces larval growth rate in both beetle species (Röder *et al.* 2007). However, in the field, the rust is not present for the entire summer, but becomes more common as the season progresses. We test how larvae respond to this situation, comparing their performance on healthy, infected and switched diets (changing from healthy to infected leaves part-way through development). This reveals a novel three-way interaction in which beetles on the switched diet seem to use the arrival of the rust fungus as a cue to accelerate their growth. We then combine the diet treatment with a photoperiod treatment mimicking early- and late-season conditions (already known to induce developmental plasticity; Margraf *et al.* 2003), in order to explain the difference between the infected and switched diets. The results demonstrate a highly flexible response in which larvae trade-off life-history traits in order to reach a critical developmental stage for overwintering. As a result of this plasticity, larval growth rate cannot be considered a good indicator of host plant quality.

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2. MATERIAL AND METHODS

(a) Study organisms

Oreina elongata Suffrian and *O. cacaliae* Schrank (Coleoptera: Chrysomelidae) are closely related, metallic blue leaf beetles found exclusively in mountain environments (Lohse & Lucht 1994). *Oreina cacaliae* is the larger of the two species and has a wider geographical and altitudinal range, with isolated populations at altitudes of 800–2300 m across the European mountains, whereas *O. elongata* is restricted to the Alps and Apennines in habitats between 1600 and 2400 m a.s.l. (Lohse & Lucht 1994; Margraf *et al.* 2007). In the studied populations, *O. cacaliae* is a specialist that spends the whole reproductive season on *A. alliariae*, while the adults and larvae of *O. elongata* move repeatedly between *A. alliariae* and *Cirsium spinosissimum*, a host that is not attacked by the rust (Gotthard *et al.* 2005; Verdon *et al.* 2007). The two species also differ in reproductive mode: *O. elongata* is oviparous whereas *O. cacaliae* is viviparous. Both face extremely short reproductive seasons of just two to three months while their habitats are free of snow, and have extended life cycles. They hibernate as larvae at the end of their first summer, pupate within the soil in spring, and spend a second summer as a non-reproductive adult before producing offspring only in the following year.

Mature adults were collected from four sites in the Alps: *O. elongata* from the dam at Emosson (Swiss Alps, Valais, 46°03'55.1" N, 06°55'24.9" E, altitude 1949 m) and the Piccolo San Bernardo Pass on the border between France and Italy (Italian Alps, Valle d'Aosta, 45°41'40.7" N, 06°53'05.9" E, altitude 2053 m), and *O. cacaliae* from Kandersteg (Swiss Alps, Ueschidental, Bern, 46°28'26.7" N, 07°38'52.7" E, altitude 1481 m) and La Fouly (Swiss Alps, Val Ferret, Valais, 45°56'11.2" N, 07°05'38.1" E, altitude 1587 m). For each population approximately 15 individuals of each sex were gathered during early June or July as a function of altitude. Adults were kept in 19 × 9 × 8 cm plastic boxes with holes for aeration, at the University of Neuchâtel (Switzerland) in an incubator (Model 250P, LMS Ltd, Sevenoaks, UK) at 6°C with 12 : 30 hour day length. Every 2 days the food was changed and the eggs (*O. elongata*) or first-instar larvae (*O. cacaliae*) removed.

Adenostyles alliariae (Gouan) A. Kern. (Asterales: Asteraceae) is a common, perennial, subalpine and alpine plant, found at a maximum altitude of 2800 m growing on damp soils. It produces secondary compounds, pyrrolizidine alkaloids, which are sequestered by both beetle species (Hartmann *et al.* 1999). *Adenostyles alliariae* is the exclusive host of *U. cacaliae* (DC) Unger (Uredinales: Pucciniaceae), a rust that produces spores from patches (telia) on the underside of leaves approximately two weeks after infection (Bisby 1920). Healthy and naturally rust-infected leaves (with visible telia) were collected twice weekly from La Fouly or Emosson, where fungal infections appear in mid-June and mid-July, respectively (as a result of differences in altitude and exposure). They were transported in a cooled box and kept in a dark, slightly humid fridge at 6°C for a maximum of 2 days until used.

(b) Larval performance on healthy, rust-infected and switched diets

For two populations of *O. elongata* and *O. cacaliae*, larval growth rate, maximum weight and development time were compared when reared on healthy, rust-infected or switched

diets. Newly emerged larvae were assigned at random to one of three diets: healthy; infected with visible fungal telia; or healthy initially but then switched to rust-infected leaves after 8 days. They were reared individually in Petri dishes (diameter 5.5 cm and depth 1.2 cm), with the base lined with plaster of Paris and a filter paper to maintain humidity. Every 3 days, they were weighed to the nearest 0.1 mg on an electronic balance and given a fresh piece of leaf. A few days after reaching the fourth instar, the larvae were moved to larger plastic pots (diameter 9.5 cm and depth 4.5 cm) with a layer of damp soil, where they were fed and weighed until they buried into the soil to hibernate. Experiments were conducted at the University of Neuchâtel in an incubator with 15 hour day length and temperatures varying gradually from 20 (day) to 6.5°C (night). Six (*O. elongata*) or five (*O. cacaliae*) larvae of each population were reared on each diet.

Growth rate was calculated as a daily growth multiplier, estimated for two separate periods for the larvae under all treatments (pre-switch from the start until day 8 and post-switch from day 8 until the maximum weight). For each larva, the successive weights were log transformed and then regressed against the time in days (these linear regressions gave a very close approximation to the growth process, with r^2 values between 0.765 and 1). Exponential back-transformation of the slope gave the daily growth multiplier, representing the coefficient by which larvae multiplied their weight each day. The larvae showed a slight decrease in weight just before they buried themselves for the winter diapause, so the maximum weight reached (mg) was used for the analysis. The development time was taken as the number of days needed to reach this maximum weight. The two growth rates, maximum weight and development time were analysed in separate ANOVAs with terms for species, diet, population nested within species, the species by diet interaction and the population by diet interaction. Terms involving population were treated as random effects. When terms with more than two levels were significant, Tukey HSD tests were used to determine which groups differed significantly. Only the post-switch growth rate required a transformation (reciprocal) to make the data conform to assumptions of normality and homogeneity of variance.

(c) Larval performance under different diets and day-length regimes

Larval growth rate, maximum weight and development time were compared on the same three diet treatments but under two different day-length regimes. The experiment used larvae from the two populations of *O. elongata* only, with 10 larvae of each population on each combination of diet and day length. The larvae were reared as described above, except they were assigned randomly at the start to one of two incubators running different day-length conditions. The first provided the day-length regime 'early', with conditions of 5 July initially (15 : 36 hour day length) and a decrease in the light period of 1–3 min each day. The second incubator simulated the day-length regime 'late', with initial photoperiod typical of 14 August (14 : 12 hour day length) and a decrease of 3–4 min d^{-1} . The temperatures were identical in both (15 hours at 17°C and 7 hours at 7°C, with a 1 hour gradient between phases). The day length was obtained from the Sion meteorological station (Swiss Alps, Valais).

The growth rate was again calculated as a daily growth multiplier separately for the pre- and post-switch periods (giving linear regressions with r^2 values of between

Table 1. ANOVAs on the four larval performance parameters for the two populations of *O. elongata* and *O. cacaliae* when reared on healthy, infected or switched diets. (The population and population by diet terms were nested within species.)

	d.f.	SS	F	p
pre-switch growth rate				
species	1	0.0180	1.017	0.419
diet	2	0.0343	12.484	0.018
pop(species)	2	0.0357	13.077	0.018
diet × species	2	0.0046	1.656	0.297
diet × pop(species)	4	0.0055	0.525	0.718
error	54	0.1403		
post-switch growth rate				
species	1	0.0665	669.426	0.001
diet	2	0.0638	41.226	0.002
pop(species)	2	0.0002	0.125	0.886
diet × species	2	0.0143	9.224	0.031
diet × pop(species)	4	0.0031	2.420	0.060
error	54	0.0174		
maximum weight				
species	1	3578.105	226.759	0.004
diet	2	365.566	58.812	<0.001
pop(species)	2	31.635	5.203	0.077
diet × species	2	21.694	3.490	0.127
diet × pop(species)	4	12.161	0.271	0.896
error	54	606.308		
development time				
species	1	206.869	2490.199	<0.001
diet	2	541.337	172.326	<0.001
pop(species)	2	0.144	0.046	0.956
diet × species	2	46.671	14.857	0.014
diet × pop(species)	4	6.289	1.135	0.350
error	54	74.800		

0.763 and 1), and maximum weight and development time were measured as described above. The two growth rates, maximum weight and development time were analysed in separate ANOVAs with terms for day length, diet, population and all two- and three-way interactions. No transformation was needed to achieve normality and homogeneity of variance. All statistical analyses were carried out using JMP v. 7.0 (SAS Institute, NC, USA).

3. RESULTS

(a) Larval performance on healthy, rust-infected and switched diets

In the pre-switch period, there was a significant effect of diet on growth rate (table 1; figure 1a). The larvae reared on healthy leaves and on the switched diet (given healthy leaves up to that point) did not differ, but both grew more rapidly than those on the rust-infected diet (healthy = switched > infected; Tukey HSD). There were also significant differences between populations.

In the post-switch period, there was again a significant effect of diet on growth rate (table 1; figure 1b). Overall, larvae on the switched diet (now feeding on rust-infected leaves) grew more rapidly than those on the healthy diet, while larvae on the rust-infected diet had the lowest growth rate (switched > healthy > infected; Tukey HSD). The species differed (with faster growth in *O. elongata*), and the species by diet interaction was also significant (with a more pronounced effect of diet in *O. elongata*).

There was a significant effect of diet on the maximum weight reached by larvae (table 1; figure 1c). Larvae on the healthy diet were the heaviest, while those on the switched and rust-infected diets did not differ from each other (healthy > switched = infected; Tukey HSD). There was also a difference between the species, with heavier larvae in *O. cacaliae*.

The development time of larvae depended on their diet (table 1; figure 1d), with significantly shorter development in larvae on the healthy diet than in those reared on rust-infected leaves, but the most rapid development on the switched diet (infected > healthy > switched; Tukey HSD). The species differed significantly, with shorter development time in *O. elongata*. The species by diet interaction was also significant, with a more pronounced effect of diet in *O. elongata*.

(b) Larval performance under different diets and day-length regimes

There was a significant effect of diet on growth rate during the pre-switch period (table 2; figure 2a). As in the first experiment, growth rates on the healthy and switched diets were similar, and higher than those on the rust-infected diet (healthy = switched > infected; Tukey HSD). There was also an overall effect of day length, with faster growth under the late-season photoperiod, and a difference between populations, with faster growth in the larvae from Piccolo San Bernardo. The interaction between population and day length was significant, because differences between day-length treatments were more pronounced for the larvae from Emosson.

In the post-switch period, there was a significant effect of diet on growth rate, consistent with that in the first experiment (table 2; figure 2b). The larvae grew more rapidly on the switched diet than on the healthy diet, and both grew more rapidly than those reared on rust-infected leaves (switched > healthy > infected; Tukey HSD). There was an overall effect of day length, with faster growth under the late-season photoperiod, and a difference between populations, now with faster growth in the larvae from Emosson. The diet by day-length interaction was also significant, with larvae on the healthy diet responding much more strongly to variation in day length than those on the switched or rust-infected diets.

For maximum weight, only the diet term was significant (table 2; figure 2c), with no difference between infected and switched diets but a greater larval weight on the healthy diet, as in the first experiment (healthy > switched = infected; Tukey HSD).

For development time, there were significant effects of day length (early > late), diet (infected > healthy > switched; Tukey HSD), and the diet by day-length interaction (table 2; figure 2d). The response to photoperiod was much stronger in larvae on the healthy diet than in those on the switched or infected diets.

4. DISCUSSION

Infection by the rust *U. cacaliae* clearly reduces the quality of *A. alliariae* as a host plant for *Oreina* beetles (Röder *et al.* 2007). In the first experiment, the larvae of both species reared on infected leaves showed reduced growth rates (the daily multiplier over the whole growth period was reduced by 2.8% on average), lower maximum weights (reduced by

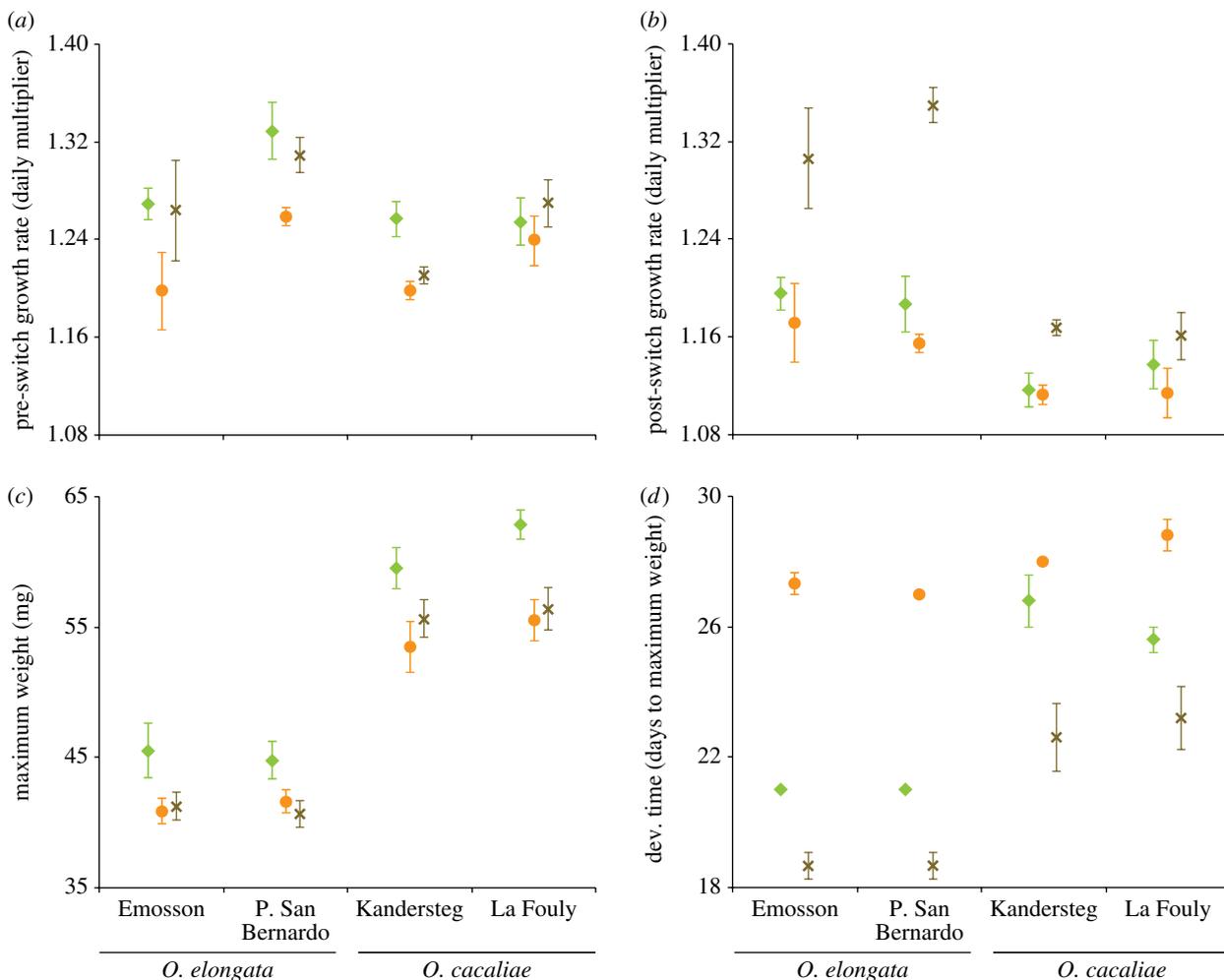


Figure 1. Larval performance of *O. elongata* and *O. cacaliae* from two populations reared on healthy, rust-infected or switched diets. Graphs show the (a) pre-switch and (b) post-switch growth rates (calculated as daily growth multipliers, see text for details), (c) the maximum weight (in mg) reached by the larvae during their development and (d) the number of days needed to reach the maximum weight (all shown as means \pm standard errors, $n=6$ for *O. elongata*, $n=5$ for *O. cacaliae*). Diamonds, healthy diet; circles, infected diet; crosses, switched diet; dev. time, development time.

9.9%) and longer development times (increased by 17.7%). This negative effect may be a direct result of compounds produced by the fungus, or an indirect consequence of changes to host chemistry or the induction of defence in the plant (Hatcher 1995; Röder *et al.* 2007).

Remarkably, moving larvae from healthy to rust-infected leaves increased their growth rate. In comparison with the healthy diet, the larvae of both species reared on the switched diet showed higher growth rates (by 7.1% in the post-switch period), lower maximum weights (by 8.8%, not significantly different from that on the infected diet) and shorter development times (by 11.9%). This switched diet was designed to mimic the natural situation as rust infection develops during the season. Our results suggest that larvae use the sudden arrival of the rust as a signal that the season is drawing to a close and that conditions will continue to deteriorate. This induces a rapid change in their pre-diapause strategy, causing them to increase their growth rate, but also shorten the development period at the expense of their final weight, to complete the larval period before the rust infection worsens or the first snow falls.

Oreina elongata is known to be able to adjust individual growth in relation to seasonal time horizons (Margraf *et al.* 2003). When reared under a photoperiod typical of late

summer, they show an increased growth rate, reduced development time and normal final weight. This ability was used in our second experiment to investigate the dramatic difference between the behaviour on the infected and switched diets, by crossing the diet treatments with day-length regimes typical of early and late in the breeding season. Larvae on the healthy diet showed the normal response to photoperiod, but there was little effect of light regime in larvae on the infected or switched diets.

Considered together, the experiments suggest several conclusions. Firstly, as has been shown before in response to photoperiod (Margraf *et al.* 2003), larvae reared on healthy leaves do not grow at their maximal rate. This implies the existence of costs of rapid growth, leading to stabilizing selection on growth rate, and indirectly on body size. It also leaves room for acceleration in larvae developing late in the season, after weather-induced delays, or when encountering rust infection. Secondly, larvae on the infected diet showed no response to photoperiod, suggesting that the difference between the infected and switched diets arises because exposure to the rust from the start of life makes larvae unable to modify growth rates in response to the normal stimuli. Further work is needed to determine whether acceleration of growth is achieved by increasing consumption or by

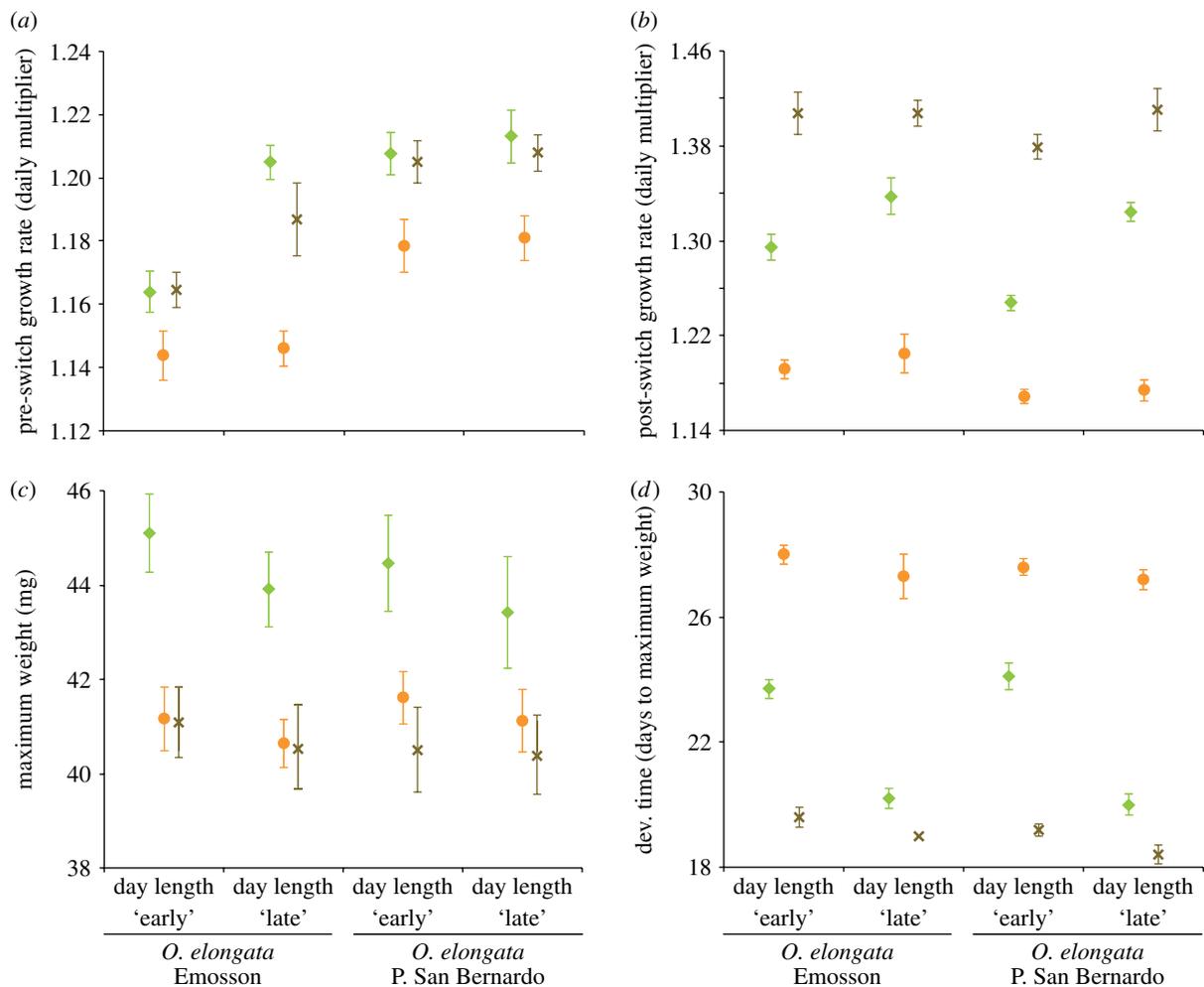


Figure 2. Larval performance of *O. elongata* from two populations reared on healthy, rust-infected or switched diets and under two day-length regimes (early and late-summer photoperiod). Graphs show the (a) pre-switch and (b) post-switch growth rates (calculated as daily growth multipliers, see text for details), (c) the maximum weight (in mg) reached by the larvae during their development and (d) the number of days needed to reach the maximum weight (all shown as means \pm s.e., $n = 10$). Diamonds, healthy diet; circles, infected diet; crosses, switched diet; dev. time, development time.

physiological means. In either case, initial exposure to rust seems to remove the ability to accelerate feeding or physiology, and hence removes the capacity for developmental plasticity. Finally, the response to the arrival of the rust was more dramatic than that to the late-season light conditions. Larvae on the switched diet already seemed to be growing at their maximum rate and showed no response to photoperiod, whereas larvae under the late-season day-length regime still showed a significant increase in growth rate on the switched diet.

The plasticity represents a trade-off among the three growth parameters. On the infected diet, the larvae compensate for their reduced growth rate by enduring a longer development time in order to reduce the impact on their maximum weight. In contrast, larvae on the switched diet use their accelerated growth to produce a short development time at the expense of a reduced maximum weight. The fact that weight is similar on the two diets suggests there may be a minimum weight that would allow hibernation and pupation. On the infected diet larvae must extend development in order to reach this weight, while on the switched diet they can stop growth at that point in order to shorten the development time.

Reducing their final weight or increasing development time would both bear costs for larvae. Prolonging

development may affect larval survival by exposing them to predation and bad weather for a longer period, whereas a reduction in larval weight is likely to lead to higher mortality during the winter, as well as to affect future reproductive success by reducing adult body size (Williams 1999; Fordyce & Shapiro 2003; Laine 2004; Blanckenhorn 2005). Larvae must therefore strike a delicate balance between the two life-history parameters. On the switched diet, they favour a reduction in development time rather than continuing growth to reach the normal weight, perhaps because rust infection signals conditions that will continue to deteriorate, or because feeding on the rust may have negative effects on post-larval fitness, so that limiting their exposure to it brings direct benefits. The response to rust is more extreme than that to the late-season photoperiod (which has no effect on maximum weight), suggesting that the optimal trade-off may differ according to the perceived threat posed by the onset of rust infection or the advancing season.

Within the genus *Oreina*, there has been repeated evolution of this trade-off between development time and final weight and, in parallel, the negative correlation between larval growth rate and final weight. It is seen here in the comparison between the species, with higher growth rate, shorter development time and lower weight

Table 2. ANOVAs on the four larval performance parameters for the two populations of *O. elongata* when reared on healthy, infected or switched diets, and under early or late-season photoperiods.

	d.f.	SS	F	p
pre-switch growth rate				
day length	1	0.0049	9.143	0.003
diet	2	0.0281	26.374	<0.001
pop	1	0.0279	52.486	<0.001
diet × day length	2	0.0022	2.059	0.133
pop × day length	1	0.0025	4.740	0.032
diet × pop	2	0.0004	0.378	0.686
diet × pop × day length	2	0.0016	1.510	0.226
error	108	0.0575		
post-switch growth rate				
day length	1	0.0240	16.173	<0.001
diet	2	0.9372	315.209	<0.001
pop	1	0.0163	10.979	0.001
diet × day length	2	0.0151	5.077	0.008
pop × day length	1	0.0027	1.844	0.177
diet × pop	2	0.0017	0.580	0.562
diet × pop × day length	2	0.0026	0.889	0.414
error	108	0.1606		
maximum weight				
day length	1	12.481	1.847	0.177
diet	2	302.111	22.350	<0.001
pop	1	0.721	0.107	0.745
diet × day length	2	3.415	0.253	0.777
pop × day length	1	0.310	0.046	0.831
diet × pop	2	5.947	0.440	0.645
diet × pop × day length	2	0.197	0.015	0.986
error	108	729.950		
development time				
day length	1	85.008	68.978	<0.001
diet	2	1480.717	600.742	<0.001
pop	1	1.408	1.143	0.288
diet × day length	2	67.317	27.311	<0.001
pop × day length	1	0.208	0.169	0.682
diet × pop	2	1.817	0.737	0.481
diet × pop × day length	2	1.017	0.413	0.663
error	108	133.100		

in *O. elongata* than in *O. cacaliae*. It also appears in comparisons between populations within *O. elongata*, where those from Bosco Gurin and Mattmark in Switzerland show the same changes in the three traits in comparison with other populations (Margraf *et al.* 2007). And it arises in the form of developmental plasticity in the response to the switched diet. The three examples are likely to be reactions to the seasonal time constraints associated with higher altitude, higher latitude and rust attack (similar to converse Bergmann clines; Blanckenhorn & Demont 2004). As a consequence, the response may represent a fundamental survival–fecundity trade-off, with future fecundity (probably related to body size) sacrificed in order to complete development within the extremely short alpine summer.

Both *O. elongata* and *O. cacaliae* suffer reduced growth rates when reared on rust-infected leaves, and they show a suite of behaviours in their dispersal and feeding preference that would allow them to avoid infected plants (Röder *et al.* 2007). However, widespread infection of their host-plant patch or development late in the season will often leave beetles with no alternative but to feed on rust-infected hosts. The plasticity of growth rate that we demonstrate here seems to represent a strategy to make the best of a bad job, allowing larvae

to complete development despite the presence of a fungal antagonist. It is a more extreme mode of phenotypic plasticity than that previously described in the form of compensatory (or catch-up) growth after a period of nutritional deficit (Metcalf & Monaghan 2001) or growth acceleration induced by photoperiod cues (Nylin & Gotthard 1998), since the response occurs while still exposed to environmental stress and as such is likely to impose greater costs. Similar behaviour is to be expected in other host–parasite systems in which host quality deteriorates irreversibly due to multiple infection or ageing, with repercussions for the outcome of competition between parasites, and the selection pressures exerted by parasites and their hosts on each other. More generally, the result highlights the complications introduced when moving from two- to three-species interactions. It also warns against the assumption of a simple correlation between host quality and larval growth rate, demonstrating that poor quality hosts may paradoxically lead to rapid growth.

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