



## Short communication

Does rapid adaptation to a poor-quality host by *Callosobruchus maculatus* (F.) cause cross-adaptation to other legume hosts?

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## ARTICLE INFO

## Article history:

Accepted 13 February 2009

## Keywords:

Adaptation

*Callosobruchus maculatus*

Grain legume

Host range

Lentil

Oviposition

## ABSTRACT

Initial assays indicated that lentil is a very poor host for an Asian population of the seed beetle *Callosobruchus maculatus* (F.). Larval survival was near zero, and females laid few or no eggs on lentil seeds. However, mass selection in the laboratory consistently produced a rapid increase in survival (from <2% to >80% in <20 generations) as well as a moderate increase in host acceptance. We investigated whether adaptation to lentil simultaneously causes cross-adaptation to other grain legumes, particularly those closely related to lentil. After 30 generations of selection, survival in lentil exceeded 90% in the lentil line, but remained near zero in a line maintained on the ancestral host, mung bean. Despite this extreme divergence in performance in lentil, the lines did not differ in their survival on eight other legume hosts, including two hosts (pea and fava bean) that belong to the same tribe (Vicieae) as lentil. Similarly, females from the lentil line laid more than three times as many eggs on lentil as females from the mung bean line did, but the lines exhibited only minor differences in their acceptance of eight alternative hosts. Lentil-line females did not show greater acceptance of artificial seeds (glass balls), as might be expected if increased egg-laying on lentil was simply due to a reduction in the overall threshold for oviposition. We conclude that the changes in larval physiology and adult behavior that permitted rapid colonization of a marginal host were largely specific to that host, and not likely to promote a further expansion of the beetle's host range.

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## 1. Introduction

Most herbivorous insects attack a fairly well defined set of host plants, but are occasionally observed to expand their host range to a novel plant (Bernays, 2001). In some cases, the insect may already be well adapted to the novel host (Agosta, 2006; Murphy and Feeny, 2006), but colonization of a new host often requires successive genetic modifications of morphological, physiological or behavioral traits (Carroll et al., 1997; Vanbergen et al., 2003; Magalhaes et al., 2007; Xie et al., 2007). In agriculture, such changes may produce distinct populations or "biotypes" that can attack crops or cultivars previously thought to be resistant to the insect (Diehl and Bush, 1984; Lushai et al., 2002). The appearance of new biotypes may require major changes in pest management strategies (Via, 1990).

Adaptation to one novel host may simultaneously affect an insect's performance on other hosts, including hosts that the population may never have encountered. For example, if a population has a means to detoxify a particular secondary compound in a novel host, it may be able to exploit closely related hosts that contain similar compounds (Agrawal, 2000). Cross-adaptation can also

occur with respect to oviposition behavior; selection for increased egg-laying on a new host may lead to greater acceptance of hosts with a comparable mixture of oviposition stimulants and deterrents (Huang and Renwick, 1993). Thus, a single host shift may have consequences for an insect's entire host range. In this study, we examine whether rapid adaptation to a marginal host by a seed beetle causes cross-adaptation to other hosts.

Females of the seed beetle *Callosobruchus maculatus* (F.) (Coleoptera: Chrysomelidae: Bruchinae) attach eggs to the surfaces of grain-legume seeds. Hatching larvae burrow into the seed directly beneath the oviposition site and complete development within a single seed. All suitable hosts for *C. maculatus* are in the subfamily Papilionoideae within the legume family Fabaceae. Within the Papilionoideae, most *C. maculatus* hosts belong to the tribe Phaseoleae, and the most severely infested crops are in the genus *Vigna* (Tuda et al., 2005). Beetles have only rarely been reported to attack lentil (*Lens culinaris* Medikus), which belongs to the tribe Vicieae within the Papilionoideae, and is thus distantly related to the insect's typical hosts (Young et al., 2003; Choi et al., 2004). Lentil is generally unsuitable for larval growth (Credland, 1987) and elicits little oviposition (Wasserman, 1986). Nevertheless, we recently demonstrated that mass selection in the laboratory could rapidly produce self-sustaining populations on lentil (Messina et al., in

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press). Larval survival rose from <2% to >65% after only 5–8 generations, and exceeded 85% in <20 generations. In addition, oviposition on lentil increased two- to three-fold in <20 generations (Messina et al., 2009).

Rapid adaptation to lentil could alter beetle performance on other common grain legumes. If increased survival in lentil depends on changes in enzymatic activity in the larval midgut (Desroches et al., 1997), lentil-adapted populations may have fortuitously acquired the ability to withstand toxins in hosts that are closely related to lentil. Similarly, greater acceptance of lentil by egg-laying females could reflect a greater sensitivity to lentil-specific cues or a lower threshold for accepting any seed-like substrate. In either case, lentil-adapted females may behave differently from non-adapted females.

Our first objective in this study was to examine whether the dramatic increase in survival in lentil caused cross-adaptation to other grain legumes. On nine legume hosts, we compared survival rates between a lentil-adapted line and a line maintained on the ancestral host, mung bean (*Vigna radiata* (L.) Wilczek). Two of the hosts belong to the tribe Viciae, and hence are more closely related to lentil than to mung bean (Choi et al., 2004). A second objective was to compare the lentil and mung bean lines with respect to host acceptance. We estimated lifetime fecundity on nine legume hosts as well as on glass balls, which elicit egg-laying in the absence of seeds (Messina et al., 1987a; Credland and Wright, 1988). If lentil-adapted females have a generally lower oviposition threshold, we might expect acceptance of glass balls to be higher in the lentil line than in the mung bean line.

## 2. Materials and methods

### 2.1. Source of beetle lines

The study population was established from infested mung beans originating from southern India (Mitchell, 1991). Each generation was produced by adding 1500–2500 adults (estimated by volume) to approximately 750 g of mung beans ( $\approx 12,000$  seeds) in a 2-L jar covered with organdy cloth. We maintained stock cultures and conducted all experiments in a growth chamber at 24 °C and under constant light. Laboratory conditions approximated the natural environment of *C. maculatus*, which has likely infested human stores of grain legumes for thousands of years (Tuda et al., 2006).

We described elsewhere the establishment of beetle lines adapted to lentil (Messina et al., 2009, in press), and provide only a summary here. Despite an initial estimate of zero larval survival in lentil seeds, we performed mass selection by adding 2000–2500 adults from each of three mung bean lines (Messina, 2004a) to jars with 750 g of lentil seeds. A few emergent beetles, representing a severe population bottleneck, were observed in each lentil line after 8 weeks. Later experiments confirmed that, for the mung bean lines, initial survival in lentil is non-zero but <2% (Messina et al., in press). By 24 weeks, one lentil line began to produce abundant adults; the other two died out. By repeating the mass selection twice more we established three lines that independently adapted to lentil. All experiments in this study used the oldest lentil line (hereafter, the L line) as well as the original mung bean line (hereafter, the M line) from which it was derived.

### 2.2. Estimation of larval survival

We compared survival from egg hatch to adult emergence on nine hosts, including lentil and mung bean (Table 1). Because it was not feasible to estimate survival on all hosts simultaneously, we conducted the assays in a staggered fashion after the L line had spent 25–30 generations on lentil. For any given host, however, the

**Table 1**

Survival to adult emergence (%) of *Callosobruchus maculatus* larvae on nine legume hosts.<sup>a</sup>

Legume tribe	Host	M line	L line
Phaseoleae	Mung bean, <i>Vigna radiata</i> (L.) Wilczek	95.5	96.0
	Adzuki bean, <i>V. angularis</i> (Willd.) Ohwi & Ohashi	74.5	70.0
	Red kidney bean, <i>Phaseolus vulgaris</i> L.	0	0
	Black turtle bean, <i>P. vulgaris</i> L.	0	0
	Lima bean, <i>P. lunatus</i> L.	0	0
	Soybean, <i>Glycine max</i> (L.) Merr.	0	0
Viciae	Lentil, <i>Lens culinaris</i> Medikus	0	92.9
	Pea, <i>Pisum sativum</i> L.	23.6	23.2
	Fava bean, <i>Vicia faba</i> L.	8.8	7.7

<sup>a</sup> Beetle lines were maintained on the ancestral host, mung bean (M), or transferred to lentil (L) for 25–30 generations. To remove non-genetic host effects, the L line was first reverted back to mung bean for a generation.  $N = 60$ –220 one-larva seeds per treatment.

L and M lines were assayed simultaneously. All assays used a subculture of the L line that was first reverted back to mung bean for a generation (Messina, 2004a; Messina et al., in press). This step reduced any host-related, non-genetic effects on survival because parents of all test larvae had developed in the same host (mung bean).

To obtain a cohort of larvae in a particular host, we first placed 3–5 pairs of newly emerged adults from the appropriate culture into each of 30–60 Petri dishes containing 75–100 seeds. Seeds of most hosts were organically grown and obtained in bulk from Azure Standard (Dufur, Oregon, USA). Newly emerged adults were obtained by sieving off all existing adults from a culture, and then returning to collect emergent adults a few hours later. Females in the dishes were allowed to oviposit for 24 h, after which all beetles were removed. After 10 days, we collected up to 10 seeds per dish that bore a single larva, as indicated by a hatched egg on the seed surface. Sample sizes varied considerably among hosts because oviposition rates during the 24-h exposure were highly variable. Across the 18 treatments (nine hosts  $\times$  two lines), we collected a minimum of 60 and a maximum of 220 one-larva seeds per treatment. Seeds were isolated in vials and inspected weekly until 120 days after oviposition; previous experiments indicated that no beetles emerge after this period (Messina et al., in press).

For one host, adzuki bean (*Vigna angularis* (Willd.) Ohwi & Ohashi), we also measured egg-to-adult development time and adult mass at emergence. Earlier experiments suggested that survival in the 'Dainagon' cultivar of adzuki bean was relatively high, so that we were likely to obtain a sufficient number of adults to compare these traits between lines, as we had already done for lentil and mung bean (Messina et al., in press). Poor or zero survival on the other potential hosts precluded obtaining robust estimates of mean mass and development time (see Section 3). In the adzuki bean experiment, vials were inspected daily, and each newly emerged beetle was weighed on an electrobalance.

Because larval survival was zero on some hosts (see Section 3), we could not conduct a three-way analysis to simultaneously examine associations between survival, selection line, and host. For each host in which survival was non-zero, we performed a separate chi-square test to determine whether adult emergence was independent of selection line. For the adzuki bean experiment, two-way analysis of variance was used to estimate the effects of selection line and sex on development time and mass. All tests were performed using SYSTAT 10 software (Wilkinson et al., 1996)

### 2.3. Estimation of host acceptance

We compared host acceptance between the L and M lines on nine legumes as well as on 6-mm diameter glass balls. Chickpea,

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