Journal of Insect Physiology 88 (2016) 24–32

Contents lists available at ScienceDirect

Journal of Insect Physiology

journal homepage: www.elsevier.com/locate/jinsphys

Adult beetles compensate for poor larval food conditions

Thorben Müller, Caroline Müller *

Department of Chemical Ecology, Bielefeld University, Universitätsstr. 25, 33615 Bielefeld, Germany

ARTICLE INFO

Article history:
Received 14 October 2015
Received in revised form 11 February 2016
Accepted 17 February 2016
Available online 18 February 2016

Keywords:
Match–mismatch
Pest
Crop
Phaedon cochleariae
Reproduction
Feeding preference

ABSTRACT

Life history traits of herbivores are highly influenced by the quality of their hosts, i.e., the composition of primary and secondary plant metabolites. In holometabolous insects, larvae and adults may face different host plants, which differ in quality. It has been hypothesised that adult fitness is either highest when larval and adult environmental conditions match (environmental matching) or it may be mainly determined by optimal larval conditions (silver spoon effect). Alternatively, the adult stage may be most decisive for the actual fitness, independent of larval food exposure, due to adult compensation ability. To determine the influence of constant *versus* changing larval and adult host plant experiences on growth performance, fitness and feeding preferences, we carried out a match–mismatch experiment using the mustard leaf beetle, *Phaedon cochleariae*. Larvae and adults were either constantly reared on watercress (natural host) or cabbage (crop plant) or were switched after metamorphosis to the other host. Growth, reproductive traits and feeding preferences were determined repeatedly over lifetime and host plant quality traits analysed. Differences in the host quality led to differences in the development time and female reproduction. Egg numbers were significantly influenced by the host plant species experienced by the adults. Thus, adults were able to compensate for poor larval conditions. Likewise, the current host experience was most decisive for feeding preferences; in adult beetles a feeding preference was shaped regardless of the larval host plant. Larvae or adults reared on the more nutritious host, cabbage, showed a higher preference for this host. Hence, beetles most likely develop a preference when gaining a direct positive feedback in terms of an improved performance, whereby the current experience matters the most. Highly nutritious crop plants may be, in consequence, all the more exploited by potential pests that may show a high plasticity in reproduction and feeding preferences.

1. Introduction

Host plant quality has a major influence on the growth and reproduction of herbivores at an individual level (Schoonhoven et al., 1998; Awmack and Leather, 2002) as well as on a large scale population level (Riolo et al., 2015). As determinants of plant quality, especially plant nitrogen content plays a key role as limiting factor for herbivore growth (Mattson, 1980; Behmer, 2009), but apart from plant nutrition, a suite of other chemical and morphological plant traits is decisive for herbivore development (Travers-Martin and Müller, 2008). Thus, herbivores reared on plants differing in quality show differences in developmental time and body mass but also in one or several reproductive traits like egg number, egg size and hatching success, which are essential fitness traits (Geister et al., 2008; Travers-Martin and Müller, 2008). Due to their high nutrient content and often reduced secondary metabolite content, which are selected for, crop plants might particularly improve the growth performance and fitness of herbivores (Schoonhoven et al., 1998; Hopkins et al., 2009).

In holometabolous insects, the morphology and physiology as well as energetic needs drastically change after metamorphosis (Ebenman, 1992). Moreover, the individual ecological niche can shift at that stage (Groothuis and Taborsky, 2015), particularly if both larvae and adults feed on plants, since the availability and quality of host plant species may vary throughout the season (Moran, 1994). Thus, adults may be exposed to other hosts than those experienced by the larvae and thereby face both a physiological and an ecological switch after eclosion. In this context, the environmental matching hypothesis postulates that individuals which are constantly reared in one condition (e.g., on one host plant species) perform better compared to individuals which are switched to a different condition (e.g., another host, which may differ in quality) (Monaghan, 2008). Alternatively, juveniles may gain a long lasting fitness advantage based on more nutritious early food conditions, which has been termed the silver spoon effect (Monaghan, 2008). Finally, the current conditions may be most decisive for life-history traits, independent of experiences gained

* Corresponding author.
E-mail address: caroline.mueller@uni-bielefeld.de (C. Müller).

http://dx.doi.org/10.1016/j.jinsphys.2016.02.009

earlier in life. This may be the case, if adults are able to compensate for poor larval conditions when they receive food of higher quality after metamorphosis (Mevi-Schütz and Erhardt, 2005). Moreover, the transgenerational interaction of maternal feeding experience with the host experience of the offspring can affect the population dynamics of insects (Rios et al., 2013), showing the importance of such effects over generations.

Different host plant experiences can also influence feeding preferences (Mayhew, 2001; Davis, 2008). However, a strong correlation between early larval experiences and host plant preferences later in life has been controversially discussed (Hopkins, 1917; Barron, 2001). The effects seem to be species-specific with examples for (Shikano and Isman, 2009; Anderson et al., 2013) and against (Rank, 1992; Janz et al., 2009) the dominant role of the larval experience. Match–mismatch experimental designs, in which individuals either stay constantly in one environment or are switched to another environment after a certain time, allow us to investigate the importance of certain life stages on shaping of various life history trajectories and preferences and thus offer insights in underlying mechanisms and functions (Groothuis and Taborsky, 2015).

The aim of the present study was to investigate the impact of constant *versus* changing larval and adult host experiences on life history traits of a holometabolous beetle, in which larvae and adults are folivorous, using a natural host and a crop plant species differing in quality. In particular, we studied whether the reproductive output as an important fitness component is highest under constant rearing conditions (i.e., environmental matching) or highest when larval food quality is high (silver spoon), or whether adults can compensate for poor larval conditions during the early or later adult stage when the food quality changes (which we term here 'adult compensation ability'). Next to developmental time and body mass, we measured different reproductive traits twice over the lifetime of the beetle to test whether the time period of food experience gained as an adult has an influence on these fitness traits. Moreover, we measured feeding preferences several times throughout life to investigate the relevance of current and earlier feeding conditions for shaping of preferences, expecting a more decisive effect of the current conditions on preferences due to a more direct feedback effect of the food choice on the performance. Water, total carbon and nitrogen content as well as characteristic secondary metabolite concentrations were analysed as estimates for plant quality.

As test organism, we used the mustard leaf beetle, *Phaedon cochleariae* F. (Coleoptera: Chrysomelidae), which serves as a model in physiological, behavioural, and chemo-ecological research (Kühnle and Müller, 2012; Stock et al., 2013; Müller and Müller, 2015; Otte et al., 2015) and can be a pest as a larva and an adult on various crops such as cabbage (Finch and Kienegger, 1997; Uddin et al., 2009). As a specialist on Brassicaceae species, *P. cochleariae* is well adapted to glucosinolates (Reifenrath and Müller, 2008), which are primarily found in the Brassicales (Halkier and Gershenzon, 2006). In nature, changes in food availability and quality after metamorphosis can potentially occur. Furthermore, adults are more mobile than larvae (Müller and Müller, 2015) and may move to other host plants in the proximity. Directly after eclosion, adults do not show any feeding preferences (Kühnle and Müller, 2011), but older adults prefer higher quality food on which they have been continuously reared (Tremmel and Müller, 2013). Here, we performed a match–mismatch experiment, in which half of the individuals were constantly fed on one of two host plant species and the other half was switched to the alternative host after metamorphosis. Using this experimental set-up allowed us to disentangle the determinants of fitness and feeding preferences and to make predictions about the likelihood that herbivores readily accept crop species, of which they could become harmful pests.

2. Materials and methods

2.1. Study organisms and rearing conditions

Mustard leaf beetles (*Phaedon cochleariae*) were collected from watercress (*Nasturtium officinale*) in different parts of Germany (public locations near Bielefeld, Berlin and Würzburg). The insects were reared for several generations in ventilated plastic boxes ($20 \times 20 \times 6.5$ cm) in a climate cabinet under constant conditions (20 °C, L16:D8, 65% r.h.). As food plants for the rearing and for the experimental setup, cabbage (*Brassica rapa* L. ssp. *pekinensis* var. Michihili; seeds from Kiepenkerl, Bruno Nebelung GmbH, Konken, Germany), watercress (seeds from Volmary GmbH, Münster, Germany) and white mustard (*Sinapis alba*; seeds from Agravis, Raiffeisen AG, Münster, Germany) were grown in pots (12 cm diameter) filled with composted soil and placed in a greenhouse (L16:D8, 60% r.h.). Insects used in this study were kept for several generations on white mustard to ensure that they had no experience with cabbage or watercress at least for a few years. For the experiment, randomly selected larvae hatching from eggs laid on white mustard were either fed with leaves of 8–10 week old non-flowering cabbage plants or of 7–8 week old non-flowering watercress plants *ad libitum*, respectively. We used only middle-aged leaves to reduce effects of within-plant quality differences.

2.2. Experimental set-up

To test the impact of constant *versus* changing environmental conditions on various developmental traits and feeding preferences of *P. cochleariae*, four different rearing treatments were set-up. Half of 280 freshly hatched *P. cochleariae* larvae ($n = 140$) were reared on cabbage (C) in six ventilated plastic boxes ($20 \times 20 \times 6.5$ cm; $n = 20$–25 larvae per box). The remaining 140 larvae were provided with watercress (W) in six additional boxes ($n = 20$–25 larvae per box). To prevent desiccation of the plant parts, they were mounted in wet sponge rubber. Food was exchanged daily or every other day. Half of the cabbage-fed larvae were constantly reared on cabbage (CC) as adults. The other half of the cabbage-fed larvae was switched after adult eclosion to watercress (CW). Half of the watercress-fed larvae were continuously reared with watercress as adults (WW) and the other half was switched to cabbage (WC) at the day of adult eclosion. For each treatment group, adults were distributed over three boxes. About 15–25 adults were kept per box in a nearly balanced sex ratio (higher group sizes in the beginning and lower group sizes at the end of the experiment).

2.3. Measurements of host plant effects on developmental and reproductive output

Developmental and fitness traits were measured at several time points [(two times during the larval stages, once in the second (L2) and once in the third instar (L3), and three times over the adult life (A0–A2)] to investigate whether the duration of feeding on one or the other host over the larval and adult stage had an influence on these traits at a given developmental stage. At day 5 (L2) and day 11 (L3) after hatching and at the day of adult eclosion (A0), the body mass was measured. The development time from hatching until the day of adult eclosion was noted. Additionally, three reproductive output traits were determined. First, the average number of eggs laid over four days in the leaves was counted twice per female (early adulthood: A1, day 10–13; later adulthood: A2, day 24–27 after adult eclosion; A1: $n_{CC} = 27$, $n_{CW} = 26$, $n_{WW} = 32$, $n_{WC} = 30$; A2: $n_{CC} = 26$, $n_{CW} = 25$, $n_{WW} = 32$, $n_{WC} = 29$). During these time periods, every female was separately kept in a Petri dish