



Research Paper

Impact of floral nectar limitation on life-history traits in a grassland butterfly relative to nectar supply in different agricultural landscapes



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ABSTRACT

Wild flower diversity and abundance are strongly reduced in intensive agricultural landscapes. Flower-visiting insects may, therefore, experience limited nectar quantities and qualities. Adult insects that rely on energy-rich nectar income for flight, survival and reproduction are expected to be much more affected than insects that rely on their larval reserves. We dealt with this issue at the intraspecific level by comparing the responses of several life-history traits to different nectar diets between meadow brown butterflies (*Maniola jurtina*) originating from relative intensively managed and extensively managed agricultural landscapes. We used outdoor flight cages in which we simulated factorial treatments of low/high nectar quality and low/high quantity. Survival was highest in the high nectar quantity and quality treatment. Individuals from intensive landscapes were heavier, which is in line with predictions on increased capital breeding, and they survived better than those from extensive landscapes, of which the females lost body mass in all treatments. Females from intensive landscapes were able to buffer, or even increase, their body mass in the high nectar quantity treatments, but the differences with females from extensive landscapes disappeared under low nectar quantities (independent of nectar quality). In males, body mass losses were always larger for individuals from extensive landscapes compared to individuals from intensive landscapes. Forty percent of the females showed complete reproductive failure in the low quantity/low quality treatment compared to c. 7% in the other treatments. In the low quantity/low quality treatment, realized fecundity decreased strongly in females from intensive, but not extensive landscapes. Egg size was not affected by landscape of origin in the high-quality nectar treatments, but showed very different responses relative to landscape of origin in the treatments with low-quality nectar. Our results showed strong effects of reduced nectar supply on fitness-related traits, and responses were different between butterflies originating from landscapes with contrasted nectar diet. Hence, different levels of agricultural intensification changing the quantity and quality of the local nectar supply could pave the way for ecological differentiation of the organism's behaviour, physiology and life history.

1. Introduction

The intensification of agriculture has worldwide resulted in simplified landscapes characterized by declines of ecological resources (i.e., consumables and utilities) that are essential to wild organisms, including those species that had previously adapted to living in agricultural landscapes of low management intensity (Benton et al., 2002). Wild flowers providing nectar are examples of essential resources that became much scarcer in intensively managed agricultural landscapes (Tscharntke et al., 2005; Potts et al., 2010). Remnant fragments of flower-rich vegetation act as source populations of insects in the surrounding landscape (Öckinger and Smith, 2007; Kohler et al., 2008). Besides reduced quantities, a different spectrum of nectar plant species (e.g. ratio of annual vs perennial sources) is typically found in

intensively compared to extensively managed agricultural landscapes (Wilson et al., 1999).

Wild flower-visiting insects are likely to face food limitation and altered food quality in intensively managed farmland. For short-living, strict nectar feeders, scarcity of nectar may have a strong impact on life-history traits (e.g., longevity and fecundity; Geister et al., 2008). Organisms vary in the amount and the type of resources acquired for reproduction and survival at their adult stage. In insects, some species rely for their adult life and for reproduction entirely on resources gathered during their larval stages (i.e., capital breeding), whereas other species depend on resources to be acquired by active adult feeding (i.e., income breeding; Stephens et al., 2009). In typical nectar-feeding insects, most nitrogen is acquired at the larval stage, and carbohydrates used for energy demanding activities such as flight

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principally come from the adult's diet (Boggs and Freeman, 2005). Such organisms experience spatial and temporal variation in nectar supply. Climatic factors and vegetation management both affect the presence, abundance and phenology of flowering species. Anthropogenic systems like agricultural regimes may impose different selection pressures on wild organisms leading to rapid evolution (Sih et al., 2011). Although many Lepidoptera rely on nectar in the adult stage, evolution has produced species that do not feed at all as adults (e.g. most Saturniidae species; Tammaru and Haukioja, 1996). Nectar-poor, intensively managed agricultural landscapes that also lack mass-flowering crops could select for life-history strategies that depend much less on adult income feeding compared to populations in nectar-rich, extensively managed agricultural landscapes. Here, we are interested in testing this idea.

Direct ecological effects of variation in nectar diet are well documented, for example in butterflies. Quantitative restriction of nectar intake reduces female fecundity, but not lifespan (Boggs and Ross, 1993; Niitpõld et al., 2014). Egg provisioning decreased with age in food limited females (Karl et al., 2007). In several butterfly species, females use carbon from the adult diet for egg production (O'Brien et al., 2004). Nectar quality may also affect life-history traits (Geister et al., 2008). Together with water, sugars are the main constituents of nectar and sugar types and concentrations vary among flower species (Baker and Baker, 1983). When fed with nectar of high sugar concentration, butterfly species lived for longer (Braby and Jones, 1995; Cahenzli and Erhardt, 2012b) and both longevity and fecundity may increase as well (Hill, 1989). Nectar amino acids also play a significant role for female butterfly fitness (Jervis and Boggs, 2005) as they may increase fecundity (Mevi-Schütz and Erhardt, 2005; Cahenzli and Erhardt, 2012a; but see Molleman et al., 2008). Nectar intake may also constrain egg size (Murphy et al., 1983).

Conditions with restricted flower supply may push butterflies to shift towards higher degrees of capital breeding (Tammaru and Haukioja, 1996). Hence, they could become heavier at emergence (i.e., larger body reserves). Other adaptations may involve changes in resource allocation patterns that allow better resistance to food stress. Recently, we demonstrated the direct negative effects of poor nectar supply for young adults of the butterfly *Maniola jurtina* (Lebeau et al., 2016a). Poor nectar supply corresponded to the quantity and quality of floral nectar as typically observed in meadows of relatively intensively managed agricultural landscapes that lack flower-rich grassland. The experiment included butterflies of nectar-rich grassland origin only, which were heavily impacted in terms of survival, activity and physiological condition (Lebeau et al., 2016a). Here, we tested the effect of nectar quantity and quality on adult *M. jurtina* males and females from both extensively managed and intensively managed agricultural landscapes to test the hypothesis of an altered ability to survive and reproduce (i.e., higher fitness indicators) under nectar stress in butterflies originating from nectar-poor, intensively managed environments. We simulated the factorial combinations of low/high nectar quality and quantity in outdoor flight cages to study life-history consequences in butterflies of the two landscape origins. Nectar quantity restriction is predicted to reduce longevity and fecundity depending on allocation trade-offs. Butterflies from intensive, flower-poor agricultural landscapes are expected to be less affected by nectar limitation. Nectar quality restriction is expected to impact females more than males, because of their nutrient investment in egg manufacturing whereas males only need calories to fuel their flight. Because nutrient pools vary between the landscapes of origin, we expect butterflies from extensively managed agricultural landscapes (i.e., flower-rich grasslands) to be more strongly impacted by nectar quality reduction assuming they rely much more on an income breeding strategy than conspecifics from the intensively managed landscape. When nectar quality and quantity are simultaneously reduced, we expect negative consequences for both longevity and fecundity in all *M. jurtina* butterflies.

2. Materials and methods

2.1. Model species

The meadow brown (*Maniola jurtina*) is a widespread European butterfly. It is univoltine and occurs in grassland habitats; caterpillars feed on a variety of grasses. Adults visit a range of species for floral nectar, but show a preference for knapweed *Centaurea jacea* in our study sites (Lebeau et al., 2016a). In the absence of the preferred species, they feed on alternatives (e.g., red clover *Trifolium pratense*; Lebeau et al., 2017). The typical action radius of an individual is 300 m or less, but movements have been observed up to 1 km (Schneider et al., 2003).

One to a few days after emergence, females start to lay eggs. Egg maturation happens progressively, as there are no mature eggs at adult emergence (Scali, 1971). Females lay their eggs one by one.

2.2. Butterfly sampling

In the summer of 2012, freshly emerged adults were sampled in two Belgian agricultural regions that differed in management intensification: extensively managed landscapes (EL) located in the Famenne (centre: 50°08'22" N, 5°03'01" E; area: ± 20 km²) and intensively managed landscapes (IL) located in Walloon Brabant (centre: 50°35'02" N, 4°39'09" E; area: ± 40 km²). Note that both regions are close to one another (< 60 km apart) and each host several local populations of *M. jurtina*. In each region, butterflies were sampled in 4 several sites distant of each other from 500 m to 10 km; so, we sampled in 8 sites in total. The first region mainly consisted of grassland and woodland. Types and intensity of management varied among sites, but a large part is composed of extensively managed hay meadows and other grasslands favourable to several grassland butterflies. The predominantly intensively managed landscape of the other region mainly consisted of arable fields and a small proportion of grasslands in the form of roadside verges, intensively grazed pastures or productive meadows like intensively managed monoculture grasslands of *Lolium perenne* (mown several times a year); there were no crop mass-flowering broadleaved plant fields. Because of the lower butterfly abundance, the actual sampling area was larger in the IL landscape compared to the EL landscape. Captured butterflies were stored in small cages and kept in the shade. Next, there were transported to our laboratory. We performed repeated trials with field-caught EL butterflies and IL butterflies in July and early August 2012 (5 and 6 trials in total, respectively). On the day of launching a trial, we collected 48 males and 48 females in one of the two landscape types and assigned them to the four diet treatments (i.e., 12 butterflies of each sex for each diet treatment). We captured only young adult individuals with a hand net; age was estimated based on wing wear (Watt et al., 1977). Before their release in the cages, butterflies were weighed (Ohaus Explorer balance; accuracy ± 0.1 mg) and marked on their ventral wings using a non-toxic permanent marker. In total 960 individuals were used (480 from IL and 480 from EL).

2.3. Experimental setup

We used two identical semi-cylindrical outdoor cages (plastic greenhouses covered by green netting; dimensions l * w * h = 9.0 m * 3.7 m * 1.8 m (at maximal height) that were each separated in two. Hence, we had four equally-sized compartments of 4.5 m * 3.7 m * 1.8 m (l * w * h). We applied four nectar treatments: i) high abundance of preferred nectar (i.e., 100 inflorescences of *C. jacea*, C100), ii) low abundance of preferred nectar (i.e., 10 inflorescences of *C. jacea*, c10), iii) high abundance of non-preferred nectar (i.e., 100 inflorescences of *T. pratense*, T100) and iv) low abundance of non-preferred nectar (i.e., 10 inflorescences of *T. pratense*, t10). Diet treatments were assigned randomly to the four compartments at each new session. Flowers of *T. pratense* contain slightly more nectar than those of *C. jacea* (mean nectar

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