



Trade-offs between fecundity and choosiness in ovipositing butterflies



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Being choosy can allow animals to find and identify the best resources or safest locations to rear offspring. Despite these benefits, individuals vary in the degree to which they are choosy. One explanation is that choosiness represents a costly form of offspring investment and is part of a suite of life history trade-offs. We examined trade-offs between choosiness and fecundity in the cabbage white butterfly, *Pieris rapae*. To test the prediction that choosiness is negatively correlated with fecundity, we presented female cabbage white butterflies with an array of host plant leaves that varied in nutrient content and conspecific density. Butterflies preferentially laid eggs on leaves with higher nutrient content and fewer conspecific models. In addition, butterflies that were choosier with regard to plant nutrition also tended to be choosy in terms of conspecific density. Choosy females were less fecund, with fecundity measured as the sum of eggs laid over 3 days plus all remaining mature eggs in their abdomen. These results are consistent with the idea that life history trade-offs include investment in costly behavioural traits that require time and energy, such as choosiness or cognition.

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Animals choose high-quality resources by attending to a range of cues, such as resource size (Ryan & Keddy-Hector, 1992), proximity to cover (Lima & Dill, 1990) or nutritional content (Bukovinszky et al., 2013; Schwarz, Durisko, & Dukas, 2014; Taylor, Schalk, & Jeanne, 2010; Yang, Walther, & Weng, 2015; Zweifel-Schielly, Leuenberger, Kreuzer, & Suter, 2012). Animals can also use social cues to avoid areas with high competition (Doligez, Danchin, Clobert, & Gustafsson, 1999; Reiskind & Wilson, 2004). Given that choosing the best resources can increase fitness of an individual or its offspring, it is unclear why all individuals are not highly choosy. For example, while animals are often choosy with respect to resources (e.g. Sims & Quayle, 1998) and mates (Bateson, 1983), some animals are not choosy in these contexts (e.g. Feinsinger, Beach, Linhart, Busby, & Murray, 1987; Jennions & Petrie, 1997). There is even considerable individual variation within species in the same context (Doak, Kareiva, & Kingsolver, 2006). One explanation for this variation in choosiness is that being choosy is costly in terms of energy or time. This potential cost could be part of a suite of life history trade-offs that may ultimately restrict choosiness in some individuals and promote variation in choosiness across individuals (Janz, 2002; Wiklund & Persson, 1983). The existence and robustness of such trade-offs could have

implications for the range of traits generally considered to be important in life history evolution.

Life history theory proposes that individuals or species might adopt a variety of different reproductive strategies that reflect the finite energy or time available for reproduction and maintenance. For example, utilizing energy for one aspect of reproduction leaves less available energy for other functions, resulting in trade-offs (Roff, 1992). In the context of choosiness, energy is expended by the cognitive and sensory machinery required to process and store information about available choices (DeWitt, Sih, & Wilson, 1998; Isler & van Schaik, 2009; Laughlin, de Ruyter van Steveninck, & Anderson, 1998; Niven & Laughlin, 2008), and by the locomotor system as it is engaged while the animal is collecting that information (Byers, Wiseman, Jones, & Roffe, 2005; Johnston, 1991; Tucker, 1970). Choosiness may therefore exhibit trade-offs with components of fitness such as offspring number or survival. If time is more limiting than energy, a similar trade-off might emerge. There may be an opportunity cost associated with identifying and choosing the best options, rather than accepting the first resource an animal encounters (Stephens & Krebs, 1986). Time spent identifying the best resources could instead be spent rearing more offspring or laying more eggs, distributing them across a wider variety of sites. This idea recalls the speed–accuracy trade-off in the context of foraging (Chittka, Skorupski, & Raine, 2009). Individuals that favour accuracy may be able to find the best resources, at a cost of time (Chittka, Dyer, Bock, & Dornhaus, 2003) and potentially the total number of resources they can visit and offspring they produce.

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Conversely, individuals that favour speed might save time by being less accurate, thus maximizing the total number of resources they exploit and offspring they produce, even if some of those resources are unsuitable (Burns, 2005). Regardless of whether energy or time is more limiting, choosiness during nest site selection or egg laying could be considered a form of costly reproductive investment that might exhibit trade-offs, especially in animals that have nonoverlapping generations such as insects. Parasitoids, for example, seem to be egg-limited with regard to fecundity. Ovipositing females with small egg loads are more selective because the cost of being choosy decreases with decreasing egg load (Driessen & Hemerik, 1992; Heimpel & Rosenheim, 1998; Heimpel, Rosenheim, & Mangel, 1996; Rosenheim, Heimpel, & Mangel, 2000). Despite potential costs, choosiness during oviposition can enhance offspring survival in some insects, especially those that require specific resources for survival during the larval stage (Doak et al., 2006; Gripenberg, Mayhew, Parnell, & Roslin, 2010). Thus, choosiness should represent an important component of a life history strategy.

Here, we used the cabbage white butterfly, *Pieris rapae*, to test the hypothesis that choosiness exhibits trade-offs with fecundity. Life history trade-offs between egg size and egg number have already been established in butterflies and other insects (Fischer & Fiedler, 2001; Fox & Czesak, 2000; Garcia-Barros, 2000; Seko, Miyatake, Fujioka, & Nakasuji, 2006). Trade-offs between adult choosiness and fecundity may stem from resources allocated either prior to adulthood (such as the majority of their protein), or during adulthood (Karlsson & Van Dyck, 2009). For instance, adult-acquired carbohydrates contribute to egg production and may exhibit trade-offs with traits involved in choosiness, such as brain metabolism or flight. In this study, we offered females different oviposition sites of varying quality. Although choosiness with regard to mate choice has also been studied in butterflies (Kemp, 2007), it is difficult to create differences in the quality of different males, and it is equally difficult to quantify male quality. Therefore, we focus solely on choosiness during oviposition in this study. As larvae, cabbage white butterflies feed on host plants in the family Brassicaceae. The nutrient content of a host and presence of conspecifics have particularly high impacts on larval survival. Thus, we focus on these two host plant characteristics. With regard to plant nutrition, adult females differentiate between highly fertilized and poorly fertilized plants (Chen, Lin, Wang, Yeh, & Hwang, 2004), potentially using plant colour or transpiration rate as cues (Myers, 1985). They also use social cues to avoid laying eggs near conspecifics, presumably to avoid competition experienced by offspring (Sato, Yano, Takabayashi, & Ohsaki, 1999), which can be extremely costly (Gibbs, Lace, Jones, & Moore, 2004; Kivela & Valimaki, 2008). Individual laboratory-reared female butterflies in this study were presented with an oviposition assay containing host plant leaves that varied in nutritional status and the presence of conspecifics. We predicted that, if there is a trade-off between choosiness and fecundity, females that were choosier with respect to host plant nutritional status and conspecific presence would have lower fecundity.

METHODS

The focal butterflies in our study were 33 female cabbage whites reared in the laboratory from wild-caught mothers. We assessed choosiness in these focal butterflies using a behavioural assay in which females were allowed to choose where to lay eggs. We investigated trade-offs of choosiness by looking at potential relationships between choosiness in the context of nutrition and density, and between choosiness in each context and estimated fecundity.

Butterfly Collection and Husbandry

Focal female cabbage whites used in the assay were reared in the laboratory from six mothers collected in gardens on the University of Minnesota St Paul campus. We kept track of the mother of each focal butterfly to determine whether there was any signal of genetic effects on choosiness. Mothers were individually placed in 61 × 61 × 61 cm Bug-Dorm cages with a damp washcloth and a cup of water covered with tulle to maintain humidity, a small sponge soaked with 10% honey solution to provide a source of carbohydrates (changed daily) and a leaf of organic cabbage to promote oviposition. Once eggs were laid on the organic cabbage leaves, they were transferred to an incubator and larvae were reared in the laboratory on an artificial diet modified from established methods (Snell-Rood, Espeset, Boser, White, & Smykalski, 2014; Troetschler, Malone, Bucago, & Johnston, 1985; Supplementary Material). Emerged adult focal butterflies were individually marked with a pen and relocated to 61 × 61 × 61 cm clear vinyl and mesh cages in the greenhouse with the same amenities given to their wild mothers. The focal females also had access to males, and 4–12 butterflies with a sex ratio of approximately 1:1 were maintained in each mating cage. Females remained in the mating cages for 3 days, a sufficient period of time for mating to occur so that females would be motivated to lay eggs in the behavioural assay.

Host Plant Preparation

Host plants for the behavioural oviposition assay were grown under natural light in greenhouse facilities at the University of Minnesota, with an extended photoperiod provided by overhead lights after September, when daylength began to decrease. As detailed below, we manipulated host plants to present focal butterflies with different options with regard to nutritional status and conspecific density.

Fertilizer was used to create high- and low-nutrition host plant options because cabbage whites can sense differences in fertilization levels (Myers, 1985) and prefer relatively more fertilized plants (Chen et al., 2004). To produce a difference in fertilization level, cabbages (*Brassica oleracea* var. Earliana) were grown from seed in Sunshine[®] Professional Growing Mix (Mix 15/LC15, Sun Gro Horticulture Canada Ltd, Seba Beach, AB) and randomly assigned to high- or low-fertilizer treatments. We applied 5 g of slow-release fertilizer (Osmocote[®] Classic 14-14-14 N:P:K, Everris, Dublin, OH, U.S.A.) twice to each high-fertilizer cabbage plant, approximately 3 weeks apart. We concurrently applied 2 g of fertilizer to low-fertilizer plants. Two batches of cabbages were grown in the early and late summer for a consistent supply of mature leaves with no signs of senescence. To verify a difference between the two fertilizer treatments, we quantified nitrogen content from plants in both batches. Three leaves from different plants in each treatment group were pooled and analysed for nitrogen content at the University of Minnesota Research Analytical Lab using the Dumas method (Matejovic, 1995). The nitrogen analysis indicated an average of 1.5605% nitrogen for the high-fertilizer cabbages and 1.3475% nitrogen for the low-fertilizer cabbages across two batches of plants. Thus, the fertilizer treatment resulted in an average difference of 0.213% nitrogen between the subset of high- and low-fertilizer cabbages tested in the two batches of plants.

To create host plants with different levels of conspecific density, we pinned dead model female cabbage whites in oviposition posture onto the cabbage leaves. Dead, pinned conspecifics are commonly used as social cues in insects, including butterflies (Jones, Ryan, & Chittka, 2015; Otis et al., 2006). Butterflies used as models were purchased from Carolina Biological Supply (Burlington, NC, U.S.A.) as eggs and reared to adulthood in the laboratory on

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