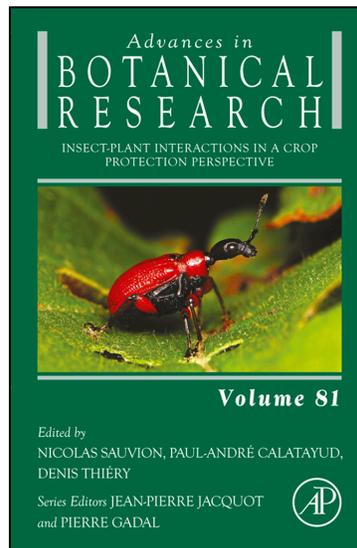


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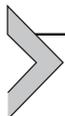
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ISBN: 9780128033180

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How Host Plant and Fluctuating Environments Affect Insect Reproductive Strategies?

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Abstract

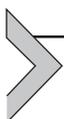
Host plants possibly represent the strongest selection pressure for the evolution of reproductive traits in phytophagous insects. In a first part of this chapter, we review how plant quality affects both female and male life history traits and their respective reproductive success, and how the production and transfer to females of male sperm and associated nongametic substances (spermatophores as nuptial gifts) also depend on the host plant choice. At first glance, it seems that reproductive traits in phytophagous insects should be selected to maximize the success of this short-term interaction between host plant and phytophagous insects. This, however, ignores the fact that variation in reproductive success is detrimental to long-term fitness, which may explain that reproductive traits depart from their short-term expectation in unpredictable environments. Bet-hedging strategies – as exemplified by spatial or temporal dispersal (e.g., prolonged diapause) – can therefore evolve in such environments, as described in the second part of this chapter. The knowledge reviewed in this chapter is also integrated in the broader applied perspective of insect pest population management.



1. INTRODUCTION

Many aspects of the phytophagous insect's life history depend on the host plant on which they develop, emerge or reproduce. Temporal seasonal and intraday variations in quality and quantity of the plants may result from many external factors (e.g., climate or soil conditions such as nitrogen contents and water resource) and internal factors (i.e., plant health or injuries). In response, phytophagous insects have evolved life-history strategies to deal with spatial and temporal variability of the host plant quality. For example, the regulation of the offspring size by insects in response to the host plant quality, or the synchrony between egg hatching and host plant phenology are keypoints to understand insect pest outbreaks, or the dynamics of trophic networks in which phytophagous insects are involved [e.g., see chapter: Food Webs and Multiple Biotic Interactions in Plant-Herbivore Models by [Corcket, Giffard, and Sforza \(2016\)](#)]. Periodic environmental variation such as seasons (i.e., predictable component of environmental variability) plays a major role in the evolution of phytophagous insect life history traits. However, environment stochasticity (i.e., unpredictable component) must not be neglected since it can explain curious insect strategies as bet-hedging.

Even if several literature reviews on reproductive strategies in response to host plant quality exist (see [Awmack & Leather, 2002](#) for an example), we attempt, in this chapter, to review the different effects of the host plants on insects' immediate fecundity, through the modulation of both female and male gamete production. We then focus on the impact of variation of host quality and availability in time and space (i.e., fluctuating environment) on their reproductive strategies, in particular through the evolution of bet-hedging strategies. We also discuss the literature in the light of crop protection against insect pests, especially in the context of climate change.



2. EFFECT OF HOST PLANT QUALITY ON MALE AND FEMALE REPRODUCTION

Reproduction is one of the most energy consuming activity for an individual during its lifetime. In most insect species, reproduction is a nutrient-limited process for both sexes, and largely relates to the individuals' energy reserves (e.g., [Boggs & Freeman, 2005](#)). The resources needed for reproduction can be acquired during the juvenile instar or adult stage. Species that can only acquire resources at the juvenile stage are referred to as *capital breeders*. For such species, the quality of the larval food plant [i.e., set of characteristics including levels of chemicals (nitrogen, carbon, defensive compounds...), reviewed by [Awmack & Leather, 2002](#)] is decisive as insect fitness is ultimately dependent on larval plant quality ([Telang & Wells, 2004](#)). Other species that can acquire additional resources during adulthood are called *income breeders*. Contrary to capital breeders, income breeders can compensate for the acquisition of poor-quality food at the larval stage; thus plant quality is generally considered more critical for capital breeders than for income breeders. However, both income and capital breeding females may complete the nutritive resource devoted to reproduction by nutrients contained in nuptial gifts or transferred by the partner during copulation ([Lewis & South, 2012](#)).

In this context, the nutrients obtained by phytophagous insects can be allocated to their somatic tissues and affect the general body condition of larvae and both adult males and females in many ways. For instance, these resources can be used to decrease their developmental duration ([Cahenzli & Erhardt, 2012](#); [Tigreros, 2013](#)) or increase adult longevity ([Cahenzli & Erhardt, 2012, 2013](#); [Fritzsche & Arnqvist, 2015](#)), body size ([Cahenzli & Erhardt, 2012, 2013](#); [Fritzsche & Arnqvist, 2015](#); [Tigreros, 2013](#)), and initial lipid, protein and glycogen contents ([Vande Velde, Schtickzelle, &](#)

Van Dyck, 2013). The reproductive output of most phytophagous insects is improved by an increase in the host plant's protein and carbon-based nutrient concentrations, and by a decrease in soluble carbohydrate concentration. The mineral content of the host plant also influences the reproduction of herbivorous insects, but this effect is complex, sometimes unclear and will not be addressed in this chapter. Among the different chemical substances contained in host plants, nitrogen has been identified as the key nutrient required by herbivorous insects (White, 1993). For instance, reproductive performance of aphid species is higher on high-nitrogen (Khan & Port, 2008). In addition to nutrients, secondary plant compounds can impact the performance of phytophagous insects (as reviewed by Hilker & Meiners, 2011). Overall, nutrient stress conditions occurring early in life (e.g., food deprivation or low plant quality) can greatly impede individual fitness (e.g., survival and fecundity) as well as less direct effects, such as a decrease in the ability to attract and locate mates (Muller, Arenas, Thiéry, & Moreau, 2016).

The host plant is thus an extremely important ecological factor for phytophagous insects of both sexes, but its gender-specific effect has been the object of scarce attention. Here we review the effect of host plant quality on female and male reproductive strategies.

2.1 Effects of the Host Plant Quality on Larval Development and Consequences on Female Reproductive Output

Host plant quality affects several female life history traits such as larval growth, diapause induction and larval defence against natural enemies (Coley, Bateman, & Kursar, 2006; Hunter & Mcneil, 1997). It is also known that the quality and quantity of plant tissues consumed during larval stages affects the reproduction of females, thus highlighting the importance of larval diet for future reproductive events (Awmack & Leather, 2002; Blanckenhorn, 2000; Honěk, 1993; Leather, 1994; Thiéry & Moreau, 2005).

For example, many essential compounds in butterfly eggs are exclusively provided by the larval diet (O'Brien, Boggs, & Fogel, 2013). When host plant consumed at the larval stage is of poor quality, females (especially income breeder females) can, to some extent, override this potential handicap by the use of high-quality plants as adults. Map butterflies [*Araschnia levana* (Linnaeus, 1758)] females, for instance, obtain amino acids required for egg production from nectar (Mevi-Schutz & Erhardt, 2005). In general, both larval residual energy derived from the host plant and the food ingested

as adult are used for egg production, such that both income and capital breeder species rely on the quality of the host plant on which larvae develop.

The effects of host plant quality on the reproductive output of herbivorous insects are generally investigated through three main proxies: the number of eggs produced, their probability of hatching and their size. For example, egg size and clutch size depend on host plant quality: females feeding on plants of poor quality generally lay smaller and fewer eggs than those feeding on plants of high quality (Fox & Czesak, 2000). These proxies of the female fitness are, however, not synonymous, and they should be interpreted differently (see below).

2.1.1 Host Plant and Clutch Size

Fecundity is the number of eggs produced by a female during her lifetime. Potential and realized fecundities are usually considered, being defined as, respectively, the number of eggs in the reproductive tract and the number of eggs laid. The first one is a good estimate of the female potential fitness and is certainly the most studied reproductive life history trait due to the convenience of its estimation (Awmack & Leather, 2002; Leather, 1994). However, its interpretation is limited as egg maturation or fertilization can fail, thus resulting in sterile or aborting eggs. Moreover, when eggs are produced during the adult stage, the number of eggs in the reproductive tract may not be representative of the total number of eggs laid during a lifetime, which may vary depending on internal and external factors such as the quality and quantity of host plant consumed. For all these reasons, realized fecundity is a better fitness proxy than potential fecundity.

Because laid eggs may fail to develop, it is preferable to estimate fitness through fertility, defined as the number of hatching eggs. The relevance of this trait as a fitness proxy was demonstrated by Moreau, Benrey, and Thiery (2006) who studied the reproduction of one of the main vine pests, *Lobesia botrana* (Denis & Schiffermüller, 1775) (Lepidoptera: Tortricidae). In this species, the female fecundity is influenced by the variety of grapes they develop on, whereby females grown on Merlot lay more eggs than those grown on Riesling (Fig. 1A). Using fecundity as a fitness proxy, one would expect Merlot to be a better host for female development than Riesling. However, eggs of females grown on Riesling have higher hatching rates than those of females grown on Merlot (Fig. 1B). These two contradicting conclusions demonstrate that both fecundity and fertility should be considered carefully. In fact, the measure of the reproductive rate per female (number of larvae produced per female) shows no relationship with the host plant

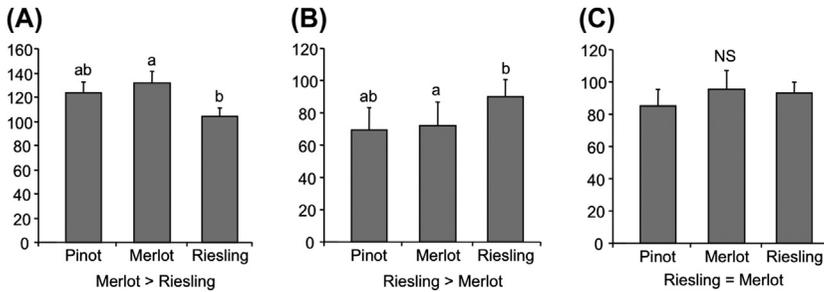


Figure 1 (A) Fecundity (number of eggs laid), (B) fertility (percentage of eggs hatched) and (C) reproductive rate (number of larvae produced per female) according to the cultivar where the larvae fed on. The text below each panel indicates the better cultivar for *L. botrana* females. Modified from Moreau, J., Benrey, B., & Thiery, D. (2006). Assessing larval food quality for phytophagous insects: Are the facts as simple as they appear? *Functional Ecology*, 20, 592–600.

on which females developed (Fig. 1C). In this species, a high fecundity is counterbalanced by a low fertility. Unfortunately, fertility is difficult to measure under field conditions, thus is often neglected. Most studies investigating the quality of the host plant on herbivore reproduction only considered female fecundity, implicitly assuming that high-quality host plants will also result in a higher or similar hatching success as low-quality plants (see Tammaru, Esperk, & Castellanos, 2002 for an exception). This missing life history trait is, however, puzzling in our general understanding on how host plant quality affects the fitness of phytophagous insects.

2.1.2 Host Plant and Egg Size

As detailed above, the effect of host plant quality on female fitness cannot be limited to egg numbers but one should also take into account the hatching probability, which is directly linked to egg size. It is commonly accepted that females face a choice between the production of a large number of small eggs and the production of a small batch of large eggs (Fox & Czesak, 2000). Indeed, although the scientific community knew about these evolutionary trade-offs for a long time, most of the studies devoted to identify the effect of host plant quality on the fitness of phytophagous insects analyzed only one or independently a few life history traits. However, it is essential to study all fitness related life history traits together to fully understand the effects of larval food quality on herbivore fitness.

Egg size is recognized as a crucial reproductive life history trait for females. Egg size is related with host plant quality by at least two distinct mechanisms. On the one hand, females that developed on plants of high quality may

accumulate enough resources to produce numerous large eggs. In this case, a direct relationship exists between the quality of host plant consumed by the female and offspring life history traits (Moreau, Arruego, Benrey, & Thiéry, 2006; Moreau, Benrey, et al., 2006). As stated above, the main sources of energy for egg production come from the resources accumulated at the larval stages, especially for capital breeder's species (Awmack & Leather, 2002; Kaspi, Mossinson, Drezner, Kamensky, & Yuval, 2002). Larger eggs are thus often associated with more nutritional provisions allocated by females (Berrigan, 1991; Fox & Czesak, 2000). On the other hand, females may express egg size plasticity in response to the host plant quality at the oviposition site. For example, females of the seed beetle, *Stator limbatus* (Horn, 1873) (Coleoptera: Chrysomelidae: Bruchinae), tend to deposit larger eggs on low rather than on high-quality host plants, thus increasing survival of larvae on low-quality host plants (Fox, 1997). In this case, the link between egg size and the host plant quality is indirect and does not involve a direct physiological relationship between the mother's condition and her reproductive output. Egg size is thus a fitness proxy linked with host plant quality by a complex relationship and depends on the quality of the plant on which the mother developed and the eggs are laid (Ekbom & Popov, 2004).

It is generally assumed that producing larger eggs gives them an advantage for they result in larger larvae. Indeed, under stressful conditions (lack of food, adverse environmental conditions...), a larger egg with more reserves is better equipped to resist desiccation or withstand stressful or variable conditions. Moreover, such large larvae should have bigger mandibles with obvious advantage in the perforation of plant tissues and thus in food acquisition (Awmack & Leather, 2002; Fox & Czesak, 2000). Ekbom and Popov (2004) thus suggested that large larvae emerging from large eggs are advantaged on poor-quality host plants in comparison with small larvae emerging from small eggs. Consequently, larger larvae may have a greater chance to successfully establish on a plant than smaller ones.

As part of an ecosystem, eggs and larvae also face many trophic threats, such as other phytophagous competitors or predators and parasitoids [e.g., chapters: Food Webs and Multiple Biotic Interactions in Plant-Herbivore Models by Corcket et al. (2016) and The Plant as a Habitat for Entomophagous Insects by Kaiser et al. (2016)]. The egg characteristics and the embryo development are influenced by secondary plant compounds, such as toxins incorporated into the eggs by females, which protect the embryo from parasitism and predation (Blum & Hilker, 2008). Considering offspring size, strong trophic pressure gives an advantage for intermediate larval size,

resulting in the selection for nonmaximized larval growth. The classic explanation of such phenomenon is that larger eggs and larvae are known to be more apparent and susceptible to predation/parasitism than smaller ones but this effect is offset by the fact that they have more energy to escape and defence against their threats (Berger, Walters, & Gotthard, 2006).

2.2 Effect of Host Plant on Male Reproductive Output

There is increasing evidence that host plants also influence the reproductive output of insect males. In phytophagous species, male reproduction is generally affected by the quality or availability of nutrients acquired by feeding on plants as larvae (Muller, Thiéry, Moret, & Moreau, 2015; Takakura, 2004; Tigreros, 2013) or adults (Cahenzli & Erhardt, 2012, 2013; Fritzsche & Arnqvist, 2015). In some cases, plants can also affect male reproduction through the chemical compounds they emit (Ali, 2012; Shelly & Epsky, 2015). Altogether, the quality of host plants on which males feed can affect their reproductive output through variations in (1) the traits involved in mate acquisition and (2) the production of sperm and associated nongametic resources (spermatophore) that impacts female reproductive output, in terms of the number and quality of offspring males sire. Due to the costs associated with the production of sexual traits, sperm and spermatophores, males may further adjust their investment in such traits according to female quality and exhibit mate choice strategies.

2.2.1 Male Attractiveness and Competitive Ability

Males' ability to attract females and secure sexual partners and mating territories against rival males can be modulated by the resources obtained during host plant feeding. In the European grapevine moth (*L. botrana*), for instance, grape cultivars on which individuals develop influence their probability of acquiring a mate (Moreau, Thiery, Troussard, & Benrey, 2007). More precisely, females discriminate males of different qualities during the precopulatory phase and they preferentially call (i.e., via pheromones) those that fed on higher quality cultivars as larvae (Muller et al., 2015). In contrast to many species where females tend to prefer larger males, the preference observed in *L. botrana* females is unrelated to male size (Muller et al., 2015). While the cues or signals females use to discriminate males' host plant origin remain to be identified in this species, it has been demonstrated in others that host plant quality can affect male sexual signals. In particular, the production of sex pheromones often relies on bioactive chemicals or chemical precursors, as illustrated by two examples: pyrrolizidine alkaloids

in arctiid moths, *Utetheisa ornatrix* (Linnaeus, 1758) (Lepidoptera: Noctuidae) (Conner, Eisner, Vandermeer, Guerrero, & Meinwald, 1981), and methyl eugenol in the oriental fruit fly, *Bactrocera dorsalis* (Hendel, 1912) (Diptera: Tephritidae) (Shelly, 2000), that males acquire when feeding on plant as adults or sequester as larvae (see Landolt & Phillips, 1997 for a review). It then confers a mating advantage to males emitting pheromones with high levels of these compounds (Shelly, 2000).

Host plant feeding can also alter other male sexual traits associated with their mating success such as colouration and vibratory signals. In the small white butterfly, *Pieris rapae* (Linnaeus, 1758) (Lepidoptera: Pieridae), females prefer more colourful males (Morehouse & Rutowski, 2010) whereby wing colouration is based on pterins, pigments rich in nitrogen which is mainly acquired during larval feeding (Tigreros, 2013). In the *Enchenopa binotata* species complex of treehoppers (Hemiptera: Membracidae), males communicate with plant-borne vibrational signals which vary according to the clone plant on which they fed as larvae (Rebar & Rodríguez, 2014). This likely affects their reproductive success, with females exhibiting strong mate preference on the basis of the features of those signals (Rodríguez, Sullivan, & Coccoft, 2004). Thus the host plant quality can condition phytophagous male reproductive output by affecting the characteristics of their sexual traits, and recent studies show that it can additionally affect male sexual behaviour. In species where males display territorial behaviours, those in better physiological conditions generally have greater chances of accessing and holding territories (Briffa & Hardy, 2013). As said above, host plant can largely affect individuals' morphology (e.g., body mass/size, wing size, flight muscle ratio) and energy reserves (i.e., lipid, protein, glycogen contents). It results in variation in male territorial success and potentially in various male sexual strategies. Experimental work conducted in the speckled wood, *Pararge aegeria* (Linnaeus, 1758) (Lepidoptera: Nymphalidae), showed that larval food plant quality is a key determinant of male adult body mass, lipid content and flight muscle ratio (Vande Velde et al., 2013). These parameters further condition the performance of perching males when defending sunlit spots on the forest floor where they wait for females. As a result, low-quality males that developed on drought-stressed plants adopt an alternative nonterritorial searching behaviour (i.e., patrolling tactic), which is less energetically demanding (Vande Velde et al., 2013).

2.2.2 Sperm and Associated Substances Production

While numerous studies have examined the effect of variation in both larval and adult nutrition of the plant on female gamete production (see above),

much less is known about the effect of plant production on sperm production. The few studies gave contrasting results and mainly concerned Lepidoptera, in which males produce two types of sperm: the eupyrene (i.e., fertile) sperm, and the apyrene (i.e., nonfertile) sperm, whose function remains unclear but could potentially play a role in sperm competition (Silberglied, Shepherd, & Dickinson, 1984). In *L. botrana*, host plant (grape cultivars) on which larvae feed affects the number of eupyrene sperm produced and males transferring more sperm have a greater reproductive output by fertilizing a greater number of eggs (Muller et al., 2015). Nevertheless, to our knowledge this result is unique since in two other cases, no link between larval nutrition on host plant and sperm production was found [in *P. aegeria* in Vande Velde et al., 2013; and *Bicyclus anynana* (Butler, 1879) (Lepidoptera: Nymphalidae) in Lewis & Wedell, 2007]. Complementary adult feeding on nectar or rotten fruit has also no apparent direct effect on eupyrene sperm production in *B. anynana* (Lewis & Wedell, 2007). This latter result is, however, not surprising because, in Lepidoptera, spermatogenesis ends before adult emergence (Friedländer, 1997). Only the production of apyrene sperm continues during the early adult life and might be affected by adult feeding. Further studies are needed to draw general conclusions on this topic.

In many insect species, not only phytophagous ones, males also provide females with nongametic resources prior to or during mating (Lewis & South, 2012; Vahed, 1998) (Fig 2). Such ‘nuptial gifts’ can take many forms such as preys captured by the male, oral secretion or spermatophores produced by the male, or body parts or the whole body of the male (see Vahed,

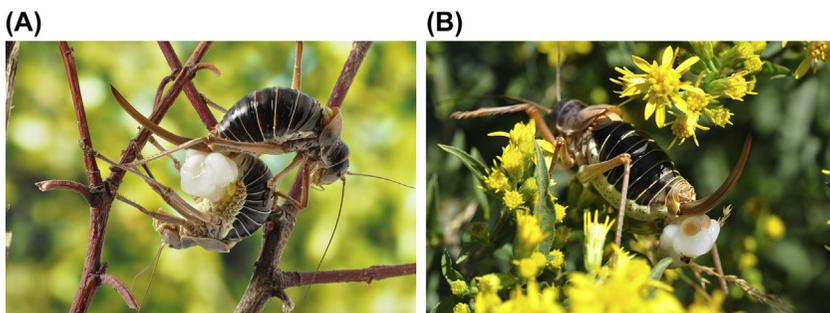


Figure 2 (A) *Ephippiger diurnus* male transferring his spermatophore to a female (on top) during mating. (B) *E. diurnus* female with a spermatophore [in orange (grey in print versions): the ampulla containing the sperm, in white: the spermatophylax containing various nutrients and water]. *Sonia Dourlot*.

1998 for a complete review). They contain a variety of compounds such as proteins, fats, carbohydrates, minerals, uric acid (Vahed, 1998) which are passed to the females and potentially affect both female and male reproductive outputs. Elegant radiolabelling experiments showed that spermatophore-derived substances (such as amino acids, zinc, phosphorus and sodium) passed to the female somatic tissue and eggs (Gwynne, 2001; Lewis & South, 2012; Vahed, 1998). In addition, other chemicals present in the spermatophore, such as plant-derived defensive compounds, such as pyrrolizidine alkaloids or cyanogenic glycosides, can also favour the protection of females, their eggs or both against predation (Eisner & Meinwald, 1995). Little is known about the impact of male diet on their spermatophore quality. One study demonstrated that, in the small white butterfly (*P. rapae*) the quality of the larval food [on two different host plants: garlic mustard, *Alliaria petiolata* (M.Bieb.) Cavara & Grande, and nasturtium, *Tropaeolum majus* L.] affected the size of the spermatophores (Cook & Wedell, 1996). Other experiments showed that supplementing male adult diet with electrolytes and amino acids enhance their spermatophore mass, size and contents (e.g., Lederhouse, Ayres, & Scriber, 1990). The subsequent consequences on the male reproductive output, in terms of the quality and quantity of eggs fertilized by the gift-giving male, have received even less attention (Delisle & Bouchard, 1995; Delisle & Hardy, 1997; Royer & McNeil, 1993; South & Lewis, 2011). In the rosaceous leaf roller, *Choristoneura rosaceana* (Harris, 1841) (Lepidoptera: Tortricidae), for instance, males fed as larvae with beaked hazel (*Corylus cornuta* Marshall), a host plant of low nutritional quality, produced smaller spermatophores than males fed with striped maple (*Acer pensylvanicum* L.), a plant of higher nutritional value (Delisle & Bouchard, 1995). In return, females mated once with hazel-fed males lay fewer eggs and produce fewer offspring than those mated once with maple-fed males. Therefore host plant quality affects male reproductive success in phytophagous species through its effect on the size and nutrient contents of the spermatophore that males transfer to females at mating (Delisle & Bouchard, 1995; Muller et al., 2015; South & Lewis, 2011). Nevertheless, the precise relationship between the quality of host plant on which males feed and the quality of their spermatophore and the associated fitness return, deserves to be extended to other species to draw general conclusions on these relationships in plant-eating insects.

Furthermore, spermatophores not always act as a paternal investment, by increasing the number or quality of males' offspring, but also as a mating effort by protecting the donors' sperm (Gwynne, 2001; Vahed,

1998). In such a case, nuptial-gift quality can modulate the female refractory period and consequently the risk of sperm competition that males face. Females receiving a large spermatophore usually show a long remating latency (Muller et al., 2016), ultimately increasing the male's fertilization success.

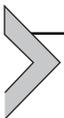
2.2.3 Consequences on Male Mate Choice

Spermatophores are highly costly to produce and can thus strongly limit males' reproductive rate (Gwynne, 2001; Lewis & South, 2012). Hence, it would be advantageous for males to adjust their reproductive investment to female quality. In line with this hypothesis, males of the bush cricket, *Ephippiger diurnus* (Dufour, 1841) (Orthoptera: Tettigoniidae), modify the size and composition of their spermatophore according to female body mass and age (Jarrige, Greenfield, & Goubault, 2013, 2015) (Fig 2). In this species presenting a last-male sperm precedence effect (i.e., the sperm of the last male to mate a female fertilizes a larger proportion of the female's eggs; Hockham, Graves, & Ritchie, 2004), gifts transferred to older females which are less likely to remate contained large amounts of nutritious protein-bound amino acids (Jarrige, Body, Giron, Greenfield, & Goubault, 2015). In contrast, younger large females, in which sperm competition risk is higher, received more diluted spermatophores, containing increased amounts of free glycine, a substance which increases female handling time of the spermatophore. This gift allocation has been suggested to represent a form of cryptic mate choice, allowing males to maximize their chances of paternity in relation to the risk of sperm competition associated with mate quality. Nevertheless, to our knowledge, the impact of host plant feeding on spermatophore quality and its subsequent consequences on male differential investment in female by manipulating its composition remains to be investigated.

Males can also show more direct mate preference, which can vary according to the plant they developed from. For instance, larval host plant experience modulates male attraction to the female sex pheromone in the cotton worm, *Spodoptera littoralis* (Boisduval, 1833) (Lepidoptera: Noctuidae). In this species, males were more attracted to the female sex pheromone when combined with the odour of the host plant species they fed on as larvae than to female sex pheromone combined with odours of host plant species they did not experience (Anderson, Sadek, Larsson, Hansson, & Thöming, 2013).

2.2.4 Effect of Exposure to Host Plant Volatiles on Male Reproductive Output

Host plant can also affect the male reproductive output without requiring males to feed on them. Plant volatiles can indeed favour male mate finding especially when females concentrate on host plants to feed and oviposit. In such a situation, plants act as 'sexual rendezvous' points (Bernays & Chapman, 1994). Additionally, the exposure to plant odours can modulate male emission of sex pheromone (e.g., Bachmann et al., 2015), male responsiveness to female sex pheromone (Binyameen, Hussain, Yousefi, Birgersson, & Schlyter, 2013), male competitiveness (Morató, Shelly, Rull, & Aluja, 2015) and, as a result, male mating success (Vera et al., 2013). Male responses to host plant volatiles are extensively studied in fruit flies, because a better understanding of such effects may permit the development of new control techniques of these pests of agronomic importance. *Ceratitis capitata* (Wiedemann, 1824) (Diptera: Tephritidae) males exposed to various *Citrus* species or common guava (*Psidium guajava* L.) show a mating advantage over nonexposed males (Shelly & Epsky, 2015). This advantage can be conferred by the increased calling behaviour and pheromone release displayed by exposed males, as observed in the South American fruit fly, *Anastrepha fraterculus* (Wiedemann, 1830) (Bachmann et al., 2015). Likewise, the reproductive success of males exposed to the essential oils extracted from different host plants is strongly enhanced (Morató et al., 2015; Shelly & Epsky, 2015). This effect could be more specifically triggered by specific compounds, such as terpenes (e.g., α -copaene; Shelly, 2001) present in the plant odour. These effects can be used to increase sterile males' competitiveness over wild males in pest management programs whereby sterile males exposed to plant oils during mass-rearing outcompete wild males for copulation with wild females up to 3 days after exposure (Shelly & Epsky, 2015).



3. INSECT REPRODUCTIVE STRATEGIES IN RISKY ENVIRONMENTS

Phytophagous insects live in varying environments and have evolved life-history strategies to deal with this variability. Only a part of this variability comes from host plant–insect interactions. Thus it would be misleading to consider this part alone in studies of the evolution of these strategies. In this section, we highlight cases where such strategies have been studied extensively or suggested in phytophagous insects. We also review

bet-hedging strategies well known in other organisms but that require more empirical and theoretical attention in phytophagous insects.

3.1 Evolutionary Strategies in Risky Environments

Plants differ in their suitability as food for a given insect species. In a stable environment where plants are abundant, one may predict that natural selection favours the ability of a female to lay its eggs in a host plant that is most suitable for her offspring's development (Bernays, 1991; Mayhew, 1997). The fitness consequences of a wrong choice are particularly severe because developing phytophagous insects are often unable to switch from one host plant to another. This leads to a positive correlation between the preference of a female for a host plant and the performance of her offspring — often referred to as the preference–performance hypothesis (PPH; Gripenberg, Mayhew, Pamell, & Roslin, 2010). This relationship has been demonstrated in several examples, but dozens of studies report a weak or no relationship between preference and performance (for a review see Gripenberg et al., 2010). This suggests that females sometimes choose less suitable or unsuitable host plants, which raises the following question: why, in some contexts, females exhibit apparent suboptimal choices? One possible explanation may be that the abundance or quality of resources varies in time, such that highly specialized females may sometimes face bad conditions that result in low reproductive success.

Genotypes with reproductive successes that vary in time are generally counterselected, even if their (arithmetic) mean reproductive success is unaffected. For instance, a genotype whose females at a given generation lay no egg under certain environmental conditions would immediately go extinct, even if this loss could be compensated by laying many eggs in the future. The negative impact of varying growth rates on the selective value of a genotype are captured by calculating fitness as the geometric instead of the arithmetic mean of growth rates. The geometric mean decreases as the temporal variance in growth rates increases, such that a genotype that reduces this variance may have a selective advantage. This is generally known as a *bet-hedging strategy*, which maximizes the geometric mean even at the cost of a reduced arithmetic mean (Cohen, 1966; Philippi & Seger, 1989; Ripa et al., 2010; Seger & Brockmann, 1987; Slatkin, 1974). Bet-hedging theory permits to explain why generalist phytophagous may evolve in an environment where resource abundance or quality varies in time. Thereby a specialist may better exploit a given resource, but at a cost of maximum variance in its reproductive success, whereas a generalist

would reduce this variance (Starrfelt & Kokko, 2012). In this case, one phenotype is expressed by the genotype, which is generally known as conservative bet-hedging.

Selection in fluctuating environments can yield more spectacular strategies where one genotype yields several phenotypes randomly – also known as *coin-flipping plasticity* (Cooper & Kaplan, 1982) – each of them being specialized to a given environmental condition that may occur. Likewise, this strategy – known as *diversifying bet-hedging* – reduces the temporal variance of the genotype's growth rates.

Another distinction between bet-hedging strategies differentiates those that buffer environmental variations 'here and now' versus 'elsewhere or later' (Hopper, 1999; Hopper, Rosenheim, Prout, & Oppenheim, 2003; Solbreck, 1978). Traits such as generalism, clutch and egg size or mating strategies can be interpreted as examples of the former, as we will show in next Section 3.2, whereas traits such as facultative dispersal or dormancy are potential examples of the latter (Section 3.3).

3.2 Dealing With Unpredictable Variation Here and Now

3.2.1 Generalism

In the context of phytophagous insects, generalism is the ability to exploit several host plant species. Such a strategy is generally considered costly, first because it requires being able to overcome the defence mechanisms (e.g., toxic compounds, physical barriers) of several host plant species and second because generalists exploit a large range of host species, such that sometimes they exploit less suitable hosts. Nonetheless, as we have seen, generalism may provide a fitness benefit when the quality and/or quantity of host plant vary temporally in an unpredictable fashion (Futuyma, 1979; Starrfelt & Kokko, 2012). Wiklund and Friberg (2009) surveyed the annual survival of the generalist orange-tip butterfly, *Anthocharis cardamines* (Linnaeus, 1758) (Lepidoptera: Pieridae) and observed that survival on its host plant species is indeed temporally uncorrelated. Generalism is nevertheless rather uncommon in phytophagous insects, with about 10% species exploiting several resources (Bernays & Graham, 1988). This may be due to the high cost of generalism, and to the existence of alternative – and possibly less costly – bet-hedging strategies that can allow specialists to buffer environmental variation (see below).

3.2.2 Egg Size and Number

These traits are often thought as being negatively correlated, or equivalently that they are part of a trade-off (see Part 2 of this chapter). In a stable

environment, the evolutionarily expected combination of these two traits linked by a trade-off is the one that maximizes the average number of viable offspring produced. [Einum and Fleming \(2004\)](#) predict that by producing higher quality (larger) – but fewer – offspring, regardless of variation in environmental conditions, may be considered as conservative bet-hedging. Indeed, these offspring will be more able to survive and reproduce when resources are scarce. This strategy comes at the cost of a lower number of offspring under favourable conditions, which can be compensated by the advantage of a reduced variance in growth rates above some threshold of environmental variations. This has been studied in birds (e.g., [Boyce & Perrins, 1987](#)), but not in phytophagous insects to our knowledge.

The reasoning above on the evolution of egg size and number neglects the variation of these traits within a clutch, although egg sizes have been found to vary within clutches ([Fox & Czesak, 2000](#)). While this may appear as nonadaptive phenotypic variation, [Olofsson, Ripa, Jonzén, and Jonze \(2009\)](#) have suggested that this might be a case of adaptive diversifying bet-hedging. Indeed, a genotype producing both large and small eggs produces specialists of good and bad conditions, respectively ([Kaplan & Cooper, 1984](#); [McGinley, Temme, & Geber, 1987](#)). Phytophagous insects – especially those who lay their eggs in extra-host batches (such as butterflies) – seem like a relevant biological model to test the hypothesis of adaptive bet-hedging ([Box 1](#)).

3.2.3 Traits That Are Often Described as Bet-Hedging but may not Be

Making many small clutches – instead of one large clutch – is often described as a bet-hedging strategy ([Freese & Zwölfer, 1996](#)). Intuitively, a female laying all her eggs in a single place risks losing all her offspring, for instance, if a predator feeds on this host plant. This is controversial because in a large well-mixed population the risk of predation would be spread among all the carriers of a genotype. In this context, making many small clutches does not buffer variations in the genotype's growth rate ([Starrfelt & Kokko, 2012](#)). The quality of a reproductive partner, possibly in interaction with host plant, may have strong impact on lifetime reproductive success. Multiple mating is therefore sometimes thought of as bet-hedging (e.g., [Fox & Rauter, 2003](#)), because it can reduce the risk that an individual mates with a low-quality partner. But similarly to the reasoning above, the risk is spread among all the carriers of a given genotype in a large population ([Starrfelt & Kokko, 2012](#)). However, [Yasui and Garcia-Gonzalez \(2016\)](#) have shown that a bet-hedging strategy consisting in mating

Box 1 Testing bet-hedging in phytophagous insects

One may think that observing such a curious strategy as a high level of iteroparity (i.e., reproducing several times) may be enough to identify a bet-hedging strategy. This is not the case for at least two reasons. First, a bet-hedging strategy is by definition a response to unpredictable environmental variation but similar strategies can evolve in response to other selection pressures; iteroparity, for instance, can provide a selective advantage if adults can acquire lots of resources between distant reproductive events, and thereby increase their net reproductive rate. Second, strategies that look like bet-hedging can evolve neutrally in the complete absence of any selection pressure (Verin, Menu, & Rajon, 2015).

The demonstration that an observed heritable strategy corresponds to an adaptive bet-hedging strategy thus requires formal testing. One way of performing such a test consists in comparing this observation with the prediction of a realistic model (Simons, 2011). Such a prediction can only be obtained through a modelling approach that incorporates observed distributions of time-varying parameters (e.g., survival rates, fecundities). Many theoretical studies also suggest that density dependency has a strong impact on the evolutionary outcome (Rajon, Venner, & Menu, 2009); thus such dependency should be quantified. The adaptive dynamics framework (Geritz, Kisdi, Meszéna, & Metz, 1998; Metz, Nisbet, & Geritz, 1992; Rajon et al., 2009) and individual-based modelling (Grimm, 1999) are appropriate in this context. The conclusion of the test would be even more robust if performed in several populations.

Experimental evolution may also be an efficient design to test if bet-hedging can evolve as an adaptation to a variable environment (Kawecki et al., 2012). The experimental setting should start with a non-bet-hedging genotype facing random sequences of some parameters – mimicking unpredictable environmental variation – and compare its evolutionary dynamics with that of a control placed in a stable environment. The de novo emergence of bet-hedging has been observed in similar experiments in microorganisms (Beaumont, Gallie, Kost, Ferguson, & Rainey, 2009). The rather short generation time of most phytophagous insects and their rearing convenience make them good models to perform such experimental evolution experiment in multicellular organisms. Combined with sequencing methods, this could provide information about the genetic and physiological mechanisms underlying bet-hedging traits (Box 2).

with different partners (i.e., being polyandrous or polygynous) may still evolve in small populations, or in structured populations with small effective populations sizes (N_e). Holman (2015) tested this prediction in 49 datasets in various taxa (including many phytophagous insects) and found that bet-hedging is highly unlikely to explain the evolution of these strategies.

3.3 Dealing With Unpredictable Variation Elsewhere or Later

3.3.1 *Spatial Dispersal*

In their model, [Levin, Cohen, and Hastings \(1984\)](#) consider that a part of the carriers of a genotype that adopt a bet-hedging dispersal strategy systematically disperses, while the others stay and reproduce in the locality they were born in. One can also consider these strategies in terms of distance: some carriers of a gene disperse far, while the others travel a shorter distance ([Snyder, 2006](#)). All these formulations for bet-hedging dispersal strategies have in commons that a single genotype systematically expresses a range of phenotypes differing in their ability to disperse; this is a form of diversifying bet-hedging.

Such a strategy may have a selective advantage if (1) the conditions for survival or reproduction may be bad locally without being predictable and (2) the probability of finding different conditions elsewhere is not zero (i.e., in a lack of spatial autocorrelation; [Bulmer, 1984](#); [Hopper, 1999](#)). In such a context, the carriers of a bet-hedging genotype encounter many environmental conditions, independently of their natal locality, which reduces the impact of locally variable conditions on the genotype's growth rate. A metapopulation structure is necessary for a spatial dispersal strategy to evolve ([Olivieri, Michalakis, & Gouyon, 1995](#)), and the selective advantage of dispersal bet-hedging generally increases with the number of localities ([Bulmer, 1984](#)). This type of structure is often found in insect populations ([Hopper, 1999](#)). However, to our knowledge no empirical study has yet shown that dispersal has evolved as a bet-hedging strategy in insects.

3.3.2 *Prolonged Diapause*

A bet-hedging dormancy genotype produces phenotypes that differ in the length of their development cycle — hence a case of diversifying bet-hedging — such that its carriers reproduce at different reproductive seasons. Therefore the carriers of the genotype experience various environmental conditions in an unpredictable environment, which reduces the temporal variance in their growth rates ([Gourbière & Menu, 2009](#); [Hopper, 1999](#); [Menu, Roebuck, & Viala, 2000](#); [Seger & Brockmann, 1987](#)). Many insect species display variance in the length of their life cycle, involving a facultative additional or prolonged diapause (e.g., [Danks, 1987](#); [Soula & Menu, 2005](#); [Tauber, Tauber, & Masaki, 1986](#)). [Hopper \(1999\)](#) found scarce evidence for diversifying bet-hedging in insects. Surprisingly, he neglected prolonged diapause strategies in his analysis. [Simons \(2011\)](#) considered these

strategies, however, and found several prospective examples in phytophagous insects. Although many of these studies suggest the presence of bet-hedging, none at the time had compared observations to a realistic model's prediction. To our knowledge, only one study since has performed such a test, namely with the chestnut weevil, *Curculio elephas* (Gyllenhaal, 1836) (Coleoptera: Curculionidae) (Rajon, Desouhant, Chevalier, Débias, & Menu, 2014). They have clearly demonstrated that the observed diapause strategies in two populations of *C. elephas* can be predicted by a realistic bet-hedging evolutionary model. This model was parameterized using a long-term estimate of several survival rates, density-dependent fecundities, resource abundances and predation pressure. Research studies have also focused on the physiological mechanisms underlying bet-hedging in this species (Menu & Desouhant, 2002; Soula & Menu, 2005; see also Box 2).

3.3.3 Hatching Asynchrony

Hatching asynchrony (or 'hatching spread') has been observed in phytophagous insects where parents provide food for their offspring (Nalepa, 1988; Smiseth, Ward, & Moore, 2006). It may provide a selective advantage if, as a consequence of this strategy, various offspring encounter different, randomly occurring environmental conditions and if these conditions determine their survival or the success of their development as suggested in birds (Laaksonen, 2004).

3.3.4 Temporal Clutching

Iteroparity (i.e., reproducing several times in a lifetime) is typically considered as a conservative bet-hedging strategy, where long-lived adults, instead of offspring, disperse in time (Bulmer, 1985; Wilbur & Rudolf, 2006). In insects, however, mating is often uncoupled from egg laying. As we have seen, multiple mating as a bet-hedging strategy is controversial. Nonetheless, laying one's eggs in multiple clutches spread in time could provide a similar evolutionary advantage as iteroparity, regardless of the mating strategy.

3.3.5 Pausing in Social Insects

Bet-hedging dispersal in time might also explain the presence of inactive workers in social phytophagous insects (Charbonneau, Hillis, & Dornhaus, 2014), who can carry a part of the workload when catastrophic unpredictable event occurs. This is predicted to increase the long-term sustainability of the colony at the expense of decreasing short-term productivity (Hasegawa, Ishii, Tada, Kobayashi, & Yoshimura, 2016). However, it remains to be

Box 2 The genetic and physiological architecture of diversifying bet-hedging strategies

The precise mechanisms that may randomly produce several phenotypes from a single genotype are poorly known in insects, despite its crucial importance for our understanding of the evolution of these strategies. Two main candidate mechanisms have been proposed (Cooper & Kaplan, 1982; Simons & Johnston, 1997; Walker, 1986): (1) developmental instability, which may amplify small differences in gene expression into different developmental routes and eventually, different phenotypes and (2) the dependency of the offspring phenotype on the value of a physiological or environmental variable it experiences, this variable being uncorrelated with – and thus impossible to foresee – future environmental conditions. In both cases, the phenotype is determined by a comparison between an underlying variable and a genetically (or possibly epigenetically) determined threshold. The frequency of each phenotype among the offspring can be changed by changing the threshold (Rajon et al., 2014).

The former mechanism (1), based on gene networks exploiting gene expression noise, has been studied extensively theoretically (Kussell & Leibler, 2005). Levy, Ziv, and Siegal (2012) have shown experimentally in yeast that the expression of a slow-growing resistant phenotype (the equivalent of a facultative dormant phenotype in insects) can be predicted by the level of expression of a single gene, such that phenotype switching may occur as this level increases or decreases randomly. To our knowledge, no study has studied this mechanism in phytophagous insects.

In phytophagous insects, however, a few empirical studies suggest that the second mechanism may be at the origin of bet-hedging dormancy strategies. For instance, a hypothetical mechanism has been proposed for *C. elephas*, in which the choice of entering into facultative dormancy is only made by larvae with high lipid content (Soula & Menu, 2005). This mechanism might ensure that those larvae with high fat content choose dormancy, as they probably are the most likely to survive an additional dormancy and still have the energy required to finish developing and reproduce. Danforth (1999) found a similar relationship between body weight and dormancy frequency in the desert bee *Perdita portalis*. Interestingly, such a mechanism makes the dormancy frequency, at a given year, dependent on the environmental conditions that year – for instance, a warm winter will make larvae consume more of their resources – which are uncorrelated with future environmental conditions. Rajon et al. (2014) modelled the evolution of bet-hedging dormancy strategies in two populations of the chestnut weevil, and they could only explain the observed dormancy frequencies with a model that included such noise. Nonetheless, we are still far from the identification of a causal relationship, and further work on the precise physiological and genetic determinants of diversifying bet-hedging is needed.

demonstrated that a genotype adopting such a strategy indeed increases the geometric mean of its growth rates.

3.4 Future Challenges: Life-History Syndromes

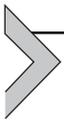
In this review, we have focused on unpredictable environments, which selects for bet-hedging. However, evidence shows that a trait involved in a bet-hedging strategy can also respond to predictable environmental cues, thus combining predictive plasticity and bet-hedging (Clausen & Venable, 2000). Reality is further complicated by the fact that several bet-hedging strategies may evolve jointly, thus forming life-history syndromes.

We have described many strategies that have the same aim, namely buffering the negative impact of environmental variance. One may expect that in this situation the traits correlate negatively. This is a typical expectation for temporal (dormancy) and spatial dispersal strategies, described as the dispersal syndrome (Buoro & Carlson, 2014). The evolution of a combination of these traits should depend on ecological parameters; for instance, the patterns of spatial and temporal autocorrelation sets the probability that better conditions may be found elsewhere or later in case the natal locality offers bad conditions, thus setting the success of one or the other strategy. Syndromes go beyond dispersal in time or space, and any of the bet-hedging traits described above are redundant as buffers of environmental variation. Venable and Brown (1988) modelled the joint evolution of the size of offspring and of their ability to disperse spatially and temporally, and generally found negative correlations between them. Pelisson, Bernstein, Débias, Menu, and Venner (2013) have shown that four species of the *Curculio* genus in a guild exhibit various combinations of three bet-hedging strategies, which supposedly have favoured their coexistence.

Nonetheless, the general prediction that seemingly emerges from these studies — that bet-hedging strategies should be negatively correlated — ignores the specificity of the interaction between these strategies (Rubio de Casas, Donohue, Venable, & Cheptou, 2015). As we have seen, large larvae of *C. elephas* are also the most likely to disperse temporally. This is a counterintuitive observation as producing offspring that are bigger on average and more likely to enter a facultative diapause combines two bet-hedging strategies, conservative and diversifying respectively. This positively correlated occurrence of two bet-hedging strategies actually has an evolutionary explanation (see Box 2).

Likewise, generalism and other bet-hedging strategies respond to a common selection pressure, such that one might expect diversifying

bet-hedgers to be more prone to specialism. However, [Kisdi \(2002\)](#) has made the exact opposite prediction, showing that local adaptation — a form of specialization in a spatial context — occurs conjointly with a decrease in the probability of dispersal — such that both bet-hedging strategies are lost when the advantage of being locally adapted overcomes that of buffering environmental variance. From these examples, we see that further theoretical developments are needed to reach a general theory of bet-hedging combining several traits.



4. CONCLUSIONS

By several aspects, the host plant affects the reproductive strategies of almost all phytophagous insects for which it has been studied. The corpus of literature attempting to characterize the insect's female life history traits affected by the plant and the mechanisms beyond thus regularly increases. However, conclusions are still limited in males by largely using artificial diets, laboratory-controlled conditions and often stock culture insects with a homogeneous genetic background. In addition, less is known concerning such relationships with plants as a natural food source varying in time and space on male reproductive outputs. Furthermore, insects adapt their fecundity, their spatial dispersive strategy or synchrony with their resource. However, we identified gaps in knowledge concerning intimate mechanisms to better understand and predict variations in phytophagous insect population dynamics. For example, understanding how plant quality tunes the plasticity in diapause duration or the variation in immune systems which regulates the resistance to natural enemies or infections has to be improved in future years. This is even more critical in insect crop pests whose damages are estimated to represent over 30% of the crop losses worldwide.

Progressing in this field of research has important for plant protection against crop insect pests and especially in the perspective of reducing pesticide use. Several alternative strategies to insecticide control exist but they all rely on a better prediction of pest populations' size and their variation. Biotechnical methods such as mating disruption or the modification of pests behavioural strategies based on the semiochemicals use, but also biological control by natural enemies, suppose to anticipate pest population variations and request a good knowledge of the their reproductive strategies. Developing agroecological practices in many crop productions also requires in depth knowledge of the interactions between the host plant and the insect

reproduction. Our current knowledge will probably be modified rather soon by the climatic environment which will profoundly affect those interactions and the insect reproductive strategies. Thus studying pest insect life history traits in interaction with the host plant in the age of unpredictable climatic changes represents for scientists and people in charge of plant protection and biodiversity an exciting and challenging period.

ACKNOWLEDGEMENTS

We thank Sonia Durlot for the two pictures of *Ephippiger diurnus* and the referee for his helpful comments.

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