Oecologia (2006) 149: 101–106
DOI 10.1007/s00442-006-0428-x

PLANT ANIMAL INTERACTIONS

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A novel trade-off of insect diapause affecting a sequestered chemical defense

Received: 19 January 2006 / Accepted: 27 March 2006 / Published online: 11 July 2006

Abstract Diapause allows insects to temporally avoid conditions that are unfavorable for development and reproduction. However, diapause may incur a cost in the form of reduced metabolic energy reserves, reduced potential fecundity, and missed reproductive opportunities. This study investigated a hitherto ignored consequence of diapause: trade-offs involving sequestered chemical defense. We examined the aristolochic acid defenses of diapausing and non-diapausing pipevine swallowtail butterflies, *Battus philenor*. Pipevine swallowtail larvae acquire these chemical defenses from their host plants. Butterflies that emerge following pupal diapause have significantly less fat, a female fitness correlate, compared to those that do not diapause. However, butterflies emerging from diapaused pupae are more chemically defended compared to those that have not undergone diapause. Furthermore, non-diapausing butterflies are confronted with older, lower quality host plants on which to oviposit. Thus, a trade-off exists where butterflies may have greater energy reserves at the cost of less chemical defense and sub-optimal food resources for their larvae, or have substantially less energetic reserves with the benefit of greater chemical defense and plentiful larval food resources.

Keywords Chemical defense · Diapause · Life-history evolution · Trade-off · Sequestration

Communicated by Richard Karban

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Introduction

Diapause is a state of dormancy widely observed in the insects where metabolic processes are substantially reduced, permitting individuals to persist in a quiescent state for months or years. Diapause has been observed in all life-history stages of insects and can be obligate or facultative (Danks 1994). Numerous studies have examined the evolutionary and ecological consequences of diapause in a cost/benefit framework and important trade-offs have been described for this life history trait (Tauber et al. 1986; Danks 1987). The propensity to diapause can vary within and among populations, and such variation provides the opportunity to examine trade-offs associated with this life-history trait and the underlying evolutionary mechanisms maintaining this variation (Tauber et al. 1986; Mousseau and Roff 1989; Hopper 1999; Wiklund et al. 1992; Danks 1994; Nylin and Gotthard 1998; Soula and Menu 2003).

Many studies have concluded that one important benefit of diapause is that it allows insects to temporally avoid unfavorable conditions, such as hostile climatic conditions, insufficient or low quality food resources, and risks imposed by natural enemies (Danks 1987; Lill 2001). Diapause can, however, impose a cost through the depletion of stored energy reserves and a reduction in fecundity, increased vulnerability to natural enemies, and lost reproductive opportunities (Danks 1987; Tauber and Tauber 1992; Ishihara and Shimada 1995; Saunders 2000; Ellers and Van Alphen 2002). The defensive benefits described in association with diapause have been largely indirect, realized through the avoidance of activity during periods of high natural enemy threat or by synchronizing activity when resource quality facilitates accelerated growth, thereby reducing the time developing juveniles remain in more vulnerable stages (Feeny 1976; Clancy and Price 1987; Williams 1999; Fordyce and Shapiro 2003). Trade-offs can exist within a tri-trophic context, for example the benefit of avoiding exposure to natural enemies through diapause can be tempered by seasonal variation in host plant quality (Lill 2001). Also