Behaviorally plastic host-plant use by larval Lepidoptera in tri-trophic food webs

Michael S. Singer^a

^aDepartment of Biology, Wesleyan University, Middletown, Connecticut, 06459, USA,

msinger@wesleyan.edu

^aCorresponding author

Abstract

Plant-insect interactions research emphasizes adaptive plasticity of plants and carnivores, such as parasitoids, implying a relatively passive role of herbivores. Current work is addressing this deficit, with exciting studies of behavioral plasticity of larval Lepidoptera (caterpillars). Here I use select examples to illustrate the diversity of behaviorally plastic host-plant use by caterpillars, including anti-predator tactics, self-medication, and evasion of dynamic plant defenses, as proof of the agency of caterpillar behavior in plant-insect interactions. I emphasize the significance of adaptive behavioral plasticity of caterpillars in the context of tri-trophic interactions. Recent research on trait-mediated indirect interactions places adaptive behavioral plasticity of herbivores at the center of community and food web dynamics, with far-reaching consequences of issues such as community stability.

Introduction

Behaviorally plastic host-plant use by herbivores demonstrates the active role of herbivores in their interactions with plants. Some have argued that herbivore behavior has been a blindspot in the plant defense literature [1], and I add here that behavioral plasticity has been especially ignored. Much more attention has been given to defensive plasticity of plants [1,2] and plastic responses of carnivores to induced plant defenses [3,4] (Fig. 1). Recently, however, studies of herbivore feeding plasticity have begun to link behavioral and physiological mechanisms to theory in evolutionary, community, and ecosystem ecology [5]. This increased attention to mechanisms of herbivore behavior in the context of adaptive plasticity theory is informing many issues old and new, such as tri-trophic interactions, nutritional ecology, and ecological immunology. Because these studies were framed in disparate ways by their original authors, one goal here is to link them under the conceptual umbrella of adaptive plasticity theory, which rests on the notion of fitness trade-offs of alternative phenotypes or behaviors under detectably different ecological circumstances. My focus here is behavioral plasticity of host-plant use by larval Lepidoptera (caterpillars), one of the most species-rich and ecologically important groups of herbivores in terrestrial ecosystems [6]. Importantly, new evidence of adaptively plastic behavior of caterpillars shows their agency in a variety of tri-trophic interactions, and offers promise for furthering understanding of tri-trophic dynamics at the community and food web levels.

Caterpillar behavior: agency and diversity

In the following sections, I describe several key examples of the active role of caterpillars in the dynamics of plant-herbivore interactions as well as the diversity of caterpillar behaviors involved (i.e. feeding and non-feeding activity) (Fig. 1). These descriptive examples provide observations needed to inform theory on the ecological dynamics of tri-trophic interactions [7]. The small set of examples here, intended to be representative but not comprehensive, reveal some patterns consistent with existing theory as well as behavioral diversity that raises questions with the potential to offer new theoretical insight. For example, how do mechanisms and ecological consequences of behavioral plasticity differ across the distribution of dietary specialization recently described for caterpillars and other insect herbivores [6]?

Feeding

Here I draw on select examples to show recent evidence for individual variation and adaptive plasticity in feeding behavior by caterpillars. Consistent with evidence from other herbivores, research on caterpillars shows that cues of carnivores (predators, parasites, pathogens) often cause reductions in herbivore feeding rate or dietary quality, which increases herbivore survival at the expense of growth or reproduction [8-10]. For example, dietary specialist *Manduca sexta* caterpillars reduced their feeding rates in response to the presence of predators, accompanied

by compensatory post-ingestive physiological changes[9]. Because the act of feeding and defecating can greatly increase a caterpillar's risk of predation [11,12], the reduction in feeding rate is likely to be adaptive for the caterpillar. However, the signature trade-off of adaptive plasticity was apparent: growth costs of these behavioral and physiological adjustments appeared later in development[9,13].

Another potentially widespread phenomenon is adaptive plasticity in diet choice by herbivores to gain resistance against parasites. As in the case described above, the adaptive change in diet in response to parasites entails other fitness costs. Recent studies in nutritional ecology show that caterpillars can change their nutrient preferences in response to microparasites. For example, the grass-specialist *Spodoptera exempta* caterpillars not only reduced their total feeding rate, but also dynamically adjusted the ratio of macronutrient intake over the course of viral infection [14]. Reduced carbohydrate intake, resulting in a high protein-to-carbohydrate ratio, increased the survival rate of infected caterpillars. This therapeutic nutrient intake pattern departs sharply from self-selected diets and optimal growth of uninfected caterpillars [15], indicating the foraging trade-off between growth and defense.

With respect to plant secondary metabolites, caterpillars show adaptive plasticity in pharmacophagy. The polyphagous grazer, *Grammia incorrupta*, increases its gustatory response to and ingestion of pyrrolizidine alkaloids (PA) when infected with tachinid parasitoids [16-18]. While PA consumption confers anti-parasitoid resistance, it also entails costs in survival [17] and growth efficiency [19]. Therefore, this therapeutic medication response is adaptive for caterpillars

battling parasitoid infections, but not for unparasitized individuals. More work is needed here to understand how medication behavior plays out in field settings [20].

Movement

Movement behavior by caterpillars reinforces the notion of their active role in insect-plant interactions, which has not always been accounted for in plant defense theory. Many caterpillars move about extensively on the plant(e.g., [21-23]) or among different plants (e.g., [24,25]), and such movements can help caterpillars feed selectively and adaptively. The focus here is plasticity in movement behavior. As a counterploy to induced plant defenses, caterpillars can avoid dynamic chemical resistance traits of plants(e.g., [26,27]), which tend to be heterogeneously distributed even when systemically induced (e.g., [28,29]). One of the functional hypotheses for induced chemical resistance in plants (moving target model, [30]) proposes that heterogeneity and unpredictability of induced defenses would be especially challenging for herbivores to overcome. However, a recent study demonstrates that caterpillars can move adaptively in response to cues of a plant's incipient increase in chemical resistance[31]. These researchers mapped in real time both induced changes in *Arabidopsis thaliana* resistance expression and preemptive avoidance behavior by polyphagous *Helicoverpa armigera* caterpillars. Interestingly, this study found no such avoidance response by *Plutella xylostella* caterpillars, which are dietary specialists adapted physiologically to mustard oil defenses of *A. thaliana* and related Brassicaceae[32].

By moving within host plants, between host plants, or off host plants altogether, caterpillars might avoid mortality or non-consumptive fitness costs from invertebrate carnivores that cue in to feeding damage, byproducts, or areas of induced plant response (e.g., [11,12,33]). Careful and extensive study of two polyphagous species of slug caterpillars (Limacodidae) revealed a general pattern of plastic movement patterns that depended on host-plant species, light environment, and predator density [23]. Interestingly, the slug caterpillars moved (and fed) more frequently in shady versus sunny microsites, the latter associated with increased attack risk from parasitoids [34]. Functional consequences of diverse caterpillar movement patterns are not well understood.

Other behaviors

Caterpillars employ a multitude of plastic behavioral defenses against their enemies [35]. Here I will illustrate this with an example that clearly qualifies as "host-plant use" while excluding others, such as facultative myrmecophily and plasticity in shelter-building (e.g., [36]), due to space limitations. Regurgitation is one of most widely observed behavioral responses by caterpillars and other insects to physical attack, such as prodding, grasping, or biting by a predator [35]. It has also been observed as a response to parasitoids, such as tachinid flies (e.g., [37]). The regurgitant is a combination of ingested plant material and caterpillar secretions. Because this behavioral response presumably uses plant material to provide defense against enemy attack at the expense of lost nutrients, water [37], and time

spent foraging, it putatively matches the predictions of adaptive plasticity theory. A more definitive test of this hypothesis awaits further study.

Consequences for communities and food webs

Each type of behavioral plasticity described above has the potential to influence the dynamics of plant-insect interactions and community structure. However, it is difficult to envision the aggregate effects of these cases within a single community. Therefore, we must turn to theory and data from experimentally tractable systems. In a tri-trophic system with herbivores at an intermediate trophic level, plasticity in behavioral traits can mediate the strength of indirect effects [38,39]. First, consider top-down effects of carnivores on caterpillars and plants. If anti-predator behavior typically reduces feeding rates of host-specialist caterpillars accompanied by delayed negative effects on herbivore growth and fitness (e.g., [9]), the resulting reductions in plant damage and herbivore population growth would benefit the herbivore's host plants over a longer time period. These dynamics are likely to exert weak, stabilizing effects on plant and insect populations and communities [8]. By contrast, if natural enemies trigger host-plant switching behavior, the result can be strong, variable effects of top-down cascades mediated by grazing herbivores, as seen in some terrestrial and many marine ecosystems [40-42]. Although elegantly demonstrated for grazing grasshoppers [38], such effects have not been studied in grazing caterpillars.

Because most caterpillar species are relatively host-specific [6], and thus not able to dynamically switch host plants, it is expected that adaptively plastic or fixed defensive behaviors of caterpillars would cause reduced feeding rates or lost feeding opportunities via the diverse behavioral mechanisms described (incompletely) in the previous section. Since these behaviors are expected to weaken plant-herbivore interactions as well as herbivore-carnivore interactions, promoting the stability of communities and food webs, it is perhaps most interesting to consider the possible destabilizing effects on plant-caterpillar interactions when the third trophic level is removed. This "experiment" has been run numerous times in intensively managed agricultural landscapes, with herbivore outbreaks more often attributed to fertilization of host plants [43] and lack of population control due to consumptive effects predicted by classic theory [44]. However, missing enemy cues to herbivores due to the loss of carnivore diversity (e.g., [45]) or recently juxtaposed carnivore-herbivore interactions could be a large source of destabilization. It is worth asking how much of the terrestrial world's "greenness" stems from herbivores sacrificing feeding voracity for risk aversion in the presence of carnivores [7, 41].

The bottom-up effects of plants on caterpillars and carnivores appear to be far more variable. If polyphagous caterpillars can move to avoid the expression of induced chemical resistance of plants [31], they might gain in food quality at the expense of increased risk of attack by visually oriented carnivores [46]. The concomitant induction of plant volatile emissions might bring the carnivores to the vicinity of the herbivore (e.g., [33, 47]), also subjecting relatively immobile herbivores (e.g., dietary specialists) to increased risk of attack. The resulting tri-

trophic interactions would be expected to suppress herbivore populations and limit or disperse damage to plants while benefiting carnivores. However, the evidence to date for these and other bottom-up trait-mediated indirect effects (e.g., slow-growth/high-mortality effects [48]) is decidedly mixed [49,50]. More work is needed in this area to detect patterns that could be related to herbivore feeding strategy or other factors.

Conclusion

The behavioral plasticity of host-plant use by caterpillars is a subject still rich with research opportunity and potential for linking biological processes that propagate across levels of organization in plant-insect interactions. Some fruitful areas of future research might address some of the following questions. What sensory/physiological cues do caterpillars use to detect dynamic enemies and changes in plant quality and how specific are they? Are sensory and behavioral tactics shared among species that are phylogenetically related, ecologically associated (e.g., sharing the same host plant), or functionally similar (e.g., shared diet breadth or other life history traits)? How do the combined dynamic effects of plant defenses and carnivores constrain herbivore behavior, fitness, and demography? While there is no doubt that the behavioral plasticity of caterpillars contributes to their active role in tri-trophic interactions, the diverse mechanisms and ecological consequences for communities and food webs are largely unknown yet potentially profound.

Acknowledgements

Thanks to Sergio Rasmann and Kailen Mooney for the invitation to contribute to this Ecology section, and to the anonymous reviewer whose comments helped improve the manuscript. I acknowledge support from Wesleyan University and the U.S.

National Science Foundation for original research related to this opinion piece: NSF IOS 0744676, NSF DEB1011503, NSF DEB 1404177, and NSF IOS 1501538.

References

- [1] Karban R: **The ecology and evolution of induced resistance against herbivores.***Functional Ecology* 2011, **25**:339-347.
- [2] Karban R, Baldwin IT: *Induced Responses to Herbivory*. University of Chicago Press; 1997.
- [3] Heil M: **Indirect defence via tritrophic interactions.***New Phytologist* 2008, **178**:41-61.
- [4] Poelman EH, van Loon JJA, Dicke M: **Consequences of variation in plant defense for biodiversity at higher trophic levels.***Trends Plant Sci* 2008, **13**:535-541.
- **[5] Sheriff MJ, Thaler JS: **Ecophysiological effects of predation risk; an integration across disciplines.***Oecologia* 2014, **176**:607-611. This special feature provides a timely overview of the sensory and physiological processes underlying non-consumptive effects of predators on prey. Each article places its physiological study in an ecological context, creating a useful complement to the behavioral perspective presented here.
- **[6] Forister ML, Novotny V, Panorska AK, Baje L, Basset Y, Butterill PT, Cizek L, Coley PD, Dem F, Diniz IR *et al.*: **The global distribution of diet breadth in insect herbivores.***Proc Natl Acad Sci USA* 2015, **112**:442-447. By compiling an astounding data set, this collaborative effort reveals the first general quantitative distribution of insect herbivore diet breadth, which serves as a foundation for new insight into plant-insect interactions. The distribution is highly skewed toward dietary

specialization, especially in the tropics, yet polyphagy persists in all ecological communities.

[7] Schmitz OJ: *Resolving Ecosystem Complexity*. Princeton University Press; 2010.

[8] Peacor SD, Cressler CE: **The implications of adaptive prey behaviour for ecological communities: a review of current theory**. In *Trait-mediated Indirect Interactions: Ecological and Evolutionary Perspectives*. Edited by Ohgushi T, Schmitz OJ, Holt RD. Cambridge University Press; 2012:131-160.

[9] Thaler JS, McArt SH, Kaplan I: **Compensatory mechanisms for ameliorating the fundamental trade-off between predator avoidance and foraging**. *Proc Natl Acad Sci* 2012, **109**:12075-12080.

*[10] Low PA, McArthur C, Hochuli DF: **Dealing with your past: experience of failed predation suppresses caterpillar feeding behaviour**. *Anim Behav* 2014, **90**:337-343. This article elegantly shows the behavioral legacy of predation encounters.

[11] Bernays EA: **Feeding by lepidopteran larvae is dangerous**. *Ecol Entomol* 1997, **22**:121-123.

[12] Weiss MR: **Defecation behavior and ecology of insects**. *Annu Rev Entomol* 2006, **51**:635-661.

*[13] Thaler JS, Contreras H, Davidowitz G: **Effects of predation risk and plant resistance on *Manduca sexta* feeding behaviour and physiology**. *Ecol Entomol* 2014, **39**:210-216. This study nicely shows the interactive effects of top-down and bottom-up ecological factors as well as the integrative behavioral and physiological responses of an herbivore as it transitions among phenotypic states.

****[14] Povey S, Cotter SC, Simpson SJ, Wilson K: Dynamics of macronutrient self-medication and illness-induced anorexia in virally infected insects.***J Anim Ecol* 2013, **83**:245-255. This study provides an extraordinarily integrative picture of the adaptive behavioral tactics employed by an insect herbivore to combat a viral pathogen. More than any other study, it records the temporal dynamics of diverse feeding tactics involved in herbivore resistance against parasites.

[15] Lee KP, Simpson SJ, Raubenheimer D: **A comparison of nutrient regulation between solitary and gregarious phases of the specialist caterpillar, *Spodoptera exempta* (Walker).***J Ins Phys* 2004, **50**:1171-1180.

[16] Bernays EA, Singer MS: **Taste alteration and endoparasites.***Nature* 2005, **436**:476.

[17] Singer MS, Mace KC, Bernays EA: **Self-medication as adaptive plasticity: Increased ingestion of plant toxins by parasitized caterpillars.***PLoS ONE* 2009, **4**:e4796.

[18] Smilanich AM, Mason PA, Sprung L, Chase TR, Singer MS: **Complex effects of parasitoids on pharmacophagy and diet choice of a polyphagous caterpillar.***Oecologia* 2011, **165**:995-1005.

[19] Singer MS, Carrière Y, Theuring C, Hartmann, T: **Disentangling food quality from resistance against parasitoids: diet choice by a generalist caterpillar.***Am Nat* 2004, **164**:423-429.

[20] de Roode JC, Lefevre T, Hunter MD: Self-medication in animals.Science* 2013, **340**:150-151. This brief article summarizes the state of the field of animal medication with several examples from insects and points the way forward.

- [21] Schultz JC: **Habitat selection and foraging tactics of caterpillars in heterogeneous trees.** In *Variable Plants and Herbivores in Natural and Managed Systems*. Edited by Denno RF, McClure MS. Academic Press; 1983:61-90.
- [22] Johns R, Quiring DT, Lapointe R, Lucarotti, CJ: **Foliage-age mixing within balsam fir increases the fitness of a generalist caterpillar.***EcolEntomol* 2009, **34**:624-631.
- *[23] Stoepler TM, Lill JT, Murphy SM: **Intraplant movement of generalist slug caterpillars (Limacodidae: Lepidoptera): effects of host plant and light environment.***Environ Ent* 2014, **43**:1561-1573. This study is notable for its careful documentation of subtle and informative movement patterns of caterpillars previously understood to be extremely sedentary.
- [24] Mason, PA, Bernardo MA, Singer MS: **A mixed diet of toxic plants enables increased feeding and anti-predator defense by an insect herbivore.***Oecologia* 2014, **176**:477-486.
- [25] Cunningham JP, Lange CL, Walter GH, Zalucki MP: **Host location behavior in the desert caterpillar, *Heliothispunctifera*.***EntomolExpAppl* 2011, **141**:1-7.
- [26] Rodriguez-Saona C, Thaler JS: **The jasmonate pathway alters herbivore feedingbehaviour: consequences for plant defences.***EntomolExpAppl* 2005, **115**:125-134.
- [27] Roslin T, Syrjala H, Roland J, Harrison PJ, Fownes S, Matter SF: **Caterpillars on the run—induced defences create spatial patterns in host plant damage.***Ecography* 2008, **31**:335-347.

[28] Orians C: **Herbivores, vascular pathways, and systemic induction: facts and artifacts.***J ChemEcol* 2005, **31**:2231-2242.

[29] Stork W, Diezel C, Halitschke R, Galis I, Baldwin IT: **An ecological analysis of the herbivory-elicited JA burst and its metabolism: plant memory processes and predictions of the moving target model.***PLoS ONE* 2009, **4**:e4697.

[30] Adler FR, Karban R: **Defended fortresses or moving targets? Another model of inducible defenses inspired by military metaphors.***Am Nat* 1994, **144**:813-832.

[31] Perkins LE, Cribb BW, Brewer PB, Hanan J, Grant M, de Torres M, Zalucki MP: **Generalist insects behave in a jasmonate-dependent manner on their host plants, leaving induced areas quickly and staying longer on distant parts.*Proc R Soc B* 2013, **280**:20122646. This remarkable study analyzes caterpillar movement in relation to the dynamics of induced plant resistance with unprecedented resolution. It sets a new standard for close observation of dynamic plant-insect interactions.

[32] Ratzka A, Vogel H, Kliebenstein DJ, Mitchell-Olds T, Kroymann J: **Disarming the mustard oil bomb.***Proc Natl Acad Sci USA* 2002, **99**:11223-11228.

[33] Thaler JS: **Jasmonate-inducible plant defences cause increased parasitism of herbivores.***Nature* 1999, **399**:686-688.

*[34] Stoepler TM, Lill JT: **Direct and indirect effects of light environment generate ecological trade-offs in herbivore performance and parasitism.***Ecology* 2013, **94**:2299-2310. This article elegantly shows the multi-

dimensionality of growth versus defense trade-offs faced by herbivores in their natural environment.

[35] Greeney HF, Dyer LA, Smilanich AM: **Feeding by lepidopteran larvae is dangerous: A review of caterpillars' chemical, physiological, morphological, and behavioral defenses against natural enemies.***Insect Survival Journal* 2012, **9**:7-34.

[36] Marquis, RJ, Lill JT: **Impact of plant architecture versus leaf quality on attack by leaf-tying caterpillars on five oak species.***Oecologia* 2010, **163**:203-213.

[37] Woods HA, Bernays EA: **Water homeostasis by wild larvae of *Manduca sexta*.***PhysiolEntomol* 2000, **25**:82-87.

[38] Beckerman AP, Uriarte M, Schmitz OJ: **Experimental evidence for a behavior-mediated trophic cascade in a terrestrial food chain.***ProcNatlAcadSci USA* 1997, **94**:10735-10738.

[39] Werner EE, Peacor SD: **A review of trait-mediated indirect interactions in ecological communities.***Ecology* 2003, **84**:1083-1100.

[40] Schmitz OJ, Ovadia O, Krivan V: **Trophic cascades: the primacy of trait-mediated indirect interactions.***EcolLett* 2004, **7**:153-163.

[41] Preisser EL, Bolnick DI, Benard ME: **Scared to death? The effects of intimidation and consumption in predator-prey interactions.***Ecology* 2005, **86**:501-509.

[42] Trussell GC, Schmitz OJ: **Species functional traits, trophic control and the ecosystem consequences of adaptive foraging in the middle of food chains.** In

Trait-mediated Indirect Interactions: Ecological and Evolutionary Perspectives. Edited by Ohgushi T, Schmitz OJ, Holt RD. Cambridge University Press; 2012:324-338.

[43] Rosenzweig ML: **Paradox of enrichment: destabilization of exploitation ecosystems in ecological time.***Science* 1971, **171**:385-387.

[44] Hairston NG, Smith FE, Slobodkin LB: **Community structure, population control and competition.***Am Nat* 1960, **94**:421-425.

[45] Steffan SA, Snyder WE: **Cascading diversity effects transmitted exclusively by behavioral interactions.***Ecology* 2010, **91**:2242-2252.

[46] Bergelson JM, Lawton JH: **Does foliage damage influence predation on the insect herbivores of birch?***Ecology* 1988, **69**:434-445.

[47] Kessler A, Baldwin IT: **Defensive function of herbivore-induced plant volatile emissions in nature.***Science* 2001, **291**:2141-2144.

[48] Uesugi A: **The slow-growth high-mortality hypothesis: direct experimental support in a leafmining fly.***EcolEntomol* 2015, **40**:221-228.

[49] Kaplan I, Thaler JS: **Plant resistance attenuates the consumptive and non-consumptive effects of predators on prey.** *Oikos* 2010, **119**:1105-1113.

[50] Mooney KA, Singer MS: **Plant effects on herbivore-enemy interactions in natural systems.** In *Trait-mediated Indirect Interactions: Ecological and Evolutionary Perspectives*. Edited by Ohgushi T, Schmitz OJ, Holt RD. Cambridge University Press;2012:107-130.

Figure legend

Tri-trophic network of plasticity, with circles representing adaptively plastic traits of two plant phenotypes or species (green, Px, Py), herbivores (black, H), and carnivores (red, C). Arrows represent possible interactions inducing or induced by trait plasticity. Behavioral plasticity of herbivores, the subject of this article, has received less attention than plasticity of plants and carnivores.

Figure