Available online at www.sciencedirect.com

ScienceDirect

Current Opinion in Insect Science

Ontogenetic strategies in insect herbivores and their impact on tri-trophic interactions

Karina Boege[1], Anurag A Agrawal[2,3] and Jennifer S Thaler[2,3]

Insect herbivores express tremendous ontogenetic variation in traits related to growth and maturation, but also as an evolutionary consequence of ecological interactions with plants and predators. These selective pressures can either reinforce or restrict expression of particular ontogenetic strategies, allowing herbivores to simultaneously cope with plant resistance and risk of predation through ontogenetic change. For example, whereas an increase in defense-sabotaging behavior, aposematism and sequestration along herbivore ontogeny seems to be reinforced by both bottom-up and top-down forces, some ontogenetic trends in anti-predator behavior can be limited by plant resistance. Communication among plants, herbivores and their natural enemies is also influenced by insect ontogenies. The study of ontogenetic strategies of herbivores requires the assessment of the genetic variation, heritability and adaptive value across herbivore development, considering the variation in plant quality and predation risk.

Addresses
[1] Instituto de Ecología, Universidad Nacional Autónoma de México, Ciudad Universitaria, Apartado Postal 70-275, Coyoacán, C.P. 04510, Ciudad de México, Mexico
[2] Department of Ecology & Evolutionary Biology, Cornell University, Ithaca, 14853, NY, USA
[3] Department of Entomology, Cornell University, Ithaca, 14853, NY, USA

Corresponding author: Boege, Karina (kboege@unam.mx)

Current Opinion in Insect Science 2019, **32**:61–67

This review comes from a themed issue on **Ecology**

Edited by **Michael Singer**, **Katerina Sam** and **Genoveva Rodríguez-Castañeda**

For a complete overview see the Issue and the Editorial

Available online 20th November 2018

https://doi.org/10.1016/j.cois.2018.11.004

Introduction

Insect herbivores undergo enormous changes in size and other traits as they develop. As a result, they face major challenges to survive, grow and reproduce. Hence, different traits are expressed as a function of the physiological priorities at each ontogenetic stage, allowing organisms to cope with their changing environments. Here we identify ontogenetic changes (hereafter ontogenetic strategies) in morphological, physiological and behavioral traits of herbivorous insects resulting from the interactions with their host plants and/or natural enemies (Table 1). We also describe how the ontogeny of insects can affect the communication and the outcome of tri-trophic interactions. Considering this, we propose several approaches to assess the evolution of ontogenetic strategies in herbivore traits.

One of the main challenges of immature herbivorous insects is maximizing their growth while minimizing the exposure to natural enemies [1]. Achieving this throughout development, as their size and nutritional needs change (for example from protein to lipid-based diets [2]), requires continuous adjustments in the expression of different traits to simultaneously cope with plant resistance and predation risk (Table 1, Figure 1) [3,4]. For some traits, both plant quality and predation risk should promote the same ontogenetic changes. In contrast, for other attributes these forces can actually represent opposing selection pressures. In this case, the most influencing selective agent should drive ontogenetic changes, or both forces can have non-additive effects.

Foraging, sabotage and shelter building behaviors

Bottom-up and top-down forces can reinforce the same ontogenetic strategies in feeding habits, sabotage strategies and shelter building behaviors. As herbivores develop, they acquire larger mandibles and are forced to take larger bites on leaf blades. As a consequence, they lose the ability to discriminate different leaf parts and may require to feed on lower quality, well-defended plant tissues (Table 1, [3,5,6]). Hence, there should be strong selection to increase mobility as they develop, to reach different tissues or plants. This must be particularly relevant in seasonal forests, in which the availability of fresh leaves decreases as the season progresses. Although larger mandibles allow larger and more mobile herbivores to feed on mature and tougher leaves, increasing sabotaging behaviors should be favored at these stages to reduce the exposure to toxic plant exudates (Table 1, [7,8]). An ontogenetic increase in sabotaging abilities can be reinforced by the third trophic level, if this behavior allows better handling of leaf blades to build more complex shelters to hide from predators [9]. Large herbivores, which are preferred by vertebrate predators [9], may build more complex leaf shelters when they are able to cut large veins and petioles (Table 1, [3,10,11]). Indeed, several studies show that the ability of sabotaging plant defenses

Table 1

Herbivore traits affecting plant herbivore interactions changing across ontogeny

Trait	Ontogenetic strategy	Mechanism/ driver	Ontogenetic Consequence	Ref.
Morphology traits				
Mandible shape	Toothed mandible edge change to smooth edge (Lepidoptera)	Plant defenses	Changes from skeletonization to cutting leaf blade feeding habits	[5]
Feeding behavior				
Host shifts	Increases	Plant induced defenses	Greater exposure to predators Adjustments for nutrient demands (growth versus storage)	[1,2,6]
Feeding habit	Switches from leaf mining to external feeders	Plant defenses and phenology	a) Young stages can have greater selectiveness to avoid poor quality (epidermis) or toxic (veins) food b) Young stages have greater parasitism risk being concealed in the leaf mines	[3,5,6]
Sabotage of plant defense (vein cutting)	Increases	Plant defenses Predation risk	Increased ability to feed on more plant tissues, better manipulation of leaf blades to build shelters	[3,7,8,10–12]
Detoxification	Increases	Plant defenses	Ability to feed on resistant plant	[19•,20]
Digestive efficiency	Decreases	Plant defenses	Need to consume more plant material	[19•]
Diet selectivity	Decreases	Plant defenses Risk of predation	Shifts from protein towards lipid biased diets	[2,3]
Anti-predator strategies				
Aposematism	Increases Decreases	Plant defenses Predation risk	Increase or reduction in conspicuousness, changes in the exposure to predators. Changes in anti-predator behavior and predator deterrence	[4,17,18,19•]
Defensive Regurgitation	Increases	Predation risk	Reduced predation risk at older stages	[18]
Release of plant VOC's	Decreases	Plant defenses	Reduced predation risk at older stages	[25,26]
Shelter building	Increase in complexity	Predation risk	Reduced predation risk at older stages	[10–12]
Starvation periods	Increases	Predation risk + plant defenses	Increased ability to respond to predators by resting and/or starving	[14]
Sequestration	Increases or decreases	Predation + plant defenses		[12,22••]

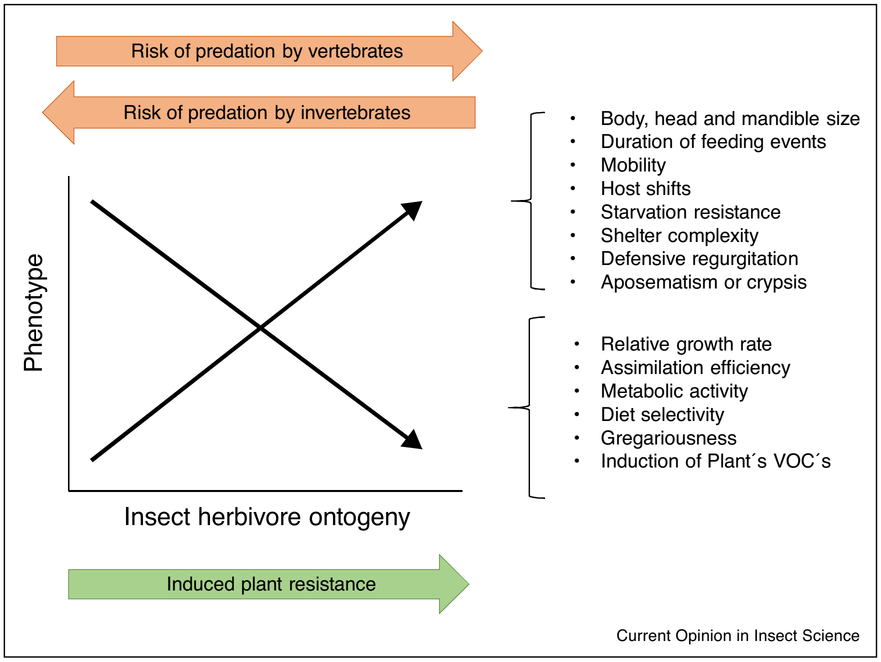
(e.g. trenching, vein-cutting) increases across larval development (Table 1, [11,12]).

Anti-predator behaviors

Plant resistance and predation may also impose conflicting section pressures on the expression of herbivore traits across development, due to trade-offs between acquiring food and avoiding predation. For example, a common mechanism for avoiding predation is reducing time spent feeding [13]. However, resting decreases food intake and can have high costs for herbivores in stages more susceptible to starvation. One model for studying these tritrophic interactions has been the predator *Podisus maculiventris* and its caterpillar and beetle prey, such as *Manduca sexta* and *Leptinotarsa decemlineata*. In the case of *M. sexta* feeding on *Solanum ptychanthum*, larvae show ontogenetic changes in anti-predator behavior. First and third instars reduce their time spent feeding in the presence of the predator [14], but no such behavior was observed in later instars.

However, this anti-predator behavior can be limited when herbivores feed on resistant plants [15•]. Thus, ontogenetic changes in herbivore likelihood of starving can be influenced by changes in their susceptibility to plant quality as they develop. Indeed, for *M. sexta*, it has been reported that reduced feeding on resistant plants is costly for individuals at the third instar, but not for younger or older stages [16]. In the case of the Colorado Potato Beetle (*Leptinotarsa decemlineata*), larvae can reduce their feeding as a response to the presence of *P. maculiventris* their whole life, but only when feeding on susceptible plants. In contrast, young instars are less likely to express this behavior on resistant plants (Thaler, unpublished). These examples highlight the importance of assessing the relative impacts of plant resistance and risk of predation to understand ontogenetic changes in feeding and anti-predator behaviors.

Figure 1



Ontogenetic patterns of traits and ecological interactions of insect herbivores, emphasizing how host plant quality and predation risk change across their development. Increasing and decreasing phenotypic traits are specified to the right of the graph, while patterns in ecological interactions are shown above and below the graph in colored arrows.

Ontogenetic changes in color

Ontogenetic changes in coloration and patterning are common in insect herbivores, and often involve a shift from crypsis to aposematism (Figure 2) [4,17,18]. This ontogenetic change can be particularly relevant to avoid risk of predation by vertebrates [9]. Because of cognitive mechanisms, birds are particularly sensitive to color and its association with prey toxicity. One adaptive hypothesis for an ontogenetic change from crypsis to aposematic colors is that the former is favored until opportunity costs are too high (due to limited foraging on restricted plant parts), at which point organisms switch to more conspicuous behavior (e.g. extensive feeding). Increased mobility and foraging on contrasting backgrounds and/or on more diverse diets should promote changes in coloration [13]. This change in appearance should occur when herbivores have accumulated enough toxic compounds from plants, which can be used against their predators (Figure 2) [4,18,19•]. Grant [18] presented an excellent test of this hypothesis with *Saucrobotys futilalis* (Crambidae), where early instars feed in silken nests and are cryptically green, whereas more mobile later instar are free-roaming on the same host plant, but exhibit highly contrasting orange and black coloration, with later instars also being the most behaviorally defended. Hence, understanding the adaptive value of ontogenetic changes in warning colors may require the simultaneous analysis of ontogenetic changes in feeding and defensive behaviors, but this awaits further investigation.

There is remarkably little data in the literature about the potential for host plant effects on ontogenetic changes in insect coloration or defense. Changes in diet across herbivore ontogeny could have direct impacts in their opportunity to sequester toxic compounds of their host plants (as discussed in the next section). In particular, aposematism should be favored in stages specialized in toxic plants [19•]. In a study of *Eumorpha fasciata*, Fink [17] showed that the larval ontogenetic color changes in this species were somewhat dependent on the host plant species it was feeding on. Nonetheless, the ecological consequences and constraints on the alternate color morphs in this species are unknown. In swallowtail butterflies, larval ontogenetic color change is frequent, but so too are changes in the volatile chemistry of defensive secretions from eversible osmeteria [20,21], and the adaptive value and dependence on plant quality await further study.

Sequestration of secondary metabolites

Caterpillars of the monarch butterfly *Danaus plexippus* do not change in color but show pronounced shifts in the sequestration of cardenolides from their milkweed host plants. Although early instars have a higher concentration (per gram dry mass) of cardenolides, they have lower

Figure 2

Ontogenetic shifts in two lepidopteran herbivores of milkweed (*Asclepias syriaca*). **(a)** and **(b)**, *Danaus plexippus* (Nymphalidae), which has consistently aposematic coloration throughout its larval development, but which uses distinct tactics for offense (deactivating latex). First instar caterpillars use a 'circle trench' to deactivate latex and eat the island of latex-free issue within. Later instars notch midribs or petioles to deactivate latex and consume the distal tissue which is free of pressurized latex [48]. **(c)** and **(d)**, *Euchaetes egle* (Arctiidiae), which is gregarious and potentially cryptic as early instars (egg clutches of several hundred), while solitary and aposematic as later instars. Although later instars of *E. egle* deactivate latex similar to later stage monarchs, the gregarious early instars of *E. egle* do not possess an obvious latex-deactivation behavior; rather, their gregarious feeding may simply overwhelm any latex response.

ability to resist the negative effects of these toxins compared to later instars. In addition, the later and larger instars end up accumulating greater total amounts of these toxins (Jones *et al*., in revision), hence they can result in more toxic prey for vertebrate predators than earlier instars (Figure 2). In the buckeye butterfly, *Junonia coenia*, the ability to sequester iridoid glycosides from their host plants also increases with larval stage [22••]. In both cases, reinforcing selection is likely to promote increased sequestration of their host plant defenses over larval development, to cope with increased plant toxicity and risk of predation by vertebrates.

Communication between plants, herbivores and their natural enemies

Volatile organic compounds are essential mediators of communication among plants, herbivores and their natural enemies [23•,24]. Interestingly, herbivore ontogeny can influence communication between plants and the third trophic level as young herbivore stages can induce more and different plant volatiles (HIPV) than older instars or adult individuals [25], perhaps increasing their likelihood of being found by their natural enemies. For example, the release of leaf volatile compounds has been reported to be greater when willow plants are eaten by larvae than when eaten by adult beetles [26], and when corn plants are eaten by young compared to older instars of *Pseudoletia separate* [25]. In both cases, volatile emission was related to the preference of natural enemies for plants infested by earlier stages of herbivores. Hence, both bottom-up (HIPV) and top-down (parasitoid preferences) forces are in synchrony to promote greater parasitism rates at younger herbivore developmental stages. This has been reported for herbivores with leaf mining feeding habits at young stages, which experience greater risk of parasitism than older, free feeding stages [3]. Consequently, the expression of insect attributes or behaviors to reduce parasitism, such as salivary traits that suppress plant induced defenses [23•,27,28] and immunity responses to parasitism (e.g. encapsulation; [29]) should be particularly important for young herbivores. For example, a negative relationship between encapsulation rate and body size has been reported for the Mediterranean Field Cricket, *Gryllus bimaculatus* [30]. However, more evidence is needed to document such developmental effects, and disentangle the role of herbivore size on such changes. Future studies should examine the relationship between insect developmental stage, size, offensive abilities, and susceptibility to plant defenses and predation.

Herbivore responses to predation risk can be also altered by factors such as the information that prey have about the presence of predators. For example, larval and adult predators produce different chemical cues, sometimes associated with aggregation pheromones in the juvenile stages [31,32] or mating pheromones as adults [33,34]. Herbivorous prey likely use these cues to respond to predators. First instar larvae of *L. decemlineata* for instance, respond more strongly to the presence of male than female individuals of its predator, the soldier bug *P. maculiventris* [34], because only the males release sex pheromones. Hence, herbivores seem to be able to adjust their behavior across their development as a function of the life stage and/or sex of predators. In this context, the impact and particular outcomes of tri-trophic systems are likely to be strongly dependent on the specific herbivore and predator interacting stages.

Approaches to investigate the evolution of ontogenetic strategies of herbivores

Despite the immense potential for herbivore and plant traits to impact offense-defense interactions, we are far from understanding the evolutionary dynamics of ontogenetic strategies and still have many unanswered questions. Does the adaptive value of herbivore traits change across their ontogeny? Are such ontogenetic changes themselves adaptive? Under which circumstances can the ontogenies/phenologies of interacting species coevolve? Below we outline some approaches for considering ontogenetic adaptations in evolution of herbivore ontogenetic trajectories to answer some of these questions.

Matching of phenologies and ontogenies

Offense-defense coevolutionary dynamics are likely to be restricted to particular ontogenetic stages of interacting species. For example, Quintero and Bowers [22••] recently have shown that later instars of *J. coenia* sequester more iridoid glycosides than young instars, but only when feeding on older stages of *P. lanceolata* [22••]. In addition, young instars have been found to be more sensitive to ontogenetic changes in leaf toughness, iridoid glycosides and nitrogen contents than late instars [35]. This constitutes a great first example of how the ecological and evolutionary outcomes of interacting species depend on the matching of phenologies and/or life spans of both plants and their herbivores. Direct manipulation of the timing of the interaction, or assessments of current phenological mismatches due to climate change [36] can provide useful information of when particular ontogenetic strategies are likely to evolve. In this context, phenology-ontogeny landscapes proposed by Yang and Rudolph [37] can be a valuable tool to visualize changes in the strength and type of species interactions and their fitness impacts.

Genetic variation in ontogenies

Describing the genetic variation and heritability of ontogenies can also provide a useful approach to assess their potential for evolutionary responses to species interactions. This requires the production of genetic families of plants, herbivores and/or natural enemies and the assessment of the variance components in the traits of interests at different ontogenetic stages. Significant family × ontogeny interactions in mixed models would suggest heritable variation for particular ontogenetic strategies, as has been reported for different defensive traits in plants [38–41,42••]. On the side of herbivores, however, there is no available information on the genetic variation of sabotaging strategies, aposematism and anti-predator behaviors across herbivore ontogeny and this warrants further investigation.

Measures of natural selection across ontogenies

Understanding the selective forces behind ontogenetic strategies requires the assessment of the adaptive value of traits at different ontogenetic stages of plants, herbivores and their natural enemies. This approach should be particularly helpful to determine when evolution in species at these trophic levels is likely to occur. Experiments where genotypes with different ontogenetic strategies are exposed to natural conditions will be most useful. Selection gradients on particular traits can then be assessed at each ontogenetic stage. This, in turn, would allow estimating both the adaptive value of traits at particular stages and of their ontogenetic changes. Although a tremendous amount of empirical evidence has demonstrated the adaptive value of plant defense traits [43–45] and herbivore counter offence strategies [46], there is currently scarce information on how the strength of natural selection changes across the development of plants and herbivores. We are aware of only one study reporting that the targets of selection on plant defensive strategies changes across ontogeny from chemical defense in seedlings, to physical defense in juvenile plants, to biotic defense in reproductive plants (Ochoa-López *et al.* unpublished manuscript).

Using comparative biology to understand adaptive nature of ontogenetic changes

Because species may be highly divergent in ontogenetic traits, examining the match between species traits and their interactions can be a powerful way to study ontogenetic adaptations. For example, larval stages in some swallowtail species are well known to exhibit ontogenetic changes in coloration (discussed above), while other related species do not show such changes. A research program examining the phylogenetic position, ontogenetic strategies, and natural biotic and abiotic interactions of multiple species would be profitable. In such comparative analyses, including multiple species with independent origins of the traits of interest is critical. On the plant side, a recent study of 12 species of *Datura* reported that alkaloids consistently increase during plant development in all species, but trichome density shows more variable ontogenetic strategies [47]. This represents an ideal system to assess biotic and abiotic correlates of the evolution of ontogenetic changes in the expression of trichomes.

Concluding remarks

Incorporating the study of ontogeny of plants, herbivores and their natural enemies into the study of evolutionary ecology can be logistically challenging, but adds a potentially predictive axis to the outcome of species interactions. Here we advocate a focus on the understudied ontogenetic strategies of herbivorous insects that are subject to selection by plants and enemies, which may be reinforcing or conflicting. Ample evidence suggests that ontogenetic strategies of herbivores may hold the answers to some unsolved mysteries of tri-trophic interactions.

Conflict of interest statement

Nothing declared.

Acknowledgements

KB research stage while writing the manuscript at Cornell University was supported by the Dirección General de Asuntos del Personal Académico (DGAPA-UNAM, Mexico) through its program 'Programa de Apoyos para la Superación del Personal Académico' (PASPA). AAA was supported by the U.S. NSF (IOS EDGE Grant 1645256). JST was supported by Agriculture and Food Research Initiative competitive award no. 2018-67013-28068 from the USDA National Institute of Food and Agriculture.

References and recommended reading

Papers of particular interest, published within the period of review, have been highlighted as:

- • of special interest
- •• of outstanding interest

1. Santana AFK, Zucoloto F: **Infuence of previous experience on the preference, food utilization and preformance of *Ascia monuste orseis* wild larvae (Godart) (Lepidoptera: Pieridae) for three different hosts**. *Neotrop Entomol* 2011, **40**:631-638.
2. Stockhoff BA: **Ontogenic change in diet selection for protein and lipid by gypsy moth larvae**. *J Insect Physiol* 1993, **39**: 677-686.
3. Gaston KJ, Reavey D, Valladares G: **Changes in feeding habit as caterpillars grow**. *Ecol Entomol* 1991, **16**:339-344.
4. Higginson AD, Speed MP, Ruxton GD: **Florivory as an opportunity benefit of a aposematism**. *Am Nat* 2015, **186**: 728-741.
5. Hochuli DF: **Insect herbivory and ontogeny: how do growth and development influence feeding behaviour, morphology and host use?** *Austral Ecol* 2001, **26**:563-570.
6. Johnson ML, Zalucki MP: **Feeding and foraging behaviour of a generalist caterpillar: are third instars just bigger versions of firsts?** *Bull Entomol Res* 2007, **97**:81-88.
7. Green ES, Zangerl AR, Berenbaum MR: **Effects of phytic acid and xanthotoxin on growth and detoxification in caterpillars**. *J Chem Ecol* 2001, **27**:1763-1773.
8. Zeng R, Sen, Wen Z, Niu G, Berenbaum MR: **Aflatoxin B1: toxicity, bioactivation and detoxification in the polyphagous caterpillar *Trichoplusia ni***. *Insect Sci* 2013, **20**:318-328.
9. Remmel T, Davison J, Tammaru T: **Quantifying predation on folivorous insect larvae: the perspective of life-history evolution**. *Biol J Linn Soc* 2011, **104**:1-18.
10. Abarca M, Boege K, Zaldivar-Riverón A: **Shelter- building behaviour of a tropical Pyralid moth (*Lepidomys* sp. near proclea Druce; Chrysauginae)**. *J Insect Sci* 2014, **14**:39.
11. Dussourd DE: **Behavioral sabotage of plant defenses by insect folivores**. *Annu Rev Entomol* 2017, **62**:15-34.
12. Clarke AR, Zalucki MP: **Foraging and vein-cutting behaviour of *Euploea core corinna* (W. S. Macleay) (Lepidoptera: Nymphalidae) caterpillars feeding on latex-bearing leaves**. *Aust J Entomol* 2000, **39**:283-290.
13. Singer MS, Lichter-Marck IH, Farkas TE, Aaron E, Whitney KD, Mooney KA: **Herbivore diet breadth mediates the cascading effects of carnivores in food webs**. *Proc Natl Acad Sci* 2014, **111**:9521-9526.
14. Thaler JS, Griffin CAM: **Relative importance of consumptive and non-consumptive effects of predators on prey and plant damage: the influence of herbivore ontogeny**. *Entomol Exp Appl* 2008, **128**:34-40.
15. • Wetzel WC, Thaler JS: **Does plant trait diversity reduce the ability of herbivores to defend against predators? The plant variability-gut acclimation hypothesis**. *Curr Opin Insect Sci* 2016, **14**:25-31.
Presents the plant variability-gut acclimation hypothesis to explain how chemical variablity can constraint anti-predator behavior in insect herbivores.
16. van Dam NM, Hermenau U, Baldwin IT: **Instar-specific sensitivity of specialist *Manduca sexta* larvae to induced defences in their host plant *Nicotiana attenuata***. *Ecol Entomol* 2001, **26**:578-586.
17. Fink LS: **Foodplant effects on colour morphs of *Eumorpha fasciata* caterpilars (Lepidoptera: Sphingidae)**. *Biol J Linn Soc* 1995:423-437.
18. Grant JB: **Ontogenetic colour change and the evolution of aposematism: a case study in panic moth caterpillars**. *J Anim Ecol* 2007, **76**:439-447.
19. • Caro T, Sherratt TN, Stevens M: **The ecology of multiple colour defences**. *Evol Ecol* 2016, **30**:797-809.
An excellent review on the ecological framework explaining color changes in several organisms, associated with different environments and microhabitats and age-related challenges.
20. Ômura H, Honda K, Feeny P: **From terpenoids to aliphatic acids: further evidence for late-instar switch in osmeterial defense as a characteristic trait of swallowtail butterflies in the tribe Papilionini**. *J Chem Ecol* 2006, **32**:1999-2012.
21. Frankfater C, Tellez MR, Slattery M: **The scent of alarm: ontogenetic and genetic variation in the osmeterial gland chemistry of *Papilio glaucus* (Papilionidae) caterpillars**. *Chemoecology* 2009, **19**:81-96.
22. •• Quintero C, Bowers MD: **Plant and herbivore ontogeny interact to shape the preference, performance and chemical defense of a specialist herbivore**. *Oecologia* 2018, **187**:401-412.

Reveals how the ontogenies of both plants and herbivores can change the outcomes of the interaction, as ontogenetic trajectories altered the behavior and physiology of its specialist herbivore, but only at particular larval stages.

23. • Blande JD: **Plant communication with herbivores**. In *Advances in Botanical Research.* Edited by Becard GBT-A in BR. Academic Press; 2017:281-304.

A recent review on the role of organic volatile compounds on tritrophic interactions and communication between plants and herbivores.

24. Magalhães DM, Borges M, Laumann RA, Woodcock CM, Pickett JA, Birkett MA, Blassioli-Moraes MC: **Influence of two acyclic homoterpenes (tetranorterpenes) on the foraging behavior of Anthonomus grandis Boh**. *J Chem Ecol* 2016, **42**:305-313.

25. Takabayashi J, Takahashi S, Dicke M, Posthumus MA: **Developmental stage of herbivore *Pseudaletia separata* affects production of herbivore-induced synomone by corn plants**. *J Chem Ecol* 1995, **21**:273-287.

26. Yoneya K, Kugimiya S, Takabayashi J: **Can herbivore-induced plant volatiles inform predatory insect about the most suitable stage of its prey?** *Physiol Entomol* 2009, **34**:379-386.

27. Musser RO, Cipollini DF, Hum-Musser SM, Williams SA, Brown JK, Felton GW: **Evidence that the caterpillar salivary enzyme glucose oxidase provides herbivore offense in solanaceous plants**. *Arch Insect Biochem Physiol* 2005, **58**:128-137.

28. Hu YH, Leung DM, Kang L, Wang C: **Diet factors responsible for the change of the glucose oxidase activity in labial salivary glands of *Helicoverpa armigera***. *Arch Insect Biochem Physiol* 2008, **68**:113-121.

29. Krzemien J, Crozatier M, Vincent A: **Ontogeny of the *Drosophila* larval hematopoietic organ, hemocyte homeostasis and the dedicated cellular immune response to parasitism**. *Int J Dev Biol* 2010, **54**:1117-1125.

30. Rantala MJ, Roff DA: **An analysis of trade-offs in immune function, body size and development time in the mediterranean field cricket, *Gryllus bimaculatus***. *Funct Ecol* 2005, **19**:323-330.

31. Hoy MA, Smilanick JM: **A sex pheromone produced by immature and adult females of the predatory mite, *Metaseiulus occidentalis*, Acarina: Phytoseiidae**. *Entomol Exp Appl* 1979, **26**:291-300.

32. Sant'Ana J, Da Silva RFP, Dickens JC: **Olfactory reception of conspecific aggregation pheromone and plant odors by nymphs of the predator, *Podisus maculiventris***. *J Chem Ecol* 1999, **25**:1813-1826.

33. Sant'Ana J, Bruni R, Abdul-Baki AA, Aldrich J: **Pheromone-induced movement of nymphs of the predator *Podisus maculivetris* (Heteroptera: Pentatomidae)**. *Biol Control* 1997, **10**:123-128.

34. Hermann SL, Thaler JS: **Prey perception of predation risk: volatile chemical cues mediate non-consumptive effects of a predator on a herbivorous insect**. *Oecologia* 2014, **176**:669-676.

35. Quintero C, Lampert EC, Bowers MD: **Time is of the essence: direct and indirect effects of plant ontogenetic trajectories on higher trophic levels**. *Ecology* 2014, **95**:2589-2602.

36. Renner SS, Zohner CM: **Climate change and phenological mismatch in trophic interactions among plants, insects, and vertebrates**. *Annu Rev Ecol Evol Syst* 2018, **49**:165-182.

37. Yang LH, Rudolf VHW: **Phenology, ontogeny and the effects of climate change on the timing of species interactions**. *Ecol Lett* 2010, **13**:1-10.

38. Bowers M, Stamp N: **Effects of plant age, genotype, and herbivory on *Plantago* performance and chemistry**. *Ecology* 1993, **74**:1778-1791.

39. Schappert P, Shore J: **Cyanogenesis in *Turnera ulmifolia* L. (Turneraceae): II. Developmental expression, heritability and cost of cyanogenesis**. *Evol Ecol Res* 2000, **2**:337-352.

40. Goodger JQD, Ades PWI: **Cyanogenesis in *Eucalyptus polyanthemos* seedlings: heritability, ontogeny and effect of soil nitrogen**. *Tree Physiol* 2004, **24**:681-688.

41. Barton KE: **Early ontogenetic patterns in chemical defense in *Plantago* (Plantaginaceae): genetic variation and trade-offs**. *Am J Bot* 2007, **94**:56-66.

42. •• Ochoa-López S, Rebollo R, Barton KE, Fornoni J, Boege K: **Risk of herbivore attack and heritability of ontogenetic trajectories in plant defense**. *Oecologia* 2018, **187**:413-426.

Presents a first report on the genetic variation and heritabilities of ontogenetic trajectories in plant defense.

43. Mauricio R, Rausher MD: **Experimental manipulation of putative selective agents provides evidence for the role of natural enemies in the evolution of plant defense**. *Evolution (NY)* 1997, **51**:1435-1444.

44. Valverde PL, Fornoni J, Núñez-Farfán J: **Defensive role of leaf trichomes in resistance to herbivorous insects in *Datura stramonium***. *J Evol Biol* 2001, **14**:424-432.

45. Agrawal AA: **Current trends in the evolutionary ecology of plant defence**. *Funct Ecol* 2011, **25**:420-432.

46. Karban R, Agrawal AA: **Herbivore offense**. *Annu Rev Ecol Syst* 2002, **33**:641-664.

47. Kariñho-Betancourt E, Agrawal AA, Halitschke R, Núñez-Farfán J: **Phylogenetic correlations among chemical and physical plant defenses change with ontogeny**. *New Phytol* 2015, **206**:796-806.

48. Agrawal AA: *Monarchs and Milkweed: A Migrating Butterfly, a Poisonous Plant, and their Remarkable Story of Coevolution*. Princeton Univ Press; 2017.