Available online at www.sciencedirect.com
ScienceDirect
Current Opinion in Insect Science

Adaptive learning in non-social insects: from theory to field work, and back

Caroline M Nieberding[1], Hans Van Dyck[1] and Lars Chittka[2,3]

We review the evidence that learning affects fitness in non-social insects. Early accounts date back from the 1970s and were based on field-based observational and experimental work, yet exploration of the ways in which various forms of learning increase fitness remains limited in non-social insects. We highlight the concerns that arise when artificial laboratory settings, which do not take the ecology of the species into account, are used to estimate fitness benefits of learning. We argue that ecologically-relevant experimental designs are most useful to provide fitness estimates of learning, that is, designs that include: firstly, offspring of wild-caught animals producing newly established stocks under relevant breeding conditions, combined with common-garden and reciprocal transplant experiments; secondly, the spatio-temporal dynamics of key ecological resources; and thirdly, the natural behaviours of the animals while searching for, and probing, resources. Finally, we provide guidelines for the study of fitness-learning relationships in an eco-evolutionary framework.

Addresses
[1] Biodiversity Research Centre, Earth and Life Institute, Université catholique de Louvain, Belgium
[2] School of Biological and Chemical Sciences, Queen Mary University of London, UK
[3] Wissenschaftskolleg/Institute for Advanced Study, Wallotstr. 19, 14193 Berlin, Germany

Corresponding author: Nieberding, Caroline M (caroline.nieberding@uclouvain.be)

Current Opinion in Insect Science 2018, **27**:75–81

This review comes from a themed issue on **Behavioural ecology**

Edited by **Eric Wajnberg** and **Emmanuel Desouhant**

https://doi.org/10.1016/j.cois.2018.03.008

2214-5745/

Adaptive value of learning in non-social insects

While multiple definitions of learning have been proposed [1] (reviewed in [2]) we take the definition by Thorpe who defined learning as an 'adaptive change in individual behaviour as the result of experience' [3]. Learning comprises various capacities from simple non-associate processes (habituation, sensitization), to associative learning (classical or operant conditioning), to cognitive phenomena that integrate multiple memories, such as rule learning and categorization [4,5]. All these phenomena can have different temporal dynamics in different species and individuals (number of trials required to learn to saturation, times over which memories fade) and be linked to different memory capacities (e.g. more information can typically be stored in long term memory, than in short term or working memory) [6]. Most scientists assume that these processes have evolved under selection [1]. Yet, relatively few studies directly show how the learning abilities of different animals affect fitness in the wild ([7,8••,9••] and refs therein). To quantify the adaptive value, one needs to provide evidence for: firstly, variability of the ability to learn, their memory capacity and durability, or their memory dynamics among individuals within populations, as it is the raw material for selection; secondly, heritability for the trait; and thirdly, selection on a non-random part of the trait distribution in the population as a result of fitness gain for some of the individuals having specific trait values. In insects, the exploration of intraspecific variation in learning ability has a long history [10,11]. Heritability for learning was demonstrated with experimental evolution experiments selecting for associative learning [12], for example, between a medium infused with two types of fruit juice and quinine, an alkaloïd produced by plants to deter insects, which increases learning rate and speed for oviposition, and decreases the decay of the memory in the fly *Drosophila melanogaster* [13]. Here, we review the evidence that learning affects fitness of insects and we focus on non-social insects because most insects are solitary and no review has targeted them specifically, as opposed to reviews on social insects including several bees, wasps and ants. Some comparisons between social insects and solitary insects have reported inferior cognitive abilities in solitary compared to social species, for example in counting abilities [14], or learning rates in a colour associative learning task [15]. In other behavioural contexts, no such differences were found. For example, colour discrimination abilities do not appear to differ between several species of solitary bees and wasps [16]. In risk-sensitive foraging, no substantial difference was found between a carpenter bee and some social bees [17]. The principle learning centres of the insect brain, the mushroom bodies, do not differ in gross neuroanatomy between the brains of social and solitary Hymenoptera, though very clear differences occur in line with foraging lifestyle [18].

Here, we first summarize the theoretical conditions under which learning is expected to evolve under selection;

second, we highlight the concerns when artificial laboratory settings are exclusively used to estimate fitness of learning. Next, we summarize the existing experimental evidence that learning affects fitness in either natural environments or in ecologically relevant laboratory settings. Finally, we provide practical guidelines for the study of fitness-learning relationships in an eco-evolutionary experimental framework.

Theoretical predictions of learning evolution in the wild

Existing theoretical models focus largely on the explorations of the conditions under which innate preferences versus associative learning guide animals most efficiently to suitable food sources. Those models suggest that the adaptive value of learning depends on how the distribution of the resources of interest in the environment varies relative to the lifetime of the organism [19–21]. Two aspects of environmental resource heterogeneity appear to matter: *certainty* refers to the fitness estimate of producing an innate behavioural response, such that high uncertainty favours learning. *Reliability* refers to the fitness associated to changing the behavioural response after experience about the focal resource. High reliability means that there is a strong correlation between specific environmental cues that may be picked up by the organism to predict the distribution of a particular resource, and it will favour learning. If certainty is high, reliability must be very high for learning to evolve adaptively (Figure 1 in [21]). Most models also suggest that reliability should be high within the lifetime of an organism, but should be low across successive generations of individuals to select for learning [19–21]. If spatial or temporal environmental changes in the distribution of the ecological resources are completely predictable, then innate behavioural responses are selected for; in case of unpredictable conditions, bet hedging strategies are the predicted outcome [22]. It would be useful to develop further models that incorporate the diversity and dynamics of learning phenomena within and across species, and link them to environmental conditions to make (and ultimately test) predictions about which forms of learning are adaptive and when [4].

Case for studying adaptive learning in the wild

We argue that field-based data or ecologically-relevant experimental designs are most useful to provide fitness estimates of learning, by which we mean that: firstly, the organisms are observed in the wild or derived from field-caught samples; secondly, the key ecological resources, and their spatio-temporal dynamics, of the studied population(s) are taken into account; and thirdly, the natural behaviours of the animals while searching for, and probing, resources are allowed to be fully expressed.

Fitness estimates based on standardized laboratory work may be attractive [23], but also problematic for several reasons. First, most studies on learning have used laboratory strains of unknown or ancient field origin, or populations provided by commercial breeders whose genetic diversity is usually unknown. This is problematic because: firstly, genetic variability for learning related genes, such as the '*for*' ('*foraging*') gene [11], may be reduced or absent in laboratory stocks and secondly, there are inter-strain or inter-population differences in learning [24•,25•]. Laboratory strains can become inbred and show reduced learning ability compared to genetically diverse natural populations [26–29]. In addition, learning ability can be costly [30,31] and may be susceptible to rapid trait loss if organisms are maintained for multiple generations under laboratory conditions under poor food quality [32–34] or limited food quantity [35]. Finally, the perception of the cues used for learning can be affected by captivity (e.g. vision [36]). These laboratory effects on learning ability can be either the result of genetic evolution [34] or of an immediate response to the environment by developmental phenotypic plasticity [33].

Second, theoretical models as explained above suggest that the adaptive value of learning depends on how the distribution of the resources of interest in the environment varies relative to the life span of the animal (e.g. [21]). Hence, the rate of environmental change relative to the life span of the animal is key to quantifying the adaptive value of the various forms of learning, yet this has been rarely tested in nature (but see [37]). It is also important to consider the natural cues that allow insects to learn about resources: for example, chemical cues are central for learning about host plant and animal prey foraging, egg-laying and mating in phytophagous and polyphagous insects and can involve larval induction, habituation, sensitization and associative learning that usually increase, often permanently, the selectivity of the experienced organisms towards (learnt preference) or against (learnt deterrence) the resource (e.g. [38]). Visual cues are also used for foraging and oviposition: solitary wasps associatively learn colour, shape, and to a certain extent brightness for foraging as shown by an increased rate of landing on the conditioned resource type [39–41]. Butterflies forage based on associative learning of flower colour (e.g. [42]), yet leaf shape or bud size also matter and differences in oviposition preference were when full plants versus cuttings were compared (see examples in Suppl. Online Table 1). However, the underlying type of learning mechanism is not always unequivocally shown. In addition, whether having a fixed resting location (nest, hive) or not, solitary insects have to navigate to find temporal and spatial heterogeneous resources, and some solitary wasps use spatial landmarks to locate their resources up to weeks in advance, like social insects [43,44]. Resources can be distantly located from the resting place of the organism, and be cryptic targets under the natural complexity of vegetation structures [45–47]. Hence, experiments should allow the natural expression of movements towards naturally distributed resources to quantify the actual costs of learning [30,31], which are likely underestimated when simplistic lab-based experimental setups are used for obvious logistic reasons.

Adaptive learning of non-social insects in the field and in ecologically-relevant setups

We focus on learning experiments that took the ecology of the species into account, but most of which did not assess fitness. Learning, at least in some form is present in virtually all animals, and is therefore found to be the rule rather than the exception (but see [48–50]). Many of these studies focused on adult foraging (e.g. flower visitation [51•]). Other behaviours include larval foraging, oviposition on hosts (e.g. butterflies or wasps), predator avoidance, mate choice, species recognition and mate attraction. Most studies focused on non-social learning, yet social learning (i.e. learning from other individuals by e.g. imitation) has also been documented in crickets, flies, butterflies, damselflies (e.g. for mate choice and predator avoidance; Box 1 in [52]; [24•,53]) and social information was shown to spread among groups of individuals [54]. Associative mechanisms are known to underlie learning in the context of oviposition as well as pollination [51•,55] and long term memory formation based on protein synthesis is recurrent (e.g. [30,56,57]). Memory formation depends on the number and type of conditioning trials, intervals between trials and on the reward value associated to the behaviour [58]. Learning ability differs between closely related species and sexes (e.g. [42]). The extent of learning differs across behaviours within a species; for example, *Euphydryas editha* butterflies can learn various characteristics of host plants for foraging but not for oviposition [59]. Learning can also affect different behaviours associated to the same resource and have effects across successive life stages if using the resource, for example when larval development on a host plant affects mating preference of adults [60•]. This may matter in, for example, many Lepidoptera where larvae usually feed on a subset of the host plant species that adults use for foraging and mating [61].

First fitness estimates of learning in insects date back from the 1970s and were based on observational field work (Suppl. Online Table 1; [23,37,42,62–74,75•,76•,77,78••,79••,80••,81–86]). These studies suggest that learning can be advantageous through improved recognition, accuracy or selectivity of feeding resources that are available at higher abundance in the environment, a strategy that maximizes energy intake. Learning chemical cues as predictors of food quality at the larval stage can improve larval growth [23,74]. Female fitness is also improved by learnt preference to plants of better quality [66,71], as larger-sized offspring that have better survival are produced. For example, females of the butterfly *Battus philenor* increased fitness by learning to avoid laying eggs on already used host plants [64]. Other case studies include evidence that avoiding sexually deceptive orchids by a wasp is associated to fitness gains [87]. Learning can occur among heterospecifics and affect fitness through tri-trophic interactions [78••].

Assessing the adaptive value of learning in the wild, in practice

How can we develop ecologically relevant setups that take the ecology of the species into account, particularly for non-social insect species?

Reliable data on the distribution of key resources over evolutionarily relevant time periods are pivotal [45]. First, a sound understanding of the ecology of the species will allow identifying the relevant life stages (larval, adult) and behaviours (foraging, mating oviposition, prey avoidance, shelter) under selection for learning relative to resource acquisition. Finding shelters to rest (roost) and overwinter remains understudied, despite the fact that insects spend significant time budgets under harsh conditions (e.g. winter in temperate regions and drought in tropical regions). Second, evolution is sometimes thought to embrace time periods too long to be amenable for experimentation [21]. Yet, associative learning was shown to evolve within as few as 30 generations of experimental evolution in *D. melanogaster* [12,13]. Therefore, learning ability may evolve within a limited timescale in nature as well, where effective population sizes are often large and multiple generations may occur within a year. This provides scope for measurable evolutionary change in learning ability linked to spatial or temporal changes in resources over years or decades. It is fortunate that detailed data on environmental changes for climate and vegetation have become available over the periods of the last 30–50 years, particularly in insects of conservation concern. Multiple replicated populations from contrasted environments in terms of spatial/temporal certainty and reliability of resource distribution are needed to avoid any confounding bias due to non-causal environmental factors that happen to differ as well between populations. For example, mapping foraging resources for the hawkmoth *Manduca sexta* in the wild revealed that olfactory associative learning to switch flower species by adult foragers during summer improved provisioning efficiency [78••]. We expect that the rate of human-induced environmental change will generate a strong selective pressure on learning ability.

Another important improvement could be to use offspring of field-caught animals and to interface lab work with field work. Using offspring of field-caught animals avoids biasing learning estimates that result from inbreeding. When feasible, rearing the animals in cages but in the field would provide the developing organisms with the natural cues (e.g. chemical, visual, mechanosensory, magnetic, electrostatic), specific range of cues (for example natural chemicals, spectral reflectance) and related perceptual biases as they developed under selection in the wild. It would also provide a more natural food composition, which affects learning [88•]. Fitness estimates (survival and number of offspring) obtained from common-garden experiments of field-derived animals, and (split-brood) reciprocal transplant experiments between environments contrasting in environmental heterogeneity, for example habitats contrasted for foraging opportunities, will assess the relative fitness benefits of various forms of learning of these populations. Finally, the presence of individual genetic variability in learning ability means that the same individuals should be tested for quantifying learning and assessing its adaptive value. This is so because working at the population level may blur the causal relationship between learning and fitness. This may be challenging with small insects that are hard to track individually in the wild. Instead, individuals could be followed for bouts of movements [66] or by making use of specific tracking technology (microdots, harmonic radar) [89,90].

Finally, we could take advantage of knowledge acquired about spatial navigation in a wide array of insects including non-social insects [91]. Researchers in this field developed interesting experimental setups that integrate the ecology of the species, including: firstly, the movements for finding resources (food, mate, shelter, predator avoidance) in the environment; and secondly, the natural cues and related perceptual biases under selection in the wild.

Conclusion

While evidence for fitness benefits arising from various learning capacities remain scarce in natural, ecologically-relevant environments, we believe that it has become both timely and feasible to invest in experimental field work to quantify the adaptive value of learning for behaviours central to fitness in a wide range of insects, including non-social insects. This is notably because the adaptive value of learning for these behaviours is likely affected by the current changes in resource distribution under human-induced rapid environmental change including fragmentation and overall reduction of suitable habitats for nesting and feeding. Notably, pollen and nectar availability has significantly decreased for flower-visiting insects worldwide [92,93] and insect densities have declined strongly in the last decades (e.g. [94]). Fluctuations of resources in space and time can produce suboptimal tracking in foraging [95] and can affect the adaptive value of memory and learning [96]. We may expect that learning biases, as documented in several social and non-social insects, for example, towards social over non-social cues to locate foraging resources [97], or in the ability to learn enhanced over reduced social cues to choose among mating partners [53], constrain the adaptive evolution of learning and memory types in response to current environmental changes to suboptimal, maladaptive strategies. The combination of carefully executed field work and laboratory experiments with controls allows the production of robust data sets with strong replication (across populations), and the exploration of causal associations between learning, fitness and resource distribution as they change over time under real-world conditions.

Funding

This work was supported by the Université Catholique de Louvain UCL and the Fédération Wallonie-Bruxelles (Grant ARC 17/22-086) to C.M.N. and H.V.D. LC was supported by ERC Advanced Grant SpaceRadarPollinator and HFSP Program Grant RGP0022/2014. This is publication BRC 421 of the Biodiversity Research Centre at UCL.

Conflict of interest statement

None

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.cois.2018.03.008.

References

1. Papaj DR, Lewis AC (Eds): *Insect Learning: Ecological and Evolutionary Perspectives*. Chapman and Hall; 1993.
2. Barron AB, Hebets EA, Cleland TA, Fitzpatrick CL, Hauber ME, Stevens JR: **Embracing multiple definitions of learning**. *Trends Neurosci* 2015, **38**:405-407.
3. Thorpe WH: *Learning and Instinct in Animals*. London: Methuen; 1963.
4. Smid HM, Vet LEM: **The complexity of learning, memory and neural processes in an evolutionary ecological context**. *Curr Opin Insect Sci* 2016, **15**:61-69.
5. Giurfa M: **Behavioral and neural analysis of associative learning in the honeybee: a taste from the magic well**. *J Comp Physiol A* 2007, **193**:801-824.
6. Menzel R: **Behavioral and neural mechanisms of learning and memory as determinants of flower constancy**. In *Cognitive Ecology of Pollination. Animal Behavior and Floral Evolution*. Edited by Chittka L, Thomson JD. Cambridge Univ. Press; 2001:21-40.
7. Raine NE, Chittka L: **The correlation of learning speed and natural foraging success in bumble-bees**. *Proc R Soc B* 2008, **275**:803-808.
8. •• Morand-Ferron J, Cole EF, Quinn JL: **Studying the evolutionary ecology of cognition in the wild: a review of practical and conceptual challenges**. *Bio Rev* 2016, **91**:367-389.

This review highlights both the practical and conceptual challenges faced by the rapidly growing field of studying cognition in the wild. The study also discusses the advantages and disadvantages of captive versus field test but mostly in vertebrates. Cognitive ecology studies reviewed in this paper have revealed the importance of natural history to understand which cognitive domain and which aspect of cognitive performance is under selection in a population.

9. •• Morand-Ferron J: **Why learn? The adaptive value of associative learning in wild populations**. *Curr Opin Behav Sci* 2017, **16**:73-79.

This opinion paper stresses the significance of the recent progress in studying intraspecific variation in learning and refers to experiments that demonstrate the adaptive value of learning information for survival in the wild.

10. Fabre JH: *Nouveaux Souvenirs Entomologiques*. Librairie Delagrave Paris; 1882.

11. Mery F: **Natural variation in learning and memory**. *Curr Opin Neurobiol* 2013, **23**:52-56.

12. Medioni J, Cadieu N, Vaysse G: **Sélection divergente pour la rapidité de l'acquisition d'un conditionnement chez la Drosophile (*Drosophila melanogaster*)** [Divergent selection for speed of conditioning in *Drosophila melanogaster*]. *Comptes Rendus des Séances de la Société de Biologie* 1978, **174**:961-967.

13. Mery F, Kawecki TJ: **Experimental evolution of learning ability in fruit flies**. *Proc Natl Acad Sci USA* 2002, **99**:14274-14279.

14. Bar-Shai N, Keasar T, Shmida A: **How do solitary bees forage in patches with a fixed number of food items?** *Anim Behav* 2011, **82**:1367-1372.

15. Dukas R, Real LA: **Learning foraging tasks by bees — a comparison between social and solitary species**. *Anim Behav* 1991, **42**:269-276.

16. Chittka L, Beier W, Hertel H, Steinmann E, Menzel R: **Opponent colour coding is a universal strategy to evaluate the photoreceptor inputs in hymenoptera**. *J Comp Physiol A* 1992, **170**:545-563.

17. Perez SM, Waddington KD: **Carpenter bee (*Xylocopa micans*) risk indifference and a review of nectarivore risk-sensitivity studies**. *Am Zool* 1996, **36**:435-446.

18. Farris SM, Schulmeister S: **Parasitoidism, not sociality, is associated with the evolution of elaborate mushroom bodies in the brains of hymenopteran insects**. *Proc Roy Soc Lond B* 2011, **278**:940-951.

19. Stephens DW: **Learning and behavioural ecology: incomplete information and environmental predictability**. In *Insect Learning: Ecological and Evolutionary Perspectives.* Edited by Papaj DR, Lewis AC. Chapman & Hall; 1993:195-218.

20. Aoki K, Feldman MW: **Evolution of learning strategies in temporally and spatially variable environments: a review of theory**. *Theor Popul Biol* 2014, **91**:3-19.

21. Dunlap AS, Stephens DW: **Reliability, uncertainty, and costs in the evolution of animal learning**. *Curr Opin Behav Sci* 2016, **12**:73-79.

22. Botero CA, Weissing FJ, Wright J, Rubenstein DR: **Evolutionary tipping points in the capacity to adapt to environmental change**. *Proc Natl Aca Sci USA* 2015, **112**:184-189.

23. Dukas R, Bernays EA: **Learning improves growth rate in grasshoppers**. *Proc Natl Acad Sci USA* 2000, **97**:2637-2640.

24. • Verzijden MN, Svensson EI: **Interspecific interactions and learning variability jointly drive geographic differences in mate preferences**. *Evolution* 2016, **70**:1896-1903.

This study exemplifies how learning may affect the probability to rejecting heterospecific males by studying sexual interactions between two closely related damselfly species (*Calopteryx spendens* and *C. virgo*).

25. • Froissart L, Giurfa M, Sauzet S, Desouhant E: **Cognitive adaptation in asexual and sexual wasps living in contrasted environments**. *PLOS ONE* 2017, **12**:e0177581.

This study addresses differences in memory and learning ability between two wasp species that differ in habitat. The wasp species living in the wild had better cognitive performance than the other species, which is confined to stored-products buildings.

26. Papaj DR, Prokopy RJ, McDonald PT, Wong TTY: **Differences in learning between wild and laboratory *Ceratitis capitata* flies**. *Entomol Exp Appl* 1987, **45**:65-72.

27. Sepulveda DA, Zepeda-Paulo F, Ramırez CC, Lavandero B, Figuero CC: **Loss of host fidelity in highly inbred populations of the parasitoid wasp *Aphidius ervi* (Hymenoptera: Braconidae)**. *J Pest Sci* 2017, **90**:649-658.

28. Nepoux V, Haag C, Kawecki TJ: **Effects of inbreeding on aversive learning in *Drosophila***. *J Evol Biol* 2010, **23**:2333-2345.

29. Nepoux V, Babin A, Haag C, Kawecki TJ, Le Rouzic A: **Quantitative genetics of learning ability and resistance to stress in *Drosophila melanogaster***. *Ecol Evol* 2015, **5**:543-556.

30. Mery F, Kawecki TJ: **Cost of long-term memory in *Drosophila***. *Science* 2005, **308**:1148.

31. Snell-Rood EC, Davidowitz G, Papaj DR: **Reproductive tradeoffs of learning in a butterfly**. *Behav Ecol* 2011, **22**:291-302.

32. Xia S-Z, Liu L, Feng C-H, Guo A-K: **Nutritional effects on operant visual learning in *Drosophila melanogaster***. *Physiol Behav* 1997, **62**:263-271.

33. Gandolfi M, Mattiacci L, Dorn S: **Mechanisms of behavioral alterations of parasitoids reared in artificial systems**. *J Chem Ecol* 2003, **29**:1871-1887.

34. Kolss M, Kawecki TJ: **Reduced learning ability as a consequence of evolutionary adaptation to nutritional stress in *Drosophila melanogaster***. *Ecol Entomol* 2008, **33**:583-588.

35. Mery F, Kawecki TJ: **A fitness cost of learning ability in *Drosophila melanogaster***. *Proc R Soc Lond* 2003, **270**:2465-2469.

36. Tan SJ, Amos W, Laughlin SB: **Captivity selects for smaller eyes**. *Curr Biol* 2005, **15**:R540-R542.

37. Papaj DR, Mallory HS, Heinz CA: **Extreme weather change and the dynamics of oviposition behavior in the pipevine swallowtail, *Battus philenor***. *Oecologia* 2007, **152**:365-375.

38. Papaj DR, Prokopy RJ: **Phytochemical basis of learning in *Rhagolethis polmonella* and other herbivorous insects**. *J Chem Ecol* 1986, **12**:1125-1143.

39. Wäckers FL, Lewis WJ: **A comparison of color-, shape- and pattern-learning by the hymenopteran parasitoid *Microplitis croceipes***. *J Comp Phys A* 1999, **184**:387-393.

40. Lucchetta P, Bernstein C, Théry M, Lazzari C, Desouhant E: **Foraging and associative learning of visual signals in a parasitic wasp**. *Anim Cogn* 2008, **11**:525-533.

41. Desouhant E, Navel S, Foubert E, Fischbein D, Théry M, Bernstein C: **What matters in the associative learning of visual cues in foraging parasitoid wasps: colour or brightness?** *Anim Cogn* 2010, **13**:535-543.

42. Kandori I, Yamaki T, Okuyama S, Sakamoto N, Yokoi T: **Interspecific and intersexual learning rate differences in four butterfly species**. *J Exp Biol* 2009, **212**:3810-3816.

43. Rosenheim JA: **Host location and exploitation by the cleptoparasitic wasp *Argochrysis armilla*: the role of learning (Hymenoptera: Chrysididae)**. *Behav Ecol Sociobiol* 1987, **21**:401-406.

44. van Nouhuys S, Kaartinen R: **A parasitoid wasp uses landmarks while monitoring potential resources**. *Proc R Soc B* 2008, **275**:377-385.

45. Stanton ML: **Spatial patterns in the plant community and their effects upon insect search**. In *Herbivorous Insects Host-seeking Behavior and Mechanisms.* Edited by Ahmad S. Academic Press; 1983:125-157.

46. Wiklund C: **Egg-laying patterns in butterflies in relation to their phenology and the visual apparency and abundance of their host plants**. *Oecologia* 1984, **63**:23-29.

47. Rausher MD: **The effect of native vegetation on the susceptibility of *Aristolochia reticulata* (Aristolochiaceae) to herbivore attack**. *Ecology* 1981, **62**:1187-1195.

48. Parmesan C, Singer MC, Harris I: **Absence of adaptive learning from the oviposition foraging behaviour of a checkerspot butterfly**. *Anim Behav* 1995, **50**:161-175.

49. Potting RPJ, Otten H, Vet LEM: **Absence of odour learning in the stemborer parasitoid *Cotesia flavipes***. *Anim Behav* 1997, **53**:1211-1223.

50. Ellis AG, Johnson SD: **Lack of floral constancy by bee fly pollinators: implications for ethological isolation in an African daisy**. *Behav Ecol* 2012, **23**:729-734.

51. • Jones PL, Agrawal AA: **Learning in insect pollinators and herbivores**. *Annu Rev Entomol* 2017, **62**:53-71.

This review paper compares different aspects of learning in pollinators and herbivorous insects and argues that insect learning has the potential to have an important, yet largely unexplored, role in plant–insect coevolution.

52. Grüter C, Leadbeater E: **Insights from insects about adaptive social information use**. *TREE* 2014, **29**:177-184.

53. Westerman EL, Hodgins-Davis A, Dinwiddie A, Monteiro A: **Biased learning affects mate choice in a butterfly**. *Proc Natl Acad Sci USA* 2012, **109**:10948-10953.

54. Battesti M, Moreno C, Joly D, Mery F: **Spread of social information and dynamics of social transmission within *Drosophila* groups**. *Curr Biol* 2012, **22**:309-313.

55. Hollis KL, Guillette LM: **What associative learning in insects tells us about the evolution of learned and fixed behavior**. *Int J Compar Psychol* 2015, **28**:1-18.

56. Tully T, Preat T, Boynton SC, Del Vecchio M: **Genetic dissection of consolidated memory in *Drosophila***. *Cell* 1994, **79**:35-47.

57. Müller C, Collatz J, Wieland R, Steidle JLM: **Associative learning and memory duration in the parasitic wasp *Lariophagus distinguendus***. *Anim Biol* 2006, **56**:221-232.

58. Kruidhof HM, Pashalidou FG, Fatouros NE, Figueroa IA, Vet LEM, Smid HM, Huigens ME: **Reward value determines memory consolidation in parasitic wasps**. *PLoS ONE* 2012, **7**:e39615.

59. McNeely C, Singer MC: **Contrasting the roles of learning in butterflies foraging for nectar and oviposition sites**. *Anim Behav* 2001, **61**:847-852.

60. • Proffit M, Khallaf MA, Carrasco D, Larsson MC, Anderson P: **'Do you remember the first time?' Host plant preference in a moth is modulated by experiences during larval feeding and adult mating**. *Ecol Lett* 2015, **18**:365-374.

61. Astegiano A, Altermatt F, Massol F: **Disentangling the co-structure of multilayer interaction networks: degree distribution and module composition in two-layer bipartite networks**. *Sci Rep* 2017, **7**:15465.

62. Rausher MD: **Search for leaf shape in a butterfly**. *Science* 1978, **200**:1071-1073.

63. Copp NH, Davenport D: ***Agraulis* and *Passiflora* I. Control of specificity**. *Biol Bull* 1979, **155**:98-112.

64. Rausher MD: **Egg recognition: its advantage to a butterfly**. *Anim Behav* 1979, **27**:1034-1040.

65. Rausher MD, Papaj DR: **Demographic consequences of conspecific discrimination by *Battus philenor* butterflies**. *Ecology* 1983, **64**:1402-1410.

66. Stanton ML: **Short-term learning and the searching accuracy of egg-laying butterflies**. *Anim Behav* 1984, **32**:33-40.

67. Rausher MD: **Conditioning and genetic variation as causes of individual variation in the oviposition behaviour of the tortoise beetle, *Deloyala guttata***. *Anim Behav* 1983, **31**:743-747.

68. Rausher MD: **Tradeoffs in performance on different hosts: evidence from within and between site variation in the beetle *Deloyala guttata***. *Evolution* 1984, **38**:582-595.

69. Lewis AC: **Memory constraints and flower choice in *Pieris rapae***. *Science* 1986, **232**:863-865.

70. Peterson SC: **Host specificity of trail marking to foliage by eastern tent caterpillars, *Malacosoma americanum***. *Entomol Exp Appl* 1986, **42**:91-96.

71. Papaj DR, Rausher MD: **Components of conspecific host discrimination behavior in the butterfly *Battus philenor***. *Ecology* 1987, **68**:245-253.

72. Papaj RD, Prokopy RJ: **The effect of prior adult experience on components of habitat preference in the apple maggot fly (*Rhagoletis pomonella*)**. *Oecologia* 1988, **76**:538-543.

73. Dethier VG: **Induction and aversion-learning in a polyphgous arctiid larvae (Lepidoptera) in an ecological setting**. *Can Entomol* 1988, **120**:125-131.

74. Dorn NJ, Cronin G, Lodge DM: **Feeding preferences and performance of an aquatic lepidopteran on macrophytes: plant hosts as food and habitat**. *Oecologia* 2001, **128**:406-415.

75. • Dukas R, Duan JJ: **Potential fitness consequences of associative learning in a parasitoid wasp**. *Behav Ecol* 2000, **11**:536-543.

Wasps learn to associate in 15 min and for several days the fruit and the presence of the prey and this affects the number of offspring produced.

76. • Coolen I, Dangles O, Casas J: **Social learning in noncolonial insects?** *Curr Biol* 2005, **15**:1931-1935.

This landmark study shows that crickets adapt their predator-avoidance behaviour after observing the behaviour of conspecific demonstrators and that the behavioural changes lasted after demonstrators were gone. This study is the first to show social learning in non-colonial insects.

77. Xue HJ, Egas M, Yang XK: **Development of a positive preference–performance relationship in an oligophagous beetle: adaptive learning?** *Entomol Exp Appl* 2007, **125**:119-124.

78. •• Riffell JA, Alarcon R, Abrell L, Davidowitz G, Bronstein JL, Hildebrand JG: **Behavioral consequences of innate preferences and olfactory learning in hawkmoth–flower interactions**. *Proc Natl Acad Sci USA* 2008, **105**:3404-3409.

Adult moths have an innate preference, which can be erased by learning towards another plant. Heterogeneity in space and time of foraging resources represented by two host plants matches (field abundance and relative nutritional content) correlate with the switch in host plant species during the season for foraging.

79. •• Guillette LM, Hollis KL, Markarian A: **Learning in a sedentary insect predator: Antlions (Neuroptera: Myrmeleontidae) anticipate a long wait**. *Behav Proc* 2009, **80**:224-232.

These two studies show that antlions predatory larvae learn to associate a vibration with the presence of the prey or its size. They become selective towards bigger prey, which increases growth rate, accelerates molting between larval stages and shortens the vulnerable larval stage by allowing sooner pupation.

80. •• Hollis KL, Cogswell H, Snyder K, Guillette LM, Nowbahari E: **Specialized learning in antlions, pit-dwelling insect predators, shortens vulnerable larval stage**. *PLoS ONE* 2011, **6**:e17958.

These two studies show that antlions predatory larvae learn to associate a vibration with the presence of the prey or its size. They become selective towards bigger prey, which increases growth rate, accelerates molting between larval stages and shortens the vulnerable larval stage by allowing sooner pupation.

81. Kuszewska K, Miler K, Filipiak M, Woyciechowski M: **Sedentary antlion larvae (Neuroptera: Myrmeleontidae) use vibrational cues to modify their foraging strategies**. *Anim Cogn* 2016, **19**:1037-1041.

82. Videla M, Valladares G, Salvo A: **Differential effects of experience on feeding and ovipositing preferences of a polyphagous leafminer**. *Entomol Exp Appl* 2010, **137**:184-192.

83. Collatz J, Dorn S: **Tritrophic consequences arising from a host shift between apple and walnut in an oligophagous herbivore**. *Biol Control* 2013, **65**:330-337.

84. Moayeri HRS, Ashouri A, Mohandesi A: **Fitness costs of cotton aphids (*Aphis gossypii*) cornicle secretion, as a defense mechanism**. *J Entomol Soc Iran* 2012, **31**:51-61.

85. Moayeri HRS, Rasekh A, Enkegaard A: **Influence of cornicle droplet secretions of the cabbage aphid, *Brevicoryne brassicae*, on parasitism behavior of naïve and experienced *Diaeretiella rapae***. *Insect Sci* 2014, **21**:56-64.

86. Stockton DG, Pescitelli LE, Ebert TA, Martini X, Stelinski LL: **Induced preference improves offspring fitness in a phytopathogen vector**. *Environ Entomol* 2017, **46**:1090-1097.

87. Whitehead MR, Peakall R: **Short-term but not long-term patch avoidance in an orchid-pollinating solitary wasp**. *Behav Ecol* 2012, **24**:162-168.

88. • Lihoreau L, Poissonnier LA, Isabel G, Dussutour A: ***Drosophila* females trade off good nutrition with high-quality oviposition sites when choosing foods**. *J Exp Biol* 2016, **219**:2514-2524.

This study shows that the learning performance of fly larvae that had to associate an odour with a food reward were higher on a balanced food diet than on high carbohydrate or high protein diets.

89. Whitehead MR, Peakall R: **Microdot technology for individual marking of small arthropods**. *Agric Forest Entomol* 2012, **14**:171-175.
90. Woodgate JL, Makinson JC, Lim KS, Reynolds AM, Chittka L: **Life-long radar tracking of bumblebees**. *PLOS ONE* 2016, **11**: e0160333.
91. Collett M, Chittka L, Collett TS: **Spatial memory in insect navigation review**. *Curr Biol* 2013, **23**:R789-R800.
92. Thomas JA, Telfer MG, Roy DB, Preston CD, Greenwood JDD, Asher J, Fox R, Clarke RT, Lawton JH: **Comparative losses of British butterflies, birds, and plants on the global extinction crisis**. *Science* 2004, **303**:1879-1881.
93. Potts SG, Biesmeijer JC, Kremen C, Neumann P, Schweiger O, Kunin2 WE: **Global pollinator declines: trends, impacts and drivers**. *TREE* 2010, **25**:345-353.
94. Hallmann CA, Sorg M, Jongejans E, Siepel H, Hofland N, Schwan H, Stenmans W, Müller A, Sumser H, Hörren T, Goulson D, de Kroon H: **More than 75 percent decline over 27 years in total flying insect biomass in protected areas**. *PLOS ONE* 2017, **12**: e0185809.
95. Dunlap AS, Papaj DR, Dornhaus A: **Sampling and tracking a changing environment: persistence and reward in the foraging decisions of bumblebees**. *Interface Focus* 2017, **7**:20160149.
96. Wallin H: **Movement patterns and foraging tactics of a caterpillar hunter inhabiting alfalfa fields**. *Funct Ecol* 1991, **5**:740-749.
97. Avarguès-Weber A, Lachlan R, Chittka L: **Bumble bee social learning can lead to suboptimal foraging choices**. *Anim Behav* 2018, **135**:209-214.