

# Considerations for Insect Learning in Integrated Pest Management

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## Abstract

The past 100 yr have seen dramatic philosophical shifts in our approach to controlling or managing pest species. The introduction of integrated pest management in the 1970s resulted in the incorporation of biological and behavioral approaches to preserve ecosystems and reduce reliance on synthetic chemical pesticides. Increased understanding of the local ecosystem, including its structure and the biology of its species, can improve efficacy of integrated pest management strategies. Pest management strategies incorporating insect learning paradigms to control insect pests or to use insects to control other pests can mediate risk to nontarget insects, including pollinators. Although our understanding of insect learning is in its early stages, efforts to integrate insect learning into pest management strategies have been promising. Due to considerable differences in cognitive abilities among insect species, a case-by-case assessment is needed for each potential application of insect learning within a pest management strategy.

**Key words:** conditioning, aversive, associative, learned behavior, memory

Learning and memory are ubiquitous among animals, including insects (Capaldi *et al.* 1999, Brown and Laland 2003, Griffin 2004, Hoppitt and Laland 2008). Most research on insect behavior and learning have focused on aspects that might improve the productivity of beneficial insects or help mediate pest insects (Capaldi *et al.* 2000; Kawaguchi *et al.* 2006; Vinauger *et al.* 2011a, b; Giunti *et al.* 2015; I' Anson Price *et al.* 2019). Numerous definitions of learning have been proposed, many of which reference a behavioral change in response to experience often involving experience-induced changes in neurophysiology (van Alpern and Vet 1986, Barron 2001, Dukas 2008). Learning requires memory, which can be described as the persistence of learning or the retention and retrieval of learned information (Menzel and Müller 1996, Okano *et al.* 2000, McCall and Kelly 2002, Frost *et al.* 2012). Factors to consider in identifying learned behavior include repeatability of behavioral changes, gradual changes with continued experience, and decay in behavioral changes in the absence of continued experience or in the presence of different experience, demonstrating that learning is a life-long process rather than an outcome (Papaj and Prokopy 1989). Here we provide an overview of the history of insect learning and potential applications.

## Insect Learning and Memory

Complex behaviors such as food- and mate-finding are adaptive responses involving the performance of multiple integrated different behaviors and can rely on a suite of innate (inherited) preferences and preferences acquired through learning in response to multimodal

environmental, physiological, or social cues (Papaj and Prokopy 1989; Turlings *et al.* 1989; Vet *et al.* 1998, 1990; Segura *et al.* 2007; Jones *et al.* 2015; Enjin *et al.* 2016). The ability of a species to learn can be closely tied to its phenotypic plasticity (e.g., behavior), which itself can be a blend of adaptability to novel experiences and complex innate programming (Kaiser *et al.* 1989, Sachse *et al.* 2007, Dukas 2008, Pfennig *et al.* 2010). Behavioral plasticity can be described as the ability of an individual to adapt to new or changing information, assess its relevance, and prioritize information according to relative reliability of available information (Kaiser *et al.* 1989, Sachse *et al.* 2007, Dukas 2008, Pfennig *et al.* 2010). In general terms, species that inhabit a more diverse or changeable habitat, or that use a wider variety of hosts, may have greater reliance on learned sensory cues associated with suitable hosts. Learning is profitable where habitats are variable among generations or change rapidly or unpredictably within an insect's lifetime, as evidenced by foraging bumblebees (*Bombus* spp. Latreille [Hymenoptera: Apidae]) observing conspecifics to identify ephemeral floral resources (Stephens 1993, Dunlap *et al.* 2016). Conversely, a uniform and unchanging habitat could limit the importance of learning in favor of evolved innate preferences. Species which rely on greater diversity of hosts (generalists) could benefit more from learning cues associated with host finding whereas specialist species could more easily rely on innate preferences (Segura *et al.* 2007).

Most studies of insect learning have focused on responses to olfactory and visual stimuli (Thorpe and Jones 1937, Wäckers and Lewis 1994, McCall and Eaton 2001, Segura *et al.* 2007, Busto

*et al.* 2010, Benelli and Canale 2012, Liu and Sakuma 2013, Vinauger *et al.* 2014). However, insects can learn using a variety of sensory cues, including olfactory, visual (color, contrast, pattern, shape, and size), gustatory/taste, tactile/auditory, temperature, and spatial/temporal signals (Table 1). In some cases, learning paradigms can be extremely complex. Dung beetles (*Scarabaeus* (Kheper) *lamarcki* MacLeay [Coleoptera: Scarabaeidae]) learn to orient using a fixed-time map of celestial cues as a navigational guide (el Jundi *et al.* 2016). Leaf-cutter ants (*Acromyrmex ambiguus* Emery [Hymenoptera: Formicidae]) learn to avoid leaves treated with fungicide, which is undetectable to the ants, based on growth patterns in their symbiotic fungal gardens (Saverschek *et al.* 2010, Saverschek and Roces 2011). Honeybees (*Apis mellifera* Linnaeus [Hymenoptera: Apidae]) are highly adaptable, continually incorporating new experiences, including weather conditions, flower availability, and colony conditions, and can learn conceptual relationships, including more/less, above/below, left/right, and same/different (Capaldi *et al.* 2000, Avarguès-Weber and Giurfa 2013).

Studies into insect learning have been focused primarily on honeybees and other pollinators (foraging behavior and sublethal effects of pesticides and toxins), predatory insects and parasitoids (host-finding behavior and potential for improved efficacy in pest management strategies), *Drosophila* spp. Fabricius (Diptera: Drosophilidae) (as a model system for understanding insect development, evolution, and genetics), and phytophagous insects (host-selection and host-finding behavior; Du *et al.* 1997, Cunningham *et al.* 2001, Schwaerzel *et al.* 2003, Fiala 2007, Leadbeater and Chittka 2009, Busto *et al.* 2010, Giunti *et al.* 2015, Charbonneau *et al.* 2016, Dunlap *et al.* 2016, Smolla *et al.* 2016). Learning and memory can be assessed via changes in insect behavior (choice tests), involuntary responses (proboscis extension reflex), or physiology (calcium imaging; electromyography and silicon multichannel electron arrays; Faber *et al.* 1999, Daly *et al.* 2004, Farina *et al.* 2005, Frost *et al.* 2012). Measuring or quantifying learning and memory can be challenging because it can be difficult to determine whether behavioral change is due to learning or other factors, such as change in motivation, fatigue, physiological changes, or injury (Barron *et al.* 2015). In addition, differences

in conditioning methods, experimental design, and measurement techniques can significantly influence results and their interpretation (Frost *et al.* 2012).

### Types of Insect Learning

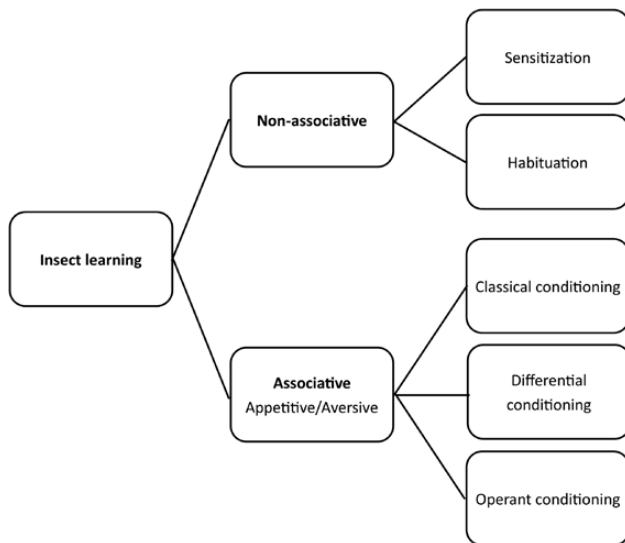
Insect learning can occur through several different processes (Fig. 1). Non-associative learning is the simplest form, comprised of becoming more (sensitization) or less (habituation) sensitive to a sensory cue through exposure. Responses can be induced by short-term exposure at critical points in development (e.g., during or shortly following emergence). Through repeated or prolonged exposure, sensitization may form the basis for sensory memory (Stopfer and Laurent 1999, Galizia and Sachse 2010). Sensitization and habituation of olfactory cues occur in the antennal lobes or mushroom bodies (Faber *et al.* 1999, Farooqui *et al.* 2003, Daly *et al.* 2004, Larkin *et al.* 2010).

Associative learning refers to conditioning the individual to associate a stimulus cue to either a positive reward (appetitive learning) or a negative punishment (aversive learning). Appetitive and, to a lesser extent, aversive conditioning have been demonstrated in most insect orders, with extensive studies involving Hymenoptera, Diptera, Blattodea, Lepidoptera, Coleoptera, and Hemiptera (Ebeling *et al.* 1966; Brodie Jr and Formanowicz Jr 1981; Meller and Davis 1996; Schwaerzel *et al.* 2003; Jørgensen *et al.* 2007; Saverschek and Roces 2011; Vinauger *et al.* 2011a, b; Buatois *et al.* 2017).

Associative learning can take the form of classical (Pavlovian) conditioning (Fig. 1), in which the stimulus induces a learned reflexive response (i.e., proboscis extension), or operant conditioning, where the stimulus induces a learned modifiable behavioral response (Garren *et al.* 2013). The strength of the response in operant conditioning varies with the value of the reward. Differential conditioning combines associative and non-associative learning paradigms (Faber *et al.* 1999). Associative memories and memories that involve a combination of olfaction, visual, spatial, and tactile cues, are retained in the mushroom body (de Belle and Heisenberg 1994, Armstrong *et al.* 1998, Hammer and Menzel 1998, Strausfeld *et al.* 1998, Schwaerzel *et al.* 2003, Farooqui *et al.* 2003). Prolonged or repeated experiences can result in permanent changes to behavior and physiology, including

**Table 1.** Although olfactory cues are most commonly used in studies of learning in insects, a variety of sensory cues have been demonstrated as effective stimuli for complex associative learning behaviors.

Order: Family	Species	Sensory System	Stimuli	Source
Diptera: Drosophilidae	<i>Drosophila melanogaster</i> Meigen	Olfactory / Tactile	Food odors and mechanical disturbance	Saumweber <i>et al.</i> 2014
Hymenoptera: Apidae	<i>Apis mellifera</i> Linnaeus (honeybees)	Tactile / Acoustic	airborne sound	Kirchner <i>et al.</i> 1991
		Visual	complex natural scenes	Dyer <i>et al.</i> 2008
	Visual	Colors and shapes	Buatois <i>et al.</i> 2017	
	<i>Bombus terrestris</i> Linnaeus (bumblebees)	Gustatory / Taste	cues in nectar	Molet <i>et al.</i> 2009
Hymenoptera: Formicidae	<i>Atta vollenweideri</i> Forel (leaf-cutter ants)	Visual	flower color	Leadbeater and Chittka 2007
		Visual	flower color	Dunlap <i>et al.</i> 2016
	<i>Cataglyphis noda</i> Brullé (desert ants)	Visual / Olfactory	flower color and blue/yellow	Smith and Raine 2014
		Temperature	thermal radiation	Kleineidam <i>et al.</i> 2007
<i>Myrmica rubra</i> Linnaeus (red ants)	<i>Myrmica rubra</i> Linnaeus (red ants)	Tactile / Acoustic	vibration and magnetic fields	Buehlmann <i>et al.</i> 2012
		Spatial / Temporal	routes to disposal sites	Diez <i>et al.</i> 2011



**Fig. 1.** Forms of insect learning. Even a single exposure to a stimulus without an associated reward or punishment can induce a familiarization effect. These non-associative conditioning events can enhance sensitivity (sensitization) resulting in increased response to innately attractive stimuli or in reduce sensitivity (habituation) resulting in decreased avoidance of innately repellent stimuli. Associative conditioning occurs when exposure to a stimulus precedes or occurs concurrently with a positive (appetitive conditioning) or negative (aversive conditioning) reward experience. Classical (Pavlovian) conditioning occurs when the induced behavioral response is involuntary or reflexive (proboscis extension in honeybees, salivation in dogs). In contrast, operant conditioning occurs when the induced response is a modifiable behavior. Differential conditioning combines any of the preceding conditioning paradigms or involves differing reward values for differing stimuli.

antennal lobes and mushroom bodies (Thorpe 1938, Hershberger and Smith 1967, Devaud *et al.* 2001, Farris *et al.* 2001, Sachse *et al.* 2007).

### Insect Life Stage and Learning

The influence of learning and memory retention across life stages in insects, particularly holometabolous insects, has been hotly debated over the past 100 yr (Hopkins 1916, 1917; Craighead 1921, 1923; Thorpe and Jones 1937; Thorpe 1939; Thompson 1988; Jaenike and Holt 1991; Tully *et al.* 1994; Barron and Corbet 1999; Barron 2001; Gandolfi *et al.* 2003a; Schroll *et al.* 2006; Blackiston *et al.* 2008; Bonduriansky and Day 2009; Davis 2008; Anderson *et al.* 2013; Aso *et al.* 2014; Ernst *et al.* 2015). Although metamorphosis dramatically alters insect physiology, including extensive degeneration, reorganization, and regrowth of antennal lobe and mushroom body structures, select underlying neuronal cells and portions of the mushroom body can be traced from larval to adult stages (Armstrong *et al.* 1998, Blackiston *et al.* 2008, Aso *et al.* 2014). Although mushroom body structures and degree of developmental continuity differ among insect taxa, potential may exist for some conservation of memory (Blackiston *et al.* 2008).

Larval insects are capable of robust but simplified odor perception and odor learning (Scherer *et al.* 2003, Hendel *et al.* 2005, Gerber and Stocker 2007). Among some taxa, natal experience is thought to influence adult behavior through imprinting (sensitization or habituation) or associative learning (Tully *et al.* 1994, Blackiston *et al.* 2008, Davis 2008). Results vary among studies and learning can sometimes be partly attributed to experience during or immediately after adult emergence, such as sensory cues located on or near

the pupal case, rather than at larval stages (Thorpe and Jones 1937; Thorpe 1939; Barron and Corbet 1999, 2000; Gandolfi *et al.* 2003a; Anderson *et al.* 2013). The relationship between larval experience and adult host preference can also be due to induced gene expression or a genetically distinct subset of the population (Thompson 1988, Jaenike and Holt 1991, Schroll *et al.* 2006, Bonduriansky and Day 2009). Residual host or environmental odors experienced during adult emergence can induce a chemical legacy association to find new hosts (Corbet 1985, Veltman and Corbet 1991, Rietdorf and Steidle 2002, Gandolfi *et al.* 2003a, Blackiston *et al.* 2008). During postemergence reconnaissance flights, adult parasitic wasps (Hymenoptera) learn olfactory and visual cues of prey's host plants associated with successful ovipositing to identify potential future oviposition sites (Tumlinson *et al.* 1993).

Recent advances in DNA sequencing technology and identification of a functional DNA methylation system in *A. mellifera* have raised questions about the role of epigenetics in host-switching (Ernst *et al.* 2015). Many insect species express different phenotypes due to seasonal or regional differences in available diet or environmental conditions during development that could explain differences in sensitivity to sensory stimuli and the resulting host preference hierarchies (Pfennig *et al.* 2010, Ernst *et al.* 2015, Kijimoto and Moczek 2016).

Among adult insects, the reliability of sensory cues as predictors for relevant aspects of environment is key to determining the value of learned cues (Dunlap *et al.* 2016). Negative courtship experiences can cause male *Drosophila melanogaster* Meigen (Diptera: Drosophilidae) to have increased sensitivity to male pheromone on female flies and improve discrimination between mated and virgin females (Keleman *et al.* 2012).

Memory is either reinforced through repeated experience or decays where memory of experience-associated odors lacks benefits (Grossmann 1973, Vet and Dicke 1992, Kaiser and De Jong 1993, McCall *et al.* 1993, Menzel and Müller 1996, Busto *et al.* 2010, l'Anson Price *et al.* 2019). Depending upon the species and habitat variability, experience can result in host preferences that vary in persistence from a few minutes to many days but tends to persist longer with subsequent repeated experience (Kaiser *et al.* 1989, Bjorksten and Hoffmann 1998, Blackiston *et al.* 2008, Collett 2008, Vinauger *et al.* 2014). Short-term, intermediate, and long-term memory phases have been identified in honeybees, mosquitoes (Diptera: Culicidae), and *Drosophila* (Meller and Davis 1996, Vinauger *et al.* 2014). Short-term (persisting minutes to hours) and intermediate memory (persisting hours to days) can be formed following a single exposure or conditioning experience (Meller and Davis 1996, Busto *et al.* 2010, Vinauger *et al.* 2014). Long-term memory (persisting days or longer) can require repeated reinforcement experiences (Grossmann 1973, Kaiser and De Jong 1993, Meller and Davis 1996, Busto *et al.* 2010, Saverschek *et al.* 2010). Simultaneous exposure to multiple conditioning experiences can force insects to prioritize, inhibiting learning of cues associated with one experience in favor of the other (Rains *et al.* 2008, Christiansen and Schausberger 2017). As experience grows, learning can serve to modify or reinforce learned or innate preferences, often by introducing local adaptations (Kaiser *et al.* 1989, Galef Jr 1995, McCall and Kelly 2002).

Within a taxonomic class of several million species, it is unlikely that a 'one size fits all' hypothesis would apply to all cases. Changes in host preferences are likely attributable to multiple factors, including genetics, selection, and conditioning (Barron 2001). In limited circumstances, larval conditioning may play a role in adult behavior but is generally superseded by adult experiences and conditioning (Barron 2001, Blackiston *et al.* 2008). Differences of opinion about timing, permanence, and basis of insect learning are likely to persist for many years

to come. However, there is growing acknowledgment of the existence of a variety of insect learning models and the importance of learning for adaptive behavior by both pest and beneficial insect species.

### Social Learning

Foraging, particularly by naïve individuals, or to locate novel food sources, is time-consuming and risky (Chittka and Leadbeater 2005, Dunlap *et al.* 2016, Smolla *et al.* 2016). Learning from conspecifics is well documented among insects, particularly social insects such as honeybees (*A. mellifera*), bumblebees (*Bombus* spp.), and ants Linnaeus (Hymenoptera: Formicidae) (Chittka and Leadbeater 2005, Coolen *et al.* 2005, Leadbeater and Chittka 2007). Learning via observation promotes the rapid spread of novel information or behaviors, such as watching conspecifics trying novel hosts or food sources (Leadbeater and Chittka 2007, Sarin and Dukas 2009, Giurfa 2012, Durisko and Dukas 2013, Dunlap *et al.* 2016).

Social learning allows individuals to reduce risks of mistakes or negative experiences that could occur through trial-and-error, provided the information source is considered reliable (Jones *et al.* 2015, Dunlap *et al.* 2016, Smolla *et al.* 2016, l'Anson Price *et al.* 2019). Naïve wasps, bees, and ants learn to recognize physical and chemical cues from novel food sources by observing nest-mates and are attracted by foraging conspecifics, but more experienced individuals will avoid conspecifics at food sources, preferring less competitive feeding sites (Slaa *et al.* 2003, Kawaguchi *et al.* 2006, Leadbeater and Chittka 2007). Social cues can include observing conspecifics at feeding sites/flowers, odor 'footprints' left at feeding sites, or floral odors carried into the nest by nest-mates (Molet *et al.* 2009). Eusocial insects, such as honeybees, bumblebees, and ants, have been observed engaging in recruitment behavior akin to mentoring, such as honey bee waggle dancing and ant trail marking (Chittka and Leadbeater 2005, Franks and Richardson 2006, Smolla *et al.* 2016). Analyses of recruitment relative to food patch distribution patterns suggest that this behavior is learned rather than innate (Heinrich 1979, Leadbeater and Chittka 2009). When recruitment messages are unreliable, foragers quickly learn to ignore social cues in favor of increased scouting activity (Dunlap *et al.* 2016, l'Anson Price *et al.* 2019). Nonsocial insects, including crickets Laicharting (Orthoptera: Gryllidae), damselflies Séllys (Odonata: Zygoptera), and flies Linnaeus (Diptera), learn to associate chemical cues of wounded conspecifics to avoid predators and learn about resources or avoid predators by observing heterospecifics (Wisenden *et al.* 1997, Chittka and Leadbeater 2005, Coolen *et al.* 2005, Leadbeater and Chittka 2007, Roberts 2012).

### Insect Learning and Pest Management Strategies

Numerous insect species are classified as pests primarily due to widespread damage to agricultural and forestry plant products and the spread of disease to human and animal hosts. Integrated pest management strategies have been developed in response to many of these threats to food safety and health. However, pesticide resistance and changing efficacy of pest management strategies continue to be a problem (Kogan 1998, Bass *et al.* 2015). The idea that biological and chemical pest controls could supplement each other was first discussed in 1939 and reintroduced in 1954 (Hoskins *et al.* 1939, Smith and Allen 1954). However, the integration of chemical and biological pest management strategies did not become widespread until the 1970s, spurred by the growing awareness of consequences of over-reliance of pesticides (Carson 1962).

Researchers have begun exploring the potential to integrate insect learning to improve the efficacy of pest management practices, primarily in the areas of agriculture and forestry, disease-vector control (medical and veterinary), and urban pest management (Dukas 2008, Menzel 2012, Leadbeater and Dawson 2017). Many insect species integrate multimodal sensory cues, including olfactory, visual, tactile, acoustic, and spatial stimuli, to identify hosts and discount nonhosts (Smith and Allen 1954, Campbell and Borden 2009). Conditioning paradigms that combine multimodal stimuli can reinforce learned preferences in parasitoids or predatory insects (Table 2). Exposure to pesticides and other pest management efforts may result in unintended avoidance conditioning experiences for pest insects. Understanding these processes could inform our efforts to limit the efficacy of these learned avoidance behaviors (Table 3).

### Agriculture and Forestry

The origins of our understanding of insect learning were in agriculture and forestry, in the works of Hopkins, Craighead, and Walsh, and this remains the most widely studied venue (Walsh 1864; Hopkins 1916, 1917; Craighead 1921, 1923). Much of the work in these areas has focused on the use of polyphagous parasitoid wasps and predatory species to control pest insects (Table 2). Strategies involving the mass release of Hymenopteran parasites could be made more effective by conditioning parasitoids to combination of olfactory, visual, and/or tactile/acoustic stimuli associated with finding hosts, food, or mates (Giunti *et al.* 2015). By tying an appropriate color cue to first ovipositioning experience of naïve female parasitoids, we can condition mass-released parasitoids to seek out hosts in the fruit of that color (Benelli and Canale 2012). Timing of experience during a parasitoid's life history can greatly influence the efficacy of learning and memory retention and will vary among species (Browne and Withers 2002, Decker *et al.* 2007, Giunti *et al.* 2015). Although some host odors may be learned by larvae, most odors, including plant-host complex odors, are learned during or after adult emergence (Caubet and Jaisson 1991, Weiss *et al.* 2004, Takemoto *et al.* 2009, Rasekh *et al.* 2010). Therefore, both the conditioning stimuli and timing of learning experiences are important for pest management efficacy.

### Disease-Vector Control

Although insects are a primary vector of many important diseases, implications of and potential applications for insect learning have received less attention in areas relating to disease control. However, there have been a few notable exceptions including research into insecticide avoidance behavior of pyrethroid-resistant *Anopheles gambiae* Giles (Diptera: Culicidae) in areas where insecticide-treated nets are in common use for malaria prevention (N'Guessan *et al.* 2007). Pyrethroid resistance combined with habituation to pesticide odors is rapidly reducing the efficacy of protective netting in malaria-prone areas of Africa. Site fidelity has been documented for feeding and oviposition sites in *Anopheles* spp. and *Culex* spp. Linnaeus (Diptera: Culicidae), suggesting that female mosquitoes have learned to recognize specific locations as suitable (McCall and Kelly 2002). Aversive conditioning has also been documented in ovipositioning site preferences of *Anopheles stephensi* Liston (Diptera: Culicidae) (Reisen 1975). Studies of *Rhodnius prolixus* Stål (Hemiptera: Reduviidae) and *Aedes aegypti* Linnaeus in Hasselquist (Diptera: Culicidae) behavior demonstrate that blood-feeding insects are capable of learning associations between olfactory cues and both positive and negative reinforcement (Vinauger *et al.* 2011a, b; Menda *et al.* 2013). It is likely that repeated



**Table 2.** A variety of studies have been completing investigating insect learning by Hymenopteran parasitoids of importance to pest management strategies. Researchers have sought to improve the efficacy of pest management efforts against a diverse range of pest insects using a variety of stimuli and conditioning paradigms.

Time of Conditioning	Parasitoid	Pest Species	Stimuli	Reference
Prior to / during emergence	<i>Hyssopus pallidus</i> Askew (Hymenoptera: Eulophidae)	<i>Cydia pomonella</i> Linnaeus (Lepidoptera: Tortricidae)	kairomones in larvae and frass	Gandolfi <i>et al.</i> 2003a, b
During / postemergence	<i>Nemeritis canescens</i> Gravenhorst (Hymenoptera: Ichneumonidae)	<i>Ephesttia kilhniella</i> Zeller (Lepidoptera: Pyralidae) and <i>E. elutella</i> Hübner (Lepidoptera: Pyralidae)	host kairomones	Thorpe and Jones 1937
Postemergence	<i>Dinarmus basalis</i> Rondani (Hymenoptera: Pteromalidae)	<i>Zabrotes subfasciatus</i> Boheman (Coleoptera: Bruchidae) and <i>Acanthoscelides obtectus</i> Say (Coleoptera: Bruchidae)	host kairomones	Caubet and Jaisson 1991
	<i>Trichogramma</i> nr. <i>Brassicae</i> Bezdenko (Hymenoptera: Trichogrammatidae)	<i>Sitotroga cerealella</i> Olivier (Lepidoptera: Gelechiidae) and <i>Helicoverpa punctigera</i> Wallengren (Lepidoptera: Noctuidae)	host kairomones	Bjorksten and Hoffmann 1998
	<i>Microplitis croceipes</i> Cresson (Hymenoptera: Braconidae)	<i>Helicoverpa zea</i> Boddie (Lepidoptera: Noctuidae)	host-plant semiochemicals	Drost <i>et al.</i> 1988
	<i>Cotesia marginiventris</i> Cresson (Hymenoptera: Braconidae)	<i>Spodoptera frugiperda</i> Smith (Lepidoptera: Noctuidae) and <i>Trichoplusia ni</i> Hübner (Lepidoptera: Noctuidae)	host-plant semiochemicals and kairomones in frass	Lewis <i>et al.</i> 1991
	<i>Cotesia marginiventris</i> and <i>Microplitis croceipes</i>	<i>H. zea</i>	host-plant semiochemicals and kairomones in frass	Turlings <i>et al.</i> 1989, 1993
	<i>Microplitis demoliter</i> Wilkinson (Hymenoptera: Braconidae)	<i>H. zea</i>	host-plant semiochemicals in frass	Hérard <i>et al.</i> 1988
	<i>Aphytis melinus</i> DeBach (Hymenoptera: Aphelinidae)	<i>Aonidiella aurantia</i> Maskell (Hemiptera: Diaspididae)	kairomone in host cuticle	Hare <i>et al.</i> 1997
	<i>Cotesia marginiventris</i>	<i>Spodoptera frugiperda</i>	kairomone in host frass	Loke and Ashley 1984
	<i>Microplitis croceipes</i> , <i>Trichogramma pretiosum</i> Riley (Hymenoptera: Trichogrammatidae), and <i>T. achaeae</i> Nagaraja (Hymenoptera: Trichogrammatidae), and Nagarkatti (Hymenoptera: Trichogrammatidae)	<i>H. zea</i>	kairomone in host frass	Gross <i>et al.</i> 1975
Pre-adult and during oviposition	<i>Trichogramma</i> nr <i>ivelae</i> Pang and Chen (Hymenoptera: Trichogrammatidae)	<i>H. punctigera</i> , <i>Papilio Aegaeus</i> Donovan (Lepidoptera: Papilionidae), and <i>Hypolimnus bolina</i> Linnaeus (Lepidoptera: Nymphalidae)	host kairomones	Bjorksten and Hoffmann 1995
During oviposition	<i>Psytalia concolor</i> Szépligeti (Hymenoptera: Braconidae)	<i>Ceratitis capitata</i> Wiedemann (Diptera: Tephritidae)	color	Benelli and Canale 2012
	<i>Leptopilina heterotoma</i> Thomson (Hymenoptera: Eucoilidae)	<i>Drosophila simulans</i> Sturtevant (Diptera: Drosophilidae)	host-infested fruit odors	Vet <i>et al.</i> 1990
	<i>Cotesia glomerata</i> Linnaeus (Hymenoptera: Braconidae)	<i>Pieris brassicae</i> Linnaeus (Lepidoptera: Pieridae) and <i>Spodoptera littoralis</i> Boisduval (Lepidoptera, Noctuidae)	host-infested plant odors	Desurmont <i>et al.</i> 2018
	<i>Lysiphlebus fabarum</i> Marshall (Hymenoptera: Braconidae)	<i>Aphis fabae</i> Scopoli (Hemiptera: Aphididae)	social cues	Rasekh <i>et al.</i> 2010
During repeated ovipositioning	<i>Trichogramma achaeae</i>	<i>H. zea</i>	kairomone in host cuticle	Lewis <i>et al.</i> 1975
Multi-generational	<i>Trichogramma maidis</i> Pintureau and Voegelé (Hymenoptera, Trichogrammatidae)	<i>Ostrinia nubilalis</i> Hübner (Lepidoptera: Crambidae) and <i>Anagasta kuehniella</i> Zeller (Lepidoptera: Pyralidae)	host kairomones	Kaiser <i>et al.</i> 1989

**Table 3.** Direct application of insect learning paradigms on integrated pest management programs.

Pest category	Target insect	Type of conditioning	IPM practice	Reference
Herbivores	<i>Acheta domesticus</i> Linnaeus (Orthoptera: Gryllidae)	aversive	necromones to condition against food odors	Shephard <i>et al.</i> 2018
	<i>Helicoverpa armigera</i> Hübner (Lepidoptera: Noctuidae)	associative	integrating host abundance into plant volatile mixture in lures	Cunningham <i>et al.</i> 1999
	generalist herbivores	associative	integrating host abundance into plant volatile mixture in lures	Shanower and Romeis 1999
		aversive	toxic / bitter / distasteful compounds as deterrents	Bernays 1993
		aversive	nutrient deficiencies as deterrents	Bernays 1993
Disease vectors	<i>Aedes aegypti</i> Linnaeus (Diptera: Culicidae)	aversive	intercropping	Verkerk <i>et al.</i> 1998
	<i>Anopheles stephensi</i> Liston (Diptera: Culicidae)	aversive	intercropping	Verkerk <i>et al.</i> 1998
	<i>Rhodnius prolixus</i> Stål (Hemiptera: Reduviidae)	aversive	olfactory cues as blood-feeding deterrent	Menda <i>et al.</i> 2013
		aversive	olfactory cues as ovipositioning deterrent	Reisen 1975
		aversive	olfactory cues as blood-feeding deterrent	Vinauger <i>et al.</i> 2011b

experience would reinforce the association and prolong the avoidance behavior. Exposure to DEET during a simulated blood-feeding experience can reduce the innate aversive response of *A. aegypti* to DEET, suggesting that habituation can reduce pest control chemical efficacy (Vinauger *et al.* 2014). A single odor can act as either an attractant or repellent dependent upon the prior experience of *Culex quinquefasciatus* Say (Diptera: Culicidae), demonstrating that experience can modify and even nullify innate preferences for specific olfactory cues (McCall and Eaton 2001). The potential influence of positive and negative experiences on insect behavior must be considered in developing pest management strategies. Because many of the insects that are disease vectors have some capacity for learning, strategies that employ aversive conditioning in relation to human-associated olfactory or visual cues could improve the efficacy of pest management efforts.

### Urban Pest Management

Insect learning has received less attention in the field of urban pest management. Much of the research has focused on the behavior of cockroaches. Early experiments demonstrated that a combination of associative learning and habituation to light helps German cockroaches (*Blattella germanica* Linnaeus [Blattodea: Ectobiidae]) avoid insecticide-treated areas (Ebeling *et al.* 1966). Cockroaches can become habituated to mildly repellent contact insecticides, improving their efficacy in the long-term (Ebeling *et al.* 1966). Experience can induce attraction to an innately neutral odor and inhibition to an innately attractive odor, including aversive conditioning from sublethal exposure to bait-insecticides (Kells *et al.* 2005, Liu and Sakuma 2013). There is also growing evidence of social learning in cockroaches (Lihoreau and Rivault 2011). The reluctance to incorporate learning paradigms into urban pest management may be due in large part to widespread fear of insects among the general population (Kellert 1993).

### Implications of Learning for Pest Management

#### Intercropping and Physical Barriers

Large single crop sites, indicative of modern industrial-style monoculture farming, are ideal venues for sensitization and associative learning by phytophagous insects. Insects have ample opportunity

for repeated stimulus-positive reward experiences to reinforce learning. Learning can lead to restricted host use or limited host preference (host constancy), especially where one host species is predominant. An individual polyphagous insect may learn host constancy to forage more efficiently (Cunningham *et al.* 1999). In contrast, intercropping (use of a variety of plants within a crop area) has been used as an effective pest management strategy for centuries (Horwith 1985, Knörzner *et al.* 2009). Application of intercropping practices varies significantly, as does its relative efficacy in limiting insect learning (Verkerk *et al.* 1998). A variety of intercropping strategies are currently in use, including alternating plants within a row, alternating rows of plants, use of multiple varieties or species of plants in a single crop area, intercropping throughout the entire crop area, or creating a border area of intercropped plants. Additionally, many intercropping programs use one or more plant species or varieties with properties that are repellent to pest species or attractive to predatory species. Intercropping can disrupt appetitive learning processes in insects by introducing unrewarded or negative experiences that limit the reliability of stimulus information (Verkerk *et al.* 1998, Finch and Collier 2000).

Physical barriers, including greenhouses, growing tunnels, and pesticide-treated barrier nets can be effective to control or reduce the inflow of pest insects. However, hymenopteran parasitoids and pollinators have demonstrated a strong aptitude for aversive learning and can associate olfactory stimuli and negative consequences of pesticide contact, which can effectively limit the movement of beneficial insects (Vergoz *et al.* 2007, Carcaud *et al.* 2009, Martin *et al.* 2014).

Careful timing of repellent semiochemicals and pesticides during critical early stages may be sufficient for newly emerging insects to develop aversive conditioning to crop plants. Insects excluded from crop areas via repellents or physical barriers during early adult stages may instead become sensitized to olfactory and visual stimuli associated with non-crop plant hosts and through repeated feeding or ovipositioning, become conditioned to seek out non-crop hosts (Cunningham *et al.* 1998, 1999). This would require considerable understanding of pest insect life history and an effective early monitoring program to ensure pest management efficacy. In the case of multivoltine pest species, growers would need to reapply repellents or exclusion mechanisms with each successive generation to ensure efficacy.

## Biological Control

A variety of parasitoid and predator insect control programs for agriculturally important pest insects are currently in use (Table 2). Most commonly, generalist parasitoid hymenopterans are reared under controlled conditions for mass-release in crop areas. For example, *Aphytis melinus* DeBach (Hymenoptera: Aphelinidae) are reared on oleander scale insects, which are usually reared on squash, and released commercially as a control agent for the citrus pest, California red scale (*Aonidiella aurantii* Maskell [Hemiptera: Diaspididae]). A single exposure of *A. aurantii* kairomones to newly emerged *A. melinus*, is sufficient to increase host preference for *A. aurantii* and improve efficacy of host finding (Hare *et al.* 1997). There is growing evidence that efficacy can be further improved in some insect species, including parasitoids, through additional temporally spaced learning experiences (Tully *et al.* 1994, Meller and Davis 1996, Kim *et al.* 2007, Campbell and Borden 2009). Combining sensitization exposure to host plants and ovipositioning experience on target host species can improve retention of parasitoids in target areas and increase host specificity. Associations with positive and negative experiences can help parasitoids learn to distinguish between similar odor blends, such as plants with and without infestations by host insects (Vet *et al.* 1990, 1998; Weiss *et al.* 2004). Other predatory insect species can be reared and conditioned in a similar manner, including lady beetles Latreille (Coleoptera: Coccinellidae) and lacewings Linnaeus (Neuroptera: Chrysopidae) (Wisenden *et al.* 1997, Reddy *et al.* 2004). Olfactory cues from both prey insects and host plants can be used to sensitize, attract, and retain predatory insects.

Naturally occurring generalist parasitoids can be induced to host-switch to invasive pest insect species through by blanketing infested crops with semiochemicals from host species or herbivore-induced plant volatiles (Barratt and Johnstone 2001). These will initially act as attractants into crop areas, where parasitoids can become conditioned to these novel hosts. Differential learning can be used to induce host-switching from a benign natural host to a related pest species.

## Challenges Associated With Insect Learning and Pest Management

### Host Shifting

Larval feeding experience can induce host preference changes for oviposition sites in female moths and for potential mating sites in male moths (Moreau *et al.* 2008, Anderson *et al.* 2013). This experience can override innate host preference hierarchies or override innate responses to deterrent compounds associated with larval food sources (Akhtar and Isman 2003, Moreau *et al.* 2008). The effects of larval experience can alter both host-finding and host-acceptance behavior (Olsson *et al.* 2006, Stamps and Davis 2006). This can result in either increased host fidelity or, under variable environmental conditions, can allow for adaptive responses that promote host-shifting and could facilitate sympatric speciation (Beltman *et al.* 2004, Beltman and Haccou 2005, Snell-Rood and Papaj 2009).

### Chemical-Induced Interference

Studies of chemical-induced interference of insect learning and memory have primarily focused on experiments with beneficial hymenopteran insects, including honeybees (*A. mellifera*) and bumblebees (*Bombus* spp.). These studies have demonstrated that sublethal exposure to a variety of chemicals and pesticides can induce persistent disruptions in learning and memory (Aliouane *et al.* 2009, Frost *et al.* 2013, Siviter *et al.* 2018). Similar patterns of reduced learning and memory in honeybees can be attributed to parasitic

infection and environmental conditions, including temperature extremes and changes in light exposure (Fitz-Earle and Sakaguchi 1986, Frost *et al.* 2011, Gegeer *et al.* 2006, Kralj *et al.* 2007, Charbonneau *et al.* 2016). Pest management strategies must, therefore, take into consideration potential negative consequences of pesticides, physical barriers, and other treatment options on pollinators and other beneficial insects. Strategies should be examined on a case-by-case basis to ensure benefits in pest management efficacy outweigh potential risks.

## Consequences of Agricultural Practices and Pest Management Strategies

Olfactory cues emanating from large-scale monoculture agricultural crops would rapidly become ubiquitous in the local environment, leading to sensitization for host odors and creating an ideal setting for learned acceptance by polyphagous insects (Smith and McSorley 2000, Potter and Held 2002, Teasdale *et al.* 2004, Marković 2013). Homogeneous forests due to replanting by commercial forestry industry pose a similar risk for learning by potential forest pest species (Jactel *et al.* 2005).

Because IPM efforts are not 100% effective, questions remain about the extent to which insects that are not killed can learn to avoid traps and lure odors that are used in monitoring or mass-trapping (Ebeling and Reiersen 1969, Kain *et al.* 2013, Menda *et al.* 2013). Further study could help identify means to pest management practices to compensate, including alternating between two or more different lures. Insect learning of avoidance cues may also be closely tied to growing pesticide resistance. Survivors of pesticide exposure could learn to use olfactory, visual, or spatial cues associated with the experience to subsequently avoid or limit future exposure (Ebeling and Reiersen 1969, Chareonviriyaphap *et al.* 1997, Rose *et al.* 2005, Cordeiro *et al.* 2013). Additionally, as insects become more resistant to a pesticide, they may also become habituated, reducing its efficacy as a deterrent. This may be particularly true in circumstances where pesticide applications were suboptimal due to dosage errors, missed treatments, or adverse weather conditions, and where insects were exposed to a negative but not lethal experience.

## Insect Life History Effects

The efficacy of using insect learning in pest management strategies can differ among species with different life histories. Lifespan, feeding lifestyle (generalist vs specialist), and reproductive lifestyle are factors to be considered. Insect learning may be less useful in pest management strategies where insects involved are short-lived, multivoltine species. However, if long-lived species are involved as either pest or predator, learning may be much more relevant to pest management efforts. Subtle differences in reproductive lifestyles of parasitoid insects can have considerable differences in the types of cues learned. Parasitoids that arrest development in host species often use sensory cues associated with host species at earlier life stages to identify future host sites (Wäschke *et al.* 2013). In contrast, parasitoids that oviposit in hosts which will continue to develop and grow may also use cues associated with healthy host-food sources for identifying prospective hosts (Wäschke *et al.* 2013).

Receptivity to sensory cues and susceptibility to learning change over the life history of an insect (Browne and Withers 2002). Age, physiological condition, and environmental conditions can all influence reliance on learning and memory. Insects that have restricted access to food, mates, or suitable oviposition sites are likely to have reduced thresholds for or reduced reliance on learned chemical cues (Browne and Withers 2002). Desperation can supersede a learned hierarchy of preferences (Davis 2007, 2008). These insects may be more willing to risk imperfect matches to remembered stimuli and

try novel hosts. Seasonal or circadian differences in host availability or environmental conditions can influence insect physiology and efficacy of learning (Decker *et al.* 2007, Garren *et al.* 2013). Learning is most productive when host availability and habitat conditions are stable during the lifetime of the insect but variable among generations (Segura *et al.* 2007, Smith and Raine 2014).

### Limitations of Parasitoids and Predatory Insects as Control Agents

Parasitoids and predatory insects are growing in popularity as chemical-free alternative pest control measures (Tauber *et al.* 2000, Cónsoli and Grenier 2009, Parra 2009). In many cases, generalist parasitoids or predators are reared on alternate hosts or artificial media before being mass released. Efficacy can be improved by sensitizing newly emerging insects to their intended target hosts or to host-associated odors (Vet and Van Opzeeland 1984, Vet *et al.* 1995). Additionally, newly emerging insects can also be cross-conditioned to host-plant odors to encourage foraging within a crop area (Coaker and Cheah 1993, Storeck *et al.* 2000).

A critical first step is to identify candidate parasitoids or predatory insects (Mills 2005). Then suitable rearing conditions must be determined so that insects develop normally but are not conditioned to the wrong stimuli (Bigler 1989, Roitberg *et al.* 2001). A suitable sensory cue must then be applied at the appropriate point in the insect's life history (e.g., at emergence or during a first oviposition experience) to ensure a persistent learned association. Assuming sufficient numbers of insects are available, timing for release is critical (Yang *et al.* 2006, Ovruski and Schliserman 2012, Pfab *et al.* 2018). If release occurs too early, no target hosts will be available, and parasitoids will disperse, or subsequent learning experiences will supersede the unreliable memory. If release occurs too late, the pest species will become too firmly established for parasitoids to effectively mitigate.

Host-insect and crop-plant semiochemicals can mediate host recognition in parasitoid wasps and improve host specificity, but effective semiochemical blends will differ depending upon parasitoids, host insects, and crops (Hare *et al.* 1993). Identifying and synthesizing effective semiochemical blends in sufficient quantities for pest management can be challenging (Hare *et al.* 1997). Costs associated with rearing, conditioning, and releasing parasitoids for pest control can also be a limiting factor for widespread use of this pest management strategy (Stevens *et al.* 2000).

### Unintended Conditioning

The environment in which parasitoids and predatory insects are mass released or encouraged through attractant semiochemicals can become sources of information about risk for the pest insects upon which they prey (Wisenden *et al.* 1997). Bumblebees (*Bombus* spp.), cockroaches (Blattodea), and flies (Diptera) can learn to identify cues that signal predators, suggesting that risk aversion learning is common among many insect species. (McCall and Eaton 2001, Durisko and Dukas 2013, Dawson and Chittka 2014). In the absence of sufficient prey species, mass-released parasitoids may learn new olfactory associations that can override initial conditioning (Lewis *et al.* 1990, Grasman *et al.* 2001).

## Future Directions for Pest Management

### Direct Use of Insect Learning

Insect learning is already in use in many mass-release programs involving parasitoids. Improvements in efficacy, specificity, and memory duration could be achieved by introducing temporally

spaced reinforcement conditioning experiences or supplementing host-odor associations with host-plant odors, particularly herbivory-induced plant odors (Steidle 1998, Ueno and Ueno 2005, Kim *et al.* 2007, Frost *et al.* 2012, Liu and Sakuma 2013, Giunti *et al.* 2015). Augmenting conditioning experiences with ferulic acid eicosyl ester, a component compound in the medicinal plant *Rhodiola rosea* Linnaeus (Saxifragales: Crassulaceae) used to improve human neurological function, could enhance memory function in diverse species (Michels *et al.* 2018). Conditioning parasitoids to multiple stimuli, including olfactory or visual cues associated with target hosts and plant crops, can have a synergetic effect on host specificity and encourage site fidelity within the crop area, reducing loss of parasitoids to dispersal (Lewis and Martin 1990, Gandolfi *et al.* 2003b, Giunti *et al.* 2015).

Endemic parasitoids and predatory insects could be reared and conditioned to prey on invasive species as they are introduced. In many cases, biological control efforts to eradicate invasive pest species have involved the use of introduced parasitoids or predators that might themselves become an invasive pest or prey on endemic benign species. Using conditioned endemic predators to control invasive pest could pose less risk to the existing ecosystem.

### Indirect Use of Insect Learning

We can use our knowledge of how insects learn to develop more effective planting and pesticide use strategies and integrate the use of chemical repellents. Because repeated positive experiences can reinforce a conditioned response but experiencing a different or negative response following the same stimuli can reduce the reliability of information, crop rotation programs, and intercropping could disrupt associative learning of potential host plants (Papaj and Prokopy 1989, Meller and Davis 1996). Periodic changes in pesticide use could interrupt development of habituation or aversive learning by pest insects.

Studies on the effects of sublethal doses of chemical pesticides, primarily on honeybees, demonstrate long-term chemical-induced interference with insect learning (Aliouane *et al.* 2009, Frost *et al.* 2013, Samuelson *et al.* 2016, Klein *et al.* 2017, Tison *et al.* 2017, Siviter *et al.* 2018). Application of chemical pesticides during nonflowering periods (to reduce risk to pollinating insects) could result in similar learning and memory deficiencies in pest insects, preventing them from learning cues associated with suitability of novel crops as a potential host. Careful study is required to ensure that any potential benefits in limiting pest insect learning are not outweighed by risks to beneficial insects.

Use of sterile males is a useful strategy to mediate a variety of insects; however, results can vary among species or populations and are limited among insect species that mate with multiple partners (Fitz-Earle and Sakaguchi 1986). Many parasites and bacterial or viral pathogens are known to affect changes in host behavior, survival, resistance, and fecundity (Hurst and Jiggins 2000, Goodacre and Martin 2012). Bacteria could be identified or modified to restrict mushroom body development in host insects and thereby also limit potential for learning. Using sterile males as an initial bacterial vector, transmission could continue during mating, maternal transfer, or through contact with infected eggs, larvae, or adults (Ebbert 1995). As infection spreads through a target insect population, the ability of that insect species to learn and remember cues associated with food sources could be limited.

### Beneficial Insects

Increased understanding of the impacts of pesticides and pest management methods on health and cognitive ability of pollinators and



other beneficial insects can inform the development of targeted pest management strategies. Neonicotinoid and pyrethroid pesticides reduce cognitive function, learning, and memory in *A. mellifera* honeybees (Aliouane *et al.* 2009, Frost *et al.* 2013, Samuelson *et al.* 2016, Klein *et al.* 2017, Tison *et al.* 2017, Siviter *et al.* 2018). Timing of pesticide applications, choice of pesticides for use during each application, and potential alternatives to pesticides should be considered.

Honeybees are susceptible to a wide variety of parasites, including *Varroa destructor* Anderson and Trueman (Parasitiformes: Varroidae) mites. These mites parasitize primarily pupal stages of developing honeybees. Bees that experienced parasitism during pupal development become habituated to odor stimuli more quickly, become sensitized to new odors more slowly, and are less responsive to non-associative learning experiences (Kralj *et al.* 2007).

### Biocontrol of Weed Plants

Classical biological control of invasive undesirable plant species (weeds) uses the intentional release of introduced phytophagous insect species as a biological control measure (Harris 1988). Prior to release, local regulators usually require that these insect species are tested for host acceptance and survival on a variety of commonly occurring native and crop plants; however, these represent only a small proportion of commonly occurring plant species in the release areas. Introduced insect species have been successful in reducing approximately one-third of the intended host weed-plant species; however, many introduced species also feed on native or crop plants (Harris 1988, Denslow and Johnson 2006). Dispersal hundreds or thousands of kilometers outside the intended control region or learning to use alternative nontarget host species are additional concerns (Pemberton 2000, Pratt and Center 2012, Suckling and Sforza 2014). We can reduce this risk by using associative conditioning with native phytophagous insect species. A large proportion of invasive plant species are suitable alternate hosts to native insect species (Bezemer *et al.* 2014). Inducing conditioned changes in host preference to favor feeding on invasive plant species could result in a host-shift that may be as effective as using introduced insect species, but with less risk of adding additional environmental stress to native plant species.

### Conclusions

A first step in developing a long-term insect pest management strategy should be to acknowledge that insects can learn and will adapt. Integrated pest management strategies must evolve to remain effective. Insects can be both pest and benefactor in agricultural and forestry applications, disease vector control, and potentially in urban pest management. Learning by parasitoids and predatory insects can be mediated to help manage outbreaks of pest insects. Similarly, learning by phytophagous insects could be used to help control invasive plant species.

Current knowledge has given us the means to make significant gains in some areas of pest management, most notably using sensitization and associative conditioning of parasitoids for mass release against phytophagous pest insects. There is still much more that a knowledge of insect learning could contribute to biological control of pest insects (in agriculture, forestry, and urban settings), pest plants, and disease vectors.

Understanding mechanisms by which pest insects learn can inform the application of integrated pest management programs. It can give insight into means of modifying the conditions that allow insects to become pests. Growth in understanding of learning by beneficials, including predatory insects and pollinators, can help to offset detrimental effects of pesticides and toxic chemicals. Continued study of

learning by parasitoids and predatory insects can lead to advances in pest management strategies that are less environmentally harmful. Understanding life history, habitat variability, and propensity to learn of insects of interest as pests or beneficials can help to identify potential areas of susceptibility and improve overall efficacy of pest management efforts. Continued growth in our knowledge of insect learning will contribute to our efforts to follow the basic tenant of integrated pest management, to 'know your insect'. Learning is a journey, not a destination; even in insects.

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