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Advancing Undergraduate Laboratory Education Using Non-Model Insect Species

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Abstract

Over the past decade, laboratory courses have made a fundamental shift to inquiry-based modules and authentic research experiences. In many cases, these research experiences emphasize addressing novel research questions. Insects are ideal for inquiry-based undergraduate laboratory courses because research on insects is not limited by regulatory, economic, and logistical constraints to the same degree as research on vertebrates. While novel research questions could be pursued with model insect species (e.g., *Drosophila*, *Tribolium*), the opportunities presented by non-model insects are much greater, as less is known about non-model species. We review the literature on the use of non-model insect species in laboratory education to provide a resource for faculty interested in developing new authentic inquiry-based laboratory modules using insects. Broader use of insects in undergraduate laboratory education will support the pedagogical goals of increased inquiry and resesarch experiences while at the same time fostering increased interest and research in entomology.

Supplemental Material >

INTRODUCTION

In 2012, a report of the United States President's Council of Advisors on Science and Technology called for the infusion of inquiry into undergraduate laboratory courses (105). Inquiry in undergraduate laboratory courses can range from guided inquiry, in which the instructor poses the research question and guides students in their experimental design; to open-ended inquiry, in which students define the research question and experimental design; to course-based research, which tends to have a greater emphasis on novel research questions (5, 12, 134). In a 2014 review of published inquiry-based exercises, Beck et al. (12) found a greater emphasis on guided inquiry than on open-ended inquiry or course-based research. While data on the degree of implementation of inquiry in laboratory courses are somewhat lacking, the results of a survey of the membership of the Association of Biology Laboratory Education (ABLE), who predominantly teach in colleges and universities in the United States and Canada, suggested that inquiry is more common in upper-level courses than in introductory courses and is least common in courses for non-majors (2).

In addition to inquiry, the Vision and Change report (led by the United States National Science Foundation, the American Association for the Advancement of Science, and the Howard Hughes Medical Institute) advocated for research experiences for all students (1). Interest in this type of pedagogy reform is emerging in higher education worldwide because it is evidence based (66), and because the necessity for scientifically literate citizens and leaders is unavoidable. The transformation of science learning and teaching involves all aspects of instructional activity (lecture and laboratory courses), but we specifically focus on research experiences in this review.

Authentic research experiences and course-based undergraduate research experiences (CUREs) are an avenue for providing research experiences at a broad scale (5, 134). Authenticity in learning how to conduct biological research contrasts with traditional laboratory pedagogies, which make students passive participants in cookbook exercises in which experiments lead to the confirmation of known and correct outcomes. Authentic research experiences can vary in their emphasis on science process skills versus exploring novel research questions of interest to the broader research community (5, 134, 135). At one end of the spectrum of student autonomy, faculty define the research question, the experimental design, and the methodology (e.g., 122) (**Table 1**). At the other extreme, students are free to define all aspects of the research, bounded only by the discipline of the laboratory course (**Table 1**). Course-based research experiences with intermediate levels of student autonomy can be bounded or scaffolded by the instructor (**Table 1**). For example, Cotner & Hebert (31) have students read several primary research articles on sexual behavior in cowpea weevils (bean beetles) (*Callosobruchus maculatus*, Coleoptera, Chrysomelidae). Students then use these articles as a starting point for developing their own research questions. In other cases, students can complete a guided-inquiry module and then propose new research questions based on the results of their guided-inquiry experiment.

Approaches to undergraduate laboratory education are in the midst of a fundamental shift away from confirmatory and cookbook exercises toward authentic inquiry-based modules and CUREs, and the undergraduate education community is in need of resources for the development of new laboratory curricula and CUREs. Insects are ideal for inquiry-based undergraduate laboratory courses (64) because research on insects is not limited by regulatory, economic, ethical, and logistical constraints to the same degree as research on vertebrates (32, 86, 148). In addition, the relatively small body size of most insects makes their handling and maintenance in a laboratory much more tractable than those of any vertebrates. Yet they are large enough to be easily manipulated without magnification (or with magnification only under a dissection microscope), and students readily view them as animals with observable traits. Furthermore, insects are the most diverse and abundant animals on Earth, so no other group of animals offers the opportunity to study such a wide range of natural variation (32). Matthews et al. (86) reviewed the use of insects

Table 1 Different approaches to course-based undergraduate research experiences (CUREs) that vary in the degree of student autonomy, from high to low degree of student control

Research question defined by. . .	Experimental design defined by. . .	Bounded by. . .	Explanation	Examples
Student	Student	Subdiscipline	Student groups define the research question and experimental design, but the research must be in a particular subdiscipline (e.g., ecology).	Independent research projects in a laboratory course
Student	Student	Previous guided inquiry experiment	Student groups define the research question and experimental design based on the results of a previous guided-inquiry experiment that they conducted.	Bean beetle oviposition substrate choice (36), pollination ecology (99)
Student	Student	Faculty-selected research paper	Instructor provides several research papers on a particular topic. After reading and discussing the papers, student groups define the research question and experimental design.	Bean beetle reproductive behavior (31)
Faculty	Student	Faculty research interest	Instructor defines the research question based on research interest or pedagogical goal, but student groups design the experiment.	Ant and butterfly pollination (94)
Faculty	Faculty	Faculty research interest	Instructor defines the research question and experimental design.	Genomics Education Partnership (122)

in teaching at the primary and secondary school levels. In this article, we review the use of model and non-model insects in laboratory education at the undergraduate level. In particular, we focus on the opportunities for authentic research in laboratory courses using non-model insects.

USE OF MODEL INSECTS IN UNDERGRADUATE LABORATORY EDUCATION

Drosophila

Drosophila melanogaster (Diptera, Drosophilidae) has been the go-to model insect system for the study of Mendelian genetics for more than a century, and much of our modern understanding of the fundamental concepts of independent assortment, linkage and recombination, and sex linkage originated with studies of this species. *Drosophila* is still an ideal organism for authentic genetics research in undergraduate laboratories, but studies have become much more sophisticated. For example, a heat-shock gene can be used to more efficiently conduct Mendelian studies (142). The entire *Drosophila* genome has been sequenced, but original research remains to be conducted annotating individual genes in this genome, which is the focus of the Genomics Education Partnership (122). Once genes have been identified, new avenues of research become possible, such as evaluating variation in gene or protein function (100, 104, 132) and the relationship between specific proteins and physiological-developmental processes (40, 74, 107, 127). *Drosophila* continues to be an excellent model organism for studying evolutionary processes (17, 23, 35), as well as behavioral (59), physiological (68), and microbiome responses (129) to the environment. Many strains of *Drosophila* are commercially available, along with culture materials and supplies. Anesthesia is essential for most work with adult flies, but alternative forms of fly anesthesia (145) and even use of flightless strains (28) may make course-based research with *Drosophila* more tractable.

The research literature contains many examples of *Drosophila* studies in which molecular biology techniques have been used to silence specific genes or to introduce novel genes to study functional genomics (91). Studies that plan to create or utilize genetically modified organisms may require prior regulatory approval to ensure biosafety containment.

Tribolium

Tribolium (Coleoptera, Tenebrionidae) first emerged as a model system in ecology in the mid-1920s (24). Since then, it has been used as a model to study classical genetics, population genetics, host–parasite coevolution, comparative development, physiology, and control of insect pests (24). In addition, *Tribolium castaneum* was one of the first insect species whose genome was completely sequenced (110). In a recent Web of Science topic search of "Tribolium," we found over 5,500 references, suggesting an extensive research literature.

Since *Tribolium* is commercially available and easy to rear in the laboratory, educators have used it in undergraduate laboratory teaching. For example, modules have been developed that examine population growth (124) and life history traits (3). In addition, Yezerski (149) proposed using *Tribolium* for molecular genetic linkage mapping. While *Tribolium* lends itself to inquiry-based laboratory modules, novel course-based research with *Tribolium* will require prior literature research, since many basic research questions have already been addressed.

NON-MODEL INSECTS IN UNDERGRADUATE LABORATORY EDUCATION

Important Characteristics of Non-Model Insects for Teaching

Model insect species, such as *Drosophila* and *Tribolium*, have been widely used in research and teaching, but use of non-model insects has potential advantages over use of model species. In particular, in courses emphasizing authentic research experiences, non-model species are relatively unexplored territory, allowing ample opportunities for undergraduates to conduct original and scientifically significant research on these species. In addition, a given non-model insect species may be very tractable for research in multiple biology disciplines (see sidebar titled Multidisciplinary Course-Based Research). Although most of the non-model insects that we describe below are used in research labs and might even be considered model species for research in particular areas, in many cases, basic research questions remain unanswered.

MULTIDISCIPLINARY COURSE-BASED RESEARCH

Working with non-model insect species in course-based research has the added benefit of providing opportunities to use the same insect in more than one course, exploring different systems or different biological processes. For example, students in an ecology course might evaluate the feeding choices of tobacco hornworms (*Manduca sexta*) on tobacco plants whose chemical defenses were induced by various levels of leaf damage. The same insects could be the subjects of a study in a physiology course evaluating the effects of plant secondary compounds on metabolism and a study in a microbiology course examining the effects of plant secondary compounds of the digestive tract microbiome communities. Giving students the opportunity to study the same species across a range of laboratory courses, in a variety of biology subdisciplines, and using different experimental methods and instrumentation would permit scaffolding of learning, which is less likely when courses are taught in isolation. Furthermore, such research permits students to use findings from their fellow students to inform and enrich their own research studies. Whether such a multidisciplinary approach to course-based research would yield better student learning than would otherwise occur is unknown and could be the subject of a worthy education research study.

Non-model insects that lend themselves to undergraduate laboratory courses have several characteristics (**Table 2**). First, many of these species can be cultured without prepared media and are inexpensive to raise in large numbers. Second, they have generation times that are very rapid (a few weeks) at room temperature, which is important given the time constraints of academic semesters, and can be maintained without specialized equipment or incubators. Third, most of these animals are not hazardous, are not human disease vectors, and can be disposed of by simply freezing cultures. Fourth, a wide variety of non-model insect species are commercially available at all times of the year or may be collected in their natural environment. Fifth, many non-model species are easily handled without the anesthesia required for handling *Drosophila*. Finally, unlike *Drosophila* and *Tribolium*, many non-model insects have sex differences that are very easily observed by undergraduate students.

Non-Model Insect Species

Blattodea.

Termites. In many introductory biology courses for both majors and non-majors, one of the first inquiry-based laboratory modules helps introduce students to the scientific method. A classical module for this first laboratory period involves trail following in subterranean termites in the genus *Reticulitermes* (Blattodea, Rhinotermitidae) (33, 88). Some, but not all, brands of ink pens include chemicals that mimic termite pheromones, such that termites will follow the ink line (88). In addition to simple behavioral experiments, termites have been used for studies of symbionts and nutritional mutualisms (96). These studies can be expanded with linkages to termite physiology and nutrient cycling in ecosystems (30). In addition, termites and their symbionts could be used for experiments related to the production of cellulases that might have commercial applications (119). Furthermore, as eusocial insects, termites can be used to further our understanding of social insects (138). Even simple molecular biology techniques that could be implemented in upper-level laboratory courses have been important in contributing to our understanding of the basic biology and ecology of termites (141). Subterranean termites are commercially available or can be easily collected in the field from damp, decaying logs (88).

Other Blattodea. Cockroaches have been widely used in inquiry-based laboratory modules on physiology (16, 78, 130, 143). However, many students might have an aversion to cockroaches that would limit their use in a teaching context. As a result, the giant Madagascar hissing cockroach (*Gromphadorhina portentosa*, Blaberidae) has become more popular as a model system and has been used to study vector ecology (62) and ecological energetics (123).

Coleoptera.

Bean beetles. Bean beetles, also known as cowpea weevils (*Callosobruchus maculatus*, Chrysomelidae), are seed beetles that lay eggs on dry legume seeds (Fabaceae). They are tropical and subtropical stored product pests with worldwide distribution (7). As a result, a vast agricultural research literature focuses on control of bean beetles and resistance of their legume hosts to infestation. In addition, bean beetles have been used as a model system for ecological and behavioral research.

Adult beetles are small (4–6 mm) and sexually dimorphic (in the sedentary phase), and females glue their fertilized eggs individually onto the surface of host seeds (7). The larva that develops in the egg is not free living and tunnels into the endosperm of the seed on which it was deposited. All larval development occurs in the host seed, as does pupation. Following metamorphosis, an adult

Table 2 Characteristics of non-model insect species for undergraduate laboratory education

Species	Commercially available?	Easily reared?	Adult size	Development time at 25°C	Food or media requirements	References
Blattodea						
Termites	Yes	Yes	Moderate	NA, worker castes will not reproduce	Rotting wood	30, 33, 88, 96
Cockroaches	Yes	Yes	Large	Months	Bread, apple, potato, rolled oats, dry dog food	16, 62, 78, 123, 130, 143
Coleoptera						
Bean beetles	Yes	Yes	Small	3–4 weeks	Dry bean seeds	8–11, 14, 18, 19, 26, 29, 48–50, 75, 80, 98, 101, 108, 131, 133
Fireflies	No	No	Moderate	NA, must be field collected	NA	81–84
Soldier beetles	No	No	Moderate	NA, must be field collected	NA	41
Burying beetles	No	No	Large	NA, must be field collected	NA	139
Ladybird beetles	Yes	No	Moderate	10 weeks	Live aphids	53
Mealworm beetles	Yes	Yes	Moderate	Months	Wheat bran meal or flour	90, 150
Diptera						
Gall-forming flies	No	No	Small	NA, must be field collected	NA	25, 89, 95, 117
Hover flies	No	No	Moderate	NA, must be field collected	NA	55
Flesh flies	Yes	Yes	Moderate	3 weeks	Rotting meat	54
Hemiptera						
Aphids	No	Yes	Small	2 weeks	Live host plant	6, 111, 125
Milkweed bugs	Yes	Yes	Large	4–5 weeks at 30°C	Sunflower seeds	103
Hymenoptera						
Jewel wasps	Yes	Yes	Small	2 weeks	Flesh fly pupae	13, 70, 146
Melittobia	Yes	Yes	Small	18–21 days	Flesh fly pupae	13, 60, 61, 87
Ants	Yes	Yes	Moderate	Months and requires queen	Species specific	34, 52, 116, 137, 153
Bees and wasps	No	No	Large	NA	NA	85, 120
Lepidoptera						
Tobacco hornworms	Yes	Yes	Large	4–5 weeks at 27°C	Host plants or prepared media	20, 37, 109, 114
Cabbage white butterflies	Yes	Yes	Large	4 weeks	Mustard plants or leaves	140, 152

(*Continued*)

Table 2 (*Continued*)

Species	Commercially available?	Easily reared?	Adult size	Development time at 25°C	Food or media requirements	References
Orthoptera						
Brown crickets	Yes	Yes	Large	Months	Dry dog food and apple slices	113
Locusts	No	No	Large	NA, must be field collected	NA	121

Commercial availability is based on vendors in the United States. Adult size is categorized as small (<10 mm long), medium (1–2 cm long), or large (>2 cm long). Development time is from eggs to mature adults. Food or media requirements refer to foods necessary to rear insects from eggs to adults. Development times and food or media requirements for many species may be found in the Carolina Arthropods Manual (**https://www.carolina.com/teacher-resources/Document/arthropods-care-handling-instructions/tr10467.tr**). Abbreviation: NA, not applicable.

chews out of the seed and emerges. Adults do not require food or water; all nutrition is obtained in the larval stage. Sexual maturity is completed 24–36 h after adult emergence, and females may mate with multiple males. Development time may be as rapid as three weeks at 30°C, but slows to four weeks at 25°C or longer depending on the seed host species. Normal development will occur on at least eight different host species [mung beans (*Vigna radiata* or *Phaseolus aureus*), black-eyed peas or cowpeas (*Vigna unguiculata*), adzuki beans (*Vigna angularis*), pigeon peas (*Cajanus cajan*), chickpeas or garbanzo beans (*Cicer arietinum*), hyacinth beans (*Lablab purpureus*), green peas (*Pisum sativum*), and lentils (*Lens culinaris*)] of readily available beans, but many species are toxic to the beetles (see **http://www.beanbeetles.org**). The sedentary (non-flying) sexually dimorphic phase that develops at temperatures less than 30°C is easily handled without anesthesia and may be slowed on a cold stage. A dispersal (flying) sexually monomorphic phase develops under crowded conditions and temperatures greater than 30°C. Detailed instructions on culturing and handling bean beetles is available (**http://www.beanbeetles.org**), and cultures are commercially available on three different host species.

More than 30 class-tested laboratory studies are available (**http://www.beanbeetles.org**) for inquiry-based laboratory courses in ecology and behavior (8, 10, 14, 18, 98, 101, 133), evolution (9, 11, 19), physiology (26), development (75, 80), genetics (108, 131), and biochemistry (48–50). Opportunities for molecular genetics studies have been aided by the recent publication of the complete genome sequence (118), which is available for BLASTing (**http://www.beanbeetles.org**). CUREs, such as microbiome research (29), are also very tractable with this species. The ease with which this species is raised in the laboratory and handled by students (7) makes it particularly attractive for introductory biology courses, even with non-science majors (31).

Other Coleoptera. In addition to the cowpea weevil (bean beetle) (*C. maculatus*), which is well-established in inquiry-based teaching at the undergraduate level, several other coleopterans are good non-model insects for teaching. For example, fireflies (Lampyridae) have been suggested as models for studies of natural history, behavior, and evolutionary ecology (81–84). Similarly, soldier beetles (*Chauliognathus pennsylvanicus*, Cantharidae) and burying beetles (*Nicrophrous tomentosus*, Silphidae) have been used to explore sexual selection in undergraduate laboratory courses (41, 139). Ladybird beetles (Coccinellidae) can be easily collected in the field or ordered through commercial suppliers. As a result, they are an amenable system for research in basic ecology and behavior, as well as studies on predatory interactions with aphids and host–parasitoid interactions with braconid wasps (53). Geoghegan (53) suggested a range of tenable research questions related to Coleoptera. Finally, the mealworm beetle (*Tenebrio molitor*, Tenebrionidae) and superworms (*Zophobas morio*, Tenebrionidae) are also commercially available and easily reared in the laboratory. They can be used for research on development, behavior, and physiology (90, 150). Superworms may be maintained as larvae for long time periods (weeks to months), making them suitable for long-time-course experiments, and a related species (*Zophobas atratus*) was found to harbor microbiome bacteria that degrade polystyrene (71). In addition, genetics and comparative genomics are possible avenues of research due to the close evolutionary relationship between the mealworm beetle and the flour beetle (*Tribolium*), which is a well-developed model system.

Diptera. While *Drosophila* is clearly the most pervasive dipteran model species for research and teaching, other fly species have been suggested for field and laboratory courses. In ecology courses, gall-forming and leaf-mining flies have been used in studies of population ecology and behavior (25, 89, 95). In addition, Sandro & Lee (117) proposed using larvae of the goldenrod gall fly (*Eurosta solidaginis*, Tephritidae) as a model for research on freeze tolerance—an interdisciplinary research program that incorporates ecology, physiology, and biochemistry. Although students generally do not think about flies as important pollinators, hoverflies (Syrphidae) can be collected from a range of flower types, and experimental methods can be used to determine what types of pollen they consume, allowing students to study pollination ecology (55). In addition to flesh flies (*Sarcophaga bullata*, Sarcophagidae) being used as hosts for some parasitoid wasps (*Nasonia*, *Melittobia*), the larval stage exhibits phototropic locomotor responses that have been used to investigate the role of light wavelength in this behavior (54).

Hemiptera.

Aphids. Species of aphids (Aphididae) have been widely studied due to their agricultural importance. However, they have been used less frequently in an undergraduate teaching context. Sharp & Andrade (125) suggested using pea aphids (*Acyrthosiphon pisum*) for behavioral studies. In addition, pea aphids have been used to allow students to explore species interactions with aphid predators, such as lacewings and ladybird beetles (111). Field observations of aphids have been proposed as a means of exploring population structure in terms of spatial dispersion (6). Aphids can be collected from the field and maintained in the laboratory (125). Parthenogenetic reproduction allows for production of large numbers of genetically identical clones. Furthermore, the genomes of several aphid species have been sequenced (**https://bipaa.genouest.org/is/aphidbase/**), making possible research related to genetics and genomics. Aphids also host obligate and facultative symbionts, which would allow students to explore research questions related to mutualisms (97).

Milkweed bugs. *Oncopeltus fasciatus* (Lygaeidae) is another hemipteran that is conducive to undergraduate laboratories. Although milkweed bugs are commercially available and long-established for research purposes (46), few inquiry-based laboratory modules using them as a model have been published. Podwall et al. (103) suggested using them for a variety of behavioral assays. Milkweed bugs are a hemimetabolous species, which makes them an ideal comparison species to other holometabolous insects for studies of development. In addition, genomic resources for milkweed bugs are being developed (**https://www.hgsc.bcm.edu/arthropods/milkweed-bug-genome-project**).

Hymenoptera.

Nasonia vitripennis. The jewel wasp (*Nasonia vitripennis*, Pteromalidae) is a small (2–3 mm) haplo-diploid parasitoid wasp that has been established as a model system for research in developmental and evolutionary genetics (146), as well as an alternative to *Drosophila* in genetics laboratory exercises (70). While the majority of research has focused on genetics, *Nasonia* is also a useful model system for exploring species interactions, such as interspecific competition, as they share hosts with other parasitoid wasp species (13). Avenues of future research include genetics, developmental biology, ecology and behavior, and evolutionary genetics and speciation (146). More specific suggestions of research directions are available (**http://www.sas.rochester.edu/bio/labs/WerrenLab/WerrenLab-NasoniainUndergraduateTeachingandResearch.html**). *Nasonia* are commercially available and can be easily reared on flesh fly (*S. bullata*) pupae. For details on rearing and use of *Nasonia*, the reader is referred to Werren & Loehlin (146).

Melittobia digitata. *Melittobia digitata* (Eulophidae), a species of small (1–1.5 mm) parasitoid wasps, has been the focus of behavioral ecology research on topics such as sex ratio evolution and local mate competition (87). In the context of undergraduate laboratory courses, *Melittobia* is a model for students to examine simple behaviors (60, 61). In addition, *Melittobia* and *Nasonia* have been used to evaluate interspecific competition (13). As *Melittobia* has traits similar to social insects, Matthews et al. (87) suggested it as an ideal model for evolutionary ecology research. In addition, its short generation time (just over two weeks) and haplo-diploidy indicate its utility for studies in genetics and development (87). Specific research questions about this species have been suggested by Matthews et al. (87). Like *Nasonia*, *Melittobia* is commercially available and can be easily reared on flesh fly (*S. bullata*) pupae. For details on rearing and use of *Melittobia*, the reader is referred to Matthews et al. (87). The flesh fly pupae that are necessary for rearing *Melittobia* and *Nasonia* may be purchased commercially, thereby avoiding the need to maintain *Sarcophaga* cultures on rotting meat or carrion.

Other Hymenoptera. Ants (Formicidae) are nearly ubiquitous in the environment and are often easily collected. As a result, they make an ideal model system for undergraduate teaching. Like termites, ants have been used in basic behavioral assays, such as pheromone trail following, to teach basic aspects of experimental design (92) and can be used to teach basic observational skills (116). In upper-level animal behavior courses, ants have been used for experiments on kin recognition (137). In addition, ants can be used to explore ecological principles, such as habitat choice (52) and nutrient cycling (153). Since ants collected in the field will most likely be workers, the life span of individuals may be compromised, and some behaviors may be abnormal, depending on the species collected. Rearing an ant colony is made possible by collecting an inseminated queen (116) or purchasing commercially available ant queens. Guidance on ant colony rearing may be found at AntsCanada (**https://www.antscanada.com/starting-your-ant-colony/**) and in the work of Czechowski & Pisarski (34).

Bees and wasps (Hymenoptera), with the exception of parasitoid wasps such as *Nasonia* (70, 146), *Melittobia* (13, 60, 61), and *Leptopilina* (51), are less commonly studied in undergraduate laboratory courses, likely due to the difficulty in collecting and maintaining them, as well as the fact that many species sting. However, these factors do not preclude their use in undergraduate teaching. Bees are most easily studied in the context of plant–pollinator interactions (120), although students would need to be trained in basic identification. Focusing on particular bee taxa and participating in citizen science projects, such as Bumble Bee Watch (**https://www.bumblebeewatch.org/**), reduce these barriers to studying bees. Among non-parasitoid wasps, mud daubers (Sphecidae) lend themselves to studying ecological interactions because their nests are widely available and easily collected (85). Matthews (85) provided information on how to identify mud daubers and other insect taxa often found in mud dauber nests.

Lepidoptera.

Manduca sexta. The tobacco hornworm, *Manduca sexta* (Lepidoptera, Sphingidae), has a very large larval stage (approximately the diameter of a human thumb and as long as 70 mm in late larval instars). Its large size and the possibility of raising individuals on either live plants or an artificial diet make it very tractable for laboratory studies. Furthermore, eggs, larvae, and pupae are commercially available year-round. Recent undergraduate laboratory modules include using tobacco hornworms in bioassays (20, 109), studies on endocrinology (114), and research on the cell biology of host–parasitoid interactions (37). The literature on *Manduca* is extensive and is summarized in numerous articles in the *Annual Review of Entomology* on research topics as varied as development, biochemistry, physiology, sensory perception, interactions with parasitoids, and endocrinology. Thus, there is ample research literature on which to build meaningful course-based research. A draft genome assembly for *Manduca sexta* is available (**https://i5k.nal.usda.gov/Manduca_sexta**), which would facilitate course-based research in genetics and genomics.

Other Lepidoptera. Lepidopterans are likely the most charismatic and well-known of insect species. As a result, they represent a good entry into research with insects. As described above, the tobacco hornworm (*M. sexta*, Sphingidae) is a well-established leptidopteran species for research and teaching. The cabbage white butterfly (*Pieris rapae*, Pieridae) is another commercially available species that is easily reared in the laboratory. It has been used in behavioral studies (140) and has been suggested as an alternative to beet armyworms (*Spodoptera exigua*, Noctuidae) in studies of plant–herbivore interactions (152). Because many butterfly species can be easily identified, students can conduct research in pollination ecology and contribute to citizen science research (77, 120). In addition, genome sequences of all North American butterflies have now been completed (154), making possible research in comparative genetics and genomics.

Orthoptera. Orthopterans, such as crickets and locusts, can be easily collected in the field, and some species (e.g., the brown cricket, *Acheta domesticus*) are available at pet stores. Crickets have been used as a model system for studying sexual selection and can be used for other areas of behavioral research (113). Both crickets and locusts exhibit developmental polymorphisms, which makes it possible to ask research questions at the intersection of ecology, evolution, and development (113). Finally, locusts have been suggested as a model for studying biomechanics and muscle physiology because of their pronounced jumping ability (121).

Other Undergraduate Laboratory Studies with Non-Model Insect Species

Field studies with non-model insect species. Field studies represent a broad category of research that is highly accessible to students, since such studies are typically conducted in the local natural environment. As natural environments vary across space and time, field studies will always generate novel findings. Furthermore, since insects are among the most abundant and easily observed animals in both terrestrial and aquatic (freshwater) ecosystems, field studies on these communities are very tractable (22, 102). Similarly, direct observation behavioral studies on insects in their natural environment are often very easily conducted (4, 52, 53, 55, 56, 73, 77, 92, 94, 99, 120, 136).

The identification of insect species is often fundamental to field studies. Smart phone apps (e.g., iNaturalist.org and Picture Insect) potentially make identifications in the field possible and may assist students in documenting insects observed in field studies. Insects collected as a part of a field study may be identified using traditional keys, as well as online tools (e.g., bugguide.net). In addition, insect identification has become an opportunity to bring molecular biology and genetics into the study of systematics and ecology through DNA barcoding (e.g., 27, 69).

Field studies that document taxon richness and relative abundance of insects in a community (21, 42, 45, 102, 106) are both scientifically valuable and tractable. Such studies often require little more than collection nets, drop traps, or Berlese funnels (42). A recent European study (65) indicating dramatic declines in insect abundance and diversity in the past three decades suggests that such basic studies are extremely important in a world being transformed by climate change, urbanization, and changing farming practices.

Field studies with insects can often be linked to other aspects of ecology. For example, the use of leaf packs in mesh bags in both terrestrial and aquatic ecosystems is an elegant means of studying the role of insects in decomposition and nutrient cycling (39). Interactions between species (reviewed below) are also important processes in shaping biological communities, and non-model insect species are often ideal for course-based research studies of competition, predator–prey relationships, and anti-predator adaptations (22, 63, 67). Non-model insects are also ideal for studies exploring the behavior diversity of social insects (56). Finally, students can be introduced to the invisible microbial communities that are associated with all metazoans through research on insect microbiomes (29).

Species interactions with non-model insect species. Interactions between species, such as competition, predator–prey relationships, and mutualisms, may all be readily studied in nature with non-model insect species. Research on competition is possible with non-model insect species for which there is a well-defined, limited resource that is easily manipulated. For example, interspecific competition can be examined in parasitoid species that use the same host (13). In addition, intraspecific competition among larvae in a seed can be studied in bean beetles (*C. maculatus*) because different numbers of eggs are laid on individual seeds (8). Plant–herbivore interactions may be studied in nature in almost all terrestrial habitats (15, 43, 115, 147, 152). Similarly, studies of plant–pollinator relationships are possible in almost any habitat in which flowering plants are present (4, 73, 94, 99). Such studies could elucidate the dynamic nature of cases of predation that have become mutualism (99). Last but not least, non-model insect species are ideal subjects for course-based research on predator–prey interactions (67, 136) and host–parasitoid interactions (87, 146). The vast research literature on host–parasite interactions in insects and their use in integrated pest management (e.g., on parasitic bacteria, fungi, protozoans, and nematodes) also provides a resource for authentic course-based research opportunities.

Physiological studies with non-model insect species. While vertebrate animals are often used in physiology laboratory courses, invertebrates, including insects, offer several advantages over vertebrates for these classes even beyond the animal use and care issues (38, 144). Deyrup-Olsen & Linder (38) noted four advantages to using invertebrates for physiology laboratories. First, physiological processes are often simpler in invertebrates, and therefore, basic physiological principles are easier to observe. Second, experiments in comparative physiology are easier with invertebrates, as they have greater variation in physiological processes than do vertebrates. Third, experiments are easier to perform with invertebrates, as specialized conditions are not necessary to observe physiological processes. Finally, and perhaps most importantly in terms of course-based research, much less is known about the physiology of non-model insects compared to vertebrates, allowing greater opportunity for student research.

In undergraduate physiology laboratory courses, insects are most widely used to examine sensory, nervous, and muscle systems. Silver & Smith (126) suggested examining photoreceptors in cockroaches, flies, or dragonflies. More recently, Krans et al. (72) described how to produce micromanipulators to study retinal physiology in houseflies and flesh flies. Similarly, Robertson (112) showed how students can use simple equipment to record the response of stretch receptors in locusts. Cockroaches are often used for recordings of action potentials (78, 79) and would lend themselves to experiments on factors that influence neural activity. As noted above, orthopterans are ideal models for studying muscle physiology because of their jumping behavior (121). In addition, houseflies have been used to examine the integration of sensory and motor systems (58).

Insects have relatively simple digestive systems compared to some vertebrates. In larger insects, such as cockroaches, removal of the digestive tract is straightforward, and students can examine the distribution of digestive enzymes (143). Cockroaches have also been used for studies of insect circulatory systems (130) and immune systems (151). Similar to digestive systems, the excretory systems of insects (Malpighian tubes) are simple physiological systems. As a result, students can conduct research on nitrogen excretion and active transport without sophisticated instrumentation (57, 128). Insects are also commonly used to examine factors that influence metabolic rates in ectotherms (76, 90, 93). In addition, Motten (93) suggested linking cellular processes to metabolism in flight muscles using honeybees (*Apis mellifera*, Apidae) as a model. Development in insects is well-described and easy to observe. As a result, insects lend themselves to research in endocrinology, particularly hormonal control of development (47, 114).

In addition to research on physiological systems, insects have been used in undergraduate laboratory courses for studies of enzyme biochemistry. Erwin et al. (44) described isolation of aminotransferases from insect cell lines. Furthermore, the role of acetylcholine esterase in bean beetles (cowpea weevils) has been studied extensively in a series of laboratory modules (48–50).

CONCLUSIONS AND FUTURE DIRECTIONS

As laboratory courses continue to shift toward an increase in inquiry and authentic research, non-model insects will become more prevalent in undergraduate laboratory courses, as they provide students with the opportunity to pursue novel research questions. This broader use of insects in undergraduate laboratory education will have the added benefit of fostering increased interest and research in entomology. The non-model insects described above are clearly not inclusive of all of the insect species that are the subject of active research. This suggests opportunities for research entomologists to collaborate with educators to develop curricular materials to bring new non-model insects into undergraduate laboratory courses. Such collaborations have the potential to lead to new authentic research experiences for students and new data on which researchers can build.

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