ANNUAL REVIEWS

*Annual Review of Entomology*

# Pest Elaterids of North America: New Insights and Opportunities for Management

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Annu. Rev. Entomol. 2024. 69:1–20

First published as a Review in Advance on August 10, 2023

The *Annual Review of Entomology* is online at ento.annualreviews.org

https://doi.org/10.1146/annurev-ento-120220-123249

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## Keywords

wireworm, integrated pest management, IPM, subterranean pest, soil health, click beetle

## Abstract

The larval stages of click beetle (Coleoptera: Elateridae) species, several of which are serious agricultural pests, are called wireworms. Their cryptic subterranean habitat, resilience, among-species differences in ecology and biology, and broad host range, as well as the lack of objective economic injury thresholds, have rendered wireworms a challenging pest complex to control. Significant progress has been made in recent years, introducing a new effective class of insecticides and improving species identification and our understanding of species-specific phenology, chemical ecology (i.e., adult sex pheromones and larval olfactory cues), and abiotic and biotic factors influencing the efficacy of biological control agents. These new developments have created opportunities for further research into improving our risk assessment, monitoring, and integrated pest management capabilities.

# INTRODUCTION

Wireworms are subterranean larvae of click beetle species (Coleoptera: Elateridae) that primarily feed on underground tissues of cultivated and noncultivated plants. There are approximately 10,000 species of click beetles (Coleoptera: Elateridae) globally, with approximately 100 known as pests of crops at their larval stage (134). Failed emergence, wilting, delayed growth, and death of crop plants reflect direct feeding damage by wireworms (117).

The adult beetles are typically <2.5 cm in length, slender, and dark and, depending on the species, may bear color patterns. The adults emerge from the ground in the spring to mate and lay eggs near the soil surface (4). The larvae can live in the soil for several years, depending on the species and environmental conditions (134). Wireworms evade unfavorable temperature or moisture by moving deeper into the soil until they can resume activity (117).

Their multiyear life cycle, cryptic living habitat, resilience, and voracious feeding on a broad range of crops make wireworms a formidable pest to manage. The reliance on broad-spectrum insecticides as a generic control method contributed to overlooking the species-specific ecology and biology for decades (73); however, knowledge of these species-specific factors is critical for developing effective integrated pest management (IPM) protocols. In this review, we introduce predominant pest species in Canada and the United States and provide an overview of advances in our understanding of their ecology and management in the recent decade. The existing challenges and areas requiring further research are discussed.

# SPECIES COMPLEXES IN NORTH AMERICA

## Identification

Species identification of larvae has long been limited by the paucity of morphological descriptions and the similarity between closely related species (for a review, see 134). Most taxonomic keys are region or genus specific and do not include descriptions of nonpest species, and there is currently no key to the larvae of all North American pest species. The increased use of molecular tools for identification has now shown that some long-established species concepts, such as *Hypnoidus bicolor* and *Limonius californicus*, consist of multiple haplotypes and/or cryptic species, with the relative abundance of these forms varying between geographic regions and with farming practices (3, 11, 26, 34). Further research is required to determine if the different haplotypes differ in their behavior, life histories, and response to management approaches (3). Further work is also required to develop reliable, species-specific primers for all pest species, which would allow for the rapid identification of larvae in the field and correlation of larval and adult forms of poorly understood taxa (e.g., *Dalopius*, *Melanotus*). The rapid and accurate identification of pest versus nonpest larvae may help reduce unnecessary insecticide use (60).

## Biology and Distributions

The majority of pest wireworm species in Canada and the United States belong to six genera, some of which include introduced species (**Figure 1**).

***Agriotes*.** Pest species of this genus include *Agriotes sputator* in eastern Canada (27, 107, 133) and *Agriotes obscurus* and *Agriotes lineatus* in eastern Canada (27), British Columbia, and western Washington (128). All three species were introduced from Europe in the 1800s (135). Recent surveys show that these species are dispersing inland, with *A. lineatus* and *A. obscurus* now established throughout southern British Columbia (128) and *A. sputator* in Quebec (107). It appears that these dispersals occurred recently, raising concerns that these species may displace native elaterids, becoming agricultural pests (107, 128). The life histories of all three species are thought to be

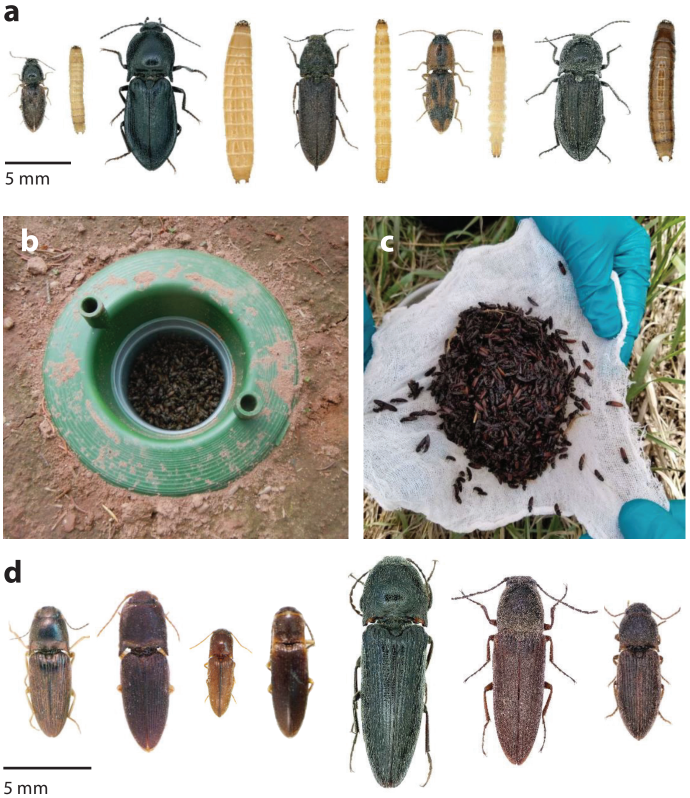

**Figure 1**

Wireworm pests in North America make up a complex of diverse species belonging to multiple genera. (*a*) Adults and late-instar larvae of the five most common pest species on the Canadian prairies. From left to right: *Hypnoidus bicolor*, *Selatosomus aeripennis destructor*, *Limonius californicus*, *Aeolus mellillus*, and *Hadromorphus glaucus*. Photos courtesy of Julien Saguez. (*b*) Vernon Pitfall Trap® containing approximately 7,000 *Agriotes sputator* in Prince Edward Island. Photo courtesy of Wim van Herk. (*c*) Pheromone trap capture of *L. californicus* in southern Alberta. Photo courtesy of David Shack. (*d*) Representative species of some of the main pest genera. From left to right: *Conoderus falli*, *Heteroderes amplicollis*, *Glyphonyx bimarginatus*, *Dalopius vagus* (photos courtesy of Blaine Mathison), *Melanotus similis*, *Limonius agonus*, *Agriotes mancus* (photos courtesy of Julien Saguez).

completed in approximately four years (134), but completion is more rapid at higher temperatures (110a). Native pest species include *Agriotes ferrugineipennis* (southern British Columbia, the Pacific Northwest) (106) and *Agriotes mancus* and potentially *Agriotes pubescens* (southern Ontario, Quebec, northeastern United States) (93, 108), which likely have life histories similar to that of *A. obscurus*. Several pest species mentioned in older literature (e.g., *Agriotes criddlei*, *Agriotes sparsus*) are no longer considered pests (132, 134).

***Conoderus*.** At least eight *Conoderus* spp. have been reported as pests in the southern United States, notably *Conoderus rudis* and *Conoderus scissus* in Georgia (18, 50); *Conoderus vespertinus*, *Conoderus lividus*, *Conoderus auritus*, *Conoderus bellus*, and *Conoderus falli* in Virginia and North Carolina (45, 84, 150); and *C. auritus*, *C. bellus*, *C. falli*, and *Conoderus exsul* in California (134). Of these, *C. falli* and *C. rudis* were likely introduced from South America, and *C. exsul* was likely introduced from New Zealand (134). The life histories of these generally small species range from two or more generations per year (*C. rudis*, *C. falli*) to one (*C. bellus*, *C. vespertinus*) to two years (*C. scissus*) (134). A closely related pest species, *Heteroderes amplicollis*, was also likely introduced from South America (72).

***Hypnoidus*.** Both *H. bicolor* and *Hypnoidus abbreviatus* are frequently collected from agricultural land in Canada and the United States, but their economic importance is unclear. Recent surveys show that *H. bicolor* comprises nearly 60% of wireworms collected from Prairie provinces overall (132) and 90% of larvae collected in Manitoba (25). In surveys conducted in Quebec, *H. abbreviatus* accounted for over 70% of wireworms collected (93). Both species also co-occur in Ontario and Alaska (81), and high populations of *H. bicolor* have been reported in Montana (76) and Idaho (88). Both sexual and parthenogenetic forms are known for *H. bicolor*, though the latter currently appears to predominate (132). Molecular analyses indicate that *H. bicolor* may be a complex of multiple cryptic species (11, 26, 34). Little is known about the life histories of these species, aside from early studies suggesting a two-year life cycle for *H. bicolor* (134).

***Limonius*.** Pest species of this genus include *Limonius canus*, *L. californicus*, and *Limonius infuscatus* in western Canada, the Pacific Northwest, Montana, and California (3, 73) and *Limonius agonus* in Ontario, Quebec, and the northeastern United States (134). The western species are responsible for most wireworm damage to crops in the Pacific Northwest. Both larval and adult activity occur later in the spring for *L. californicus* than for the other two species (69, 74, 125). To date, only the life histories of *L. agonus* and *L. californicus* have been studied, suggesting a four-year development period (see 134). Some confusion occurs in the literature regarding two historic pest species, *Limonius ectypus* and *Limonius dubitans*; some consider these synonyms of *L. infuscatus* and *L. agonus*, respectively, and others treat these four as separate species (32). Most recently, restriction site–associated DNA sequencing along with mitochondrial DNA analysis indicated that cryptic species complexes exist within the *L. californicus* and *L. infuscatus* species concepts (3).

***Melanotus*.** Approximately 10 pest *Melanotus* spp. are known in North America (134); of these, *Melanotus depressus*, *Melanotus verberans*, *Melanotus similis*, and *Melanotus communis* are of economic importance in the eastern and central United States and Canada (19, 134, 149). The single western pest species, *Melanotus longulus oregonensis*, is no longer economically important (73). Life history studies for these species are scant but suggest a 3–4-year development period for *M. longulus* and an even longer period for *Melanotus pilosus* and *M. communis* (134).

***Selatosomus*.** *Selatosomus aeripennis destructor* is the most damaging pest wireworm on the Canadian prairies (126, 134), and *Selatosomus pruininus* is the predominant dryland species in the Pacific Northwest (73, 134). Larval development likely takes 4–5 years but may require 10 or more under adverse conditions, during which larvae can molt regressively (i.e., become smaller) (134). Until recently, both *S. aeripennis* and *S. pruininus* were placed in the genus *Ctenicera*, with *Ctenicera destructor* and *Ctenicera aeripennis* treated as separate species due to differences in size, color, distribution, and soil preferences (126). However, molecular barcoding suggests the two may be a single species, i.e., *S. aeripennis* (34). Relatively less prevalent historic pest species placed in *Ctenicera* until recently include *Hadromorphus glaucus*, *Hadromorphus callidus*, *Hadromorphus inflatus*, and *Corymbitodes lobata* (17, 33, 34, 73).

**Other pest species.** Two species of *Glyphonyx* are pests in the southeastern United States, notably *Glyphonyx bimarginatus* and *Glyphonyx recticollis* (19). The life cycle of the latter is likely completed in 1 year (134). Larvae of *Dalopius* spp., including *Dalopius pallidus*, *Dalopius parvulus*, and *Dalopius mirabilis*, were found in low numbers in surveys in Quebec, Montana, and the Prairie provinces (34, 93, 132), and larvae of *Dalopius asellus* constituted 2% of wireworms collected in the Pacific

Northwest (73). Other less prevalent historic pest species include *Hemicrepidius memnonius* and *Sylvanelater limoniiformis* (73, 93, 132). Larvae of *Ampedus* spp. are relatively common on agricultural land in Quebec (e.g., 93), but these species are generally saprophytic and unlikely to be crop pests. Similarly, larvae of *Aeolus mellillus* are common on farmland throughout Canada and the northern United States (34, 67, 71) but are primarily predaceous (134). A recent review of the elaterids of Montana indicates that most records of *A. mellillus* are actually *Aeolus livens* (33), suggesting that some *A. mellillus* reported from elsewhere in western North America may have been misidentified.

### Species Co-Occurrence

Wireworm species commonly co-occur on farmlands (73, 132). In some cases, the co-occurring species may be considerably different in their life histories and seasonal activity (e.g., *G. recticollis*, *M. communis*, and *C. bellus* in Florida; *S. a. destructor* and *H. bicolor* in Alberta and Saskatchewan), potentially complicating wireworm management for producers. Co-occurring pest species can also differ considerably in their damage potential and response to insecticides, and disproportional changes in the species composition in the field may influence the population dynamics of the pest species (134). For example, *A. mellillus* may reduce populations of *S. a. destructor* and *H. bicolor* and other crop pests (134). Analysis of agronomic practices and landscape factors can help predict pest abundance and the composition of species assemblages (86); increases in soil moisture and organic carbon content following minimal tillage have led *H. bicolor* to surpass *S. a. destructor* as the predominant pest species in the Canadian prairies (132).

## CLICK BEETLE MOVEMENT AND MONITORING

### Tracking and Monitoring Adult Click Beetles

Mark-recapture techniques have been used for monitoring click beetle dispersal across landscapes; examples include monitoring of *A. obscurus*, *A. lineatus*, *A. sputator* (12, 139), *H. bicolor*, and *S. a. destructor* (24).

Although sticky cards and window traps can be effective for some flying species (e.g., *Glyphonyx bimarginatus*) (84), effective monitoring for click beetles is best achieved using pheromone-baited pitfall traps (133). Our knowledge of click beetle movement and landscape ecology has benefited from the recent identifications of species-specific sex pheromones.

**Sex pheromones.** Female-produced sex pheromones have recently been identified for several native North American species, including *M. communis* (149), revealing new insights into elaterid chemical ecology. For example, traps baited with a pheromone analog captured considerably more male *Cardiophorus edwardsi* than traps baited with the natural pheromone (100, 101). All four pest *Limonius* spp. appear to produce the same single-constituent sex pheromone, limoniic acid (40), raising the question of how species specificity is maintained in areas where these species co-occur (125). Limoniic acid and an analog compound are also attractive to related nonpest species such as *Gambrinus seminudus* and *Gambrinus ursinus* (125). The major sex pheromone constituent for *S. a. destructor*, (*Z*,*E*)-α-farnesene, attracts male beetles but is moderately repellent to females, while a second female-produced farnesene compound is moderately repellent to males (41). This may be a mechanism to prevent males, which only mate once, from being attracted to mated females and for females to avoid areas with high numbers of conspecific females. Recent work has shown the sex pheromone of *A. mancus* (108) to be similar to that of *A. obscurus*, *A. lineatus*, and *A. sputator* (113) but not to that of *A. ferrugineipennis* (106). The recent development in our understanding of sex pheromones has improved our ability to monitor population dynamics, movements, and the swarming periods of native species (12, 69, 84, 125). Sex pheromones for the introduced *Agriotes* species were identified in the 1980s (113), allowing for various ecological studies and the development of monitoring tools (e.g., 128, 133, 137, 139).

**Kairomones and female attractants.** Females of two European *Agriotes* species (*Agriotes sordidus* and *Agriotes brevis*) are attracted to their own pheromones (116, 146), suggesting that these pheromones have an aggregation function and could potentially be used for monitoring movements of females (146). Low-level, early season attraction of female *A. obscurus* to their own pheromone has also been reported (120). To date, the only plant-derived attractants for female click beetles are blends of (*E*)-anethol and (*E*)-cinnamaldehyde (for *A. ustulatus*) (115) and of (*Z*)-3-hexenyl acetate, methyl benzoate, (*Z*)-3-hexenol, and methyl salicylate (for *A. brevis*) (145). Combining these plant compounds with the respective sex pheromones did not reduce captures of male *A. brevis* and *A. ustulatus*, allowing for the creation of lures attractive to both sexes (114). Interestingly, these plant compounds decreased captures of male *A. obscurus* and *A. lineatus* (122).

## Beetle Swarming and Movement Across Landscapes

Mature larvae of pest *Agriotes*, *Limonius*, *Melanotus*, and *Selatosomus* species pupate in the fall, overwintering as adults and emerging in the spring when the soil warms (e.g., approximately 10°C for *A. obscurus* and *A. mancus*; 63). It appears that the emergence of some species is delayed in areas where several congeneric pest species co-occur, e.g., *Limonius* spp., possibly to reduce interspecific competition and/or maintain species specificity (69). For spring-emerging species, the beetle activity lasts for 3–4 months [e.g., *Agriotes mancus* (63); *S. a. destructor* (24, 41)], with male beetles in some species dying shortly after mating [e.g., *S. a. destructor* (126)]. Adults of species with a shorter life cycle or that do not overwinter as larvae (e.g., *A. mellillus*, *C. vespertinus*) may appear later in the year (150), whereas adults of species in the southern United States and/or that are multivoltine (e.g., *C. falli*) may be present in farmland for most of the year (134). Most of what is known about beetle movement is based on pitfall trap data (e.g., *S. a. destructor*, *Limonius* spp., *Agriotes* spp.) (129), although blacklight traps have also been used for some species (e.g., *C. falli*, *M. communis*) (80, 149).

The ability of pest click beetles to disperse across the landscape depends largely on their ability to fly. Species in *Conoderus*, *Melanotus*, *Limonius*, and *Hypnoidus* are generally strong fliers, but others rarely fly (e.g., *S. a. destructor*) (24) or fly only when a threshold internal temperature is reached (e.g., >25°C for *A. obscurus*) (127). For nonflying species, males are generally more active than females (e.g., *S. a. destructor*) (24) and/or active earlier in the season (e.g., *A. mancus*, *S. a. destructor*) (23, 63). Dispersal of walking species depends on the vegetation type, but male *A. obscurus* can travel approximately 40 m in 24 h (12), and male and female *S. a. destructor* can travel up to 110 m in 1 and 9 days, respectively (24). The relatively limited mobility of nonflying species may permit the development of mass trapping tactics (127, 137). Considerable work is still needed for all pest species to understand the effect of vegetation and landscape structure on beetle movements, the onset and duration of beetle activity periods, mate search behaviors, oviposition site preferences and preferred host plants, and the timing and duration of female pheromone release; these ecological factors are also influenced by climate change, highlighting the importance of continuous re-evaluation of the ecological outcomes. Further work is also required to determine the extent of movement of infested soil and landscaping plants, which may contribute to the range expansion of invasive species (e.g., the European *Agriotes* from coastal British Columbia) (128), particularly as there are currently no regulatory restrictions on the movement of these species within North America.

### Tracking and Monitoring Larvae

Soil windows (i.e., horizontally placed plates of glass separated by a thin layer of soil) (e.g., 123) and stable isotopes (e.g., 118) are examples of earlier methods used to monitor wireworm movement and feeding behaviors. More recently, wireworm behavior studies successfully used X-ray computed tomography to visualize movement (13, 66).

Monitoring for pest wireworms in the field is done by either taking soil cores or using bait traps (17, 117, 134). Soil cores typically capture far lower numbers than bait traps because the latter can attract wireworms from the surrounding area for 1–2 weeks by releasing $CO_2$ and other volatile organic compounds (VOCs) (90, 134). Larval attraction to $CO_2$ has long been known, and more recent studies demonstrate that wireworms (*A. sordidus*) are also attracted to VOCs such as hexanal produced by barley (*Hordeum vulgare*) roots (10, 39); the relative composition of these VOCs may account for the differences in corn seedling susceptibility to wireworm injury (59). Similarly, larvae of *Melanotus cribricollis* are attracted to VOCs such as α-humulene produced by bamboo (*Phyllostachys violascens*) shoots (151). Advances in our knowledge of larval ecology and orientation cues can be used to improve bait trapping, which is most effective when the soil temperatures are above 10°C, wireworms are in an active feeding state, and fields do not contain high levels of green manure or vegetation (90, 134).

## RISK ASSESSMENT AND CONTROL

### Risk Assessment

Assessing the risk of wireworm injury to crops is complicated by wireworms' seasonal vertical movements in the soil, periods of inactivity, patchy distributions in the field, and distraction by competing $CO_2$ sources and green manure (134). Although recent developments in pheromone traps facilitated monitoring for click beetles (38, 129), developing a field risk index based on adult numbers requires understanding how these correlate with larval numbers and crop damage. Correlations between larval numbers and injury will also depend on multiple biotic and abiotic environmental factors discussed elsewhere (e.g., 134). Furthermore, as pest species differ in damage potential (e.g., 35), such correlations will need to be both species and location specific (132, 134). The landscape, field history, and cropping systems also contribute to damage risk (46, 82). A comprehensive risk index must therefore consider an array of variables and their interactions to develop case-specific economic injury levels and thresholds (85, 135).

### Control

Several approaches can be used to mitigate the negative impacts of wireworms on the productivity of our agroecosystems. Below, we introduce the existing control recommendations and discuss recent research developments that can contribute to their improved efficacy.

**Chemical control.** The deregistration of effective chemistries for wireworm management, such as lindane, led to the resurgence of pest populations and an urgent need for new effective control products (117, 140). Early lab and field tests of pyrethroids, diamides, and neonicotinoids on *A. obscurus* and *Limonius* spp. have shown that these compounds generally induce temporary morbidity (123, 144). In fields with low to moderate populations, this may allow for plant establishment in the spring but will not cause significant population reductions (140, 141). At high populations, these compounds may provide poor or no stand protection (124). Similar responses have been reported for *M. communis* (20) and *H. bicolor* (75, 77).

Effective plant protection and population reduction can be achieved with low rates of fipronil, a phenyl pyrazole, and broflanilide, a novel meta-diamide. In multiyear efficacy studies, these compounds, when applied at planting, reduced *A. obscurus* populations and potato tuber damage by >90% (131, 142) and, when applied as seed treatments, protected wheat stands and reduced populations to an extent equivalent to lindane (130, 140). Work on other species has shown similar efficacy of fipronil against *Conoderus* spp. in sweet potatoes (98) and *L. californicus* and *H. bicolor* in wheat (77). It is notable that fipronil, broflanilide, lindane, and effective organochlorines used historically for wireworm management all target GABA-gated $Cl^-$ channels (134). Unfortunately, the resurgence in wireworm populations in recent decades has also led to widespread prophylactic, and often unnecessary, use of seed treatments for their management in cereals, corn, and soybeans (31, 60, 109).

Several new application methods to reduce insecticide application rates and increase efficacy have been developed. Work done with sweet potato has shown that the proportion and severity of wireworm (predominantly *C. vespertinus*) damage can be reduced when insecticides are delivered through drip irrigation (8). Seeding of fipronil-treated wheat seed into furrows at potato planting provided comparable or greater blemish and population reductions to granular applications of phorate, the industry standard, but with nearly 1,000 times less active ingredient (143). Combinations of a nonlethal insecticide that induces temporary morbidity (e.g., thiamethoxam) with a low rate of a lethal insecticide (e.g., fipronil) applied as a blended seed treatment can provide stand protection and reduce wireworm populations to eliminate the economic threat of wireworm injury for multiple years (141). The relative rates of these compounds are critical: Using high rates of thiamethoxam would induce morbidity before the larvae can ingest a lethal amount of fipronil if the latter is applied at a very low rate (77, 123).

**Host plant resistance.** Plant species may vary in their susceptibility to wireworm damage (e.g., 42, 75, 89), and identifying sources of resistance has been the topic of several recent studies (47, 51, 59). Langdon & Abney (65) reported low susceptibility in some potato cultivars to *M. communis* and *G. bimarginatus*, an effect that could be partially influenced by differences in glycoalkaloid concentrations (51). The variation in susceptibility to *A. sordidus* among corn cultivars was attributed to differences in the diversity and the concentration of root volatiles such as hexanal, heptanal, and 2,3-octenanedione (59). Finally, although differences in crown depth, root size, and growth rate were used in wheat to explain the possible lower susceptibility of a few cultivars to *L. californicus* and *L. infuscatus* (47), additional controlled studies are needed to confirm this effect.

**Cultural control.** Reducing agroecosystem suitability for wireworm activity and development and/or alternating the environment to enable vigorous crop development can reduce losses to this pest complex.

***Trap crops and intercropping.*** Although wireworms feed on a wide range of host plants, their host preference can be exploited to redirect them away from the main crop toward a secondary cultivated host, which may or may not be harvested (96). An effective trap and/or intercrop must release cues that are more attractive to the wireworms than those of the main crop and promote extended feeding (90). However, the latter might be less critical if trap crops are used to bait wireworms in an attract-and-kill strategy (see the section titled New Developments and Wireworm Control). Studies that demonstrated that trap cropping can be successful have been previously reviewed (85); notable examples include the luring of *A. obscurus* to rows of untreated wheat in the spring, significantly reducing damage to strawberries transplanted 8 days later (138). Recent studies demonstrate the attractiveness of legumes as trap crops in potatoes (64) and cereals (2).

***Crop rotation and cover crops.*** To reduce the risk of wireworm damage, the susceptible crops must follow crops that are known to be less supportive of wireworm populations (85). For example, yellow mustard (*Sinapis alba*), cabbage (*Brassica oleracea*), flax (*Linum usitatissimum*), clover (*Trifolium pratense*), pea (*Pisum sativum*), and bean (*Vicia faba*) are reported as plants with low susceptibility to wireworm damage (42). Brown mustard (*Brassica juncea*) plants, as a soil-incorporated cover crop, and their defatted seed meal, as manure, have been shown to be effective in reducing wireworm populations (37, 148). This mortality effect is due to sinigrin (glucosinolate), which, upon exposure to moisture, hydrolyzes to the wireworm-toxic 2-propenyl isothiocyanate (148).

The role of alfalfa rotation in managing wireworms has yet to be determined. After multiple years, and with appropriate irrigation management, the dense roots of established alfalfa promote soil drying and compaction (105), making the environment unfavorable to wireworms. Challenges with this approach include weeds and stand decline in older alfalfa and the differential response of various wireworm species to this practice (A. Rashed, unpublished observations). Another challenge is that crop rotation options may be limited in dryland production where wireworms are important pests (e.g., in the intermountain west and the Pacific Northwest); there, rotation schedules may benefit from weed- and residue-free fallow (31). Despite differences in susceptibility among small grains (75, 89), continuous wheat, oat, and barley combinations are not considered compelling rotation sequences agronomically. In addition, incorporating different crop types into rotations allows for the application of a wider variety of insecticides, which may reduce wireworm populations in the field for the subsequent susceptible crop in rotation. The choice of appropriate rotation crops compatible with other control tactics is an important consideration in IPM against semivoltine wireworms.

***Tillage.*** Because of their sensitivity to desiccation and limited mobility, click beetle eggs and early instar larvae can be negatively impacted by tillage, as it exposes them to open air and natural enemies (4, 99, 105). For tillage to be effective as a control method, species-specific knowledge of click beetle larvae and seasonal activity is needed. In field plots infested with *Agriotes* spp., meadow plowing before corn seeding reduced crop damage (36). This effect can be explained by the alternative food sources provided by the soil incorporation of the plant tissue (36) and likely the confusion resulting from the added $CO_2$ interfering with the ability of larvae to locate the seeded corn. Plowing just before planting did not prevent wireworm damage to potato crops later in the season, at which time the plowed-down vegetation has decomposed (134). No-tillage and reduced-tillage farming have been promoted to improve soil health and conserve water and soil in most dryland production systems. This practice, however, can increase wireworm populations compared to conventional tillage operations because the higher soil moisture favors the survival of eggs, and higher levels of organic matter favor the survival of larvae by providing alternative food sources. The effect of changes in agronomic practices on wireworms is species dependent and is known to impact wireworm species dynamics in fields (132).

**Biological control.** Wireworms are exposed to a variety of natural enemies in their subterranean habitat. Entomopathogenic nematodes and fungi are some of the better-studied organisms to be used or conserved as biological control agents. Below, we introduce some of the important natural enemies of wireworms, as well as new developments in understanding biotic and abiotic factors that can affect their efficacy as biological control agents.

***Predators and parasitoids.*** Previous reviews of the existing literature (90, 117, 134) list birds, rodents, and amphibians as vertebrate predators and arthropods including carabid beetles (Coleoptera: Carabidae) and rove beetles (Coleoptera: Staphylinidae) as invertebrate predators of click beetle larvae. Recent reports of wireworm predators include the generalist larvae of the stiletto fly *Thereva nobilitata* (Diptera: Therevidae) (134) and the soil-dwelling predatory mites *Macrocheles robustulus* (Mesostigmata: Macrochelidae) and *Gaeolaelaps aculeifer* and *Stratiolaelaps* *scimitus* (Mesostigmata: Laelapidae) (83). Field parasitism of wireworms is often attributed to the wasp families Proctotrupidae, Bethylidae, and Ichneumonidae and the fly family Tachinidae; the rates of parasitism, however, appear to be limited (117).

***Entomopathogenic bacteria.*** Recent developments in evaluating bacterial entomopathogens against wireworms beyond those reviewed by Traugott et al. (117) are scarce. *Enterococcus mundtii*, *Staphylococcus pasteuri*, *Arthrobacter gandavensis*, *Bacillus thuringiensis*, and *Pseudomonas plecoglossicida* are examples of the bacterial species that showed potential as biological control agents against *A. lineatus* (22). Spinosad, a botanical insecticide produced from the actinobacterium *Saccharopolyspora spinosa*, has been shown to be ineffective against *A. obscurus*, *L. californicus*, and *H. bicolor* (7, 123).

Our understanding of elaterid endosymbionts is also limited. Using ribosomal RNA phylogenies and multilocus sequence typing, Schuster et al. (97) characterized a new wireworm-pathogenic *Rickettsiella* pathotype (*Rickettsiella agriotidis*) from field-collected *Agriotes* spp. Earlier work in *L. canus* identified *Bacillus megaterium* and *Rahnella aquatilis* as the most frequently isolated bacteria (61). The microbiomes of larvae of *A. obscurus* and *A. lineatus* infected with *Metarhizium brunneum* contain at least 394 bacteria species, including four—*Pantoea agglomerans*, *Pandoraea pnomenusa*, *Nocardia pseudovaccinii*, and *Mycobacterium frederiksbergense*—that appear to suppress *M. brunneum*–induced wireworm mortality and have known antimicrobial mechanisms (55). Of these, *P. agglomerans* had previously been isolated from *L. canus*, suggesting that it may serve an antifungal purpose in elaterid larvae (55, 61).

***Entomopathogenic nematodes.*** Numerous studies have investigated the susceptibility of several wireworm species to the two nematode genera *Steinernema* and *Heterorhabditis*, with the efficacy of the entomopathogenic nematodes (EPNs) shown to vary with nematode species and/or strain, environmental factors, and wireworm species (79, 117). Lehmhus (68) demonstrated that *Heterorhabditis bacteriophora* and *Steinernema carpocapsae* are effective against *Agriotes* spp., but *Steinernema feltiae* had no efficacy against either *Agriotes* spp. or *Selatosomus aeneus*. In contrast, *H. bacteriophora* and *S. carpocapsae* showed no efficacy against *L. californicus*, while a field-collected isolate of *S. feltiae* caused significant mortality (78). The reported *L. californicus* mortality from *H. bacteriophora* and *S. carpocapsae* was higher when experiments were conducted in 31-ml cups (95). It is conceivable that the naturally occurring EPNs, under constant selection by biotic and abiotic environmental factors for improved efficacy (16), may be more effective in overcoming the structural barriers of wireworms (28) and show a higher efficacy than laboratory-reared and -maintained nematodes (16, 78). Comparative studies with several field-collected isolates and commercial strains are required to evaluate this proposition.

***Entomopathogenic fungi.*** The emerging pattern from the existing literature is that entomopathogenic fungi (EPFs) are more efficacious than EPNs against wireworms. *Metarhizium* spp. and *Baeuveria bassiana* are two of the most-studied entomopathogens against the wireworm species *H. bicolor* and *S. a. destructor* (112), *Agriotes* spp. (62), and *Limonius* spp. (29). Some studies suggest that *B. bassiana* is a less efficacious pathogen of wireworms than *Metarhizium anisopliae* (7), even when nonpathogenic (5), and that the efficacy of *M. anisopliae* isolates against *Agriotes* spp. varies significantly (5, 56). However, Reddy et al. (91) found no difference in the effectiveness of *B. bassiana*, *M. brunneum*, and *Metarhizium robertsii* when they were applied in farrow in experimental plots infested with *L. californicus* and *H. bicolor*; all EPFs resulted in a significant reduction in wireworm numbers collected in bait traps.

***Soil attributes and biological control.*** Physical soil characteristics such as porosity, compaction, moisture, and temperature have long been known to affect the activity and survival of wireworms and their soil-inhabiting natural enemies (46, 82, 89). Porous, sandy texture favors EPNs because it facilitates their movement and contributes to their foraging success (29). In contrast, organic matter contributes to moisture retention in the soil, likely favoring the efficacy and survival of EPFs (87). Soil temperature and moisture can also influence the biology of soil-inhabiting organisms, a species-dependent effect demonstrated in several EPN and EPF species (54, 57, 92). Unfavorable conditions that impact wireworm activity (110) or presence can influence the degree of exposure to entomopathogens. Understanding the species-specific ecology of wireworms and identifying the most suitable biological control agents for the environment are prerequisites to a successful biocontrol approach.

***Biotic interactions and biological control.*** EPNs and EPFs have been reported to be more efficacious in sterilized than in nonsterile soil (102, 111), likely due to interactions with soil-inhabiting microorganisms. Moreover, the presence of multiple species of natural enemies does not necessarily translate into more effective control; the coapplication of EPNs and EPFs may lead to synergistic (6), additive (49), or antagonistic (103) outcomes. The reported variability in outcomes can be influenced by the time and order of the applications (9), the developmental stage of the pest (147), the species and strain of the entomopathogens (1), and soil temperature at the time of applications (9). Further applied research in this area is warranted, especially in organic production.

***Wireworm biological control as an integrated pest management component.*** Various naturally occurring EPFs (e.g., 54) and EPNs (16, 78) are known to be effective against wireworms (but see 94), and preserving their populations is expected to contribute to agroecosystem health. Similarly, promoting the persistence of the introduced biological control agents could justify their applications in conventional production systems. Frequent disturbance of the topsoil and biofumigation with cover crops are examples of agricultural practices that may interfere with the activity and persistence of soil-inhabiting natural enemies. For example, continuous soil cultivation can negatively impact EPFs in conventional fields (14). Incorporating cover crops into the soil as biofumigants can also negatively influence the activity of both EPNs (44) and the soil microbiome (43).

Several studies have evaluated the effectiveness of entomopathogen and insecticide coapplications. In the laboratory, the mixed application of *M. anisopliae* with spinosad (bioinsecticide) increased the mortality of *A. obscurus* and *A. lineatus* (30). However, corn seed treated with *M. anisopliae* and either spinosad or clothianidin (neonicotinoid) was ineffective against *A. obscurus* (54). A more recent study that put the application of various combinations of entomopathogens (i.e., *B. bassiana* and *M. brunneum*), other bioinsecticides (e.g., spinosad and azadiractin), and the synthetic imidacloprid into a field test reported no significant reductions in *L. californicus* and *H. bicolor* populations (7), although *M. brunneum* alone or in combination with imidacloprid appeared to improve yield in spring wheat.

Finally, increased concentrations of microbials (54) and improved timing and application methods (117) can help increase contact between wireworms and the applied entomopathogens. For example, in-farrow and soil drench applications of EPFs can be more effective than the seed coating method in limiting wireworm damage (91).

## NEW DEVELOPMENTS AND WIREWORM CONTROL

### Developments in Adult Beetle Chemical Ecology and Control

Research on semiochemical-based control tactics in North America has primarily focused on *Agriotes* species. The development of a mass trapping strategy for male *A. obscurus* and *A. lineatus* included studies to determine the optimum pheromone trap spacing (121, 139), the ability of trap arrays to trap male beetles in field margins (139), the invasion of male and female beetles into cropland (12), and the depletion of local populations by traps used for monitoring (127). It has been demonstrated that broadcast applications of pheromone-impregnated cellulose or wax granules can disorient male *A. obscurus* for two weeks or longer (120). Sex pheromones have also been combined with entomopathogens in an attract-and-kill approach (53). For example, exposure to pheromones increased the uptake of *M. brunneum* spores by *A. obscurus* males (70). An earlier study also demonstrated that *A. obscurus* males were recaptured at a lower rate following exposure to pheromone-impregnated granules and rice conidiated with *M. brunneum* (52).

Because pheromone-based mass trapping, mating disruption, and attract-and-kill tactics are designed only to target male beetles, to reduce populations of the semivoltine click beetle larvae effectively, they need to be applied for several years. The effectiveness of these tactics will also depend on the vegetation phenology and weather conditions (120, 121). The development of semiochemical-based control tactics can be challenging for species that are strong flyers (e.g., *Limonius* spp., *Conoderus* spp.), mate more than once (e.g., *Limonius* spp.), or do not require mating to lay eggs (e.g., *H. bicolor*) (125, 134).

## Developments in Wireworm Chemical Ecology and Control

Progress in understanding the behavioral ecology of click beetle larvae has enabled the development of effective attract-and-kill approaches to reduce crop damage. Placing $CO_2$-releasing beads in the soil has successfully lured wireworms away from seedling roots or potato tubers, and research is ongoing to determine if these beads can be combined with phagostimulating substances, EPFs or EPNs, and/or neem extract to kill wireworms (15, 48, 58). Vernon (136) planted insecticide-treated wheat seeds to lure *A. obscurus* and reduce their populations in fallow fields. This formed the basis of two attract-and-kill strategies for managing wireworms in potatoes, in which insecticide-treated wheat seed was either planted and removed shortly before or placed directly in furrow at the time of potato planting (131, 143). Brandl et al. (15) used yeast as an artificial source of $CO_2$ to attract *Agriotes* spp. and expose the larvae to *M. brunneum*. Millet grain (104) and germinating wheat (56) have also been used to attract several species of wireworms and expose them to EPFs. La Forgia et al. (58) provide the most recent successful example of the attract-and-kill approach, where potato extract was used to increase *A. obscurus* exposure to EPNs. Identification of compounds that are attractive to wireworms not only has contributed to the development of targeted attract-and-kill tactics, but can also help with field monitoring and risk assessment, which are essential components of any successful IPM protocol (135).

## RNA Interference Technology and Wireworm Control

Sequencing-specific RNA interference (RNAi) offers a promising tool to combat agricultural pests, especially coleopterans (21). Identifying a target gene(s), designing an effective double-stranded RNA (dsRNA) construct, and determining the most effective delivery method are the steps to develop an RNAi control tactic; this development is at its early stages for wireworms. Some preliminary results have been promising, as the microinjection of dsRNA to target *L. californicus* homologs to genes vital to *Tribulium castaneum* (119) increased the mortality rate. Evaluating host plants genetically modified to express this dsRNA would be the next appropriate step in the process. However, efforts to develop transgenic plants to target wireworms have a long way to go to ensure the environmental safety of the approach (i.e., impact on nontarget organisms) and overcome challenges regarding market acceptability. Such limitations also apply to other approaches involving genetically modified microorganisms; for example, genetic modification of the endosymbiont *R. aquatilis* to express wireworm-active toxins reduced wireworm damage in potatoes (61).

## RESEARCH NEEDS AND FUTURE DIRECTIONS

While recent developments in effective classes of insecticides may provide temporary relief, research must continue to identify species- and location-specific IPM approaches to ensure both control and production sustainability.

The effectiveness of molecular techniques in population genetic studies and species identification has been demonstrated (e.g., 3). Additional gene bank data, especially full genome sequences, can improve species identification and help determine the impact of agricultural practices and other ecological variables driving adaptations and dispersal.

It is evident from the species-specific research in recent decades that there are considerable among-species differences in ecology influencing action thresholds (e.g., 35), monitoring, and control (73, 134). Recent developments in GPS-guided yield monitors and aerial imaging can be used with ground data to develop action thresholds and predict losses to wireworms.

Developments in identifying sex pheromones and larval attractants have improved our ability to monitor and manage wireworm damage. Such species-specific studies should continue, as they contribute to a more targeted management approach.

To achieve production sustainability, we need to improve our understanding of the impacts of our management practices on the rhizosphere and soil microbiome. The presumption that all nonchemical control methods contribute to production sustainability to a greater extent than insecticides has yet to be confirmed (79).

Finally, our knowledge of click beetle endosymbionts needs to be improved to determine the potential role of endosymbionts in wireworm survival, parthenogenesis, and response to environmental stress and the potential for developing novel control methods.

## DISCLOSURE STATEMENT

The authors are not aware of any affiliations, memberships, funding, or financial holdings that might be perceived as affecting the objectivity of this review.

## ACKNOWLEDGMENTS

We would like to thank A. Nikoukar for assistance with sorting literature; C. Barbera for editing; the *Annual Review of Entomology* Editorial Committee for reviewing; and Julien Saguez, Blaine Mathison, and David Shack for providing illustrations used in this article.

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