

BIOLOGY AND MANAGEMENT OF THE JAPANESE BEETLE

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■ **Abstract** The Japanese beetle, *Popillia japonica* Newman, an introduced scarab, has become the most widespread and destructive insect pest of turf, landscapes, and nursery crops in the eastern United States. It also damages many fruit, garden, and field crops. This review emphasizes recent research on the beetle's biology and management. Adults feed on leaves, flowers, or fruits of more than 300 plant species. Adaptations mediating their host finding, dietary range, mating, and oviposition are discussed. We also address abiotic and biotic factors affecting population dynamics of the root-feeding larvae. Japanese beetle grubs are widely controlled with preventive soil insecticides, but options for remedial control of adults and larvae presently are limited. Advances in understanding host plant resistance, entomopathogens, and other biorational approaches may provide more options for integrated management. Despite ongoing regulatory efforts, the Japanese beetle remains a threat as an invasive species.

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INTRODUCTION

The Japanese beetle (JB), *Popillia japonica* Newman (Coleoptera: Scarabaeidae) was first discovered in North America in 1916 during a routine inspection of a nursery near Riverton, New Jersey (47). As an introduced pest, it proved to be spectacularly successful. Despite concerted federal and state efforts to eradicate it, and then to limit its spread, the JB progressively extended its range. It now is the most widespread and destructive insect pest of turf and landscape plants in the eastern United States (144, 190). More than \$450 million is expended each year for direct control costs and for renovating or replacing damaged turf and ornamental plants (181). The JB also damages fruit crops, soybeans, maize, and other garden or field crops (46). Both larvae and adults are targets for substantial insecticide usage, especially on home lawns, golf courses, and in urban landscapes (144, 146).

Recognizing the potential impact of *P. japonica* on American agriculture, the former U.S. Bureau of Entomology established the Japanese Beetle Laboratory in 1917 to study the biology of this pest in its new environment and to develop methods for its control (47). Much of the early research on biological, cultural, and chemical control of the JB was conducted by USDA entomologists affiliated with that laboratory, often collaborating with other federal and state agencies. As the pest expanded its range, work also was conducted at state agricultural experiment stations and other universities.

The JB also is a valuable model for research in insect-plant relationships. Japanese beetles, being highly polyphagous, mobile, and relatively long-lived, offer insights on the behavior, physiology, and nutritional ecology of herbivores that are dietary generalists as adults. Root-feeding JB larvae are useful subjects for studies concerning the spatial ecology of soil insects, their interactions with natural enemies, and adaptations for below-ground herbivory.

The substantial body of research on JB conducted before 1975 was summarized by W.E. Fleming in a series of landmark reviews (44–47). Our review emphasizes more recent work on the beetle's ecology, and its association with host plants and natural enemies, as well as present and future management strategies.

HISTORY AS A PEST; CURRENT GEOGRAPHIC DISTRIBUTION

It is uncertain exactly when or how the JB was first introduced into the United States. It probably arrived about 1911, possibly as grubs in soil clinging to the rhizomes of Japanese iris (38). Previously, the JB occurred only on the main islands of the Japanese archipelago (47), where it was regarded as a minor agricultural

pest, probably because much of the terrain is unsuitable for larval development, and because natural enemies are adequate to keep its populations low (25). In the eastern United States, however, the JB found a new and favorable environment, with expanses of lush turf and pasture grasses for the development of its root-feeding larvae, hundreds of species of adult food plants and, at that time, no native natural enemies (44, 47). The pest increased in numbers and spread naturally, and inadvertently by human commerce, into new areas. By 1998, the JB was established in all states east of the Mississippi River except for Florida, as well as parts of Wisconsin, Minnesota, Iowa, and Nebraska, and into southern Ontario and Quebec, Canada (132). Three infestations in California—in Sacramento (1961–64), San Diego (1973–75), and near Sacramento (1983–85)—were chemically eradicated (23, 190). Local outbreaks of *P. japonica* in northern Japan since the mid-1970s have been attributed to increased cultivation of grassy areas (11).

Elsewhere in the world, the JB is established on Terceira Island (Azores, Portugal), where it escaped from a United States air base in the early 1970s (95). Although its endemic or introduced range has been reported to include northeastern China, the Hunan Province of China, the Korean Peninsula, northern India, and the South Kuril region of Sakhalin, Russia (166), these records apparently are based upon misidentifications, and its establishment on the Asian mainland is questionable (4).

In North America, the JB remains the target of quarantines restricting interstate shipment of nursery stock with soil and movement of aircraft from regulated airports to California and six other western states, as well as British Columbia (133). The European and Mediterranean Plant Protection Organization lists it as a quarantine pest (166), and it has similar status with other international regulatory organizations (145). Temperature and soil moisture likely are important factors limiting the pest's potential spread into new areas (46). A modified Match Index model (4) predicts that most of continental Europe, the United Kingdom, and Ireland are climatically suitable, as are parts of the Caucasus region, eastern central China, and the Korean Peninsula. In the Southern Hemisphere, parts of Australia, New Zealand, South Africa, and South America also are suitable. Establishment of the JB in these areas, or in the western United States, could result in enormous economic loss.

BIOLOGY AND ECOLOGY

Seasonal Biology

The JB is univoltine throughout most of its range in the United States (46). In southern Ontario, northern New England, and the Adirondack and western regions of New York, or in unusually cool years in southern New England, a portion of the population may take 2 years to complete a generation (187, 190). Appearance of adults and timing of subsequent oviposition and larval development vary by latitude and from year to year (46). Emergence typically begins in May in southern Georgia,

early to mid-June in northern Georgia, eastern North Carolina, and Kentucky (56, 131, 156, 157), but not until July in eastern Massachusetts (187). Males begin to emerge a few days earlier than females (46, 156). The sex ratio of adults emerged in the field is about 1:1 (156).

Virgin females normally are inseminated as they first emerge from the soil (100). Emerging females carry an average of 20 mature eggs and begin to lay eggs soon after mating, probably before feeding (155). After this initial oviposition, which lasts for about 3 days (155), females fly to host plants, often ones upon which other adults have aggregated, to feed and remate (14, 46, 123). Females alternate between periods of feeding and oviposition, typically entering the soil a dozen or more times and depositing 40–60 eggs over a 4–6 week adult life span (46). Eggs are laid singly, generally in the upper 7.5 cm of soil. When plants, which the beetles have been feeding on, are near a site that is suitable for oviposition, departing females tend to oviposit in that vicinity (35, 46). Otherwise, they may disperse to more suitable sites for oviposition (159). These typically are areas with moderate to high soil moisture so long as it does not exceed field capacity (5, 149, 155), moderate soil texture (5, 46, 155, 158), sunlight, and short grass cover (149).

Eggs hatch in about 10–14 days; development of the first and second instars requires about 2–3 weeks and 3–4 weeks, respectively (46). Thus, most grubs are third instars by mid-September. Eggs and first instars are sensitive to temperature and moisture extremes, especially desiccation (5, 46, 158). Variation in their survival in heterogeneous soils is believed to be a major determinant of spatial and temporal fluctuations in population density (5, 35, 46, 159). Older larvae are less susceptible to environmental stress, partly because of their ability to move downward in the soil profile (183).

The grubs feed well into October and most are nearly full-sized before the onset of winter. They are susceptible to freezing, with a supercooling point of about -7°C (74). They move deeper into the soil in late autumn. They overwinter 5–15 cm below the surface, although a few may be 20–25 cm deep. Movement upward in the soil profile usually begins in March as soil temperatures rise above 10°C (46). The grubs feed for another 4–8 weeks, then go slightly deeper and form an earthen cell in which to pupate (46, 187). The prepupal stage occurs in May and lasts about 10 days. The pupal stage lasts 7–17 days, and teneral adults may remain in the pupal cell for 2–14 days before emerging from the soil (46). In northern states where a portion of the population has a 2-year life cycle, those individuals overwinter as second and third instars during the first and second winters, respectively (187).

Pheromonal Communication

SEX PHEROMONE Virgin female JB emerging from the soil are highly attractive to males, particularly early in the summer (46). Field studies with tethered beetles, beetle-baited traps, and severed body portions confirmed that unmated females

emit a volatile sex pheromone that is produced in the abdomen (100). Males do not attract other males (100). Ladd (100) showed that females cease to produce the attractant shortly after mating, and subsequent tests with mated females gave no indication of recommencement of pheromone production (80).

The attractant compound subsequently was isolated from virgin females and tentatively identified as (*Z*)-5-(1-decenyl)dihydro-2(3H)-furanone (180). However, this racemic lactone did not attract male beetles in the field and even inhibited their response to virgin females (180). Preparation and field testing of its two enantiomeric forms confirmed that the (*R*)-enantiomer (japonilure) was active, whereas admixtures of as little as 1% of the (*S*)-enantiomer greatly inhibited male response (180). Synthetic japonilure (39) acts synergistically with food-type lures to increase trap captures (109, 110).

Histological and morphological studies revealed female-specific glands composed of epithelial cells lining the inner surfaces of anal plates and two apical sternites. Numerous pores connect these cells to the cuticle surface (174). The sex pheromone was detected by GC-MS in extracts from these glands (174). Unlike northern and southern masked chafers (*Cyclocephala borealis* and *Cyclocephala lurida*, respectively) in which the adult female sex pheromone is produced in both sexes of larvae (70), hexane extracts of JB grubs did not attract JB or *Cyclocephala* spp. males (69; D.A. Potter & K.F. Haynes, unpublished data).

Comparative studies with the Osaka beetle (*Anomala osaka*), a scarab that shares a common habitat with *P. japonica* in Japan, revealed an interesting mechanism of mutual inhibition. The two species use opposite enantiomeric forms of the chiral pheromone (114). Osaka beetles produce and respond to (*S*)-japonilure, the activity of which is completely inhibited by as little as 5% (*R*)-japonilure. Chiral gas chromatography with an electroantennogram detector showed that males of both species have olfactory receptor neurons specific for each enantiomeric form of the lactone (113). Antennae of males of each species have only a single pheromone-binding protein that recognizes both enantiomers to a similar degree (114). However, both species possess olfactory receptor neurons, colocalized in a single sensillum, that are specific to either enantiomer (196). In the JB, the receptor neuron tuned to (*R*)-japonilure is characterized by a large action potential amplitude, whereas a small-spiking receptor is tuned to the behavioral antagonist, (*S*)-japonilure. The opposite pattern occurs in the Osaka beetle. Thus, chiral discrimination evidently is achieved through the specificity of ligand-membrane receptor interactions (196). This mechanism provides species-specific chemical signals for the two sympatric species. Ultrastructure of the pheromone-detecting sensilla placodea and morphological properties of their olfactory neurons have been described (79).

PUTATIVE AGGREGATION PHEROMONE On the basis of electroantennogram responses to male extracts (1) and beetles' response to conspecifics tethered on plants (75), Iwabuchi & Takahashi (75) proposed that male JB release an aggregation pheromone that attracts both sexes. Field studies, however, have failed to

support the presence of a male attractant (80, 100). More recently, it was shown that both sexes of JB are strongly attracted to blends of plant volatiles released from beetle-damaged leaves (119, 122–124). This phenomenon may explain the aggregative behavior without invoking a beetle-produced aggregation pheromone. Such responses may facilitate mate location on host plants because, once they are mated, females themselves do not seem to attract flying males although they may mate multiple times (100, 123).

Mating Behavior

Japanese beetles engage in both polygyny and polyandry (14, 46). Males attempt to copulate with virgin females as they emerge from the ground, and females also remate on plants where they feed between periods of oviposition (46). Ladd (99), working with chemosterilants, showed that sperm contributed by a female's last mate were used to fertilize her eggs until her next mating and that sperm from a single mating remain viable for at least several weeks. Sequential pairings of females with normal or sterilized males confirmed that there is sperm displacement (99). Barrows & Gordh (14), who described courtship, copulatory, and postcopulatory behavior in JB, noted that males often remain mounted for up to 2 h after copulation. This behavior likely represents mate guarding in response to sperm competition. Males on leaves may mount a mating or postcopulatory pair and, after pushing and grappling, displace the original male (authors' observations). The fact that repeated mating is unnecessary for continued production of fertile eggs (102) suggests that polyandry in JB reflects selection for increased variability in offspring, rather than depletion of sperm reserves in females.

Nutritional Ecology and Determinants of Host Range

Japanese beetles are among the most polyphagous of plant-feeding insects. Adults feed on foliage, fruits, or flowers of >300 species of wild and cultivated plants in 79 families, especially in the Aceraceae, Anacardiaceae, Ericaceae, Fagaceae, Gramineae, Hippocastanaceae, Juglandaceae, Lauraceae, Leguminosae, Lilaceae, Lythraceae, Malvaceae, Onagraceae, Plantanaceae, Polygonaceae, Rosaceae, Salicaceae, Tiliaceae, Ulmaceae, and Vitaceae (46, 103, 105). Feeding on different species or cultivars of acceptable host plants can dramatically affect the beetles' longevity and fecundity (77, 102, 169).

HOST LOCATION BY ADULTS Olfaction is important in host location by JB (2, 46) and may also be important in their discrimination between preferred and nonpreferred plants (2). Many volatile compounds with floral or fruit-like character are attractive (45), with the most effective known lure being a 3:7:3 blend of phenethyl propionate, eugenol, and geraniol (111). As with all of the earlier "food-type" lures (45), this blend was identified and refined by field-screening without regard to whether the component compounds are present in preferred host plants, or play

a role in host location. Notably, geraniol, phenethyl propionate, and eugenol have not been found in volatile blends from several preferred host plants (119, 121–124).

Loughrin et al. (124) compared the volatile aroma compounds emitted by intact leaves of crabapple (*Malus* spp.) cultivars that differ markedly in susceptibility to JB. Although some differences in yields of individual compounds were noted, the relative attractiveness of the cultivars, as determined by a short-range pitfall assay, was not related to their susceptibility in the field (169). Indeed, leaves of some resistant cultivars were at least as attractive as foliage from highly susceptible ones. Similarly, intact leaves of two resistant maple species, *Acer rubrum* and *Acer saccharinum*, were as attractive as those of the susceptible species *Acer palmatum* and *Acer platanoides*, and the species' constitutive volatile blends were generally similar across resistance groupings (122). These studies suggest that JBs are attracted to a wide array of plants, regardless of their acceptability as hosts.

Japanese beetles exploit feeding-induced volatiles as aggregation kairomones (119, 122, 123). Detached crabapple leaves that had been damaged overnight by JB or fall webworms attracted more JB than did undamaged or artificially damaged leaves (119). JB-damaged maple leaves were more attractive than undamaged leaves (122). Attraction to induced volatiles was confirmed in field studies in which grapevines that had been damaged overnight by JB recruited 10–20 times more beetles than did intact vines. This occurred even when the intact vines were “baited” with a mesh bag containing 30 JB of mixed sex (123). For dietary generalists, plant odors induced by the feeding of conspecifics may be more reliable indicators of host suitability than are volatiles released constitutively from plants (119).

Volatiles induced by JB feeding on host leaves are typically complex mixtures of terpenoids, aliphatics, and aromatics, as compared with the relatively low levels of less complex volatile blends emitted by intact leaves of the same plants (119, 121–123). Many of the compounds released by skeletonized leaves were either floral or fruit-like in character. Odor induction from JB-damaged leaves occurred in a delayed manner (119, 121). Experiments with beetle-damaged grape plants showed that release of most compounds followed a diurnal pattern, with the period of peak emission from 1200 to 1500 hours, which coincides with the period of the adults' greatest flight and feeding activity (92). During peak emission, volatile production from JB-damaged vines was about 50 times higher than that of undamaged vines. Field trapping with single compounds and blends of compounds typical of those released by intact or insect-damaged angiosperm leaves suggested that JB are attracted to many structurally dissimilar plant volatiles, and as the complexity of the volatile blend increases, so does its attractiveness (120).

DETERMINANTS OF HOST PLANT SUITABILITY FOR ADULTS The fact that JB are attracted to a range of plants regardless of their suitability suggests that acceptance or rejection of hosts occurs mainly in response to stimuli at the leaf surface. Several ubiquitous plant sugars, including sucrose, maltose, fructose, and glucose, are phagostimulants for JB (101). Their presence causes the beetles to consume

substrates such as agar/cellulose media or glass/fiber filters (78, 101). Adults show no response to sorbitol (101), a polyhydric alcohol that is widespread in Rosaceae, which includes many favored hosts. Comparison across a range of susceptible or resistant plant species revealed no consistent correlation between host suitability and levels of leaf toughness, nitrogen, water content, sugars, protein-binding capacity, or saponins (77). Effects of supplemental dietary potassium and sodium were studied by topically treating leaves with salt solutions. Survival and fecundity generally were lower on treated foliage (171).

Studies with JB support the view that host range in dietary generalists is controlled mainly by the presence of deterrents in nonhost plants. The beetles are deterred by cucurbitacins, the bitter triterpenes characteristic of cucurbits (175). Neriifolin, a cardenolide found in yellow oleander (*Thevetia thevetiodes*) is a strong antifeedant (153). Keathley et al. (78) showed that leaves of normally resistant Bradford callery pear (*Pyrus calleryana*) could be rendered palatable and suitable as food by freezing and thawing or other manipulations that induced enzymatic tissue browning. This phenomenon evidently resulted from decompartmentalization and enzymatic degradation of feeding deterrents, probably phenolics. Phenolic glycosides were implicated in resistance of willows, *Salix* spp., to JB (140). The beetles are deterred by the latex secretions of milkweed, *Asclepias syriaca*, but will consume the leaves if the plants' laticiferous defense is experimentally disabled by vein cutting (40). Stinging trichomes of two plant species, *Urtica dioica* and *Laportea canadensis*, did not deter or interfere with feeding by JB (179).

Feeding deterrents may also determine variation in resistance to JB among closely related plant species or cultivars. Feeding intensity, as measured by adult fecal production, on various taxa of *Prunus* decreased exponentially as endogenous foliar cyanide potential increased (143). The cyanogenic glycoside prunasin and two other compounds, herniarin and coumarin, that occur in resistant *Prunus* taxa were potent antifeedants for JB in artificial diet (143). Other endogenous allelochemicals found in rosaceous plants may be stimulatory, inhibitory, or neutral (142). No significant relationship was found between total phenolic content in foliage of crabapple (*Malus* spp.) cultivars and resistance to JB (49). When eight individual phenolics present in *Malus* were tested in artificial diets, however, phloridzin, phloretin, naringenin, and catechin were antifeedants, whereas quercetin and rutin were feeding stimulants (49). Analysis of endogenous foliar phenolics, followed by stepwise multiple regression, indicated that phloridzin is the phenolic most closely associated with resistance of *Malus* to JB (50).

Earlier reports (46) of narcotic effects and paralysis of JB following feeding on zonal geranium (*Pelargonium × hortorum*) recently were confirmed (147). Early claims that castorbean (*Ricinus communis*) is acutely toxic and effective as a trap crop were experimentally discredited (46). Despite anecdotal accounts that flowers of bottlebrush buckeye (*Aesculus parviflora*) are toxic (46), we found that adults readily consume them with no adverse effects (D.W. Held & D.A. Potter, unpublished data).

PHYSIOLOGICAL AND BEHAVIORAL ADAPTATIONS FOR POLYPHAGY Ahmad (3) showed that the gut microsomal cytochrome P450 monooxygenase system (P450) of adult JB is rapidly induced, attaining maximal level within 24 h of feeding. Laboratory-simulated polyphagy and especially natural polyphagy on field hosts produced much higher levels of P450 enzymes than did single-plant feeding. This system likely provides an effective biochemical defense against the many secondary compounds present in the JB's broad range of host plants.

Potter & Held (147) tested the beetles' capacity for food-aversion learning using geranium flowers, which, when consumed, cause rapid paralysis generally lasting for 12–16 h (see above). Naive females strongly preferred geranium petals over foliage of linden, *Tilia cordata*, a highly suitable host. Surviving experienced females maintained this preference despite undergoing repeated bouts of paralysis and reduced fecundity. JB have shown some potential for habituation to a feeding deterrent. In laboratory tests, beetles exposed for 4 h per day to linden foliage treated with an initially deterrent rate of neem extract showed increased acceptance of treated foliage over successive days (71).

FACTORS AFFECTING FLIGHT AND ADULT FEEDING ACTIVITY Flight activity is greatest on clear days when temperature is between 29° and 35°C, relative humidity is >60%, wind is <20 km/h, and solar radiation is >0.6 Langleys/min (46, 95). Flight is strongly depressed by overcast or windy conditions and by rainfall (46, 95, 187). Adults feed most actively from mid-morning to late afternoon (92). Beetles also feed substantially in evening (1800–2200 hours) and sparingly throughout the night and early morning so long as ambient temperature is >15°C (92).

Roses planted in full sunlight sustained more foliar damage than did experimentally shaded plants (162). Shaded plants contained lower concentrations of foliar sugars, which act as phagostimulants, and may also have been less apparent or accessible to host-seeking adults. Despite their proclivity to attack plants growing in sunlight (46, 162), individual JB often move to abaxial leaf surfaces or shade patches during warm periods of the day (92). They are capable of physiological thermoregulation, adjusting thoracic temperature by endogenous heat production or evaporative cooling (92, 138). Minimum thoracic temperature for flight is about 27°C (92). As ambient temperature warms from dawn through late morning, beetles' response to disturbance changes from falling at <23°C to flying at >25°C (92).

Japanese beetles usually begin feeding at the top of a plant, regardless of its height (46). Rowe & Potter (161) showed that defoliation by JB was much greater in the upper canopy of linden trees (*Tilia cordata*) than on sun-exposed or shaded lower-canopy leaves. This pattern, however, could not be explained by differences in foliar toughness, nutrients (nitrogen, water, sugars), or protein-binding capacity, nor did the beetles discriminate, out of spatial context, between leaves from different canopy zones. Clonal grape plants presented on poles in a vertical array sustained similar, height-stratified damage, which suggests that visual orientation

to a host's silhouette, rather than nutritional factors, accounts for the JB's initial attraction to the tops of trees (161). Once consumed, upper leaves release damage-induced volatiles, attracting additional JB (123).

LARVAL FEEDING ECOLOGY JB larvae, like adults, are polyphagous (46), but they tend to occur as facultative monophages because their limited mobility restricts them to plant roots where the female deposits her eggs. Roots of a variety of grasses, weeds, garden and nursery crops, and ornamental plants are consumed (31, 46, 148, 167). Larval feeding is stimulated by various plant sugars (104). The larval gut is alkaline (173), and its P450 activity is inducible, becoming higher under facultative polyphagy than under monophagy (3). The gut contains proteolytic enzymes that can be inhibited, *in vitro*, with serine proteinase inhibitors (19). Chronic ingestion of a soybean trypsin inhibitor resulted in elevated larval mortality (19). Third instars oriented to seeds of wheat or maize in the soil (18). Third instars will develop to pupation on an artificial diet based on lima beans and casein (84).

MANAGEMENT

Management of JB is complex because the adults and grubs cause different types of damage. Because the adults are so mobile, controlling one life stage will not necessarily preclude problems with the other. The pest's destructive potential has led to extensive efforts to develop biological, chemical, and other methods for its control. Fleming (47) summarized integrated control studies prior to 1974, so we will emphasize more recent research.

Sampling, Spatial Distribution, Damage Thresholds

Assessment of JB grub populations requires sampling of soil and roots, often with a spade, golf cup cutter, or a motorized sod cutter (144). Larval populations are typically aggregated (34). Distributions of all instars in turf were best fitted by the negative binomial distribution (135). Extensive sampling of fairways on one central New York golf course suggested that patches with perennially high JB grub densities tended to occur near plants that attracted adult feeding aggregations, whereas low-density patches were correlated with high soil organic matter (35). Other factors positively influencing site suitability include close mowing (149), moist, well-drained, moderately textured soils (5, 155), and possibly sunlight (35, 162).

Dalthorp et al. (34) compared several methods of taking advantage of spatial autocorrelation to estimate local population densities of JB grubs on golf course fairways. Directional kriging, a geostatistical algorithm for estimating local means as weighted averages of samples, provided more accurate and consistent estimates than use of moving averages or inverse distances. Sequential sampling plans for the grubs have been proposed based upon common Ks from the negative binomial

distribution (134). For turf managers, however, extensive sampling tends to be prohibitively time consuming and destructive.

Practical application of sampling for JB larvae is limited in that damage thresholds vary across grass species, soil types, soil moisture levels, and management regimes (30–32, 106). Defoliation of grapevines by natural populations in Virginia did not significantly reduce fruit quality, yield, or shoot growth (16). However, damage thresholds or impacts of the adults' feeding on growth or physiology of woody landscape plants have not been quantified.

Attractants and Trapping

The JB is attracted to a variety of volatile oils with floral or fruit-like character (148). Field-screening for more effective lures was carried on for many years (45, 47), culminating in development of a highly attractive food-type lure, a 3:7:3 mixture of phenethyl propionate, eugenol, and geraniol (111). Use of this three-part mixture with japonilure, the synthetic sex pheromone, provides significantly greater trap captures than the sum of the captures with either lure singly (110). Configuration of the standard mechanical trap was also extensively tested and refined (45, 80), and modifications that may increase trap efficiency have been evaluated (8). Trap yields increased when traps were emptied daily, possibly because the odor of decomposing beetles is repellent or masks the lure activity (9). Sampling statistics (e.g., mean-variance relationships) for JB caught in traps baited with food-type lures, japonilure, or a combination of both lures have been determined (6).

The value of lures and traps for plant protection or area-wide suppression of JB populations has long been debated (47, 80). Gordon & Potter (56, 57) found that use of single traps or small-scale multiple trap arrangements did not prevent or reduce damage to nearby landscape plants, nor did it reduce larval densities in surrounding turf. In fact, defoliation was much greater when traps were present on a site. Mass trapping was credited with reducing small, recently established, or isolated infestations under some circumstances (e.g., 45, 47, 194).

Traps probably are most useful for monitoring populations, detecting new infestations, or for mass collecting beetles for research. California annually deploys 10,000 traps (41) in their JB detection programs. The ability of traps to detect isolated infestations in Oregon and California was a key to successful eradication efforts (9). Traps are also an important component of the Japanese Beetle Harmonization Plan (133), which regulates shipment of nursery crops from infested states to the western United States and Canada. Absence of JB in survey traps operated in nurseries allows certification of plants as being free of JB grubs and suitable for shipment. Nursery fields in counties of Michigan and Ohio with the highest adult catches were most likely to be infested with JB grubs (167). Modified traps might also be used to infect large numbers of adult JB with fungi (e.g., *Metarhizium anisopliae*) or other entomopathogens, with subsequent autodissemination into larval habitats (86, 95, 96).

Host Plant Resistance

RESISTANCE TO ADULTS Fleming (46) classified 435 plant species in 95 families into four categories ranging from plants for which there is no record of JB feeding, to ones that are highly susceptible. These ratings were based upon general field observations and anecdotal accounts. Laboratory leaf disk assays, however, showed considerable variation in feeding response among plants classified in the historical lists as either favored hosts or as minor or nonhost species (103, 105).

Replicated field trials, together with laboratory assays, have revealed significant variation in susceptibility to JB among taxa of birch (151), elm (128), flowering crabapple (150, 151, 168, 169), linden (129, 150), and soybean (62). Significant resistance, however, has not been found in roses (150).

RESISTANCE TO GRUBS Larvae consume roots of all common cool-season turfgrasses, as well as various lawn weeds (30, 31, 33, 148). Third instars consistently preferred perennial ryegrass [*Lolium perenne*] over other turfgrasses in choice tests (29). Turfgrasses can tolerate substantial root feeding in the absence of other stresses (30, 32, 33). Recovery of grub-damaged grasses is enhanced by soil moisture and remedial N fertilization (32, 106).

Infection of perennial ryegrass or fescues by fungal endophytes (*Neotyphodium* spp.) enhances resistance to certain stem- and leaf-feeding insect pests (17). Endophyte effects on JB grubs, however, are equivocal. Although low levels of pyrrolizidine or ergot alkaloids, similar to those occurring in roots of endophytic tall fescue [*Festuca arundinacea*], deterred feeding by third instars on agar-based medium (61, 141), such grubs did not discriminate between endophytic and nonendophytic tall fescue in choice tests (29). Feeding in endophytic field plots did not adversely affect larval survival or weight gain, or fecundity of JB females that emerged from the turf (36, 148). Endophytes may, however, have subtle sublethal effects. For example, grubs fed endophytic fescue grasses were rendered more susceptible to entomopathogenic nematodes (61). In contrast, grubs feeding in endophytic versus nonendophytic perennial ryegrass were equally susceptible to milky disease (191).

Mass Sterilization

Both sexes of JB can be sterilized by topical application or fumigation in chemosterilants (99), or by exposure to gamma irradiation (47). Chemosterilization of male beetles was cumulative, permanent, and did not reduce mating competitiveness. Replacing normal males with sterilized ones in laboratory pairings caused a rapid decline in production of viable eggs until only infertile ova were produced. Viability of eggs was restored when females remated with a normal male. Thus, the fertility of eggs was dependent on whether a female's last mating partner was normal or sterile (99).

The feasibility of using releases of sterile males to stabilize or reduce JB populations in isolated or newly infested areas was tested against a small, natural

infestation inhabiting an isolated valley in eastern Tennessee (107). More than 235,000 sterilized males were released weekly from June to mid-August in two successive summers. Ratios of sterile to normal males increased progressively and fertility of field-collected females declined, but these effects did not occur early enough in either summer to suppress the native population. Dependence on field-collected beetles prevented the release of adequate numbers of sterile males earlier in the summer. Release of sterile males has not been further explored as a management strategy.

Cultural Control

Females seek moist sites for egg laying, so withholding irrigation during peak beetle flight may help to reduce grub populations in turf (149). In contrast, irrigation or rainfall in late summer and autumn promotes recovery of grub-damaged turf (32, 106). Fertilizing in autumn to promote root growth also enhances tolerance (32). Raising cutting height to 18 cm, or spring application of aluminum sulfate to acidify the soil, significantly reduced subsequent grub populations in tall fescue (149). Applying dolomitic limestone to elevate soil pH, however, did not affect ovipositional preference, survival of eggs or young larvae (186, 188, 189), or abundance of JB grubs in turf (149, 186). Use of a heavy (2247 kg) roller on turf to compact the soil before beetle flights also did not reduce subsequent grub populations, nor was it effective for crushing third instars in autumn (149). Nitrogen fertilization had no effect on density or mean weight of JB grubs in tall fescue (36, 149).

Smitley (167) found that JB larvae were fourfold more abundant in grassy areas bordering nursery fields in Michigan and Ohio than in the fields themselves. Weedy nursery fields supported tenfold more larvae than did clean fields. Nursery fields in counties with the highest adult catches were most likely to have larval infestations.

Several studies have examined effects of previous cropping history, tillage, or strip-cropping on abundance and movement of JB adults in row crops. In soybeans, adults tended to be more abundant when corn, rather than soybeans, was the previous crop, in no-till or reduced-till plots where broadleaf weeds provided alternative food, and where a no-till rye cover crop was planted in fall (63, 165). In contrast, abundance of JB was similar on monoculture corn versus strips of corn alternated with soybean regardless of tillage regime (178). Lower densities were found on soybeans that were strip-intercropped with dwarf or tall sorghum than in soybean monocultures (72). Even though the dwarf sorghum was no taller than the soybeans, the intervening strips of nonhost vegetation apparently discouraged the beetles' movement and dispersal (15, 72). These studies suggest that JB recognizes and responds to sharp boundaries between host and nonhost patches irrespective of whether they form a physical barrier.

Biological and Microbial Control

PREDATORS AND PARASITOIDS From 1920–1933, USDA entomologists imported 49 species of natural enemies of *P. japonica* and related scarabs from Asia and

Australia and released them into the northeastern United States (44). Only a few became established, the most widely distributed being *Tiphia vernalis*, a tiphiid wasp that parasitizes overwintered grubs in the spring; *Tiphia popilliavora*, which attacks young grubs in late summer; and *Istocheta aldrichi*, a tachinid fly that parasitizes the newly emerged adults. These parasitoids occur sporadically and they cannot be relied on for site-specific control. Although there has been little subsequent research on their biology, recent studies with *T. vernalis* indicate that its females use species-specific larval odor and frass to locate JB grubs in the soil (M.E. Rogers & D.A. Potter, unpublished data).

Endemic, generalist predators, especially ants, staphylinids, and carabids, cause substantial mortality of JB eggs and young larvae (118, 176, 199, 200). Moles, skunks, and racoons prey on the grubs, but their foraging is often highly destructive to turf (144). European starlings, crows, grackles, gulls, and other birds feed on the grubs or adults (44). Free-range chickens kept in an apple orchard with intercropped potatoes fed on several potential crop pests, including JB. Although JB were less abundant on apple trees when chickens were present, the proportion of damaged fruit was not reduced (24).

MILKY DISEASE BACTERIA Pathology of *Paenibacillus* (formerly *Bacillus*) *popilliae* and *Paenibacillus lentimorbus*, causal agents of milky disease in JB grubs, has been extensively studied (82, 85). Grubs ingest spores of these bacteria along with soil and roots. Once in the gut, the spores germinate and vegetative cells invade the hemocoel, causing fat body depletion (164) and fatal bacteremia. Proliferation of refractile spores and parasporal bodies during the final stage of infection gives the hemolymph a milky-white color. Genetic relationships between *P. popilliae* and *P. lentimorbus* have long been debated, but DNA similarity analysis has validated the existence of the two species (160). A new strain of *P. popilliae* recently was isolated, the first report of natural incidence of milky disease in JB larvae in Japan (127).

Following development of methods for in vivo production of *Paenibacillus* spores, an extensive program was conducted from 1939 to 1953 to disseminate and establish *P. popilliae* in the eastern United States (44). Although this effort was credited with helping to suppress JB populations in treated areas (44, 81), low incidence of disease and upsurges in JB subsequently occurred. This raised doubts about the persistence and possible loss of virulence of *P. popilliae* in the field (43, 64, 65, 81). Small-scale use of commercial spore dusts did not increase milky disease incidence nor did it reduce localized grub infestations in turf (152).

Lack of methods for in vitro sporulation has limited commercial production of *P. popilliae* (81, 82). Products containing spores produced by a patented in vitro process were marketed during the 1980s, but they were recalled following the discovery that they contained only a different, noninfective bacterium (170). Recombinant DNA technology may yet provide strains of *P. popilliae* with enhanced virulence or broader host range. Until then, *P. popilliae* is probably best regarded

as one of many factors that contribute to population suppression of JB, rather than as an effective microbial insecticide (152).

BACILLUS THURINGIENSIS A novel isolate of *Bacillus thuringiensis*, designated serovar *japonensis* strain Buibui (*Btj*), isolated from Japanese soils, is highly toxic to JB larvae (139, 172). Delta-endotoxin proteins of *Btj* have been purified and characterized (73). Two formulations, one containing free protein toxin crystals (parasporal inclusions) and live spores, and another containing the toxin expressed in killed recombinant *Pseudomonas fluorescens*, were effective in suppressing JB grubs in turf plots (7). Commercial development, however, has been hindered by formulation and marketing issues, especially competition from highly effective synthetic insecticides.

NEMATODES The entomopathogenic nematodes *Steinernema glaseri* and *Heterorhabditis bacteriophora* can be effective biological insecticides for controlling JB grubs in turf (10, 42, 184, 198) or potted nursery stock (197). Implementation, however, has been hindered by high cost, limited availability, short shelf-life, and the inconsistent performance of commercial formulations (54, 83). Nematodes are sensitive to heat, soil moisture, exposure to sunlight, and biotic factors that can compromise their field efficacy (54, 55, 83). Some of their past inconsistency resulted from improper use by applicators who failed to understand their limitations, such as need for pre- and post-treatment irrigation (42). New nematode isolates may prove to be more effective. For example, *Steinernema kushidai*, which is relatively persistent and specific to scarab larvae, has given good control of JB grubs in turf (90).

Entomopathogenic nematodes also occur naturally in the soil. *Steinernema glaseri*, an unidentified mermithid, and a hindgut-inhabiting thelastomtid were found infecting JB grubs in North Carolina (154). Campbell et al. (21, 22) compared the temporal and spatial distributions of endemic *H. bacteriophora* and JB larval populations in turf fields. Although both species were patchily distributed, JB grubs tended to be less abundant in samples where the nematode was recovered. Infective juvenile nematodes can infect and be dispersed by JB adults (97), but the value of this approach for large-scale augmentation or establishment of new foci of infection is uncertain.

Being relatively sedentary, JB grubs are more vulnerable to nematodes that use a cruise foraging strategy (e.g., *S. glaseri*, *H. bacteriophora*) than to species such as *Steinernema carpocapsae* that use more stationary ambush foraging to infect mobile hosts (60, 115, 117). Host-recognition cues used by JB-adapted nematodes include CO₂ (52), host volatiles (116), contact cues (115), host feces (59) and host gut contents (58). Selection of *S. carpocapsae* for greater sensitivity to CO₂ enhanced its ability to locate JB larvae (52).

JB grubs possess defense mechanisms against entomopathogenic nematodes. These include grooming with the legs, mouthparts, and raster when nematodes are present on the cuticle (53, 192), behavioral avoidance (53, 163), and high pH gut

fluid that may also contain proteases (192). There may also be an immune response involving melanotic encapsulation within the hemolymph (193). Sieve plates on spiracles and a thick peritrophic membrane may act as morphological barriers to nematode invasion (48).

Efficacy of nematodes for grub control may be enhanced by using them in combination with other stressors such as *Btj* (88), milky disease (177), or certain insecticides. For example, *S. glaseri* and *H. bacteriophora* can synergistically interact with imidacloprid, a chloronicotynyl insecticide, against JB grubs (87, 89). Sluggishness of imidacloprid-intoxicated grubs facilitates host attachment and subsequent penetration of infective juvenile nematodes. Grooming and evasive behavior in response to nematode attack also were reduced in treated grubs (87). In contrast, no interaction occurred when the nematode *Heterorhabditis marelatus*, which is highly infective to JB, was used in combination with a molt-accelerating compound, halofenozide (126). Feeding on endophytic grasses also may increase JB grubs' vulnerability to nematodes (61).

OTHER ENTOMOPATHOGENS JB grubs are naturally infected by various microorganisms other than *P. popilliae* or nematodes. Bacteria in the genus *Serratia* colonize the gut, causing depletion of fat body, starvation, and development of an amber color (44). Low incidence of infection by a blue iridovirus was found in the Azores (94). Trophozoites and gamonts of a cephaline eugregarine were associated with JB larvae in North Carolina (154).

Hanula & Andreadis (65) conducted an extensive survey of pathogens of JB larvae in Connecticut. *P. popilliae*, *P. lentimorbus*, a rickettsia, *Rickettsiella popilliae*, and the fungus *Metarhizium anisopliae* occurred at low incidence. In contrast, cephaline eugregarines were found in the guts of larvae from nearly every site. Because they were ubiquitous, these protozoans are presumed not to be highly pathogenic in host grubs. A microsporidian, *Ovavesicula popilliae* (12), also was widespread, infecting 25% of the total JB larvae sampled, but as many as 80–90% of the grubs from some locations. This organism infects the Malpighian tubules, fat body, epidermis, and pericardial cells of larval and adult JB, as well as oenocytes and tracheal epithelial cells of adults (66). It is transmitted horizontally and appears to produce a chronic, debilitating disease. Infection by *O. popilliae* did not affect larval weight or development in the laboratory, but under field conditions, emergence of infected adults was delayed. Fecundity of heavily infected females was reduced by 50% (64).

Several species of fungi may infect JB larvae (65, 67, 76, 93, 182). Pathogenicity of *Metarhizium anisopliae* is affected by soil temperature and water content (93). Adult JB are also susceptible to *M. anisopliae* and *Beauveria bassiana* (96, 98). Infected beetles do not die for several days, so there is potential for autodissemination within populations (86, 96, 98). Villani et al. (182) showed that JB larvae avoided soil that contained high concentrations of *Metarhizium* for as long as 20 days after application. Conversely, incorporation of mycelial particles resulted in increased oviposition (182). These variable responses to inundative applications

of *M. anisopliae* help explain the erratic performance of fungi applied for control of soil-inhabiting insects.

Plant-Derived Antifeedants

Metzger and Grant applied extracts of 390 JB-resistant plant species to apple and peach leaves to test for protection from JB. Although a few extracts seemed somewhat repellent, the tests were not extensive enough to be conclusive (47). Feeding on sassafras was deterred by extracts of nonripe holly fruits (*Ilex opaca*), which contain high levels of saponins (91). Extracts of neem seeds (*Azadirachta indica*) containing the limonoid azadirachtin were strongly deterrent (108). Topical application of such extracts was toxic to JB larvae, causing death and severe deformity, or disrupting development to the adult stage (112). Although commercial formulations deterred feeding by JB in laboratory choice tests (68, 71), weekly applications of neem-based products did not adequately protect crabapple trees or roses exposed to high JB populations in the field (68). Similarly, microencapsulated pyrethrum derived from *Tanacetum cinerariifolium* did not reduce defoliation of field-grown Himalayan birches, nor did commercial extracts of garlic (*Allium sativum*), cayenne pepper (*Capsicum anuum*), or neem (195).

Insecticidal Control

INSECTICIDES AGAINST LARVAE JB grubs infesting lawns or golf courses typically are controlled by applying a soil insecticide, followed by watering to leach the residues into the root zone (144, 146). Short-residual organophosphates and carbamates were standards for grub control during the 1970s and 1980s. These products work best when applied soon after egg hatch, but they also control second and third instars after damage appears. Even when properly timed, they are variably effective (e.g., 27, 185). Moreover, their use can be detrimental to nontarget organisms, including predators of JB eggs and larvae (118, 176, 200). Most of these fast-acting, curative insecticides were restricted or canceled for turf usage during the 1990s in response to environmental concerns and the 1996 Food Quality Protection Act. These restrictions, and the relative ineffectiveness or slower activity of alternative products against third instars, has left the turf industry with few options for remedial grub control.

Imidacloprid, a chloronicotinyl analog, and halofenozide, a bisacylhydrazine ecdysteroid agonist that causes accelerated molting, were registered during the 1990s and became widely used for preventive control of scarabaeid grubs (144). Because of their persistence, either product can be applied preventively, in spring or early summer, to control grubs that eclose in July or August (144). Both compounds are highly active against early-instar JB (26, 28). Their broad application window and low vertebrate toxicity make them attractive to the turf care industry. RH 5849, a diacylhydrazine ecdysone agonist that is closely related to halofenozide, was previously tested against JB larvae (130). Symptoms of its toxicity included weight loss, cessation of feeding, and induction of a developmentally premature,

lethal molt. One-time feeding on treated foliage reduced subsequent egg production by JB females (130).

Presence of JB grubs in balled and burlapped nursery stock, container-grown plants, or in grass sod can result in rejection of such commodities for interstate and international commerce (133). Immersion of root balls in chlorpyrifos can control larvae in nursery stock, but the procedure is difficult, messy, and potentially hazardous (125). It also may be phytotoxic to some tree species (125). Preplant incorporation of bifenthrin or tefluthrin into potting media, or mid-summer drench with imidacloprid, controlled grubs in nursery containers (137).

INSECTICIDES AGAINST ADULTS Adult JB traditionally have been controlled by treating foliage or flowers of susceptible plants with short-residual insecticides, especially carbaryl (144). Because this generally is effective, there has been little motivation to develop alternative remedial controls. In California, however, area-wide spray programs for JB precipitated secondary pest outbreaks on citrus trees (37). Insecticidal soap kills adults that are hit by the spray, but it provides no residual effectiveness (136). Horticultural oil was ineffective whether applied to foliage or sprayed on the adults (136).

Regulatory Control

Although the federal Japanese beetle quarantine was rescinded in 1978, seven western states and British Columbia maintain quarantines governing importation of regulated commodities from JB-infested areas (13, 20, 133). These quarantines prohibit entry of soil, humus, compost, or manure (except when commercially packaged), grass sod, and nursery commodities unless they are free from soil that could conceal any life stage of JB. Such materials may be approved for entry if accompanied by either a Certificate of Treatment or Certificate of Origin issued by an authorized state agricultural official. The former certifies that the plants were treated for JB by approved methods prior to shipment. The latter certifies that they were produced in an approved, JB-free greenhouse, or in counties of quarantined states surveyed and free of JB, and transported in a manner that would prevent them from becoming infested. The U.S. Domestic Japanese Beetle Harmonization Plan outlines criteria for determining states' infestation status, as well as guidelines for consistent and uniform implementation of regulatory control measures (133).

The Animal and Plant Health Inspection Service (APHIS) also may regulate airport facilities in quarantined states during the JB flight season (13). An inspector may declare an airport to be regulated when he or she determines that adult JB populations are present to the extent that departing aircraft constitute a threat to spread the pest to protected states. West-bound aircraft, especially military and commercial cargo carriers, may be required to be loaded while enclosed inside a hangar, or at night. Aircraft opened and loaded during daylight may be subject to inspection, insecticide treatment, and safeguarding prior to departure. Requirements

may vary among carriers at the same airport based on varying degrees of perceived risk.

FUTURE DIRECTIONS FOR RESEARCH AND MANAGEMENT

Despite many years of research on integrated control methods for the JB, landscape managers, growers, and millions of homeowners still largely rely on insecticides to manage the adult beetle and its grubs. As insecticide use on landscapes is increasingly restricted and registrations of traditional products are lost, alternative products will be needed. Antifeedants (e.g., azadirachtin) may help to fill this void, but formulations marketed to date have been expensive and ineffective. Although use of JB traps often is counterproductive, further testing may reveal spatial configurations in which traps can help to reduce plant damage. Cultural controls that could be deployed by home gardeners (e.g., trap cropping, companion planting, repellent mulches) warrant study. For urban landscapes where potential hazards and liability of spraying are concerns, alternative application methods (e.g., trunk or soil injections) should be evaluated.

Cancellation of traditional soil insecticides has left the turf and nursery industries with few options for remedial control of JB grubs. Fast-acting, reduced-risk products that can be used for spot or curative treatments are sorely needed. Without this safety net, professionals and homeowners may increasingly favor preventive treatments as insurance against grub damage. Being able to predict in which years, and where, damaging grub infestations will occur would allow golf superintendents, lawn care providers, and homeowners to be more selective with treatments. Better understanding of the factors that drive annual and spatial variability of JB populations may provide this capability. Entomopathogenic nematodes show promise for grub control, but issues of cost, shelf-life, and reliability must still be overcome. Microbial insecticides containing *Metarhizium*, *Btj* strain buibui, or other pathogens warrant further study. Milky disease bacteria may also play a role if their virulence can be genetically enhanced and in vitro production methods are developed. The nursery industry needs better methods to ensure that nursery stock shipped to western states is grub free.

Host plant resistance offers the greatest promise for low-input, sustainable management of JB adults and grubs. Extension agents should convey information on resistant plants to landscape architects, city foresters, and retail personnel who advise homeowners on plant selection. Field-screening the diverse species and cultivars of woody ornamentals that already are on the market will likely reveal additional resistant ones, even within generally susceptible plant genera. Research on host finding by adult JB, and on the plant factors that determine its dietary range, may facilitate the development of JB-resistant plants through conventional propagation or transgenic plant technology. Although significant antibiosis

or antixenosis of turfgrasses to JB grubs has not been found, such resistance might be gained by transgenic expression of either bacterial toxins (e.g., *Btj* strain buibui), insecticidal plant proteins (51), or endophyte-associated alkaloids in grass roots.

Conservation biological control of JB grubs also warrants study. Establishment of *Tiphia* spp. or other introduced parasitoids might be enhanced by incorporating nectar-producing plants or honeydew sources into JB-infested landscapes. Information on comparative toxicity of insecticides to endemic natural enemies might encourage the use of least-disruptive compounds. Research on low-input, sustainable lawn-care practices that may help to suppress JB grub populations is needed.

As the JB spreads into new regions, it has the potential to disrupt indigenous ecosystems, including native herbivores and plant species. For example, its flower-feeding habits might compromise the reproduction of threatened or endangered plants. Another key question concerns the observation that JB often exhibits widely fluctuating populations over time. Do epizootics of pathogens such as *Ovavesicula popilliae* regulate populations of JB, or are environmental factors (e.g., rainfall) more responsible for cycles of outbreak and decline?

Finally, we suggest that analyses (e.g., 4, 46) that have projected the JB's probable ultimate spread in North America and elsewhere in the world may be overly conservative. Such models match the pest's temperature and soil moisture requirements with seasonal rainfall and other regional climatic factors. They do not take into account the expanses of irrigated turf and crop lands that now characterize many of the semiarid regions of United States that formerly were too dry to be suitable for the JB. This patchwork of suburban, grassy oases and irrigated agricultural lands may facilitate the JB's spread into Nebraska, Kansas, Oklahoma, Texas, and irrigated areas of the Great Basin; such spread has already occurred in parts of Japan (11). In southern and central California, extensive irrigation makes large areas vulnerable to the JB's establishment, and the climate of western Oregon, Washington, and southwestern British Columbia also is suitable (4, 46). Establishment of the JB in the Azores and the finding of beetles in aircraft arriving from the eastern United States in western states, Bermuda, and Europe (13) show its capacity to invade new areas. Refinement of quarantine, eradication, and management methods will help limit the JB's impact as an invasive species.

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