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SCARABS AS PESTS: A CONTINUING PROBLEM

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Abstract

The beetle family Scarabaeidae has a high diversity of species, and some of these have become important pests. Endemic scarab pests are known from all habitable continents but represent no more than a small percentage (probably 1–2%) of the total number of species. Some species have become international pests through human transport to new habitats. Scarab pests cause damage through larval feeding on plant roots or adult feeding on the aerial parts of plants. The pests are difficult to control due to the cryptic position of the larvae in the soil and the usually nocturnal activity of the adults. Chemical control is now focussed on specific chemicals with less residual activity. Biological control, especially with pathogens, has proven highly effective against some species, but control agents are often specific to a single species. Attractants ranging from sex pheromones to food lures have been isolated for scarabaeid species. Integration of control methods (IPM) has provided effective control of some species but there is a need for continued research to refine control measures and develop new options for management of this important group of pests.

The spectacular coloring, features, and size of the Scarabaeidae have long captured human imagination. “Sacred” scarabs have been viewed as symbols of life and were worshiped as early as the 1st Egyptian Dynasty (Cambefort 1994). This fascination continues today, with a collector recently paying US$ 90,000 for a black diamond scarab (Dunn 2000). However, not all scarabs are so appreciated. Some species feed on crop plants, and when these occur in high numbers they become pests in agriculture, forestry, and horticulture. The economic impact of these beetles has led to major research programs aimed at limiting their damage. Much has been learned in the 50 years since Ritcher (1958) reviewed scarab biology, but changes in land use, pest management practices, and the movement of pests to new regions has assured their continuing economic importance (Jackson 1992). In this paper we examine the characteristics of scarabs as pests and review advances in control and management of these insects.

The scarab beetles belong to the insect superfamily Scarabaeoidea that, during 200 million years of evolution (Morón 2004) have diversified into more than 31,000 species (Jameson and Ratcliffe 2002). Most pest species are found within the family Scarabaeidae, which includes 16 subfamilies (Smith 2006) and 2,300 genera. Adult scarabs are easily recognized by their distinctive, lamellate club antennae that can be fanned out when the insect is active. The larvae have slightly to strongly curved, C-shaped bodies, distinctive legs, and hardened head capsules. They are often referred to as white grubs. Pest species are within the Pleurosticti, or chafers. Adult beetles of this group are mostly phytophagous with a variety of different feeding habits (*i.e.*, Dynastinae which feed on stems or roots; Cetoniinae which feed on sap, fruit and flowers; Rutelinae which feed on foliage, fruit and flowers; and Melolonthinae which feed on foliage). The soil-dwelling larvae of chafers mostly feed on live roots and may be destructive to crops, although larvae of some Cetoniinae and Dynastinae feed only on organic matter in soil humus or litter.

Scarabs occupy many habitats, and infestations can often be recognized by signs of their feeding. Coconut palms frequently show signs of frond notching in areas endemic for the rhinoceros beetle, *Oryctes rhinoceros* (L.), while patches of pasture damage can always be found in young pastures susceptible to the grass grub, *Costelytra zealandica* (White), in New Zealand. These pests are common within their endemic range and will cause consistent, chronic damage. Other species, such as May beetles (*Phyllophaga* spp.) or European cockchafers (*Melolontha melolontha* L. and *M. hippocastani* [Fabr.]), occur in less frequent outbreaks where they totally strip foliage from large areas of forest. These pests have been recorded and monitored in central Europe for hundreds of years (Keller 1984). In Switzerland and Germany, these outbreaks have occurred in approximate 30 year cycles for the last 200–300 years. Major outbreaks were recorded in Western Europe in the 1940s and 1950s after World War II, but by the 1980s the insect was considered rare, perhaps endangered, and its loss was lamented in newspapers and labelled an indicator of environmental pollution. The insect has since recovered, with high populations throughout Switzerland, Hungary, Austria, and Germany, and a range that extends through the Rhine Valley to the Baltic Sea.

Although spectacular outbreaks can occur, scarab populations are generally at low densities. Most of their life cycle is spent as larvae concealed in the soil, with adults emerging at night during a short flight season. In an ecological sense, scarabs follow a K-strategy; they have a relatively low reproductive capacity and occur in stable populations with limited movement and mixing between populations. This is a successful strategy because scarab beetles are found in habitats as varied as tropical rainforests and desert-like grasslands and on all continents except Antarctica.

The success of scarabs lies in the ability of the larvae to feed on a range of low energy foods—grass roots and organic matter—with little competition from other insects. Larvae are able to turn these substrates into energy through microbial action in a modified gut. This has allowed scarab larvae to exploit a variety of niches, ranging from rotting organic matter and dead tree trunks to freshly growing roots. Using these resources, they have become highly successful, but when a niche coincides with human activities they may become pests even in their native habitat (Table 1).

Endemic Scarabs as Pests

Endemic species can cause damage to natural ecosystems during outbreaks. However, the landscape changes that result from cultivation and crop production often exacerbate the situation. The ability of species to emerge as pests is a function of their evolution and biology. Many scarab species are grass root-feeders in the larval stage and occur naturally in habitats that are subject to periodic changes. For example, river flood plains covered with native grasses appear to be the natural habitat of a broad range of endemic Australian scarab species. The planting of sugar cane, *Saccharum officinarum* (L.), in these zones

Table 1. Major endemic scarabs as pest species in their native habitat. (Adapted from Jackson 1992).

Region	Species	Crops attacked
Australia	*Adoryphorus couloni* (Burm.)	Pasture
New Zealand	*Costelytra zealandica* (White)	Pasture
North America	*Cyclocephala* spp., *Tomarus subtropicus (Blatchley) (=Ligyrus subtropicus)*	Turf, sugar cane
South America	*Diloboderus abderus* (Sturm)	Pasture, cereals
South Africa	*Heteronychus arator* (Fabr.)	Maize and other cereals
South Asia	*Holotrichia* spp.	Groundnut, pulses, and cereals
Western Europe	*Melolontha melolontha* L.	Trees (fruit and forestry)
Asia/Pacific	*Oryctes rhinoceros* (L.)	Palms
Mesoamerica (Mexico-Colombia)	*Phyllophaga* spp.	Maize

provided an excellent resource for these insects and led to a large complex of damaging pests (Robertson *et al.* 1995).

In Mexico, maize, *Zea mays* (L.), has been selected and developed by humans for 3,000 years and has become a dietary staple. Intensification of maize production provided an opportunity for species that can adapt to this new, human-modified, environment. While Mexico is a center of diversity for Scarabaeidae (Morón 1986) and a large number of pest species have been recorded, it is surprising that economic damage is dominated by relatively few species, predominantly from the genus *Phyllophaga*. Of 369 species of *Phyllophaga* listed by Morón (2003), less than 20 are considered to have pest status. These include *P. obsoleta* (Blanchard), *P. ravida* (Blanchard), and *P. vetula* Horn, which are distributed throughout the Mexican highlands. Other species, like *P. menetresi* (Blanchard), are severe pests in Central America. *Phyllophaga crinita* (Burmeister) is a pest of grassland and cereals in northern Mexico. Its distribution crosses into Texas and other southern states of the U.S.A. where it can damage natural rangeland as well as high maintenance turf.

The U.S.A. has a broad diversity of native scarabs, and several are recorded as pests. These include turfgrass pests such as *P. anxia* (LeConte), *P. rugosa* (Melsheimer), *Cyclocephala borealis* Arrow, *C. lurida*, Bland, *C. hirta*, LeConte, *C. parallela* Casey, *Anomala flavipennis* Burmeister, A. *marginata* (Robinson), *Macrodactylus subspinosa* (Fabr.), *Cotinus nitida* (L.), and *Ataenius spretulus* (Haldeman) (Vittum *et al.* 1999). *Tomarus subtropicus* (Blatch.) (=*Ligyrus subtropicus*) can be an important pest of sugar cane in Florida (Cherry *et al.* 1990).

Yadava (1992) listed seven major white grub pests for India, all native species, including five species of *Holotrichia*. The major pests of groundnut in southern India include *H. reynaudi* (Blanchard) and *H. serrata* (Fabr.) while in northern India, *H. consanguinea* (Blanchard) is the predominant pest species in crops. The genus *Holotrichia* occurs throughout the Palearctic region, and species are also of concern in China and Japan. About 20 of China's 2,000 scarab species are pests (J. Cui, pers. comm.). In northern Asia, *Holotrichia* is replaced by *Popillia* as the predominant pest genus, but only a few of the hundreds of recorded endemic *Popillia* species are considered pests. These include: *P. quadriguttata* (Fabr.) and

P. atrococrula Bates in China; *P. japonica* Newman and *P. lewisi* Arrow in Japan; *P. uchidai* Niijimi and Kinoshita and *P. indigonacea* Motschulsky in Korea.

Of about 150 scarab species recorded in Central Europe, damage is dominated by just four native species; *M. melolontha*, *M. hippocastani*, *Amphimallon solstitialis* (L.), and *Phyllopertha horticola* (L.) (Zimmermann 1992). In Australia, less than 30 of its 3,000 endemic scarabaeid species are considered pests (Lawrence and Britton 1991). In New Zealand, only one (*C. zealandica*) of more than 100 recorded endemic scarab species (Given 1952) is considered a major pest, with one or two others reaching occasional minor pest status.

Thus, while scarab pests are important and have been reported from all continents (with the exception of Antarctica), the number of pests in relation to the total scarab species is only *ca.* 1–2%. This implies that characteristics leading to pest status are relatively rare within the Scarabaeidae, and that it takes a particular combination of diet, environmental conditions, and structure to enable pest status.

Exotic Scarabs as Invasive Pests

Scarabs can also become pests in new habitats, and their spread has been assisted by human activity (Table 2). One of the best known invasive scarab pests is the Japanese beetle, *Popillia japonica* Newman. This insect was not considered a pest in its home country, but has caused severe problems through the eastern United States since its accidental introduction in the early 1900s (Fleming 1972). The United States Department of Agriculture (USDA) conducted extensive research programs on this insect (*e.g.*, Fleming 1972, 1976). But despite nearly a century of research and control (as recently reviewed by Potter and Held 2002), the Japanese beetle is still considered a major pest. It is one of few pests subjected to internal quarantine regulations within the United States, and it causes restricted movement of fruits and plants. Despite these attempts, the zone of infestation now covers approximately half of the country.

Other exotic pest scarabs in the United States include the European chafer (*Amphimallon majalis* [Razoum]), the oriental beetle (*Anomala orientalis* Waterhouse), and the Asiatic garden beetle (*Maladera castanea* [Arrow]) (Vittum *et al.* 1999), all of which were probably introduced in the root balls of imported nursery stock. The European chafer has never been a pest in its native Europe but is of increasing importance in the United States. It is expanding its range and has spread along the northern tier of US states and Canadian provinces as far west as Michigan, with a new population recently established in British Columbia. The European chafer is becoming a particular concern in nursery crops (Smitley 1996) because it is more difficult to kill by insecticides and biological agents than are most other pest scarabs. The oriental beetle is also expanding its range from the east coast of the United States towards the west (Alm *et al.* 1995, 1999) and is of concern as a pest of turfgrass and plant nurseries.

North America has several invasive scarab pests from Europe and Asia, yet there has been no report of North American scarabs establishing in Asia or Europe. Despite a lack of movement of North American scarabs, the Japanese beetle has moved from the U.S.A. to become established in the Azores. It is predicted that much of the world could support this pest (Allsopp 1996).

Maladera matrida Argaman, native to India, has become a serious pest in the Middle East. This polyphagous pest was first recorded in Israel in 1983 and later from Saudi Arabia (Harari *et al.* 1997). Adult beetles feed on foliage of ornamental plants, orchard trees, and irrigated crops after sunset, while the larvae

Table 2. Scarab species accidentally introduced to become pests in new environments.

Common name	Scientific name	New location	Year
Chinese rose chafer	*Adoretus sinicus* Burm.	Hawaii	1891[a]
Rhinoceros beetle	*Oryctes rhinoceros* (L.)	Burma	1895[a]
Oriental beetle	*Anomala orientalis* Waterhouse	Hawaii	1908[a]
Rhinoceros beetle	*Oryctes rhinoceros*	Samoa	1909[a]
Indian rose beetle	*Adoretus versutus* Harold	Samoa	1914[a]
Tasmanian grass grub	*Aphodius tasmaniae* Hope	New Zealand	1916[a]
Japanese beetle	*Popillia japonica* Newman	U.S.A.	1916[a]
Oriental beetle	*Anomala orientalis*	Continental U.S.A.	1920[a]
Asiatic garden beetle	*Maladera castanea* (Arrow)	U.S.A.	1921[a]
Black beetle	*Heteronychus arator* (Fabr.)	Australia	1930[a]
Taro beetle	*Papuana huebneri* (Fairmaire)	Kiribati	1934[a]
Black beetle	*Heteronychus arator*	New Zealand	1937[a]
European chafer	*Amphimallon majalis* (Razoum)	U.S.A.	1940[a]
Argentinian scarab	*Cyclocephala signaticollis* Burm.	Australia	1950[b]
Rhinoceros beetle	*Oryctes rhinoceros*	Fiji	1953[a]
Rhinoceros beetle	*Oryctes rhinoceros*	Mauritius	1962[a]
Red-headed cockchafer	*Adoryphorus couloni* Burm.	New Zealand	1963[a]
No common name	*Hoplochelus marginalis* (Fairmaire)	Reunion	1972[a]
Emerald beetle	*Protaetia pryeri* (Jensen)	Midway	1972[c]
Japanese beetle	*Popillia japonica*	Açores	1974[a]
Rhinoceros beetle	*Oryctes rhinoceros*	Reunion	1978[a]
Indian rose beetle	*Adoretus versutus* Harold	Vanuatu, Futuna Is.	1982[a]
No common name	*Maladera matrida* Argaman	Israel	1983
Taro beetle	*Papuana uninodis* Prell	Fiji	1984
Taro beetle	*Papuana* spp.	New Caledonia	1993[d]
No common name	*Maladera matrida*	Saudi Arabia	1997[e]

[a] Jackson 1992.
[b] www.ecogrow.com.au
[c] Nishida 1999.
[d] B.M. Thistleton pers comm.
[e] Harari *et al.* 1997.

are pests of potatoes, sweet potatoes, and groundnut (Gol'berg *et al.* 1989). Like many invasive insects, its population exploded after introduction before settling back into a lower level of infestation.

In the tropical Pacific, the rhinoceros beetle (*O. rhinoceros*) has spread from Asia into the Central Pacific and to Islands in the Indian Ocean, most likely by copra transport on small ships between islands. Massive outbreaks took place on Samoa in the early part of the 20th century and later in Fiji (Waterhouse and Norris 1987). Taro beetles (*Papuana* spp.) have also moved through the Pacific by human activity, with outbreaks bringing an end to taro growing and use as a staple food crop in Kiribati and severely damaging economic production in Fiji (B. M. Thistleton pers. comm.).

Protaetia spp. are distributed throughout Asia and Africa, where they are generally not considered pests. An exceptional case occurred on Midway Atoll where there was a population explosion of the Emerald beetle, *P. pryeri* (Jansen) after rat eradication programs (Klein 2003). The beetles decimated crops and clung to tourists, causing discomfort and increasing the chances of inter-island dispersal. The insect is now also established on Guam.

The Southern Hemisphere also suffers from invasive species. The South African black beetle, *Heteronychus arator* (Fabr.), is an important pest in maize crops and has spread thoughout southern Australia and northern New Zealand. In addition, the Australian pests, red-headed cockchafer, *A. couloni* (Burmeister), and Tasmanian grass grub, *Acrossidius tasmaniae* (Hope), have entered New Zealand (Emberson and Stephenson 1999; Townsend *et al.* 1999). Tasmanian grass grub is a sporadic pest of pastures, particularly in the drier east coast area of New Zealand. The red-headed cockchafer is still confined to a relatively small area but is steadily spreading from its initial point of entry. Australia also has been invaded by the Argentinian dynastine, *Cyclocephala signaticollis* Burmeister, which has established in lawns and amenity turf in New South Wales and even on the parliamentary lawn in the capital, Canberra.

While most invasive scarab pests are also known as pests within their home range, it is interesting that some species, such as the Japanese beetle, are not recognized as severe pests within their native habitat. The Japanese beetle and other invasives have shown a pattern of massive numbers generated during the outbreak phase in new areas after which the population declines to a lower level. A similar pattern is seen with outbreaks of endemic scarabs after major land use changes (*e.g.*, irrigation or the establishment of golf courses). The pattern of outbreak and decline appears to be due to a founder population arriving in a location with abundant resources and few natural enemies. This leads to rapid population growth and high population densities, followed by a decline due to a biotic response from antagonist invertebrates and microbes. Further studies are needed to better understand this phenomenon in order to predict outbreaks and develop methods to manage them.

Given the large numbers of scarab species, the high occurrence of endemism, and the success of scarabs as pests, the numbers of invasive scarab pest species appears low. It could be that the very factors that lead to endemism somehow limit success as an invasive species, such as reducing the suitability of a few individuals to found a population. Excluding tropical species, there have been no invasive scarab pests recorded that have crossed the equator to establish in the alternative hemisphere. This is in marked contrast to the Curculionidae, where many damaging species have a worldwide distribution. Perhaps the potential success of invading species is limited by the strict seasonality of scarabs, which makes behavior asynchronous between hemispheres. Alternatively, the lack of an aestivating stage and a limited egg load among scarabs may limit the success of establishment after long journeys to new habitats.

Management and Control

Scarab pests have often been controlled by persistent chemicals, but concern over safety and environmental contamination has emphasized other forms of control, such as biological control and trapping.

Trends in Use of Chemical Pesticides

Management of soil dwelling scarab pests was revolutionized after the development and use of highly persistent, chlorinated hydrocarbons (DDT, chlordane, dieldrin) from the 1950s to the 1970s. These could be applied prophylactically and gave long-term control but led to the development of insect resistance after continued use. Worse were the non-target effects and environmental contamination by these pesticides, which led to them being banned from most countries. Organochlorine residues have persisted in soils for many years after application, and their gradual dissipation has correlated with increasing scarab problems in the northeast United States, particularly in nurseries. The organochlorines were followed by less persistent, but more toxic, carbamate and phosphate-based insecticides. These have proven difficult to use for scarab larvae concealed in the soil. Drenching and soil incorporation have been used, but it is difficult to obtain contact between pest and chemical in the complex soil environment. Soil injection around plant roots has been used to protect nursery plants from root damage (Reding *et al.* 2004). However, to obtain the high mortality levels required for quarantine treatments, balled and burlapped nursery stock are dipped in vats of liquid chloropyrophos (Mannion *et al.* 2000), but even this is not always effective. A slow release formulation of chlorpyrophos on a plastic pellet has been used for control of scarabs in sugar cane (Robertson *et al.* 1995).

Insecticides developed in recent years, such as insect growth regulators and neonicotinoid compounds, are more "green" in nature. These are based on insect-specific pathways and require only small amounts of active ingredient (Cowles and Villani 1996; Shetlar 1999; Potter and Held 2002). They are most effective against early larval instars, and must be applied before grub damage is visible. Once damage is evident, it is very difficult to obtain chemical penetration of the soil to kill the pests. In addition, some species of scarabs, particularly *M. castanea*, are more resistant to these new chemicals (Cowles *et al.* 1999).

Biological Control

Biological control has often been proposed as an alternative to chemical control and is an attractive option because it involves manipulation of "natural enemies" of the pest, such as parasitoids, predators, and pathogens. Biological control, through the introduction of new species, has been used extensively for control of exotic pests when a pest has entered a new habitat without its specific cohort of natural enemies. Biological control can also be used to augment or redistribute natural enemies through either habitat modification or the application of mass produced organisms, such as biopesticides. All these approaches have been used in scarab pest control and are discussed below.

Parasitoids

Insect parasitoids, those that grow on or within their hosts, can be found attacking scarabs, but they are not usually abundant in scarab populations. The most common parasitoids are found in the families Tiphiidae and Scoliidae (Hymenoptera) and Tachinidae (Diptera).

Tiphia wasps (Tiphiidae) are solitary ectoparasites of the larvae of numerous scarab beetles (Krombein *et al.* 1979) and include four species that were successfully introduced to the United States for control of exotic scarab pests (Fleming 1968). After initial establishment, the wasp populations were greatly reduced by the heavy use of chlorinated hydrocarbons in the 1950s and 1960s. Today, however, numbers of the spring tiphia, *T. vernalis* Rohwer, have recovered, and it is the most widespread parasitoid of the Japanese beetle. *Tiphia pygidialia* Allen is often found attacking *Cyclocephala* spp. (Rogers and Potter 2003*a*). *Tiphia* wasps find their hosts by following kairomones from the grub's frass in the soil (Rogers and Potter 2002). In addition, rates of parasitism are increased if food plants are available for the adult wasps (Rogers and Potter 2003*b*). The spring tiphia will also attack the oriental beetle and other exotic scarabs, but it does not parasitize endemic species, either in the field or the laboratory (R. McDonald, pers. comm.).

Tachinid flies are endoparasites of scarab adults and larvae. They have large larvae that develop within the body cavity of the host. The tachinid, *Istocheta aldrichi* (Mesnil), lays its eggs on the thorax of adult Japanese beetles. In New Zealand, *Prociscio cana* Hutton lays its eggs on the larvae of *C. zealandica* but can only parasitize two-year life cycle populations where the third instar larvae coincide with summer fly emergence (Merton 1982).

Predators

Predators can have a significant impact on larvae in the soil and can be used to manage pest levels. For example, ants (Formicidae), ground beetles (Carabidae), and rove beetles (Staphylinidae) have been shown to reduce populations of *Ataenius spretulus* (Haldeman), *A. granarius* (L.), *P. japonica*, and *C. lurida* (Smitley *et al.* 1998; Rothwell and Smitley 1999; Zenger and Gibb 2001; Potter and Held 2002; Jo and Smitley 2003). Predators are highly sensitive to chemical pesticides, and limiting their use can lead to increases in predator populations (Potter and Held 2002). Habitat manipulation by planting wildflower mixes will also increase Japanese beetle predator levels (Braman *et al.* 2002).

Pathogens

There are a large number of insect pathogens associated with the Scarabaeidae, and several have been used in pest management (Jackson and Glare 1992). Well-studied species, such as the New Zealand grass grub, are natural hosts for more than 20 different species of pathogenic microbes and nematodes (Glare *et al.* 1993). The reason for this high pathogen potential of some species may be due to the general pattern of steady incremental population growth resulting in high insect densities as well as the long term occupation of suitable sites. These factors favor both horizontal transmission of pathogens among beetles of the same generation and vertical transmission between generations by pathogens surviving in the soil. Soil-dwelling scarabs are in close association with the reservoir of microbes in the soil, which also supports transmission of pathogens. Scarabs are infected by microorganisms from all of the major phyla: virus, bacteria, fungi, and protozoa. Entomopathogenic nematodes, although strictly parasites, are also included in this section due to their symbiotic associations with entomopathogenic bacteria, similarities in the methods of study, and their potential use in biological control. To study microorganisms and develop their use as control agents, methods for collecting, identifying, and testing scarab pathogens in the laboratory and field have been compiled by Lacey (1997) and Klein *et al.* (2000).

Scarabs are infected by a number of viruses, with the most well-known of these being the *Oryctes* virus of the rhinoceros beetle, *O. rhinoceros* (Huger 2006). This is a unique, non-occluded virus that lacks a protective protein coating. While this limits its persistence in the environment, the virus is highly infective and is readily transmitted between adult beetles. By recognizing these characteristics, it has been possible to use the virus in pest management. Viruses can be isolated, and purified fresh stocks can be used to infect adult beetles. The infected beetles are then released into healthy populations, where the virus will spread naturally into the population. The virus infects the insect gut cells and will reduce feeding and fecundity. When the virus reaches high levels, larvae will be infected in their compost breeding sites. The virus is effective because it is transmitted during aggregating behavior of the adult beetles. Despite the success of this program over five decades, the virus has not been used for pest species outside the scarab genus *Oryctes* due to low levels of infection and transmission, and no similar viruses have been found in other species. Current research is focused on examining strain differences within the virus to determine those with the greatest persistence and effect (Jackson *et al.* 2005). Scarabs are also infected by pox viruses and iridescent viruses, but the impact of these on scarab populations is unknown, and they have not been used in pest management (Glare and Crawford 1992).

Milky disease is distinctive and is found only in scarab larvae. It is caused by the bacterium, *Paenibacillus popilliae* (Dutky) (Klein and Jackson 1992). The bacterium colonizes the haemolymph of scarab larvae, producing a refractile spore that gives the haemolymph a distinctive milky color. Milky disease organisms are found in scarab populations on all continents, but, like their hosts, they have radiated into different forms that appear to show specificity for different species. Milky disease bacteria were cultured and introduced into Japanese beetle populations in the eastern United States in a major campaign from the 1940s–1960s (Fleming 1968). Formulations of the bacterium have been commercialized but use of the bacterium has been limited by the high cost of *in vivo* production and the slow uptake of disease. Redmond and Potter (1995) suggested that the bacterium would be best used as an inoculative agent as part of wider pest management programs. This approach would take advantage of the persistent nature of the *P. popilliae* spores which can survive for many years in the soil and require specific conditions of the host insect gut for germination.

Interestingly, most strains of the well-known pathogen *Bacillus thuringiensis* Berliner have little or no effect on scarabs. This resistance may have evolved through close association of larvae with bacterial spores in the soil. The organism is, however, the source of a wide and expanding range of toxins, and one recent isolate, the Buibui strain, has been shown to be effective against ruteline scarab pests, including Japanese beetle (Alm *et al.* 1997). Protein/spore mixes of this organism have been shown to be effective against scarab larvae, but it has yet to be developed for commercial scarab biocontrol.

In New Zealand, strains of the non-sporeforming bacteria, *Serratia* spp., cause amber disease in the New Zealand grass grub, *C. zealandica* (Jackson *et al.* 1993, 2001). Pathogenic strains contain a specific plasmid (Hurst *et al.* 2000), and ingestion brings about a cessation of feeding, clearance of the gut, and eventual death. Natural epizootics of amber disease develop over several seasons in grass grub populations, with populations in newly sown pastures generally disease-free. This opens an opportunity for biological control, where artificially-produced bacteria can be applied to healthy populations to promote epizootics and prevent the occurrence of pasture damage. Strains of *S. entomophila* Grimont *et al.* have been commercialized and successfully used for grass grub biological control for more than a decade (Jackson 2006). Despite intensive testing, no other scarab species has been found susceptible to the plasmid-bearing strains.

Protozoan diseases are also known in scarabs (Hanula and Andreadis 1992). In Australia and New Zealand, microsporidians (*Nosema* spp., *Vavraia* spp.), coccids (*Adelina* spp.), and neogregarines (*Mattesia* spp.) are commonly found, sometimes causing epizootics (Popay 1992). A similar complex has been isolated from scarabs in Europe. In North America, the recorded occurrence of intracoelomic protozoans as diseases of scarabs is very low. Reports are limited to a microsporidian, *Ovavesicula popilliae* Andreadis and Hanula, infecting the malpighian tubules of Japanese beetle (Hanula and Andreadis 1988). Gut-inhabiting gregarines, however, are found in the alimentary tract of scarab larvae in most parts of the world.

Entomopathogenic fungi of the genera *Metarhizium* and *Beauveria* are ubiquitous in soils, but consistent infection of scarabs is limited to specific strains mostly within the species *B. brongniarti* (Saccardo) Petch and the large spored variety of *M. anisopliae* var. *majus* (Metch.) Sorokin. For example, the scarab *Hoplochelus marginalis* (Fairmaire) has been a severe pest of sugar cane on the island of Reunion since its accidental introduction in the 1960s. The insect was resistant to a wide range of fungal isolates but highly susceptible to a strain of *B. brongniartii* isolated from the insect in its original habitat of Madagascar (Maurer *et al.* 1996). It was by far the most effective of a wide range of strains tested, yet it had little effect on other insects. Other strains of *B. brongniartii* have been isolated from *M. melolontha* and have been used for control of this pest in Europe. Cane grubs in Australia have also been a target for control by fungi. The cane grub, *Dermolepida albohirtum* (Waterhouse) is highly susceptible to a particular strain (FI-1045) of *M. anisopliae* that has been commercialized for the pest (Logan *et al.* 2000).

A wide range of nematodes have been isolated from scarabs (Poinar 1992), but attention has been focused on nematodes of the families Steinernematidae and Heterorhabditidae for pest control (Klein 1990, 1993). These species carry symbiotic bacteria that are "injected' by the nematode into the target host, thus bringing about bacterial septicaemia and death. The nematodes then reproduce in the ensuing "bacterial soup". Nematodes have been evaluated in numerous laboratory and field trials with best results obtained with the larger, "cruiser" nematodes, *e.g.*, *Steinernema glaseri* (Steiner), *Heterorhabditis megidis* Poinar *et al.*, and *H. bacteriophora* Poinar, which move through the soil to locate their hosts. Unfortunately, these large, active nematodes are the most difficult to rear, formulate, and store. Production and storage requirements may limit the successful use of the recently-discovered, scarab-active nematode, *S. scarabaei* Stock and Koppenhofer (Stock and Koppenhöfer 2003). This nematode was isolated from the oriental beetle and is effective against a range of important scarab pests, including the European chafer. To date it only has been successfully reared in live scarab larvae. Techniques for the use of entomopathogenic nematodes can be found on the Ohio Agricultural Research and Development Center web site (http://www.oardc.ohio-state.edu/nematodes) or in the training video, "Entomopathogenic Nematodes: Tools for Pest Management" (Gaugler and Klein 1998). A general problem with nematodes is that their effectiveness is often limited by the cool soil temperatures where scarab larvae are still active. Efficacy, however, can be significantly increased when combined with low rates of neonicotinoid pesticides (Koppenhöfer *et al.* 2000) that cause behavioral changes in the target insect (Grewal *et al.* 2001).

Thus, while there is a high diversity of pathogens associated with scarabs, it appears that many occur at low levels, and that scarabs appear to show intrinsic resistance to many generalist pathogens as shown by a high degree of intrinsic resistance among scarabs to commercial strains of *B. thuringiensis* or entomopathogenic fungi. This has probably arisen as a result of frequent challenges to scarab larvae by microbes during their long evolution in the soil. This means that to use a pathogen effectively against scarab pests, we must select strains that have evolved to overcome host resistance. These will be relatively rare and likely host specific (Jackson 1999). This hypothesis is supported by the lack of instances where commercial microbial products or widely used pathogens have been effective in field programs against more than one pest species (Table 3).

Table 3. Diseases and nematodes used in the biological control of Scarabaeidae.

Microorganism or Nematode	Target	Product name	Reference
Metarhizium anisopliae	*Adoryphorus couloni* Burm.	Biogreen	Rath *et al.* 1995
Serratia entomophila	*Costelytra zealandica*	Invade/ Bioshield	Jackson *et al.* 1992; Jackson (in press)
Metarhizium anisopliae	*Dermolepida albohirtum*	BioCane	Logan *et al.* 2000
Beauveria brongniartii	*Hoplochelus marginalis*	Betel	Vercambre *et al.* 1994
Beauveria brongniartii	*Melolontha melolontha*	Engerlingspilz	Keller 2000
Beauveria brongniartii	*Melolontha melolontha*	Melocont	Strasser 1999
Oryctes virus	*Oryctes rhinoceros*	—	Bedford 1980
Heterorhabditis bacteriophora	*Phyllopertha horticola*	Nema-green	Ehlers *et al.* 2003
Paenibacillus popilliae	*Phyllophaga* spp.	—	F. Badilla, pers. comm. 2005
Paenibacillus popilliae	*Popillia japonica*	Doom Milky Spore	Klein 1992
Bacillus thuringiensis var. *buibui*	*Popillia japonica*, *Anomala* spp.	—	Alm *et al.* 1997

Pheromones and Food Lures

The characteristic lamellate antennae of scarabs suggest an important role for volatile chemicals in scarab behavior and ecology, and attractant chemicals have been found that range from sex and aggregation pheromones to plant kairomones. The chemical ecology of phytophagous scarabs was reviewed by Leal (1998), and here we provide additional comments on the use of attractants in scarab control.

Sex Pheromones

The attraction of male beetles to individual females in prominent positions on plants or on the soil is a strong indicator of the presence of sex attractants in the Scarabaeidae. The isolation of these sex attractants, however, has often proven difficult due to the complex behaviors of the adult beetles and the complexity of isolated mixtures of chemicals. Pheromones can be related to insect phylogeny. Beetles of the subfamily Rutelinae generally use fatty acid derivatives as sex pheromones. The sex pheromone of the Japanese beetle, (*R*)-japonilure, is a lactone produced by desaturation of fatty acids, followed by hydroxylation, chain shortening, and ring formation (Leal 1998). Similar lactones and chemical blends have been isolated from *Anomala* spp. Sex pheromones in the subfamily Melolonthinae have been more variable in chemical structure. In New Zealand, *C. zealandica* females utilize a bacterial-produced phenol in the attraction of males (Hoyt and Osborne 1971). Females of *Holotrichia* spp. produce amino acid-derived pheromones from glands that are everted in pre-reproductive calling behavior (Leal *et al.* 1992).

Aggregation Pheromones

Adult beetles of some large, horned species of Dynastinae, such as *Xylotrupes gideon* (L.), can be found on trees in aggregations where males will fight to occupy prominent positions to attract females. The occurrence of such groups suggests the production of an aggregation pheromone. A single compound, ethyl-4-methyloctanoate, has been isolated as the aggregation pheromone produced by both *O. rhinoceros* in Asia and *O. monoceros* (Olivier) in Africa (Gries *et al.* 1994; Hallet *et al.* 1995).

Food Lures

A characteristic of many scarab beetles during their flight season is the aggregation of large numbers of feeding adults around specific trees. This has been attributed in some cases to specific visual cues, such as horizon interrupters. Aggregation may, instead, be a response to volatiles produced from damaged leaves as suggested by Loughrin *et al.* (1995) to explain Japanese beetle aggregations. The Japanese beetle is strongly attracted to fruit and flowers, and this has been used in trapping strategies. Recently, Reinecke *et al.* (2002), Ruther and Hilker (2003), and Ruther and Mayer (2005) have shown that adults of *M. melolontha*, *M. hippocastani*, and *Phyllopertha horticola* (L.) are strongly attracted to alcohols produced from damaged leaves, which may explain the plague-like aggregations of these insect on specific forest margins during the flight season.

Use of Pheromones and Food Lures in Trapping

Pheromones and food lures have been extensively used in scarab pest management for monitoring and control. More than 20,000 Japanese beetle traps are distributed through the western U.S.A. and are monitored to identify and destroy any invasive foci of the pest. The traps are baited with a combination of Japonilure and a three-part combination of phenethyl propionate, eugenol, and geraniol originally identified by Ladd *et al.* (1981). While there is little doubt that pheromone and lure traps can catch large numbers of beetles, the evidence of their effect on preventing damage and reducing pest populations has been more controversial (Potter and Held 2002). There is now evidence that pheromones can be used to disrupt scarab behavior and reduce the populations of some species. Alm *et al.* (1999) used the pheromone (Z)-7-tetradecene-2-one to evaluate the distribution of oriental beetles in the United States. The pheromone has subsequently been used in New Jersey to successfully disrupt the mating of the oriental beetle in turf, highbush blueberries, and ornamental nurseries (Polavarapu *et al.* 2002; Koppenhoffer *et al.* 2005; Sciarappa *et al.* 2005).

Aggregation pheromones are widely used for trapping the damaging adults of the rhinoceros beetle, *Oryctes* spp., in oil palm plantations in southeast Asia. Chung (1997) reported the reduction of damage in young palms by traps baited with ethyl-4-methyloctanoate. The pheromone is used in combination with *Oryctes* virus for management of rhinoceros beetles in Malaysia (Ramle *et al.* 2005).

Williams *et al.* (1990) identified a three-part lure containing octyl butyrate, and valeric, and hexanoic acids as an attractants for the rose chafer, *Macrodactylus subspinosus* (Fabr.). The attractant power of this combination was improved by the addition of trans-2-nonenol and alpha ionone (Williams *et al.* 2000), and this combination was used in Ecuador for mass trapping of beetles and protection of maize crops from damage.

The pheromone L-isoleucine methyl ester (LIME), originally isolated from *Holotrichia parallela* (Motchulsky), has been used for trapping of *Protaetia pryeri* from Midway Atoll. The compound attracted beetles of both sexes, and thousands of beetles were trapped and removed every few weeks for two years until the population crashed to very low levels (N. Garon, pers. comm.). Recently, attractants based on LIME and L-isovaline methyl ester have been used to map the distribution of a several *Phyllophaga* species in North and Central America (Robbins *et al.* 2006).

Scarabs as Pests in the Future

Scarabs will continue to be important economic pests, particularly with the intensification of crop production and increased consumer demand for pesticide-free produce. Changes in crop management and the introduction of exotic crops into new environments will result in the emergence of new scarab pests. It is here that the huge diversity among the Scarabaeidae is likely to bring unwelcome surprises to the agriculturalist. Increasing globalization and world trade will result in more opportunities for scarabs to hitch-hike to new locations where they can become damaging pests. Heightened awareness of the damaging potential of these insects has led to improvements in quarantine systems and fewer new recent outbreaks. However, once established, scarab pests are extremely difficult to dislodge, and a full range of technologies is needed for their elimination.

Chemical control will continue to be used as a quick fix for scarab problems, but management through IPM is a better long-term solution. The range of control techniques is expanding with chemical lures, biopesticides, and environmental management options. It is the combination of these technologies that will reduce the worst excesses of scarab population explosion in our crops and leave us to enjoy the diversity of this amazing group of insects.

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