

UC Riverside

UC Riverside Previously Published Works

Title

Restoring Balance: Using Exotic Species to Control Invasive Exotic Species

Permalink

<https://escholarship.org/uc/item/1qv8k7c7>

Journal

Conservation Biology, 18(1)

Author

Hoddle, M S

Publication Date

2004

Peer reviewed

Restoring Balance: Using Exotic Species to Control Invasive Exotic Species

MARK S. HODDLE

Department of Entomology, University of California, Riverside, CA 92521, U.S.A., email mark.hoddle@ucr.edu

Abstract: *Invasive species threaten natural habitats worldwide, and active human management is required to prevent invasion, contain spread, or remediate ecosystems following habitat degradation. One powerful technology for invasive species management in sensitive habitats is biological control, the use of carefully selected upper-trophic-level organisms that utilize the exotic pest as a resource, thereby reducing it to less harmful densities. Many in the conservation biology community view this pest-management technology as a high-risk enterprise because of potential collateral damage to nontarget species. The potential benefits arising from successful biological programs are reduced pesticide use, significant pest suppression, and a return to ecological conditions similar to those observed before the arrival of the pest. Biological control as a pest-management strategy has limitations: some pest species may not be suitable targets for biological control because natural enemies may not be sufficiently host-specific and may pose a threat to nontarget organisms. In some instances, substantial effects on nontarget species have occurred because generalist natural enemies established as part of a biological control program heavily utilized other resources in addition to the target pest. To minimize nontarget impacts, regulations governing releases of natural enemies are becoming more stringent, as evidenced in New Zealand and Australia. Voluntary codes of good practice are being advocated by the Food and Agriculture Organization to promote wide adoption of safety measures, which, if followed, should result in the selection of agents with high levels of host and habitat fidelity. Biological control programs in support of conservation have traditionally targeted weed species that threaten natural areas. More recently, exotic arthropod pests that compete with native wildlife or damage native plants have become targets of conservation-oriented biological control programs. Extension of biological control to new targets of conservation importance, such as invasive aquatic invertebrates and pestiferous vertebrates, is warranted. In many instances, once prevention, containment, and eradication options have been exhausted or deemed infeasible, carefully orchestrated biological control programs against appropriately selected targets may be the only feasible way to control invasive species affecting communities under assault from exotic species.*

Restaurando el Balance: Utilización de Exóticos para Controlar Exóticas Invasoras

Resumen: *Las especies invasoras amenazan los hábitats naturales en el mundo y se requiere de manejo humano para prevenir la invasión, contener la expansión o remediar ecosistemas después de la degradación de hábitats. El control biológico, el uso de organismos de niveles tróficos superiores cuidadosamente seleccionados que utilizan la especie exótica como recurso reduciéndola a densidades menos dañinas, es una poderosa tecnología para el manejo de especies invasoras en hábitats sensibles. Muchos en la comunidad de biólogos de la conservación consideran esta tecnología de manejo de plagas como de alto riesgo por el daño colateral potencial a otras especies. Los beneficios potenciales de programas biológicos exitosos son la reducción de usos de pesticidas y un regreso a condiciones ecológicas similares a las observadas antes de la llegada de la plaga. El control biológico como estrategia de manejo de plagas tiene limitaciones; algunas especies de plagas pueden no ser blancos adecuados para el control biológico porque sus enemigos naturales pueden no ser lo suficientemente específicos y constituir una amenaza para otras especies. En algunos casos han ocurrido impactos sustanciales porque los enemigos naturales generalistas, utilizados como parte de un programa de control biológico, utilizaron otros recursos intensivamente además de la especie focal. Para minimizar los impactos no deseados, las regulaciones de la liberación de enemigos naturales son cada vez más estrictas*

Paper submitted June 6, 2002; revised manuscript accepted November 19, 2002.

como se evidencia en Nueva Zelanda y Australia. La Organización de Alimento y Agricultura está impulsando códigos voluntarios de buenas prácticas para promover la adopción generalizada de medidas de seguridad, que, de ser observadas, deben resultar en la selección de agentes con altos niveles de fidelidad de huéspedes y de hábitat. Los programas de control biológico en apoyo a la conservación se han enfocado tradicionalmente en especies herbáceas que amenazan las áreas naturales. Más recientemente, las plagas de artrópodos exóticos que compiten con la fauna nativa o dañan plantas nativas se han convertido en el blanco de programas de control biológico orientados a la conservación. La extensión del control biológico a nuevas especies de importancia para la conservación, tales como los invertebrados acuáticos invasores y vertebrados plaga, está garantizada. En muchos casos, los programas de control biológico cuidadosamente orquestados contra especies seleccionadas apropiadamente pueden ser la única forma factible de controlar especies invasoras que afectan a comunidades bajo asalto de exóticas cuando las opciones de prevención, contención y erradicación se hayan agotado o se consideren no factibles.

Introduction

Invasive species cause major environmental damage, and associated economic losses can amount to billions of dollars per year (Pimental et al. 2002). Environmental damage caused by invasive species manifests itself through biodiversity reduction and species extinctions because exotics displace and reduce populations of native species (Kupferberg 1997; Wilson 1997), modify trophic structures within communities (Holland 1993), or induce perturbations, crippling healthy ecosystems (Vitousek et al. 1996). Economic losses occur because of the costs of border inspections to prevent incursion by unwanted species, eradication programs, ongoing control, reduced productivity, and habitat restoration (Pimental et al. 2002).

Sources and introduction routes of invasive organisms are varied and include the following: (1) accidental introductions via commerce and human travel, (2) global trade in living organisms (e.g., nursery, pet, and aquarium industries), (3) acclimatization societies that promote hunting and fishing of exotic animals that are mass-reared and redistributed as game; and (4) farming (e.g., animals and annual and perennial plants). Invasions by pestiferous organisms via these routes are generally unplanned, and subsequent management often involves reactive strategies to deal with incipient or existing pest problems and may include localized eradication or suppression efforts with pesticides, imposition of regional quarantines, or biological control. Biological control is a fifth invasion route for exotic organisms. Science-based biological control programs are deliberate and carefully orchestrated attempts to establish perennial exotic populations to reduce densities of target pest species with upper-level trophic organisms. Worldwide, classical biological control projects have resulted in more than 5000 introductions for control of pestiferous arthropods and over 900 for weed control (Hill & Greathead 2000). This pest-control technology has been successful in controlling some weed, arthropod, and vertebrate pests. There is growing disquiet, however, over unplanned effects on native organisms by introduced bi-

ological control agents, and this has raised concerns that the environmental safety of this pest-control practice may not be as risk-free as previously thought (Howarth 1991, 2000; Follet & Duan 2000; Henneman & Memmott 2001; Lockwood et al. 2001; Wajnberg et al. 2001).

My intent is to provide background on biological control, demonstrate that biological control is a valuable tool for managing invasive species of conservation importance, and suggest that this technology deserves consideration and greater application in the battle against new groups of exotic pests that have not been targets of biological control in the past.

The Practice of Biological Control

Biological control is the intentional use by humans of parasitoid, predator, pathogen, antagonist, or competitor populations to suppress a pest population, thereby making the pest less abundant and damaging than it would be in the absence of these organisms (DeBach 1964; Van Driessche & Bellows 1996). Most biological control programs address the following simple premise: an exotic organism becomes an invasive pest, in part, because it has left behind the guild of natural enemies that regulated its population growth in its home range. Biological control is an exercise in community re-assembly and involves the addition to the invaded habitat of new species that use the invasive pest as a resource.

Usually, few native natural enemies attack an adventive pest, and those that do are native generalist predators or herbivores that have utilized other resources in the environment prior to the arrival of the pest. In most cases, extant native organisms in the upper trophic level are not adversely affected by the introduction of specialized natural enemies because they can utilize other pre-existing resources for survival. With successful biological control programs, both the pest and the specialized natural enemy decline in abundance over time and reach densities similar to those seen in the pest's home range (Bellows 2001).

Biological control has been used as a management tool for control of crop, rangeland, and forest pests and for the restoration of natural systems affected by adventive pests (Van Driesche 1994). Classical biological control programs are those that attempt to reassociate natural enemies from the pest's home range, and they involve the following steps: (1) correct identification of the adventive pest; (2) foreign exploration for specialized natural enemies in the pest's home range; (3) importation into a secure quarantine facility and removal of pathogens, parasites, and hyperparasites that attack candidate natural enemies; (4) host-specificity testing in quarantine, and (5) mass rearing, establishment, redistribution, and impact monitoring of imported biological control agents following release from quarantine (Van Driesche & Bellows 1993).

The addition of exotic natural enemies to the environment has three primary impacts on the target system: (1) the number and function of food web links that connect the pest to other members of the community are permanently changed; (2) natural enemies can radically reduce pest densities and alter population dynamics; and (3) reduction in pest density by natural enemies changes the community structure of the affected system. In successful biological control programs, reduction of pest densities and recovery of adversely affected flora or fauna lead to a system with a community structure similar to that seen before the invasion of the pest (Bellows 2001; Headrick & Goeden 2001). Following their establishment, successful natural enemies can provide enduring pest control; replicate and disperse without continued human management, and persist when pest populations are stabilized at very low densities. Highly successful biological control programs against noxious insects, weeds (aquatic and terrestrial), plant pathogens, and vertebrates have been executed (see chapters in Bellows & Fisher 1999; also Gurr & Wratten 2000).

Economic and Environmental Benefits of Biological Control

A compelling motivation for adoption of biological control is potentially a permanent return to ecological conditions more similar to those seen before the arrival of the invasive pest and reduced ongoing expenditure for pesticides, labor, and specialized equipment. Economic analyses indicate that cost-benefit ratios for successful biological control of arthropod pests are high, can exceed 145:1, and accrue annually (Norgaard 1988; Jetter et al. 1997).

Comparisons of costs for biological control programs indicate that benefits amassed from successful projects outweigh the combined costs of unsuccessful projects, even though the latter are more numerous. For example, just 10% of arthropod biological control programs have

provided full control of the target pest (Gurr et al. 2000). For weed programs, less than 30% of projects have resulted in either total or partial control of the target (Syrett et al. 2000a). Projects sponsored by the Australian Center for International Agricultural Research had a cost-benefit ratio of 13.4:1 for 10 projects that spanned 1983–1996, even though just 4 of these projects were documented successes (Lubulwa & McMeniman 1998).

Biological control of agricultural pests can indirectly benefit native wildlife through the reduction of pesticides released into the environment because of natural enemy suppression of economically important targets. The acute impact of insecticides on wildlife because of aerosol drift from agricultural areas, runoff into waterways, food-chain accumulation, or indiscriminant application has been well documented and was brought to the public's attention 40 years ago (Carson 1962). An insidious, chronic, side-effect from pesticide use that has been recently postulated is the potential ability of synthetic chemical pollutants in the environment to accumulate in the bodies of vertebrates, including humans, where these sequestered compounds mimic or block the actions of endogenous hormones, thereby causing wildlife declines, reproductive ailments, and behavioral abnormalities (Colborn et al. 1997; Schettler et al. 1999; Krimsky 2000).

An additional ecological benefit to indigenous organisms resulting from successful biological control can be the reduction of generalist natural enemies that maintain high population densities by utilizing an abundant exotic pest without providing control. These generalists subsequently "spill over" onto lower-density, nonpestiferous or desirable native species, causing abnormally high mortality rates; this phenomenon is termed *apparent competition* (Holt & Lawton 1993; Holt & Hochberg 2001). Under conditions of apparent competition, density-dependent regulation of ineffective generalist natural enemies does not occur and populations of nontarget species can decline (Bonsall & Hassell 1998).

Effects on Nontarget Species and Biota Dilution Resulting from Biological Control Programs

Natural enemies that exhibit high levels of host and habitat fidelity ensure strong links and maximal impact on the target species, while ensuring weak links and minimal impacts to nontarget species. When biological control projects stray from this fundamental ecological principle of high host specificity, or when the technology is applied without ecological justification to poorly chosen pest targets (e.g., neoclassical biological control attempts to utilize exotic natural enemies to suppress native pest populations and the theoretical basis for this practice differs markedly from classical biological control [Hokkanen & Pimental 1989; Lockwood 1993]), then undesired outcomes such as effects on nontarget species

and lack of control are more likely to occur. Generalist natural enemies lack high levels of host and habitat specificity and are frequently cited as examples of the inherent and unpredictable risks associated with releasing biological control agents because of their adverse effects on native organisms and lack of impact on the pestiferous target (Howarth 1983, 1991; Simberloff & Stiling 1996; Stiling & Simberloff 2000). Although nontarget attacks by natural enemies, in particular parasitoids, have been documented (Boettner et al., 2000; Henneman & Memmott 2001; Benson et al. 2003a), strong experimental evidence also exists that deliberately released generalist natural enemies have not been responsible for population declines of nontarget species, as has previously been suggested (Barron et al. 2003; Benson et al. 2003b). Database analyses indicate that pronounced nontarget population changes brought about by deliberately released arthropod biological control agents are low (approximately 1.5% of projects have data on the realized field specificity of agents). This result is due, in part, to a lack of carefully planned studies that have sought specifically to quantify the effect of natural enemies on nontarget organisms. This shortcoming needs to be addressed to ensure that nontarget organisms are not at undue risk and that legislation governing the introduction of biological control agents supports responsible projects (Lynch et al. 2001). Although the exact ecological impact of biological control agents on native invertebrate populations is often uncertain, detailed studies that use trophic spectra analyses (i.e., food webs) could be a powerful way to determine the effects of natural enemies on the communities into which they are introduced (Memmott 2000; Henneman & Memmott 2001; Strong & Pemberton 2001).

Examination of the commonly cited "rogue" biological control agents presented in Table 1 demonstrates that these biological control projects were ill conceived, not necessarily because the pests were unsuitable targets but primarily because the natural enemies selected had very broad host ranges and substantial nontarget impacts should have been predictable. In some instances, agricultural interest groups (e.g., sugar cane growers, ranchers, and farmers) carried out the projects listed in Table 1 with little or no scientific grounding, and government oversight was lax either because of noninvolvement or lack of regulatory infrastructure (i.e., governing legislation) through which to identify suitable targets and assess the safety of imported natural enemies before their release or their subsequent redistribution following establishment.

Selection of natural enemies with narrow host ranges protects nontarget species because physiological, behavioral, ecological, or geographical attributes make native organisms unsuitable for exploitation by natural enemies (Strand & Obrycki 1996; Frank 1998). Furthermore, high levels of host specificity on the part of natural enemies ensure that, as social climates change, the perceived benefit of the natural enemy for pest control will not wane unless

the perceived value of the pest changes. Host-range expansion by specialized natural enemies to exploit novel hosts through evolutionary adaptation is considered rare (Nechols et al. 1992; Onstad & McManus 1996). One possible reason for the low probability of host shifts occurring with specialized natural enemies is canalization, the capacity to regulate developmental pathways against genetic mutation and environmental perturbations. Canalization results in stabilizing selection that preserves the phenotypic and genotypic status quo of the population (Debat & David 2001). As a result, the more specialized or complex the system under selection, the greater the degree of canalization and subsequent robustness to change (Siegal & Bergman 2002). Consequently, canalization of networks (e.g., genetic regulation of behavior and physiology) controlling host range for generalist natural enemies may not be as rigid as that of specialist natural enemies and may be more likely to evolve over time. Although documented host shifts and host-range expansions by some types of natural enemies are rare, such possibilities may warrant consideration, and increased research effort could help in predicting the likelihood of such events by biological control agents (Secord & Kareiva 1996; Simberloff & Stiling 1998; Howarth 2000).

Introductions of biological control agents have also been criticized for diluting endemic biodiversity and contributing to homogenization of global biota. In New Zealand, 13% of the country's insects are exotic. Of these exotic species, 2.5% have been intentionally introduced for biological control, and these natural enemies comprise 0.35% of New Zealand's total insect fauna. Intentional introductions of natural enemies are negligible in comparison to the numbers of adventive insects established in New Zealand. Consequently, biological control agents are not considered a major source of biological pollution diluting native biodiversity (Emberson 2000). Similarly, for the contiguous 48 U.S. states, deliberate establishment of new species of exotic natural enemies constitute <0.25% of the described insect fauna (Sailer 1978).

The Safety Net: Regulating the Introduction of Natural Enemies

The importation of candidate biological control agents by scientists into most countries is regulated, and highly secure quarantine facilities are used to contain, screen, and test the safety of candidate natural enemies prior to release. Government-level clearances are needed to move organisms from quarantine to less secure facilities for mass rearing and eventual release. In contrast, such procedures are generally not required for the importation of the exotic and potentially invasive aquatic, terrestrial, and arboreal species that constitute the pet, nursery, and aquarium trades, especially in the United States (Van Driesche & Van Driesche 2000).

Table 1. Generalist biological control agents, target pests, and country and year of first introduction and unintended impacts on nontarget wildlife.

Biological control agent	Target pest	Country and year of first introduction	Nontarget impacts	Reference
European red fox, <i>Vulpes vulpes</i> L. (native range: Palaearctic regions)	rabbits, <i>Oryctolagus cuniculus</i> L.	Australia, 1871	eat native marsupials and birds, and lambs	Saunders et al. 1995
Stoat, <i>Mustela erminea</i> L. (native range: Eurasia and North America)	rabbits	New Zealand, 1884	eat native birds, insects, and lizards	King 1990a
Ferret, <i>Mustela putorius</i> L. (native range: Central Europe and the Mediterranean)	rabbits	New Zealand, 1879	eat native birds	Lavers & Clapperton 1990
Weasel, <i>Mustela putorius vulgaris</i> Erxleben (native range: Eurasia and North America)	rabbits	New Zealand, 1884	eat native birds, insects, and lizards	King 1990b
Small Indian mongoose, <i>Herpestes javanicus</i> (Saint-Hilaire), (= <i>auripunctatus</i> [Hodgson]) (native range: Iraq to the Malay Peninsula)	rats, <i>Rattus</i> spp.	Trinidad 1870; Jamaica, 1872; Cuba, 1886; Puerto Rico, 1877; Barbados, 1877; Hispaniola, 1895; St. Croix, 1884; Surinam, 1900; Hawaii, 1883	eat native birds and reptiles	Hinton & Dunn 1967; Loope et al. 1988
Cane toad, <i>Bufo marinus</i> L. (native range: northwestern Mexico through southern Brazil)	white grubs, <i>Phyllophaga</i> sp.; sweet potato hawk moth, <i>Agrius convolvuli</i> L.; grey backed cane beetle, <i>Dermolepida albohirtum</i> (Waterhouse)	Jamaica, 1844; Bermuda 1855; Puerto Rico 1920; Hawaii, 1932; Australia, 1935; Fiji, 1936; Guam, 1937; New Guinea, 1937; Philippines, 1934.	eat native insects, amphibians, and reptiles, are toxic to native wildlife that consume it, and out compete native amphibians for shelter and breeding sites	Easteal 1981; Freeland 1985
Mosquito fish, <i>Gambusia affinis</i> (Baird & Girard) (native range: eastern U.S. and Mexico)	worldwide dissemination of <i>G. affinis</i> for control of mosquito larvae promoted by the World Health Organization until 1982	intensive releases began worldwide around 1900, approximately 70 countries now have permanent <i>G. affinis</i> populations including: Afghanistan, Australia, Canada, China, Ethiopia, Grand Cayman Island, Greece, Hawaii, Iran, Korea, New Zealand, Somalia, Turkey, Ukraine	attack native aquatic invertebrates and vertebrates outside its native range	Meisch 1985; Walton & Mulla 1991; Diamond 1996; Gamradt & Kats 1996; Legner 1996; Rupp 1996
Predatory snail, <i>Euglandina rosea</i> (Ferrusac) (native range: southeastern U.S.A.).	giant African snail, <i>Achatina fulica</i> Bowdich	Hawaii, 1955; Tahiti, 1974; Moorea, 1977; New Caledonia, 1978; Guam, 1957; Vanuatu, 1973; Papua New Guinea, 1952; Japan, 1958; Taiwan, 1960; Madagascar, 1962; Seychelles, 1960; Mauritius, 1961; Reunion, 1966; India, 1968; Bermuda, 1958.	eat native snails (e.g., native <i>Achatinella</i> spp. and <i>Partula</i> spp.), probably leading to extinction of some native species	Simmonds & Hughes 1963; Davis & Butler 1964; Clarke et al. 1984; Murray et al. 1988; Kinzie 1992; Griffiths et al. 1993

continued

Table 1. (continued)

Biological control agent	Target pest	Country and year of first introduction	Nontarget impacts	Reference
Tachinid fly, <i>Comptosiluna concinata</i> Meigen (native range: Europe).	gypsy moth, <i>Lymantria dispar</i> (L.) and other lepidopteran pests	U.S., 1906	parasitize larvae of saturniid moths, causing regional declines of the native moths	Boettner et al. 2000
Tachinid fly, <i>Bessa</i> (= <i>Ptychomyia</i>) <i>remota</i> (Aldrich) (native range: Indo-Malay archipelago)	coconut moth, <i>Levuana iridescens</i> Bethune-Baker	Fiji, 1925	cause possible extirpation of the native Fijian zygaenid <i>Heterophan dolens</i> and reduce abundance of other native zygaenids	Tothill et al. 1930; Robinson 1975; Howarth 1991; Sands 1997
Seven spotted lady beetle, <i>Coccinella septempunctata</i> L. (native range: Palearctic regions)	pestiferous aphid spp.	U.S., 1957; accidentally established in U.S. in 1973	displaces native aphidophagous coccinellids in agricultural crops and predate nontarget native lepidopterans	Elliott et al. 1996; Obrycki et al. 2000
Cactus moth, <i>Cactoblastis cactorum</i> (Bergroth) (native range: northern Argentina, Uruguay, Paraguay, and southern Brazil)	<i>Opuntia</i> spp. of cacti	Australia, 1925; Caribbean, 1957; Hawaii, 1950; Mauritius, 1950; South Africa, 1932; accidental introduction into the U.S. in 1989 from the Caribbean. U.S., 1968	attack native <i>Opuntia</i> spp., threatening survival of endangered native spp.	Bennett & Habeck 1992; Holloway 1964; Pemberton 1995
Flowerhead weevil, <i>Rhinocyllus conicus</i> Fröelick (native to Eurasia).	<i>Carduus</i> spp. thistles.		attacks seed heads of native <i>Cirsium</i> spp. thistles, potentially limiting regeneration of plants and displacing native thistle head feeders	Gassmann & Louda 2001; Louda 2000
Crazy ant, <i>Paratrechina</i> (= <i>Nylanderia</i>) <i>fulva</i> (Mayr) (native range: Brazil)	leaf-cutting ants and poisonous snakes	Colombia 1969–1970	attacks and displaces native reptiles, ants, and other insects, tends honeydew-producing scales, and attacks cattle	Zenner-Polania 1990

Laws governing biological control vary by country, or they may not exist at all. In the United States, biological control has been facilitated by the recent Invasive Species Executive Order 13112 (1999), which established a Cabinet-level Invasive Species Council to provide guidance on rational and cost-effective control measures for exotic pests. The Animal and Plant Health Inspection Service (APHIS; an arm of the U.S. Department of Agriculture) examines the potential environmental impacts of introduced biological control agents before authorizing their release in order to comply with statutes such as the National Environmental Policy Act (1969) and the Endangered Species Act (1973). Additionally, the U.S. Department of Interior is required by Invasive Species Executive Order 11987 (1977) to restrict the introduction of exotic species into natural ecosystems unless it has been shown that there would be no adverse effects. Despite these regulations, the United States does not have an encompassing "biological control law" and no legal mandate or agency to explicitly oversee the importation and release of exotic organisms (Howarth 2000).

New Zealand has one of the most stringent legislative requirements for importation of potential biological control agents. The Hazardous Substances and New Organ-

isms Act of 1996 has greatly increased the obligations incumbent on proponents of new biological control agents, requiring them to provide adequate data on which to base approvals for importation and release (Fowler et al. 2000). This legislation provides a solid framework within which risks and benefits of proposed natural-enemy introductions can be weighed and decisions made in accordance with presented data. The Environmental Risk Management Authority administers the review process for the importation and release of biological control agents in New Zealand.

International agreements designed to prevent the process of introducing biological control agents from causing economic and environmental damage may lead to increased restrictions on the release of natural enemies. The Food and Agriculture Organization's International Code for the Import and Release of Exotic Biological Control Agents was approved by all member states in 1995, and these guidelines should be adopted worldwide. Under the provisions of this code, not only must approval for the introduction be gained from the government of the importing country, but other countries in the region must also be consulted because natural enemies may cross international boundaries. The host range of the proposed

Table 2. Examples of invasive weed species of conservation importance that are subjects of biological control programs.

Target weed species	Natural enemies	Environmental problem	References
European heather, <i>Calluna vulgaris</i> (L.)	heather beetles, <i>Lochmaea suturalis</i> (Coleoptera: Chrysomelidae)	dense stands displace native tussock grasses in Tongariro National Park, New Zealand	Syrett et al. 2000b
Old man's beard, <i>Clematis vitalba</i> L.	leaf mining fly, <i>Phytomyza vitalbae</i> (Diptera: Agromyzidae); pathogenic fungus, <i>Phoma clematidina</i> (Pleosporaceae)	creeping vine disrupts forest structure, reduces indigenous biodiversity, and promotes weed invasion in New Zealand forests	Ogle et al. 2000; Hill et al. 2001
Mist flower, <i>Ageratina riparia</i>	mist flower gall flies, <i>Procecidochares alani</i> (Diptera: Tephritidae); mist flower fungus, <i>Entyloma ageratinae</i>	invades and kills understory forest flora in New Zealand and Hawaii	www.landcareresearch.co.nz
Scotch broom, <i>Cytisus scoparius</i> Link	seed beetle, <i>Bruchidius villosus</i> (F) (Coleoptera: Chrysomelidae); broom psyllid, <i>Arytainilla spartiophylla</i> (Förster) (Homoptera: Psyllidae)	invades river and stream beds and disturbed habitats, displaces native vegetation in New Zealand, Australia, and the U.S.	Fowler et al. 2000
Paperbark tree, <i>Melaleuca quinquenervia</i> (Cavanilles)	leaf feeding weevil, <i>Oxyops vitiosa</i> Pascoe (Coleoptera: Curculionidae)	adversely affects water tables and displaces native flora and fauna in the Florida Everglades, U.S.	Wheeler 2001
Water hyacinth, <i>Eichborina crassipes</i>	water hyacinth weevils, <i>Neochetina bruchi</i> and <i>N. eichborinae</i> (Coleoptera: Curculionidae)	floating water weed, chokes lakes and slow moving rivers in Africa, the southeast U.S., and Papua New Guinea, disrupts visual color-based mating systems in cichlid fishes in Lake Victoria in east Africa due to reduce light quality caused by weed mats	Galis & Metz 1998; Van Thielen 1994

Table 3. Examples of invasive terrestrial arthropod pests of conservation importance that are subjects of biological control programs.

Target pest	Natural enemies	Environmental problem	References
Ensign scale, <i>Ortbezia insignis</i> Browne	<i>Hyperaspis panterina</i> Fürsch (Coleoptera: Coccinellidae)	kills endemic gumwood tree, <i>Commidendrum robustum</i> , on St. Helena	Booth et al. 1995
Hemlock wooly adelgid, <i>Adelges tusgae</i> Annand	<i>Scymnus sinuanodulus</i> Yu et Yao and <i>Pseudoscymnus tsugae</i> Sasaji and McClure (both Coccinellidae) and <i>Diapterobates humeralis</i> (Hermann) (Acari: Oribatidae)	kills native eastern hemlocks, <i>Tsuga canadensis</i> L. in the northeastern U.S.	Lu & Montgomery 2001
Bromeliad weevil, <i>Metamasius callizona</i> (Chevrolat)	<i>Admontia</i> sp. (Diptera: Tachinidae)	kills native bromeliads in Florida, U.S.	Frank & Thomas 1994; Frank 1999; Salas & Frank 2001
Yellow jacket wasps, <i>Vespula vulgaris</i> L.	<i>Spbecophaga vesparum vesparum</i> (Curtis) (Hymenoptera: Ichneumonidae)	out competes native nectar-feeding birds in New Zealand forests for honeydew	Barlow et al. 1996
Red imported fire ant, <i>Solenopsis invicta</i> Buren	decapitating flies, <i>Pseudacteon curvatus</i> Borgmeier (Diptera: Phoridae)	reduces biodiversity of ants and ground-dwelling vertebrates and invertebrates	Porter 2000
Cottony cushion scale, <i>Icerya purchasi</i> Maskell	<i>Rodalia cardinalis</i> Mulsant (Coleoptera: Coccinellidae)	causes decline of indigenous plants on the Galapagos Islands, Ecuador	www.darwinfoundation.org/news/

biological control agent must be adequately measured before it is released, and an evaluation of the impact of the organism must be made following its establishment (Food and Agriculture Organization 1996).

Biological Control Programs in Support of Conservation

Following a failure to prevent species incursion, and subsequent eradication of incipient pest populations, biological control is perhaps the best—and in some instances the only—technology available for the management and restoration of ecosystems degraded by exotic invasive species. Suppression of weeds in natural areas is the most prominent application of biological control in support of conservation, and examples are numerous. The practice has grown out of earlier use of weed biological control for range and agricultural management (McFadyen 1998) (Table 2). Invasive arthropods that threaten native flora and fauna have recently become subjects of biological control programs (Table 3). Biological control projects for arthropod pests of natural areas have not been evaluated in terms of economic costs and sociological benefits to conservation. This will undoubtedly change as the success of recently initiated projects is evaluated and the numbers of new projects increase.

New Targets and Novel Biological Control Techniques

Use of specialized natural enemies in the context of a classical biological control program against nonmammalian

vertebrates and freshwater and marine invertebrates is nonexistent because there are no precedents for these groups, and specialists studying these invasive organisms may be unfamiliar with the concept of biological control and the benefits it offers. This situation is beginning to change, however, and “nontraditional” pests are now being studied as candidates for biological control (Table 4).

Vertebrate pests, especially mammals, have proven notoriously difficult to control because of their ability to learn and their secretive habits. The use of generalist vertebrate predators to control vertebrate pests has exacerbated many problems because the biological control agents have in turn become problematic (Table 1). Many vertebrate species that become pests are distinguished from nonpestiferous species by their higher intrinsic rates of increase. Agents that reduce vertebrate reproductive rates without causing mortality are receiving increased attention because this approach may present fewer risks to nontarget species. For example, sexual transmission of diseases may guarantee host specificity in biological control programs against vertebrate pests, and the potential of genetically engineering sexually transmitted viruses to sterilize infected hosts without killing them is being investigated as a novel biological control technology (Barlow 1994). Immunocontraception (also referred to as immunosterilization) as a means to control noxious vertebrates (e.g., foxes, rabbits, and mice) is being actively pursued by Australia and New Zealand (McCallum 1996). An alternative approach to immunocontraception is to use genetically modified pathogens to prevent lactation in females so that juveniles are not successfully weaned or to interfere with hormonal control of reproduction (Jolly 1993; Cowan 1996; Rodger 1997).

Table 4. List of “nontraditional” targets that are subject to biological control programs in various stages of development.

<i>Target pest</i>	<i>Description of problem</i>	<i>Potential natural enemies</i>	<i>Reference</i>
Brown tree snake, <i>Boiga irregularis</i>	responsible for extirpation of native bird species on Guam	Suitability of debilitating viruses are being evaluated for use in Guam.	T. Fritts 2001, personal communication.
Cane toads, <i>Bufo marinus</i>	out competes native Australian amphibians and is toxic to a variety of predators	Viral and bacterial diseases from the home range of the pest are being evaluated for safety and efficacy in Australia.	www2.open.ac.uk/biology/froglog/FROGLOG-15-4.html
Feral cats, <i>Felis domesticus</i>	attack native mammals, birds, and reptiles on oceanic islands and elsewhere	Feline panleucopaenia virus, and immunocontraception with genetically engineered viruses are being evaluated for use on remote islands.	van Rensburg et al. 1987; Courchamp & Cornell 2000
<i>Caulerpa taxifolia</i>	monotypic stands are threatening marine biodiversity in the Mediterranean Ocean	Herbivorous ascoglossan sea slugs native to the Caribbean are being assessed for use in the Mediterranean Ocean.	Meinesz 1999
Feral goats, <i>Capra hircus</i>	selectively browse native vegetation and cause soil erosion	Sexually transmitted flagellated protozoans may lower the reproductive potential of feral goats.	Dobson 1988
Green crabs, <i>Carcinus maenas</i>	out competes native crustaceans and threatens viability of commercial shellfish and crab industries	Castration of rhizocephalan barnacles is being evaluated for safety and efficacy.	Lafferty & Kuris 1996; Thresher et al. 2000
Mice, <i>Mus musculus</i>	plagues in southeast Australia cause large financial losses in wheat-growing areas	The rodent-specific nematode, <i>Capillaria hepatica</i> , is the subject of research in Australia.	Singleton & McCallum 1990
Rabbits, <i>Oryctolagus cuniculus</i>	high densities in Australia and New Zealand damage pasture and compete with native animals for resources	Myxoma virus is being genetically engineered to sterilize rabbit hosts in Australia.	Twigg et al. 2000
Zebra mussels, <i>Dreissena polymorpha</i> and <i>D. bugensis</i>	high densities foul water-dependent infrastructure, alter benthic communities, increase native bivalve mortality rates	Obligate host-specific ciliates and trematodes are being assessed for use in the U.S.	Molloy 1998
Mediterranean snail, <i>Cermeuella virgata</i>	high densities destroy crops and aestivating snails on ears of cereals foul harvesting equipment and contaminate grain in Australia	The parasitic fly, <i>Sarcophaga penicillata</i> , has been screened for specificity against native Australian snails and approved for release.	Port et al. 2000 http://www.sardi.sa.gov.au/bb

Conclusions

The rate at which invasive species degrade valued habitats continues to accelerate, and human management is essential if areas and species of conservation importance are to be preserved. In many instances, biological control may be the best management tool for these problematic organisms. Biological control projects should be designed and executed within a regulatory framework that requires peer-reviewed assessment of the need for biological control of the proposed target, project feasibility, and determination of what data are acceptable for demonstrating host specificity and the potential magnitude of impact on target and nontarget populations. Approved projects subject to this level of scrutiny will cost more to execute, and a balance needs to be reached that ensures the safety

standards of biologically feasible projects are met without making these projects economically infeasible.

Location, selection, and evaluation of natural enemies are difficult and require the expertise of highly trained scientists, overseas collaborators, and complex quarantine and research facilities, and projects can span many years before suitable natural enemies are located and cleared for release. Consequently, the desire for quick fixes to pest problems has prompted agriculturists and land managers to side-step these rigorous procedures and import generalist natural enemies that have high probabilities of establishment, voracious appetites, and weak associations with the target pest. Such reckless practices cannot be considered science-based biological control programs.

Biological control is a technology that can greatly benefit conservation efforts, and—given the devastating

impacts of an ever-increasing multitude of invasive organisms—the risks of doing nothing are unacceptably high. Well-targeted biological control projects can make a real difference in the battle against the stealth destroyers of the world's wilderness areas.

Acknowledgments

I thank D. Sands and R. Goeden for critically reviewing the manuscript. Comments from three anonymous reviewers were also very helpful.

Literature Cited

- Barlow, N. D. 1994. Predicting the effect of a novel vertebrate biocontrol agent: a model for viral-vectored immunocontraception of New Zealand possums. *Journal of Applied Ecology* **31**:454–462.
- Barlow, N. D., H. Moller, and J. R. Beggs. 1996. A model for the effect of *Spbecophaga vesparum vesparum* as a biological control agent of the common wasp in New Zealand. *Journal of Applied Ecology* **33**:31–44.
- Barron, M. C., N. D. Barlow, and S. D. Wratten. 2003. Non-target parasitism of the endemic New Zealand red admiral butterfly (*Bassaris gonerilla*) by the introduced biocontrol agent *Pteromalus puparum*. *Biological Control* **27**:329–335.
- Bellows, T. S. 2001. Restoring population balance through natural enemy introductions. *Biological Control* **21**:199–205.
- Bellows, T. S., and T. W. Fisher, editors. 1999. *Handbook of biological control*. Academic Press, San Diego, California.
- Bennett, F. D., and D. H. Habeck. 1992. *Cactoblastis cactorum*: a successful weed control agent in the Caribbean, now a pest in Florida? Pages 21–26 in E. S. Delfosse, and R. R. Scott, editors. *Proceedings of the eighth international symposium on biological control of weeds*. Commonwealth Scientific, Industrial, and Research Organization, Melbourne, Australia.
- Benson, J., R. Van Driesche, A. Pasquale, and J. Elkinton. 2003a. Introduced braconid parasitoids and range reduction of a native butterfly in New England. *Biological Control* **28**:197–213.
- Benson, J., A. Pasquale, R. Van Driesche, and J. Elkinton. 2003b. Assessment of risk posed by introduced braconid wasps to *Pieris virginiensis*, a native woodland butterfly in New England. *Biological Control* **26**:83–93.
- Boettner, G. H., J. S. Elkinton, and C. J. Boettner. 2000. Effects of biological control introduction on three nontarget native species of saturniid moths. *Conservation Biology* **14**:1798–1806.
- Bonsall, M. B., and M. P. Hassell. 1998. Population dynamics of apparent competition in a host-parasitoid assemblage. *Journal of Animal Ecology* **67**:918–929.
- Booth, R. G., A. E. Cross, S. V. Fowler, and R. H. Shaw. 1995. The biology and taxonomy of *Hyperaspis pantherina* (Coleoptera: Coccinellidae) and the classical biological control of its prey, *Orthezia insignis* (Homoptera: Ortheziidae). *Bulletin of Entomological Research* **85**:307–314.
- Carson, R. 1962. *Silent spring*. Houghton Mifflin, Boston.
- Clarke, B., J. Murray, and M. S. Johnson. 1984. The extinction of endemic species by a program of biological control. *Pacific Science* **38**:97–104.
- Colborn, T., D. Dumanoski, and J. Peterson Myers. 1997. *Our stolen future: are we threatening our fertility, intelligence, and survival? A scientific detective story*. Penguin Books, New York.
- Courchamp, F., and S. J. Cornell. 2000. Virus-vectored immunocontraception to control feral cats on islands: a mathematical model. *Journal of Applied Ecology* **37**:903–913.
- Cowan, P. E. 1996. Possum biocontrol: prospects for fertility control. *Reproduction, Fertility and Development* **8**:655–660.
- Davis, C. J., and G. D. Butler. 1964. Introduced enemies of the giant African snail, *Achatina fulica* Bowdich, in Hawaii (Pulmonata: Achatinidae). *Proceedings of the Hawaiian Entomological Society* **18**:377–389.
- DeBach, P., editor. 1964. *Biological control of insect pests and weeds*. Reinhold, New York.
- Debat, V., and P. David. 2001. Mapping phenotypes: canalization, plasticity, and developmental stability. *Trends in Ecology & Evolution* **16**:555–561.
- Dobson, A. P. 1988. Restoring island ecosystems: the potential of parasites to control introduced mammals. *Conservation Biology* **2**:31–39.
- Easteal, S. 1981. The history of introductions of *Bufo marinus* (Amphibia: Anura); a natural experiment in evolution. *Biological Journal of the Linnean Society* **16**:93–113.
- Elliot, N., R. Kieckhefer, and W. Kauffman. 1996. Effects of an invading coccinellid on native coccinellids in an agricultural landscape. *Oecologia* **105**:537–544.
- Emberson, R. 2000. Endemic biodiversity, natural enemies, and the future of biological control. Pages 875–880 in N. R. Spencer, editor. *Proceedings of the 10th international symposium on biological control of weeds*. Montana State University, Bozeman Montana.
- Follet, P. A., and J. J. Duan, editors. 2000. *Nontarget effects of biological control*. Kluwer Academic Publishers, Boston.
- Food and Agriculture Organization (FAO). 1996. *Code of conduct for the import and release of exotic biological control agents*. Publication 3. Secretariat of the International Plant Protection Convention, FAO, Rome.
- Fowler, S. V., P. Syrett, and P. J. Jarvis. 2000. Will expected and unexpected non-target effects, and the new Hazardous Substances and New Organisms Act, cause biological control of broom to fail in New Zealand? Pages 173–186 in N. R. Spencer, editor. *Proceedings of the 10th international symposium on biological control of weeds*. Montana State University, Bozeman, Montana.
- Frank, J. H. 1998. How risky is biological control? *Comment. Ecology* **79**:1829–1834.
- Frank, J. H. 1999. Bromeliad feeding weevils. *Selbyana* **20**:40–48.
- Frank, J. H., and M. C. Thomas. 1994. *Metamasius callizona* (Chevrolat) (Coleoptera: Curculionidae) an immigrant pest, destroys bromeliads in Florida. *Canadian Entomologist* **126**:673–682.
- Freeland, W. J. 1985. The need to control cane toads. *Search* **16**:211–215.
- Galis, F., and J. A. J. Metz. 1998. Why are there so many cichlid species? *Trends in Ecology & Evolution* **13**:1–2.
- Gamradt, S. C., and L. B. Kats. 1996. Effect of introduced crayfish and mosquito fish on California newts. *Conservation Biology* **10**:1155–1162.
- Gassmann, A., and S. V. Louda. 2001. *Rhinocyllus conicus*: initial evaluation and subsequent ecological impacts in North America. Pages 147–183 in E. Wajnberg, J. K. Scott, and P. C. Quimby, editors. *Evaluating indirect ecological effects of biological control*. CABI Publishing, Wallingford, United Kingdom.
- Griffiths, O., A. Cook, and S. M. Wells. 1993. The diet of the introduced carnivorous snail *Euglandina rosea* in Mauritius and its implications for threatened island gastropod faunas. *Journal of Zoology* **229**:79–89.
- Gurr, G., and S. Wratten, editors. 2000. *Biological control: measures of success*. Kluwer Academic Publishers, Dordrecht, The Netherlands.
- Gurr, G. M., N. D. Barlow, J. Memmott, S. D. Wratten, and D. J. Greathead. 2000. A history of methodical, theoretical and empirical approaches to biological control. Pages 3–37 in G. Gurr and S. Wratten, editors. *Biological control: measures of success*. Kluwer Academic Publishers, Dordrecht, The Netherlands.
- Headrick, D. H., and R. D. Goeden. 2001. Biological control as a tool for ecosystem management. *Biological Control* **21**:249–257.

- Henneman, M. L., and J. Memmott. 2001. Infiltration of a Hawaiian community by introduced biological control agents. *Science* **293**:1314–1316.
- Hinton, H. E., and A. M. S. Dunn. 1967. *Mongoose: their natural history and behavior*. University of California Press, Berkeley.
- Hill, G., and D. Greathead. 2000. Economic evaluation in classical biological control. Pages 208–223 in C. Perrings, M. Williamson, and S. Dalmazzone, editors. *The economics of biological invasions*. Edward Elgar, Cheltenham, United Kingdom.
- Hill, R. L., R. Wittenberg, and A. H. Gourlay. 2001. Biology and host range of *Phytomyza vitalbae* and its establishment for the biological control of *Clematis vitalba* in New Zealand. *Biocontrol Science and Technology* **11**:459–473.
- Hokkanen, H., and D. Pimental. 1989. New associations in biological control: theory and practice. *Canadian Entomologist* **121**:829–840.
- Holland, R. E. 1993. Changes in planktonic diatoms and water transparency in Hatchery Bay, Bass Island area, Western Lake Erie, since the establishment of the zebra mussel. *Journal of Great Lakes Research* **19**:617–624.
- Holloway, J. K. 1964. Projects in biological control of weeds. Pages 650–670 in P. DeBach, editor. *Biological control of insect pests and weeds*. Reinhold, New York.
- Holt, R. D., and M. E. Hochberg. 2001. Indirect interactions, community modules and biological control: a theoretical perspective. Pages 13–37 in E. Wajnberg, J. K. Scott, and P. C. Quimby, editors. *Evaluating indirect ecological effects of biological control*. CABI Publishing, Wallingford, United Kingdom.
- Holt, R. D., and J. H. Lawton. 1993. Apparent competition and enemy free space in insect host-parasitoid communities. *The American Naturalist* **142**:623–645.
- Howarth, F. G. 1983. Classical biological control: panacea or Pandora's box? *Proceedings of the Hawaiian Entomological Society* **24**:239–244.
- Howarth, F. G. 1991. Environmental impacts of biological control. *Annual Review of Entomology* **36**:485–509.
- Howarth, F. G. 2000. Non-target effects of biological control agents. Pages 369–403 in G. Gurr and S. Wratten, editors. *Biological control: measures of success*. Kluwer Academic Publishers, Dordrecht, The Netherlands.
- Jetter, K., K. Klonsky, and C. H. Pickett. 1997. A cost/benefit analysis of the ash whitefly biological control program in California. *Journal of Arboriculture* **23**:65–72.
- Jolly, S. E. 1993. Biological control of possums. *New Zealand Journal of Zoology* **20**:335–339.
- King, C. M. 1990a. *Stoat*. Pages 288–312 in C. M. King, editor. *The handbook of New Zealand mammals*. Oxford University Press, Auckland, New Zealand.
- King, C. M. 1990b. *Weasel*. Pages 313–320 in C. M. King, editor. *The handbook of New Zealand mammals*. Oxford University Press, Auckland, New Zealand.
- Kinzie, R. A. 1992. Predation by the introduced carnivorous snail *Euglandia rosea* (Ferussac) on endemic aquatic lymnaeid snails in Hawaii. *Biological Conservation* **60**:149–155.
- Krimsky, S. 2000. Hormonal chaos: the scientific and social origins of the environmental endocrine hypothesis. John Hopkins University Press, Baltimore, Maryland.
- Kupferberg, S. J. 1997. Bullfrog (*Rana catesbeiana*) invasion of a California river: the role of larval competition. *Ecology* **78**:1736–1751.
- Lafferty, K. D., and A. M. Kuris. 1996. Biological control of marine pests. *Ecology* **77**:1989–2000.
- Lavers, R. B., and B. K. Clapperton. 1990. *Ferret*. Pages 320–330 in C. M. King, editor. *The handbook of New Zealand mammals*. Oxford University Press, Auckland, New Zealand.
- Legner, E. F. 1996. Comments on adverse assessments of *Gambusia affinis*. *Journal of the American Mosquito Control Association* **12**:161.
- Lockwood, J. A. 1993. Environmental issues involved in biological control of rangeland grasshoppers (Orthoptera: Acrididae) with exotic agents. *Environmental Entomology* **22**:503–518.
- Lockwood, J. A., F. G. Howarth, and M. F. Purcell, editors. 2001. *Balancing nature: assessing the impact of importing non-native biological control agents (an international perspective)*. Thomas Say publications in entomology. Entomological Society of America, Lanham, Maryland.
- Loope, L., O. Hamann, and C. P. Stone. 1988. Comparative conservation biology of oceanic archipelagos. *BioScience* **38**:272–282.
- Louda, S. M. 2000. Negative ecological effects of the musk thistle biological control agent, *Rhinocyllus conicus*. Pages 215–243 in P. A. Follet and J. J. Duan, editors. *Nontarget effects of biological control*. Kluwer Academic Publishers, Boston.
- Lu, W., and M. E. Montgomery. 2001. Oviposition, development, and feeding of *Scymnus (Neopullus) sinuanodulus* (Coleoptera: Coccinellidae): a predator of *Adelges tsugae* (Homoptera: Adelgidae). *Annals of the Entomological Society of America* **94**:64–70.
- Lubulwa, G., and S. McMeniman. 1998. ACIAR-supported biological control projects in the South Pacific (1983–1996): an economic assessment. *Biocontrol News and Information* **19**(3):91N–98N.
- Lynch, L. D., et al. 2001. Insect biological control and non-target effects: a European perspective. Pages 99–125 in E. Wajnberg, J. K. Scott, and P. C. Quimby, editors. *Evaluating indirect ecological effects of biological control*. CABI Publishing, Wallingford, United Kingdom.
- McCallum, H. I. 1996. Immunocontraception for wildlife population control. *Trends in Ecology & Evolution* **11**:491–493.
- McFadyen, R. E. 1998. *Biological control of weeds*. *Annual Review of Entomology* **43**:369–393.
- Meinesz, A. 1999. *Killer algae: the true tale of a biological invasion*. The University of Chicago Press, Chicago.
- Meisch, M. V. 1985. *Gambusia affinis affinis*. Pages 3–17 in H. C. Chapman, editor. *Biological control of mosquitoes*. Bulletin 6. American Mosquito Control Association, Fresno, California.
- Memmott, J. 2000. Food webs as a tool for studying nontarget effects in biological control. Pages 147–163 in P. A. Follet and J. J. Duan, editors. *Nontarget effects of biological control*. Kluwer Academic Publishers, Boston.
- Molloy, D. P. 1998. The potential for using biological control technologies in the management of *Dreissena* spp. *Journal of Shellfish Research* **17**:177–183.
- Murray, J., E. Murray, M. S. Johnson, and B. Clarke. 1988. The extinction of *Partula* on Moorea. *Pacific Science* **42**:150–153.
- Nechols, J. R., W. C. Kauffman, and P. W. Schaefer. 1992. Significance of host specificity in classical biological control. Pages 41–52 in W. C. Kauffman and J. E. Nechols, editors. *Selection criteria and ecological consequences of importing natural enemies*. Thomas Say publications in entomology. Entomological Society of America, Lanham, Maryland.
- Norgaard, R. B. 1988. Economics of the cassava mealybug (*Phaenacoccus maniboti*; Hom.: Pseudococcidae) biological control program in Africa. *Entomophaga* **33**:3–6.
- Obrycki, J. J., N. C. Elliot, and K. L. Giles. 2000. Coccinellid introductions: potential for and evaluation of nontarget effects. Pages 127–145 in P. A. Follet and J. J. Duan, editors. *Nontarget effects of biological control*. Kluwer Academic Publishers, Boston.
- Ogle, C. C., G. D. L. Cock, G. Arnold, and N. Mickleson. 2000. Impact of an exotic vine *Clematis vitalba* (F. Ranunculaceae) and of control measures on plant biodiversity in indigenous forest, Taihape, New Zealand. *Austral Ecology* **25**:539–551.
- Onstad, D. W., and M. L. McManus. 1996. Risks of host range expansion by parasites of insects. *BioScience* **46**:430–435.
- Pemberton, R. W. 1995. *Cactoblastis cactorum* (Lepidoptera: Pyralidae) in the United States: an immigrant biological control agent or an introduction of the nursery trade? *American Entomologist* **41**:230–232.
- Pimental, D., L. Lach, R. Zuniga, and D. Morrison. 2002. Environmental and economic costs associated with non-indigenous species in the

- United States. Cornell University, Ithaca, New York. Available from http://www.news.cornell.edu/releases/Jan99/species_costs.html (accessed November 2002).
- Port, G. R., D. M. Glen, and W. O. C. Symondson. 2000. Success in biological control of terrestrial molluscs. Pages 133–160 in G. Gurr and S. Wratten, editors. *Biological control: measures of success*. Kluwer Academic Publishers, Dordrecht, The Netherlands.
- Porter, S. D. 2000. Host specificity and risk assessment of releasing the decapitating fly *Pseudacteon curvatus* as a classical biocontrol agent for imported fire ants. *Biological Control* 19:35–47.
- Robinson, G. S. 1975. *Macrolepidoptera of Fiji and Rotuma*. Claxsey, Oxon, United Kingdom.
- Rodger, J. C. 1997. Likely targets for immunocontraception in marsupials. *Reproduction, Fertility and Development* 9:131–136.
- Rupp, H. R. 1996. Adverse assessments of *Gambusia affinis*: an alternate view for mosquito control practitioners. *Journal of the American Mosquito Control Association* 12:155–166.
- Sailer, R. I. 1978. Our immigrant insect fauna. *Entomological Society of America Bulletin* 24:3–11.
- Salas, J., and J. H. Frank. 2001. Development of *Metamasius callizona* (Coleoptera: Curculionidae) on pineapple stems. *Florida Entomologist* 84:123–126.
- Saunders, G., B. Coman, J. Kinnear, and M. Braysher. 1995. *Managing vertebrate pests: foxes*. Australian Government Printing Service, Canberra, Australia.
- Schettler, T., G. Soloman, M. Valenti, and A. Huddle. 1999. *Generations at risk: reproductive health and the environment*. The MIT Press, Cambridge, Massachusetts.
- Secord, D., and P. Kareiva. 1996. Perils and pitfalls in the host specificity paradigm. *BioScience* 46:448–453.
- Siegal, M. L., and A. Bergman. 2002. Waddington's canalization revisited: developmental stability and evolution. *Proceedings of the National Academy of Science of the United States of America* 99:10528–10532.
- Simberloff, D., and P. Stiling. 1996. Risks of species introduced for biological control. *Biological Conservation* 78:185–192.
- Simberloff, D., and P. Stiling. 1998. How risky is biological control? Reply. *Ecology* 79:1834–1836.
- Simmonds, F. J., and I. W. Hughes. 1963. Biological control of snails exerted by *Euglandia rosea* (Ferrussac) in Bermuda. *Entomophaga* 8:219–222.
- Singleton, G. R., and H. I. McCallum. 1990. The potential of *Capillaria hepatica* to control mouse plagues. *Parasitology Today* 6:190–193.
- Strand, M. R., and J. J. Obrycki. 1996. Host specificity of insect parasitoids and predators. *BioScience* 46:422–429.
- Strong, D. R., and R. W. Pemberton. 2001. Food webs, risks of alien enemies and reform of biological control. Pages 57–79 in E. Wajnberg, J. K. Scott, and P. C. Quimby, editors. *Evaluating indirect ecological effects of biological control*. CAB International Publishing, Wallingford, United Kingdom.
- Syrett, P., D. T. Briese, and J. H. Hoffmann. 2000a. Success in biological control of terrestrial weeds by arthropods. Pages 189–230 in G. Gurr and S. Wratten, editors. *Biological control: measures of success*. Kluwer Academic Publishers, Dordrecht, The Netherlands.
- Syrett, P., L. A. Smith, T. C. Bourner, S. V. Fowler, and A. Wilcox. 2000b. A European pest to control a New Zealand weed: investigating the safety of heather beetle, *Lochmaea suturalis* (Coleoptera: Chrysomelidae) for biological control of heather, *Culluna vulgaris*. *Bulletin of Entomological Research* 90:169–178.
- Thresher, R. E., M. Werner, J. T. Høeg, I. Svane, H. Glenner, N. E. Murphy, and C. Wittwer. 2000. Developing options for managing marine pests: specificity trials on the parasitic castrator, *Sacculina carcini*, against the European green crab, *Carcinus maenas*, and related species. *Journal of Experimental Marine Biology and Ecology* 254:37–51.
- Twigg, L. E., T. J. Lowe, G. R. Martin, A. G. Wheeler, G. S. Gray, S. L. Griffin, C. M. O'Reilly, D. J. Robson, and P. H. Hubach. 2000. Effects of surgically imposed sterility on free-ranging rabbit populations. *Journal of Applied Ecology* 37:16–39.
- Van Driesche, R. G. 1994. Classical biological control of environmental pests. *Florida Entomologist* 77:20–33.
- Van Driesche, R. G., and T. S. Bellows, editors. 1993. *Steps in classical arthropod biological control*. Thomas Say publications in entomology. Entomological Society of America, Lanham, Maryland.
- Van Driesche, R. G., and T. S. Bellows. 1996. *Biological control*. Chapman and Hall, New York.
- Van Driesche, J., and R. Van Driesche. 2000. *Nature out of place: biological invasions in a global age*. Island Press, Washington D.C.
- Van Rensburg, P. J. J., J. D. Skinner, and R. J. van Aarde. 1987. Effects of feline panleucopaenia on the population characteristics of feral cats on Marion Island. *Journal of Applied Ecology* 24:67–73.
- Van Thielen, R., O. Ajuonu, V. Schade, P. Neuenschwander, A. Adite, and C. J. Lomer. 1994. Importation, releases, and establishment of *Neochetina* spp. (Col.: Curculionidae) for the biological control of water hyacinth, *Eichhornia crassipes* (Lil.: Pontederiaceae), in Benin, West Africa. *Entomophaga* 39:179–188.
- Vitousek, P. M., C. M. D'Antonio, L. L. Loope, and R. Westbrooks. 1996. Biological invasions as global environmental change. *American Scientist* 84:468–478.
- Wajnberg, E., J. K. Scott, and P. C. Quimby, editors. 2001. *Evaluating indirect ecological effects of biological control*. CABI Publishing, Wallingford, United Kingdom.
- Walton, W. E., and M. S. Mulla. 1991. Integrated control of *Culex tarsalis* larvae using *Bacillus sphaericus* and *Gambusia affinis*: effects on mosquitoes and nontarget organisms in field mesocosms. *Bulletin of the Society of Vector Ecology* 16:203–221.
- Wheeler, G. S. 2001. Host plant quality factors that influence the growth and development of *Oxyops vitiosa*, a biological control agent of *Melaleuca quinquenervia*. *Biological Control* 22:256–264.
- Wilson, E. O. 1997. Foreword. Pages ix–x in D. Simberloff, D. C. Schmitz, and T. C. Brown, editors. *Strangers in paradise: impact and management of nonindigenous species in Florida*. Island Press, Washington D.C.
- Zenner-Polania, Z. 1990. Biological aspects of the "hormiga loca" *Paratechina (Nylanderia) fulva* (Mayr) in Colombia. Pages 290–297 in R. K. Vander Meer, K. Jaffe, and A. Cedeno, editors. *Applied myrmecology: a world perspective*. Westview Press, Boulder, Colorado.

