
How Much Information on Population Biology Is Needed to Manage Introduced Species?

DANIEL SIMBERLOFF

Department of Ecology and Evolutionary Biology, University of Tennessee, Knoxville, TN 37996-1610, U.S.A.,
email dsimberloff@utk.edu

Abstract: *Study of the population biology of introduced species has elucidated many fundamental questions in ecology and evolution. Detailed population biological research is likely to aid in fine-tuning control of widespread and/or long-established invasions, and it may lead to novel control methods. It will also contribute to an overall understanding of the invasion process that may aid in the formulation of policy and help to focus attention on invasions that are especially prone to becoming problematic. But the importance of intensive population biological research in dealing with introduced species, especially those recently introduced, is often limited. In the worst instances, the absence of population biological data can be an excuse for inaction, when a prudent decision or quick and dirty operation might have excluded or eliminated an invader. The most effective way to deal with invasive introduced species, short of keeping them out, is to discover them early and attempt to eradicate or at least contain them before they spread. This approach has often been successful, but its success has usually relied on brute-force chemical and mechanical techniques, not on population biological research.*

¿Cuánta Información sobre Biología Poblacional Se Necesita para Manejar Especies Introducidas?

Resumen: *El estudio de la biología poblacional de las especies introducidas ha aclarado muchas preguntas fundamentales en ecología y evolución. La investigación detallada de la biología poblacional probablemente ayude a afinar el control de invasiones ampliamente distribuidas y/o establecidas tiempo atrás, y puede conducir a métodos originales de control. También contribuirá al conocimiento general del proceso de invasión que puede ayudar en la formulación de políticas y ayudar a enfocar la atención en invasiones que son especialmente propensas a convertirse en problemáticas. Sin embargo, la importancia de la investigación intensiva sobre biología poblacional en el combate a las especies introducidas, especialmente las recientemente introducidas, es frecuentemente limitada. En el peor de los casos, la ausencia de datos de biología poblacional puede ser una excusa para no actuar, cuando una decisión prudente o una operación rápida podría haber excluido o eliminado a un invasor. La forma más efectiva de hacer frente a las especies invasoras introducidas, a falta de mantenerlas fuera, es el descubrirlas temprano, e intentar erradicarlas o al menos contenerlas antes de que se dispersen. Este enfoque ha sido frecuentemente exitoso, pero su éxito ha recaído generalmente en técnicas químicas y mecánicas usando la fuerza bruta y no en investigación sobre la biología poblacional.*

Introduction

That invasive introduced species are a global scourge is well-publicized in both the scientific and the popular lit-

eratures (e.g., Williamson 1996; Bright 1998; Cox 1999; Devine 1999; Low 1999; Mooney & Hobbs 2000). Less understood are the various approaches used to deal with such invaders and particularly the degree of success achieved. In fact, some authors see global homogenization as inevitable because of rapidly increasing travel and trade (e.g., Quammen 1998). However, there have been many successes in keeping out introduced species

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(e.g., Parliamentary Commissioner for the Environment 2001), in eradicating them completely (Myers et al. 2000; Forsyth et al. 2001; Simberloff 2002a; Veitch & Clout 2002), and in controlling them at acceptably low levels (Simberloff 2002b). Species can often be eradicated early with little or, at most, superficial knowledge of their population biology, and failure to do so is rarely a consequence of inadequate knowledge in this realm. Once the opportunity for rapid eradication has been lost, it is more likely that population biological details will be important in creating procedures for effective maintenance management (or even eradication). Even then, the important population biology may sometimes be of the most basic kind, and sometimes population biological information is unnecessary. I examined some successes and failures in introduced species policy and management, beginning with exclusion and continuing through maintenance management, in an attempt to clarify and project the role of population biological research.

Failure to Exclude

The World Trade Organization's (WTO) Agreement on the Application of Sanitary and Phytosanitary Measures is fashioned to balance the interests of nations in keeping out threats to plant, animal, and human health, including those posed by introduced species, with the desire to remove impediments to the international movement of goods (National Research Council 2000). The agreement stipulates that a nation wishing to exclude a non-native species, or a product that might carry such a species, must conduct a quantitative risk assessment to demonstrate that the species to be excluded does propose a substantial threat. The risk assessment should include much information that is not population biological, such as whether a potential invader is problematic elsewhere, as well as information on potential economic costs of its exclusion. But the standards for such a risk assessment are so high that they can scarcely be met without also including substantial population biological research that would give estimates of various demographic parameters. In fact, an Australian attempt to exclude fresh or frozen Canadian salmon, on the grounds that they might carry pathogens that would threaten native fish, was rejected by the WTO Appellate Body, partly on the grounds that the Australian risk assessment lacked exactly this sort of quantitative approach (Victor 2000). Not only is demand for such population research in this instance a contradiction of the precautionary principle enshrined in the Convention on Biological Diversity ("Noting also that where there is a threat of significant reduction or loss of biological diversity, lack of full scientific certainty should not be used as a reason for postponing measures to avoid or minimize such a threat" [Convention on Biological Diversity 2000

Preamble]), it also connotes an unwarranted sense of security when the risk assessment standards are met. The technology of risk assessments for introduced species is immature, and confidence limits about estimates of likelihood that a species will become a pest are so large as to render them a poor instrument when the cost of a Type II error (false hypothesis of no effect) is high (Simberloff & Alexander 1998).

When the risk is posed by a particular species rather than a pathway that might carry several unknown species, it is possible that intense population biological research could provide a useful risk-assessment procedure, in spite of occasional pronouncements (e.g., Sharples 1983) that the outcome of an introduction is inherently unpredictable. Early efforts, such as the "Baker list" (Baker 1965) of traits that suggests when a plant species will be an invasive "weed," fundered, largely because of too many exceptions—species that should have been invasive that were not or those that should have been harmless but became scourges. And it is still true that the best predictor of whether a nonindigenous species will have negative effects is whether it has had such effects where it has already been introduced (Daehler & Gordon 1997). But recent efforts focused more narrowly on particular groups of plants (e.g., Rejmánek & Richardson 1996; Reichard & Hamilton 1997) seem successful at distinguishing between species that become invasive and those that do not. These successes suggest that if enough of the biology of most species were known, risk assessments could be very useful in pinpointing proposed introductions needing close attention. But for two reasons, it is unlikely that such a tool by itself could automatically suffice as the sole basis for decisions. First, the impact of a potential invader depends not only on the species but on the recipient ecosystem (Simberloff 1986; Rejmánek 1999). Second, even a few false positives—species predicted to become invasive that in fact would not have—can be very expensive (Smith et al. 1999).

Failure to Eradicate Early

The tropical alga *Caulerpa taxifolia* was first observed in a tiny area in front of the Oceanographic Museum of Monaco in 1984; it surely had not been there more than a couple of years (Meinesz 2001). It almost certainly could have been eliminated soon after its discovery, when it was restricted to a few square meters, simply by hand-removal with great care that little pieces did not float away (divers now do this successfully for small infestations at the Port-Cros National Marine Park). But the effort was delayed for years and the alga now infests several thousand hectares of the coasts of Spain, France, Monaco, Italy, Croatia, and Tunisia. The effort was delayed for two reasons. First, the various French government agencies tried to avoid taking re-

sponsibility for it, each trying to foist it off on the others. Second, when the Institut Français de Recherches pour l'Exploitation de la Mer (IFREMER), the main French marine research institute, finally got around to taking responsibility, it argued that much more study was needed to determine if *Caulerpa* was going to be a problem and, if so, to figure out how to manage it.

By contrast, the Caribbean black-striped mussel (*Mytilopsis sallei*) was discovered in 1999 in Cullen Bay (12.5 ha), Darwin Harbor, within 6 months of its arrival and before it had spread further in Australia. Within 9 days the bay had been quarantined and treated with 160,000 L of liquid bleach and 6000 tonnes of CuSO_4 . All living organisms were believed killed, and the mussel population was eradicated (Bax et al. 2001). The Australians did no empirical research before this campaign, conducting only a literature search that turned up little information relevant to control.

The South American solanaceous plant *Lycianthes asarifolia* was found on a few Houston lawns in 1997. In 1998 it infested the yards around just four homes in a 4-block area. By the summer of 2001, it overran several residential yards in one area of Houston and was nearing a big Houston city park. So far, it has not been seen elsewhere in Texas, although it has been found without fruit in one New Orleans park. It tolerates the winter in Houston and suffers a little dieback during the hottest days of the summer. It appears to be highly competitive with various lawn grasses used in Houston. This case has been publicized vociferously by Ketchersid (2001) and Westbrooks (personal communication) of the U.S. Geological Survey, but the U.S. Department of Agriculture's Animal and Plant Health Inspection Service and the state of Texas have done nothing to control this potential invasion. They point to a lack of definitive knowledge and a shortage of funds. My impression is that no one is willing to take charge. What is most alarming is that even though individual residents have attempted to control the plant by hand-pulling, mowing, applying herbicides, and removing infested sod, they have had little success. I believe a coordinated effort could eradicate this infestation fairly promptly, and I doubt it would require much detailed knowledge of population biology. It would probably take systematic herbicide tests, which Ketchersid (2001) is doing, and practice with digging techniques.

After all, this type of action has been taken before, on much tougher problems. For instance, the sandbur *Cenchrus echinatus* was introduced to Laysan in 1961. By 1989 it completely dominated 30% of the 85 vegetated ha of the island. Now it appears to be completely eradicated, with no sprouts this year, after much skepticism on the part of botanists and ecologists that it could be done (Flint 2001). The team tried several methods, including saltwater, but settled on glyphosate applications and hand-pulling. As they learned more biology, they

were able to operate more cheaply. For instance, when they determined the time from sprouting to setting seed, they were able to increase the rotation period for visiting plots. But they never engaged in detailed population biological research, and the whole project was fairly inexpensive (\$150,000/year since 1991), given that Laysan is 5 days by boat from Honolulu.

The United States has already let nonindigenous plants spread that could have been controlled easily with little or no knowledge of population biology. The story of common crupina (*Crupina vulgaris*) (Westbrooks et al. 2000) eerily resembles that of *Caulerpa taxifolia* in France. It was first noticed in 1968 in Idaho, and the first survey in 1970 showed that crupina dominated approximately 16 ha. No one acted for years, and by 1981 it infested 9000 ha and was listed as a federal noxious weed. That year an eradication feasibility study was launched, but it was not completed until 1988. The results suggested that eradication was feasible. A federal/state task force to consider eradication did not meet until 1991, by which time crupina had spread to four states and dominated 25,000 ha. But the task force decided against immediate action because of concerns about the effects of herbicides on salmon. Now crupina has spread further, and there is no comprehensive plan to deal with it. No biological control agent has been found. I cannot prove it, but I suspect it could have been eradicated in 1970 without detailed understanding of its population biology. Managers have eradicated many plant populations from small areas, simply by ripping them up and/or using herbicides and by taking care not to spread seeds or tubers during the process.

Koster's curse (*Clidemia birta*) in Hawaii is another example of a highly invasive plant that probably could have been eradicated early, without much population biological research. It was first discovered in 1941 in one small area of Oahu (Anonymous 1954), and right into the 1950s it was still restricted to this area and still infested <100 ha. It was immediately recognized as a threat (Hosaka & Thistle 1954), but no one did anything about it, not because of absence of scientific knowledge but because of overconfidence (Mack & Lonsdale 2002). Koster's curse had been well-controlled on Fiji by the thrips *Liothrips urichi*, so the biological control experts in Hawaii saw no reason for alarm or immediate action, because they were confident the thrips would control it in Hawaii (Pemberton 1957). In 1954 they released the thrips, which was a dismal failure, and several other introduced biological control agents have also had little or no effect (Wester & Wood 1977; Smith 1992). Now Koster's curse has spread to other islands, infests more than 100,000 ha, and is sometimes viewed as the second worst weed in Hawaii (Smith 2000).

The monk parakeet (*Myiopsitta monachus*), introduced to the United States in the late 1960s as a pet, is a good example of an animal species that could probably

have been eradicated early without any population biological research, by shooting, the most effective method among many tried (Roscoe et al. 1973; Neidermeyer & Hickey 1977). Unfortunately, other populations were allowed to proliferate, generally because of the controversies surrounding killing a charismatic vertebrate (e.g., Faber 1973; Welch 1973). The monk parakeet was established locally in 7 states by the early 1970s and occupied 15 states by 1995 (Neidermeyer & Hickey 1977; Long 1981; Van Bael & Pruett-Jones 1996). There are now thought to be approximately 100,000 of them in Florida alone (B. Pranty, unpublished data). In Argentina and Uruguay they have long been known as a major agricultural pest; even Darwin noted this (Bucher 1992).

It is important to acknowledge that there will be some failures when people act quickly without much research, and sometimes research might have either predicted the failure or led to a different approach that would have succeeded. To return to the *Caulerpa taxifolia* case, in June 2000, an infestation of this alga was found in Agua Hedionda Lagoon near San Diego (Meinesz 2001; K. Merkel & R. Woodfield, unpublished data). It was located in about 20 distinct patches ranging from <1 m² to approximately 500 m², all in one area in the northern part of the lagoon. The alga is believed to have arrived there because someone dumped aquarium contents into the lagoon within the last 2–3 years. Within 6 months, an interagency task force was formed and hired a contractor, who ran a series of rapid tests for sensitivity to several herbicides and tested the effectiveness of suction-dredging and hand-removal. The contractor found that bleach seemed most promising and covered all infestations with a thick, anchored tarpaulin and pumped in bleach. The tarpaulins were to be left in place for 1 year. Throughout this process, information was difficult to obtain from the contractor or the interagency task force, and several scientists complained that adequate tests of the efficacy of the bleach method were not planned to run simultaneously with the eradication effort.

Now there are shoots of *Caulerpa* in a several places, possibly from rhizoids that were not killed and grew out from under the tarpaulins (S. Williams, personal communication). The shoots are being covered and bleached further. So the outcome of this operation is as yet uncertain, as is an attempt to eliminate a larger infestation in Huntington Harbor near Los Angeles. I emphasize two points. First, the task force was right to have acted quickly rather than demanding more information on the biology of the alga. If they had not, based on the Mediterranean experience, one could assume that the alga would be much more widespread today. Second, the argument over testing the efficacy of the method was not centered on the need for more population biological research, but rather over protocols to determine just what is needed to kill the alga.

Some Successful Early Interventions

So far I have discussed failures—plus two contrasting successes—of early eradication. There may be some hazards in acting quickly, by brute force, to eradicate invasions when they are initially limited to a small area. For example, the economic cost of a failed effort may be substantial, and there may be considerable collateral damage to nontarget organisms, as in the eradication of *Mytilopsis sallei* discussed above. But many case histories demonstrate that eradication is often possible, and the ecological and economic savings, though rarely explicitly calculated, are surely great in some of these cases.

A young boy returning from Hawaii in 1966 brought two or three individuals of the giant African snail (*Achatina fulica*) to Miami (Mead 1979). The resulting infestation of 42 city blocks was discovered in 1969, and another infestation was soon discovered 40 km away. The state of Florida quickly mounted an eradication campaign using hand-picking, poison baits, quarantine, and a publicity campaign. Despite some setbacks, including the discovery of three other infestations as far as 5.6 km away and perhaps 2–3 years old, the state persevered. Success was achieved by 1975, at a cost of approximately \$1 million, though frequent surveys, baiting, and carbaryl drenches continued for many months after the last snail was seen. This project inspired another successful eradication of the giant African snail in Queensland, Australia (Colman 1978). An important population biological fact was crucial to the success of these campaigns, but it was easily determined: *Achatina fulica* does not self-fertilize.

The white-spotted tussock moth (*Orgyia thyellina*) invaded New Zealand in approximately 1996 and was restricted to a suburban residential area of Auckland when the government launched an eradication campaign in 1997. At a cost of \$5 million, the moth was eradicated in 1997 through the use of *Bacillus thuringiensis* sprays. In addition to determining the susceptibility of the moth to the bacterium, researchers used caged females in sticky traps to catch males, and local areas where males appeared were sprayed again (Anonymous 1998, 1999; Clearwater 2001). The fact that females emit a pheromone had already been determined with other tussock moths, and no other population biological research was conducted for this campaign. The government did not wait for completion of research on possible effects of the moth on New Zealand plants before conducting the eradication.

Many invasive nonindigenous plants have been eradicated after fairly early detection. The New Zealanders have a string of successes on various islands, involving very small populations of some legendary invaders, such as pampas grass (*Cortaderia selloana*), ragwort (*Senecio jacobaea*), and prickly hakea (*Hakea sericea*) (Timmins & Braithwaite 2002). Australians have also eradicated fa-

mous nonindigenous plants that were detected early, karo thorn (*Acacia karoo*) in Western Australia and parthenium (*Parthenium hysterophorus*) in the Northern Territory (Weiss 1999). In all of these cases, success was not a question of population biological research but of acting quickly with brute-force methods.

Eradicating Longstanding Invasions

Further, there are success stories in which an invasion was not caught early but was nevertheless eradicated and success stories in which effective management was achieved without eradication. At least some examples in both categories seem to have relied on superficial population biological understanding.

A dedicated group of scientists, the Island Conservation and Ecology Group, has succeeded in removing long-established populations of various combinations of feral cats (*Felis catus*), Norway and black rats (*Rattus norvegicus* and *R. rattus* respectively), house mice (*Mus musculus*), rabbits (*Oryctolagus cuniculus*), goats (*Capra hircus*), sheep (*Ovis aries*), and burros (*Equus asinus*) from several islands in northwestern Mexico by using traps, hunting dogs, and rifles (Donlan et al. 2000; Wood et al. 2001). They have not engaged in detailed population biological studies but in what might be called applied ethology, such as determining where to place traps. The entire project has cost about \$700,000 so far.

There have been successful eradication campaigns against invaders established over much larger areas. An African malaria vector, the mosquito *Anopheles gambiae*, was eradicated from northeastern Brazil (Soper & Wilson 1943; Davis & Garcia 1989). The mosquito was recorded in 1930, but the eradication campaign did not begin until after major malaria outbreaks in 1938. By then, *A. gambiae* had spread over 31,000 km². The project featured chemical treatments for adults and larvae and achieved the complete eradication of *A. gambiae* by late 1940. Several aspects of the mosquito's natural history, including the facts that in Brazil it dispersed poorly and its microhabitat requirements were satisfied almost exclusively in human habitations, contributed to the success of the campaign. However, detailed population biological study was not necessary.

The African root parasite witchweed (*Striga asiatica*) reached the Carolinas in the 1950s. It has been reduced from 162,000 ha in the 1950s to approximately 2800 ha and will almost certainly be eliminated (Westbrooks 1993; Eplee 2001). This project entailed the massive support and cooperation of the U.S. government and the state governments of North and South Carolina, and it cost about \$250 million. The basic biology of the plant was known, but the control strategy did not rely on much of it. The program entailed a rigorous quarantine on the movement of anything that could carry soil out-

side the infested area, various herbicides to kill the plants, and soil fumigation with ethylene gas to kill the seeds.

However, there have been eradications of invasive introduced plants established over large areas that cost nowhere near \$250 million. A recent example is the eradication from Western Australia of *Kochia scoparia*, described by Randall (2001; R. Randall, personal communication). It was introduced in 1990 and promoted as a living haystack, in spite of its well-known status as a major weed elsewhere. It was widely planted on 52 properties, and by 1992 it was recognized as a pest and an eradication campaign was started. By 1993 it had reached 270 properties spread out over a linear distance of over 900 km. The eradication team searched over 20,000 ha, finding more than 3200 ha to be infested. By 1995 that area was reduced to 139 ha and by 2000 to 5 ha, at a total cost of \$250,000. A variety of herbicides was used, and the project did not entail population biological studies.

In each of these eradications, it was important to know something about the biology of the target to avoid wasting a lot of time and money, but it was unnecessary to know very much. For *Anopheles gambiae*, it was important to know that it disperses poorly and that in Brazil it was found exclusively around homes. For the various plants, it was important to know whether they had soil seed banks and which herbicides worked. For the giant African snail, it was important to know that it does not self-fertilize. For many mammals, it was important to know how to trap them. These and other eradication campaigns suggest the conditions that must be met for such a campaign to be successful (Myers et al. 2000; Forsyth et al. 2001; Simberloff 2002a), which is not the same question as whether a campaign is worth undertaking (Simberloff 2002a).

Often, substantial population biological knowledge at the outset would have allowed a better estimate of the probability of success of an eradication campaign or even improved the likelihood of success. For example, release of massive numbers of sterile males has frequently been used successfully to eradicate insect populations. Some failures and temporary setbacks have arisen, however, because males have evolved in domestication to be less competitive than wild males in mating (e.g., in the campaign against the apple codling moth [*Cydia pomonella*] in British Columbia [Myers et al. 2000]) and wild females have evolved to discriminate against sterile males (e.g., in the eradication of the melon fly [*Bactrocera cucurbitae*] from the Ryukyu Archipelago [Iwahashi 1996]). Detailed population study and modeling in several instances has led to improved success through the use of initial procedures to reduce the number of wild males and better estimates of just how many sterile males must be released (e.g., Iwahashi 1996). Gleaning such knowledge will frequently necessi-

tate a long research effort, however, and the ability of some invasions to spread quickly suggests that we should often proceed with an eradication attempt even with very uncertain prospects for success.

Of course, the methods deployed in such a rapid response are likely to resemble a blunderbuss attack rather than a surgical strike. But because of their population growth and dispersal abilities, introduced species are one target of resource management at which it is often better to shoot first and ask questions later. The methods I have described were generally preemptive strikes by brute force. I am not arguing that more elegant methods were not possible in some instances but that we do not know what would have worked. Many supposedly theoretically surefire methods turn out not to work when tried. But by acting quickly, without much biological knowledge, these projects saved a huge amount of trouble and expense and avoided uncertain prospects for successful subsequent management. Because many invaders have a distinct lag time before they start to spread (Kowarik 1995; Crooks & Soulé 1996), this entire litany of successes constitutes a strong argument for an effective early warning and rapid-response mechanism (cf. Braithwaite 2000; Westbrooks et al. 2000; Timmins & Braithwaite 2002). They also argue for applying the precautionary principle when a relatively recent invasion is found. Absence of knowledge should rarely be used to justify an attempt at quick action.

Successful Maintenance Management

In many more instances, species are managed at low levels even though they are not eradicated. Sometimes such management necessitates substantial population biological knowledge; other times it does not. Water hyacinth (*Eichhornia crassipes*) in Florida is a good example of effective control after widespread invasion that did not require extensive population biological research (Schardt 1997). Arriving in Florida in the early 1880s as a horticultural curiosity, it was rapidly spread by farmers who mistakenly thought it would make good cattle fodder, so by the end of the nineteenth century it was already a major pest. Starting in 1899 the Army Corps of Engineers tried many techniques to control it. They mostly used mechanical devices, but these worked only locally because water hyacinth grows very rapidly (it can double in weight every 2 weeks) and because 1 ha of water hyacinth weighs approximately 363 tonnes, making removal from a site difficult. Meanwhile, after extensive study of aspects of the biology of the plant and insects proposed for biological control, two beetles and a moth were introduced to control water hyacinth in the early 1970s. They had almost no effect, certainly no sustained, wide-ranging, or effective impact.

In the mid-1970s, in desperation, the Florida legislature approved a program by the Florida Department of Environmental Protection to control water hyacinth statewide. The department conducted little research on the basic biology of the plant, but, with the Corps of Engineers, they found that the herbicide 2,4-D killed it. With secure annual state funding, using mechanical harvesters and 2,4-D, the state quite quickly reduced the coverage of water hyacinth from approximately 50,000 ha to <1000 ha, which is the approximate coverage now. Every year small infestations are destroyed, but others crop up elsewhere the next year. The cost is approximately \$2.7 million per year, which is a relatively small amount in this state.

In Kentucky the State Nature Preserves Commission has had substantial success managing Eurasian musk thistle (*Carduus nutans*) in certain areas. Some people convicted of driving under the influence of alcohol volunteer to help with the thistle eradication (J. Bender, personal communication). There was virtually no population biological research involved in this effort at all, just the willingness to persevere for the first couple of years even though early results were not impressive.

Control efforts against introduced sea lampreys (*Petromyzon marinus*) in parts of the Great Lakes and associated waterways initially relied heavily on chemical lampricides. Progressive improvement in the effectiveness of eradication methods and reduced reliance on chemicals have resulted from a substantial research effort on the biology, including the population biology, of this invader (Christie & Goddard 2001).

There are many instances in which biological control has been used successfully to control a pest (e.g., alligatorweed [*Alternanthera philoxeroides*], Center et al. 1997). In some of these instances, there has been substantial population biological research of the natural enemy. But most of the time biological control does not work (Williamson 1996), and when it does not work, or does not work as well as planned, subsequent population biological research may explain the failure (e.g., Luck & Podoler 1985). Many times, however, even a very well-researched natural enemy fails to control its target pest.

Effectiveness of Population Biological Research

There are also many high-impact invaders whose population biology has been intensively studied but whose successful control remains elusive. A good example is *Hydrilla verticillata*, introduced to the United States in 1960 (Langeland 1996). It was recognized quickly that this plant is a major pest, and a huge amount of research was done on its biology, including its population biology (Langeland 1996; Schardt 1997), that made it clear why it had become a pest. But a fair argument can be made that there

was really no substantial successful control until the introduction in the mid-1980s of fluridone (Sonar), which works well in whole-lake settings (Langeland et al. 1991; Langeland 1996). Fluridone can be made somewhat selective by carefully adjusting concentrations, but it is certainly no panacea. Mechanical control is too expensive in most circumstances, and many biological control introductions have failed to provide substantial control. It could be that some further piece of population biological research on *Hydrilla verticillata* will provide a much better solution. But my point is that although the population biology of *Hydrilla verticillata* is well known, this knowledge has not yet been translated into effective control.

The brushtail possum (*Trichosurus vulpecula*) is another species for which a plethora of population biological research (Montague 2000 and papers therein) has failed to yield substantial control. Introduced to New Zealand in 1858, possums were first suspected of damaging the native biota in the 1920s, and the 1940s saw a concerted effort by the government to control them (Clout & Ericksen 2000). Hunting and many other nontoxic approaches (Montague & Warburton 2000) failed to reduce populations substantially. Deployment of bait containing 1080 (sodium monofluoroacetate) beginning in the 1950s was effective in lowering populations, although the possum remains a conservation problem (Clout & Ericksen 2000; Eason et al. 2000). Extensive research on the population biology of the possum, particularly in New Zealand, contributed heavily to an understanding of why it became a pest (Clout & Ericksen 2000), and it has helped fine-tune the use of 1080 through the modeling of population recovery rates (Veltman & Pinder 2001). But the basic control method—aerial spread of 1080 bait—did not rest on such research. Current efforts to improve control seem focused in two directions. First, there is research to enhance the efficacy of the poison approach and somehow to make the public like 1080 better (Eason et al. 2000; Morgan & Hickling 2000). Second, there are a variety of methods that entail genetic engineering and interference with various physiological processes (Parliamentary Commissioner for the Environment 2000). It is possible that some of the latter efforts will bear fruit and that this production will have been fertilized by population ecological research. But in the near and intermediate term, if there is enhanced control it will come from poison. The possibility of a future technological fix, especially one that would probably take a long time to be approved for use, is no reason not to act with the tools at hand.

Conclusion

I emphasize that I am not implying that population biology is unnecessary for dealing with all invasive species problems. I have pointed out that such research is a

technical requirement of the World Trade Organization, even though the agreement stipulating this research is ill-founded. In addition, intensive population biological research can be needed simply to establish that some sort of invasive species problem exists. Although Howarth (1983, 1991) has argued persuasively that introduced biological control agents threaten nontarget native species, the importance of this phenomenon has been disputed on the grounds that his evidence was anecdotal and not quantitative (e.g., Funasaki et al. 1988; Lai 1988; Center 1995). Intensive, long-term population ecological research by Louda and her colleagues (Louda et al. 1997; Louda 1999; Louda & Arnett 2002) established that the introduced weevil *Rhinocyllus conicus* not only threatens at least one nontarget native thistle but may also indirectly threaten native herbivores who eat that thistle. This series of papers has changed the focus of the debate, with many advocates of biological control shifting from skepticism to a view that this sort of problem really happens and that we should plan our research so as to determine how often it happens and in which cases (e.g., Memmott 1999; Nechols 1999).

Further, population biological research on introduced species can provide major insights into other areas of ecology, evolution, and conservation biology, such as the relationship between population size and risk of extinction, the relationship between mating system and risk of extinction, the role of competition in shaping community structure, the role of natural enemies in limiting population size, the determinants of biogeographic ranges, the nature of character displacement and release, and the speed of evolution by natural selection (Blackburn et al., unpublished). Some exciting recent advances in both “academic” and applied ecology come from the study of introduced species (e.g., Huey et al. 2000; Forsyth & Duncan 2001). Such research will doubtless yield many further insights. The frequent presence of serendipity in science ensures that some fraction of these insights will ultimately aid management. But most will have little direct relevance to introduced species problems.

What I am arguing is that the science required for a decision on a fast course of action is often minimal, and that waiting to do more can make control more difficult or impossible. A quick and dirty response, mechanical or chemical or both, often solves the problem at the outset by eliminating the invader. At least a few times, the absence of biological research on the potential effects of a new invader has even been used as an excuse to impede exclusion or to delay doing anything after a species has been introduced.

After an invasion has become more or less metastatic, it is sometimes possible to control it by eliminating it or managing it at an acceptably low level; sometimes that management requires intensive population biological research, but sometimes it does not. I suggest that it is

here that population biological research can play a much greater role than it has. So far, we have not usually been effective at dealing with metastatic invasions. Sometimes biological control works beautifully, but usually it does not. Occasionally some approach based on profound knowledge of the population biology of a species may provide an answer. A recent striking example is the eradication of the South African sabellid polychaete worm, *Terebrasabella heterouncinata*, which parasitizes abalone and other gastropods (Culver & Kuris 2000). This species became established at Cayucos, California, near the outflow of an abalone mariculture facility. Substantial basic biological investigation showed that (1) it is specific to gastropod shells, (2) two species of *Tegula* were by far the most commonly parasitized hosts in this area, and (3) large snails were most susceptible. An army of volunteers removed 1.6 million large hosts and thereby seems to have reduced the density of susceptible hosts below that needed to maintain transmission of the parasite, which disappeared. Doubtless, other successful management methods could be based on approaches like this, methods that are tailored to the idiosyncrasies of particular species and that can be deduced only by intensive research.

And finally, intensive population biological research by no means guarantees a solution to an introduced species problem. This fact makes it all the more important that the need for more research should not be casually invoked as an excuse for inaction, especially with new invasions.

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