Biological Invasions **5:** 133–141, 2003.

Did biological control cause extinction of the coconut moth, *Levuana iridescens*, in Fiji?

Armand M. Kuris
Department of Ecology, Evolution and Marine Biology, and the Marine Science Institute, University of California, Santa Barbara, CA 93106, USA (e-mail: kuris@lifesci.ucsb.edu; fax: +1-805-893-4724)

Received 10 September 2001; accepted in revised form 7 March 2002

Key words: Bessa remota, biological control, coconut moth, coconut palm, collateral damage, extinction, Fiji, host specificity, *Levuana iridescens*, non-target impact

Abstract

In 1925, J.D. Tothill and two colleagues set out to manage *Levuana iridescens*, the coconut moth of Fiji, using biological control. By 1930, they had succeeded so completely that this pest of the copra crop had been reduced to almost undetectable levels by the tachinid fly, *Bessa remota*, introduced from Malaya, and they had summarized their campaign in a thoroughly documented and well-illustrated monograph. The example of the coconut moth is presented in the modern literature as the first and best documented extinction of a species due to scientific biological control. The program has been severely criticized because the moth was unique, beautiful, and considered endemic to Fiji. Thus, this program is also portrayed as an example of the highly controversial practice of neoclassical biological control. However, a careful reexamination of this event discloses that the moth was likely not native to Fiji, appeared to be spreading through the Fijian Archipelago, and might have spread to other island groups in the South Pacific. Also, *L. iridescens* is probably not extinct. Collateral damage, that is, non-target impacts, did occur as native zygaenid moths have been attacked by the tachinid, and they may be extinct. The reasons for the control campaign of *L. iridescens* were not primarily economic. Tothill and colleagues were trying to protect copra so that ethnic Fijian culture, so dependent on the coconut palm threatened by *L. iridescens*, could be sustained. Hence, this control program represents a difficult clash of values: preservation of insect biodiversity *versus* preservation of indigenous Pacific Islander cultures. A strategy to search for *L. iridescens* populations is proposed and development of biological control of *B. remota*, using hyperparasitoids, is possible, but would require careful evaluation since it might release *L. iridescens* from suppression, have non-target impacts on native tachinids, and lack an economic motivation.

Introduction

As a generally cost-effective means of pest control, particularly compared to chemical control alternatives (pesticides, herbicides), biological control is clearly safe for humans. However, natural enemies, once they become established, are probably permanent faunal components. Hence, the impact of biological control agents on non-target native species is a cause for environmental concern (Louda et al. 1997; Follett and Duan 2000; Wajnberg et al. 2001; Henneman and Memmott 2001).

It is probably a safe generalization that native species are valued in most cultures. However, all are not valued equally (e.g., salmon or pandas vs. aphids and malaria), and pest status may be accorded some native species. Still, at least among environmentalists (and this probably includes most ecologists), collateral damage to non-target indigenous species poses a substantial and severe threat causing some critics to consider the use of biological control only as a last resort, or only to be used under very restricted circumstances, for the control of invasive species (Howarth 1991; Simberloff and Stiling 1996;

Louda et al. 1997; Cowie and Howarth 1998; Hager and McCoy 1998).

One historical example stands out as a worst case scenario. A biological control agent, scientifically evaluated, has been portrayed as the poster child for the great risk of the use of natural enemies for biological control of a pest. This example is the extinction of the coconut moth, *Levuana iridescens* Bethune-Baker, by a tachinid fly parasitoid, *Bessa* (= *Ptychomyia*) *remota* (Aldrich). This example was recognized by Roberts (1986) and highlighted by Howarth (1991), and his perspective has been repeatedly cited in the recent cautionary literature (e.g., Simberloff and Stiling 1996; Barratt et al. 2000; Lynch et al. 2001; Holt and Hochberg 2001). Howarth made the following case:

> The control of the coconut moth, *L. iridescens*, on Fiji by the purposeful introduction of the tachinid fly *Bessa remota* from Malaysia in 1925 was described in great detail (Tothill et al. 1930) and is often cited as a classic example of biological control (DeBach 1974; Rao et al. 1971; Sweetman 1958). The last authentic specimen of this endemic monotypic genus of Zygaenidae was collected in 1929 (Robinson 1975; Tothill et al. 1930), although the species may have survived until the 1940s (Roberts 1986; Robinson 1975). The species, a widespread local pest, became endangered in less than 2 years, *and its demise is probably the best documented study of extinction among the insects* [italics mine] (Tothill et al. 1930). Another unrelated zygaenid, *Heteropan dolens*, was extirpated from Fiji at the same time (Robinson 1975). The impacts on other non-pestiferous native Fijian Lepidoptera were not recorded, even though the fly still occurs on Fiji, parasitizing non-target species (Russell 1986). Tothill et al. (1930) were unable to find the major alternative hosts in Fiji.

To this, I will add that *L. iridescens* was a distinctive species with some unique biological attributes (Tothill et al. 1930). From my personal aesthetic perspective, it was also a beautiful species, colored an iridescent dark blue (Figure 1).

Fortunately, the campaign against the coconut moth in Fiji has been described in eloquent detail by the Canadian entomologist J.D. Tothill and his two young British graduate assistants, T.H.C. Taylor and R.D. Paine who undertook the assignment and reported their studies in a monographic report on the coconut moth, and the history of its control by means of the

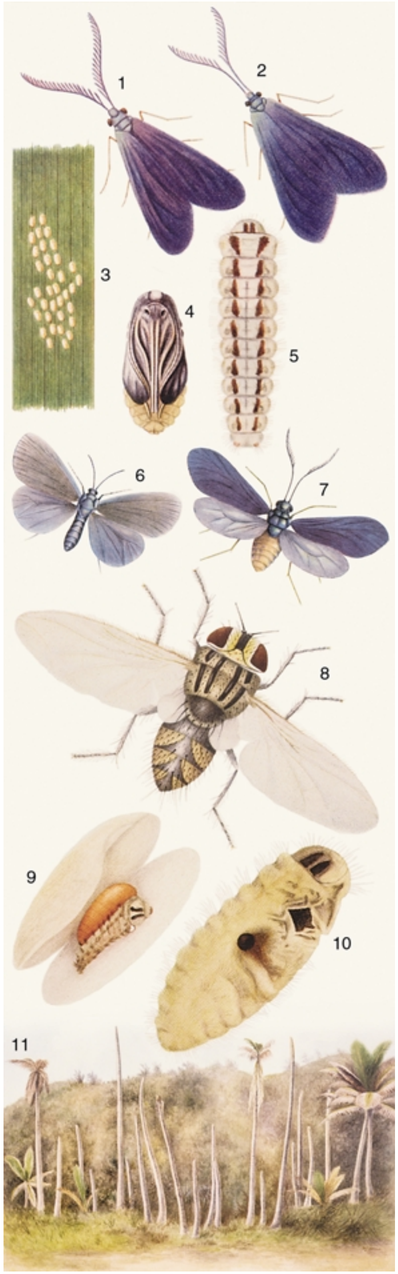

Figure 1. (1) *L. iridescens*, male, resting, (2) *L. iridescens*, female, resting, (3) *L. iridescens* egg cluster on coconut palm leaf, (4) *L. iridescens*, pupa, (5) *L. iridescens*, fifth instar larva, (6) *H. dolens*, wings spread, (7) *L. iridescens*, female, wings spread, (8) *B. remota*, adult, (9) cocoon of parasitized *L. iridescens*, opened to show dead larva of *L. iridescens* and pupa of *B. remota*, (10) larval corpse of *L. iridescens* with exit hole for *B. remota*, (11) death of coconut palms on Ovalau, after successive outbreaks of *L. iridescens,* prior to control by *B. remota*. (From Tothill et al. [1930]; paintings of insects by H.W. Simmonds; painting of shoreline by W.J. Belcher.)

parasitoid, *B. remota*, to the Government of Fiji and the Imperial Bureau of Entomology. Some invaluable additional comments are provided in a memoir by Paine (1994), who stayed on in Fiji until 1936, and then returned, as an entomologist, from 1956 to 1966.

Much has changed from the time of the pest control efforts of Tothill and his colleagues (1925–1930). In addition to the many technological advances, values on matters such as damage to native insects, have changed; often in ways difficult to discern. It is because of these social aspects that we are particularly indebted to Tothill, Taylor and Paine, for they very carefully specified their motivation for undertaking their control efforts. They were also conscious of some of the issues that provide us a perspective bridging the past 75 years.

To evaluate what happened to the coconut moth, and consider whether a comparable campaign would be appropriate in the environmental climate of today, five matters must be addressed:

1. Was the coconut moth actually endemic to Fiji?
2. Did collateral damage occur?
3. Is the coconut moth actually extinct?
4. Why did they attempt to control the coconut moth?
5. Was the control campaign conducted with human and environmental safety in mind?

The campaign against the coconut moth in Fiji

Was the coconut moth an endemic species?

Tothill et al. (1930) recognized that evaluating the zoogeography of *L. iridescens* would be critical to the development of a successful biological control strategy. The most effective biological control agents generally come from the region of origin of the pest, and prospecting for useful natural enemies is conducted in this region. The practice of detection of natural enemies in the region of origin of the pest, followed by their importation, evaluation and release, is termed 'classical' biological control (Smith 1948; Garcia et al. 1988).

The determination of the native zoogeographic status of *L. iridecens* is also key to a modern evaluation of the conduct of the coconut moth biological control campaign. If the moth were native to Fiji, then importation of a natural enemy form elsewhere would be an example of 'neoclassical' biological control (Lockwood 1993). Hokkanen and Pimentel (1984, 1989) have argued for the use of such 'new associations' precisely because they are not co-evolved, and the natural enemy may have a great impact on a 'naïve' pest. However, as Lockwood (1993) stresses, neoclassical biological control agents are selected *a priori* because they have low host specificity. Hence, their potential impacts on non-target species are potentially severe, and unbounded, with unintended consequences difficult to predict.

If the coconut moth were not native to Fiji, this would explain why it had recently become abundant and caused such severe economic and ecological problems. Weighing the evidence, Tothill et al. (1930) decided that *L. iridescens* was probably *not* a Fijian native endemic; but, more likely, represented a cryptic invasion from the Malayan/Melanesian regions to the west of Fiji (Figure 2). They based this conclusion on five points.

First, the zoogeography of *L. iridescens* in Fiji was odd. Unlike most Fijian endemics, it was not found widely among the main islands of the archipelago, but only on Viti Levu and a few small islands near its coast (Figure 2).

Second, extensive dissections of *L. iridescens* found it to be unparasitized. This was very unusual, as other zygaenid lepidopterans, especially its closest relatives, were frequently attacked by parasitoids. In contrast, introduced species are commonly unparasitized, and classical biological control aims to re-associate missing upper trophic level organisms with pestiferous exotic target species.

Third, the reason it was a serious pest of coconut trees was that it had repeatedly exhibited population outbreaks – periods of great abundance, causing defoliation and even death of many trees over long stretches of coast (Figure 1). But, these outbreaks had never been observed prior to 1877, during the time of the sandlewood trade that produced considerable shipping traffic between Fiji and the east coast of Asia. After that time, outbreaks of *L. iridescens* became regular occurrences. Coastal coconut trees on Viti Levu experienced repeated trunk constrictions associated with the greatly slowed growth that results from the repeated defoliation episodes caused by *L. iridescens*. Although trunk constrictions can be caused by other growth inhibiting factors, the greatly increased frequency of trunk constrictions on trees after the 1870s confirms the lack of reports of outbreaks in the early colonial and pre-colonial periods.

Fourth, *L. iridescens* relatives in Malaya, Java, New Guinea and the Solomon Islands are generally rare species with infrequent localized sporadic outbreaks.

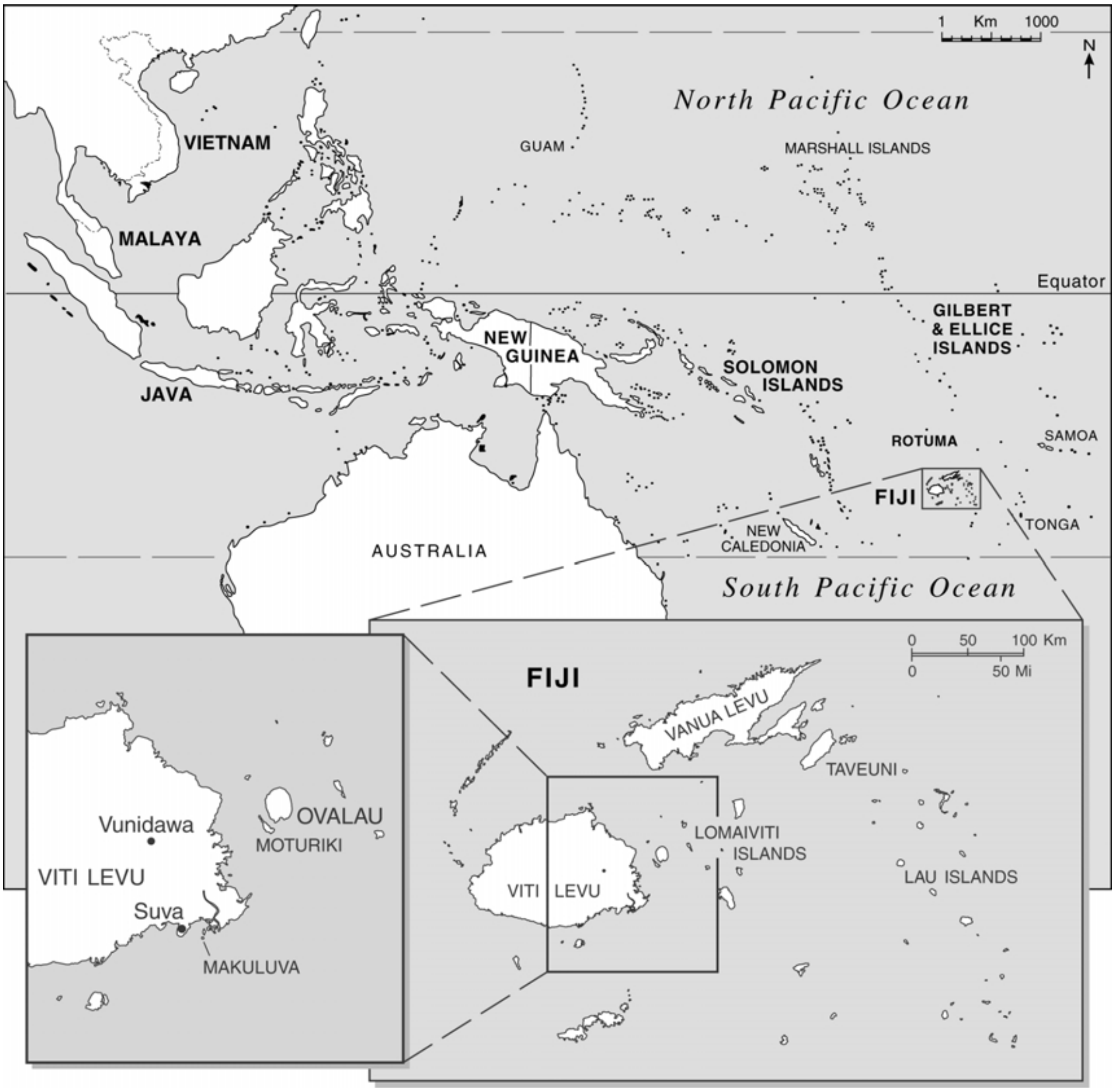

Figure 2. Places named in text are shown with historic names on a map of the Western Pacific with nested insets of the Fiji Archipelago, and eastern Viti Levu with offshore islands. Spelling of Fijian locations is modernized.

Hence, the outbreaks of *L. iridescens* from 1877 on are unusual life history features of these zygaenids, whose abundances are presumably generally held in check by natural enemies in their native ranges.

Fifth, *L. iridescens* had recently spread from Viti Levu to Ovalau and Moturiki (Figure 2), devastating copra plantations on those islands. Such an explosive range expansion is characteristic of recently established invaders. It also strongly suggested that other islands were at risk of coconut moth invasion and establishment.

While these points, particularly in the aggregate, support the hypothesis that *L. iridescens* was not, in fact, native to Fiji, they do not disprove the alternative that it was endemic. A few native endemic species do have odd restricted distributions within the archipelago. A search for *L. iridescens* in Malaya, Java and New Guinea did not detect it there. But, that is a lot of territory to search for a possibly rare species, and its recent outbreaks in Fiji might be caused by unknown changes in cultivation practices for copra (Tscharntke 2000).

Evaluating the possibilities, Tothill et al. (1930) concluded that *L. iridescens* was most likely not native to Fiji. Hence, they assumed they were working in the mode of classical biological control, rather than the more contentious (Hokkanen and Pimentel 1989; Lockwood 1993) neoclassical biological control strategy (using introduced natural enemies against native pests).

The issue of the endemicity of the coconut moth is central to an evaluation of its putative eradication as a tragedy. The conclusion remains elusive. Kalshoven (1981) considered *L. iridescens* to be conspecific with *Cathartona* (=*Artona*) *catoxantha* (Hampson), a widespread Indo-Malayan species (and the source host for *B. remota*). However, this taxonomic assignment is considered unlikely (Sands 1997).

Did collateral damage occur?

Since *L. iridescens* was the target of a classical biological control program, reduction of its population densities to undetectable levels was deliberately planned. Only its extinction might be regarded as 'collateral'. However, the parasitoid, *B. remota*, is a low host specificity natural enemy (unlikely to be released in the current regulatory and cultural climate of some Western countries (Sands 1997)). Tothill et al. (1930) reported that it readily attacked other zygaenid moths native to Fiji; one of which, *H. dolens* Druce, is now rare and may be extinct (Robinson 1975; Howarth 1991). So, collateral damage to non-target native species from *B. remota* clearly occurred. It is important to note that, to date, no comprehensive survey of native zygaenid moths for *B. remota* parasitism has been undertaken, as has recently been conducted for Hawaiian biological control agents attacking native species (Henneman and Memmott 2001). It would be valuable to also quantify the nature and extent of the collateral damage to native Fijian Lepidoptera in this influential case.

Over the past 75 years, other changes have come to Fiji that could have had a additive negative impact on abundance of *L. iridescens*, and the other related native moths that serve as hosts for the *B. remota* (Sands 1997). For example, coconut plantations have displaced native palms over most of the lowland regions of Viti Levu. This may have reduced habitat for these moths and could have decreased access to possible host plant refugia for the coconut moth. Pesticide use to control pest insects may also have negatively affected these zygaenids.

Is L. iridescens *actually extinct?*

Despite Tothill et al.'s (1930s) suspicions, and Howarth's (1991) claim, that the last specimen was collected in 1929, the coconut moth may still persist in Fiji. A specimen was collected in 1941 (Sands 1997). More importantly, Paine (1994) reported an outbreak of *L. iridescens* (soon followed by *B. remota* parasitism) on coconut palms near Vunidawa in 1956 (Figure 2). Since Paine was one of the original participants in the *L. iridescens* campaign, responsible for rearing the moths and the parasitoids, his identification of *L. iridescens* in 1956 must be considered highly reliable. Hence, its pattern of long periods of rarity, with occasional sporadic outbreaks, now resembles the temporal pattern of abundance of its relatives, such as *C. catoxantha*, on other palms in Java (Sands 1997).

Many exotic species go through an initial population outbreak phase, but then decline, sometimes below pestiferous levels, sometimes even to extinction. In some cases, this has been attributed to apparently successful biological control (Beirne 1975). However, the 50 year record of outbreaks of *L. iridescens* in Fiji, without a hint of decline (that is why the call for its control came in the 1920s), followed by its collapse to perhaps eradication, with very high levels of parasitization by *B. remota*, indicate that we can reject the hypothesis of decline to extinction due to causes other than its control by *B. remota.*

Why was L. iridescens *the target of a biological control campaign in Fiji?*

To assess the unquantified significance of the non-target impacts, and to evaluate the risks associated with this venture, it is necessary to appreciate the motivation for the control program against *L. iridescens*. Fortunately, the reasons are very clearly specified by Tothill et al. (1930) and are somewhat surprising for such an early agricultural pest control campaign. Tothill et al. (1930) note that the principle economic crop of Fiji was sugar cane. It used immigrant Indian labor and was an export crop important to colonial planters, merchants and the Government. However, ethnic Fijians would be little affected by changes in the cane economy. However, they crucially relied on copra for subsistence, many cultural practices and as a source of cash. The loss of copra was seen, by the colonial Administration, as tantamount to the demise of Fijian culture. Tothill et al. (1930) remark on these matters extensively and with clarity. Other than their archaic use of some terms, their views are quite modern. They quote Sir Morris Hedstrom, Senior Member of the Legislative Council:

> Any serious check to our sugar industry would have a disastrous effect on the Colony, particularly upon the Administration and the mercantile community, but, speaking broadly, it would not have a crushing effect on the native race, whereas the loss of the copra industry would utterly impoverish the natives of Vanua Levu, Taviuni, Lomaiviti, and Lau, and render conditions of life and Administration of those districts very difficult.
>
> Owing to the central position of Ovalau and Moturiki, and the constant traffic from those islands to Vanua Levu, Taviuni and Lau, it would be unsafe to reckon on any definite period of immunity for the other coconut-bearing areas in the group.

Tothill et al. (1930) add:

> Another respect in which coconuts are more important to this Colony than cane is that from time immemorial the coconut palm has been a mainstay of the Fijian race. In times of failure of taro and yams the coconut has provided meat and in times of drought has provided drink for populous villages in outlying islands. In a degree the tree has been the dairy cow of the Native Race and has enabled healthy children to be raised without the aid of the domestic cow. Thus the coconut is the chief source of material wealth – of ready cash – of the Fijians, and it enables islands to be inhabited and prosperous that would otherwise be unpopulated and barren.
>
> Finally, the wealth derived from coconut palms remains largely in the Colony, while part of that derived from sugar cane goes out of the Colony to shareholders of a Company that has headquarters in Sydney.

Hence, they conclude:

> We are inclined to think that the most important result of the campaign is the one least capable of measurement, namely, that coconuts can now be grown on Viti Levu.

Tothill et al. (1930) also recognized that more was at stake than just the preservation of ethnic Fijian culture on Viti Levu. They expressed a prescient concern for the future spread of *L. iridescens* and its consequent potential to impact other Pacific island cultures, since it had already spread to the neighboring islands of Viti Levu.

> The alarm was caused by *L. iridescens* breaking its traditional bounds on the large island of Viti Levu and finding its way to Ovalau and neighbouring islands. It had been present on Viti Levu for so many years that coconuts were there not regarded as a source of wealth.
>
> Another result of the campaign, also not calculable in money terms, is that it helps to ensure the prosperity of the native races of the South Pacific depending so largely upon the coconut palm. *Levuana* introduced without parasites to the Lau islands of Fiji, into Rotuma or into the Gilbert and Ellice group and into many other islands of Polynesia and Micronesia might have caused these islands gradually to become depopulated, and, as transportation by sea became more rapid and more frequent, such introductions might have occurred.

The islands of the Pacific, particularly the atolls, are deficient in resources, have depauperate floras, and can sustain only very limited agriculture. Copra, with all its uses, is the crop that permits indigenous subsistence cultures to flourish on those islands. Expansion of the range of *L. iridescens* due to increased boat traffic – a concern expressed by these scientists in 1930! – seems a foregone conclusion. It appears that the near eradication of *L. iridescens* by Tothill, Taylor and Paine prevented a probable cultural catastrophe from occurring had the copra industry collapsed because of *L. iridescens*.

The biology of the outbreaks on Viti Levu and then on Ovalau and Moturiki support these worst case concerns. Tothill et al. (1930) document massive and repeated defoliation of coconut trees, reducing their growth considerably and often killing even large trees. Their illustrations show long coastal views with nearly all coconut palms showing all but the newest leaves dead.

How were human health and environmental safety concerns evaluated during the Levuana *campaign?*

The control program was carefully developed with a concern for environmental safety. As they attempted a variety of control procedures Tothill et al. (1930)

clearly demonstrated an Integrated Pest Management (IPM) philosophy 40 years before the IPM concept was explicitly developed. In the 1920s, few chemical pesticides were available. Only arsenate of lead exhibited efficacy, and spraying this up into coconut palms was tested (using a fire hose pump and nozzle). This was rejected as unsafe (and costly). The use of generalist bird predators was proposed by avian enthusiasts, and this was vigorously (and successfully) opposed by Tothill et al. (1930). They were also careful to not introduce other pests (recall the parasitoid was isolated from *C. catoxantha*), and they also carefully cultured their initial stocks to ensure that no hyperparasitoids were introduced.

Conclusions

It is uncertain whether *L. iridescens* was native to Fiji. It also may not be extinct. So, the repeatedly cited story of the extinction of *L. iridescens* by a biological control agent as a worst-case scenario is also uncertain, perhaps even unlikely. Collateral damage to other moths did certainly occur, but the extent and severity of the non-target impacts have not been quantified. How great a loss this is depends on whether these native zygaenids are, in fact, extinct.

It seems probable that there would be further host-specificity testing of potential control agents today, and other, perhaps more specific control agents than *B. remota* would be selected.

The primary goal of the biological control campaign against *L. iridescens* was to protect the cultures of indigenous Fijian, and other South Pacific island peoples. In this it was spectacularly successful. Historically, the campaign against the coconut moth can be viewed as an antecedent to the gardenification concept. According to Janzen (1998), humans have had an overwhelming impact on the biota of the world, and it is our responsibility to actively manage it in perpetuity to the best of our ecological ability. To do this requires explicit consideration of values, costs and benefits. In this spirit, Tothill et al. (1930) attempted to preserve biodiversity and minimize impacts on human health. So, to evaluate this history from the vantage point of today forces a poignant clash of values: insect biodiversity *versus* indigenous culture. In my opinion, reasonable people may differ as to which value has the greater merit.

Future work

While this review recounts history, the story is not yet complete. There is something to consider and something to do.

If the *H. dolens*, other native zygaenids, and perhaps *L. iridescens* are not actually extinct, but have become so rare as to be threatened with extinction by *B. remota*, and this loss of biodiversity is judged to be excessive collateral damage to non-target native species, a remedy is potentially available. It is possible that *B. remota* itself might be brought under biological control. Tothill et al. (1930) remark that hyperparasitoids (= secondary parasites) were common in *B. remota* collected in Malaya, and that these hyperparasitoids 'detract considerably from the efficiency of *B. remota* in Malaya, and had these been allowed to escape in Fiji the victory over *Levuana* might have been much less prompt and decisive than it had proved to be'. Of course, such a consideration would itself require careful evaluation and safety tests. A reduction in the efficacy of *B. remota* as a natural enemy might boost *L. iridescens* populations and those of the native zygaenids that are not already extinct. Of course, it might also risk the effective economic control of a serious copra pest. Collateral damage of a hyperparasitoid release to native Fijian tachinids would also have to be evaluated.

Use of a biological control agent to remedy impact of a biological control agent will likely strike advocates on both sides of this contentious issue as unwarranted. However, as a policy modeling exercise, it would provide an evaluation of the relative weights of the values that are in conflict in the history of the biological control of the coconut moth in Fiji.

Finally, a rationally designed search should be conducted in Fiji to seek the coconut moth in potential refugia. Tothill et al. (1930) considered that the remarkable efficacy of *B. remota* as a biological control agent for *L. iridescens* was primarily due to the strong flying ability of the tachinid compared to the very poor flight dispersal ability of the coconut moth. Likely places to seek relict populations of *L. iridescens* would be small offshore islands with limited floras and few alternative lepidopteran hosts for *B. remota*. Tothill et al. (1930) specifically noted that, as *L. iridescens* became vanishingly rare, the last numerous populations could be found on small leeward islands, such as Makuluva in the delta of the Rewa River. Prior to biological control by *B. remota*, *L. iridescens* was rare on windward islands and abundant on leeward islands. A search for

L. iridescens elsewhere in the western Pacific might also be fruitful.

Sands (1997) noted that *Levuana* also fed on other species of native palms. These species should also be examined for *L. iridescens* and also *H. dolens*.

To determine if *L. iridescens* and the less well known endemic *H. dolens*, are extinct in Fiji, a coherent search for them should be initiated. Its design should be based on elements of the ecology of *L. iridescens* and *B. remota* that may point to refugia of the former from the latter species. For example, Tothill et al. (1930) note the common occurrence of *L. iridescens* on several other species of palms. The key ecological attribute of *B. remota* that promoted its spectacular efficacy against *L. iridescens* is its much greater dispersal capacity. *B. remota* is a strong flier, while *L. iridescens* is a poor flier (Tothill et al. 1930), supporting that moth's near absence on the windward side of Viti Levu and of small islands on the leeward coast.

A dedicated searching strategy for *L. iridescens* should include:

(1) The discovery of an outbreak of *L. iridescens* at a copra plantation near Vunidawa suggests that this may be near a possible refugium for *L. iridescens* and perhaps for *H. dolens*. Vunidawa is deep in the interior of Viti Levu. This sort of location may offer a more diverse palm flora for zygaenid moths than does the maritime flora associated with naturally distributed coconut palms. This, and other similar locations, should be explored with considerable attention paid to the several other native palm species known to be hosts for *L. iridescens* and related zygaenids (Tothill et al. 1930).

(2) Small leeward islands should be explored for *L. iridescens*. Before the release of *B. remota*, *L. iridescens* was most abundant on the small islands too the east of Viiti Levu, and on those islands its populations were concentrated on the leeward side, suggesting that these moths had limited ability to disperse windward. After the release of *B. remota*, these leeward islands retained some of the last abundant populations of *L. iridescens* suggesting that *B. remota* had some difficulties reaching them, or sustaining its populations on them (perhaps because alternate hosts were less available on these small depauperate islands. Some of these small islands are uninhabited or little visited (Kuris, pers. obs.).

(3) In order to find a rare and patchily distributed organism, leeward and interior areas should be explored extensively, looking at relatively few host plants from many sites, rather than intensively searching many plants at relatively few (the most probable) sites.

Acknowledgements

I thank Kevin Lafferty, Mark Torchin and James Carlton for discussions of the *Levuana* story, and Bill Reece, and other Fijians on the island of Galoa, for describing to me the importance of the coconut palm to South Pacific islanders. Mark Rigby, Mark Hoddle, and an anonymous review made valuable comments on the manuscript. This research was funded by a grant from the National Sea Grant College Program, National Oceanographic and Atmospheric Administration (NOAA), US Department of Commerce under grant number NA06RG0142, project number R/CZ-162 through the California Sea Grant college system, and in part, by the California State Resources Agency. The views expressed herein are those of the author and do not necessarily represent the views of NOAA or any of its sub-agencies. The US government is authorized to reproduce and distribute this paper for governmental purposes.

References

Barratt BS, Goldson SL, Ferguson CM, Phillips CB and Hannah DJ (2000) Predicting the risk from biological control agent introductions: a New Zealand approach. In: Follett PA and Duan JJ (eds) Nontarget Effects of Biological Control Agents, pp 59–75. Kluwer Academic Publishers, Boston

Beirne BP (1975) Biological control attempts by introductions against pest insects in the field in Canada. Canadian Entomologist 107: 225–236

Cowie RH and FG Howarth (1998) Biological control: disputing the indisputable. Trends in Ecology and Evolution 13: 110

DeBach P (1974) Biological Control by Natural Enemies. Cambridge University Press, London, 323 pp

Follett PA and Duan JJ (2000) Nontarget Effects of Biological Control Agents. Kluwer Academic Publishers, Boston, 316 pp

Garcia R, Caltagirone LE and Gutierrez AP (1988) Comments on a redefinition of biological control. BioScience 38: 692–694

Hager HA and McCoy KD (1998) The implications of accepting untested hypotheses: a review of the effects of purple loosestrife (*Lythrum salicaria*) in north America. Biodiversity and Conservation 7: 1069–1079

Henneman ML and Memmott J (2001) Infiltration of a Hawaiian community by introduced biological control agents. Science 293: 1314–1317

Holt RD and Hochberg ME (2001) Indirect interactions, community modules and biological control: a theoretical perspective.

In: Wajnberg E, Scott JK and Quimby PC (eds) Evaluating Indirect Ecological Effects of Biological Control, pp 13–37. CABI Publishing, Wallingford, UK

Hokkanen H and Pimentel D (1984) New approach for selecting biological control agents. Canadian Entomologist 116: 1109–1121

Hokkanen H and Pimentel D (1989) New associations in biological control: theory and practice. Canadian Entomologist 121: 829–840

Howarth FG (1991) Environmental impacts of classical biological control. Annual Review of Entomology 36: 485–509

Janzen D (1998) Gardenification of wildland nature and the human footprint. Science 279: 1312–1313

Kalshoven LGE (1981) Pests of Crops in Indonesia, revised and translated by Van der Laan PA and Rothschild GHL. PT Ichtiar Baru-Van Hoese, Jakarta, Indonesia, 701 pp

Lockwood JA (1993) Environmental issues involved in biological control of rangeland grasshoppers (Orthoptera: Acrididae) with exotic agents. Environmental Entomology 22: 503–518

Louda SM, Kendall D, Connor J and Simberloff D (1997) Ecological effects of an insect introduced for the biological control of weeds. Science 277: 1088–1090

Lynch LD, Hokkanen HMT, Babendreier D, Bigler F, Burgio G, Gao Z-H, Kuske H, Loomans A, Menzler-Hokkanen I, Thomas MB, Tommasini G, Waage, JK, van Lenteren JC and Zeng Q-Q (2001) Insect biological control and non-target effects: a European perspective. In: Wajnberg E, Scott JK and Quimby PC (eds) Evaluating Indirect Ecological Effects of Biological Control, pp 99–124. CABI Publishing, Wallingford, UK

Paine RW (1994) Recollections of a Pacific Entomologist 1925–1966. Australian Centre for International Agricultural Research, Canberra, 126 pp

Rao VP, Ghani MA, Sankaram T and Mathur KC (1971) A Review of the Biological Control of Insects and Other Pests in South-East Asia and the Pacific Regions. Commonwealth Agricultural Bureau, London, 149 pp

Roberts LIN (1986) The practice of biological control – implications for conservation, science and the community. Weta Bulletin of the Entomological Society of New Zealand 9: 76–84

Robinson GS (1975) Macrolepidoptera of Fiji and Rotuma. Classey, Faringdon, UK, 362 pp

Russell DA (1986) The role of the entomological society in insect conservation in New Zealand. Weta Bulletin of the Entomological Society of New Zealand 9: 44–54

Sands DPA (1997) The safety of biological control agents: assessing their impact on beneficial and other non-target hosts. Memoirs of the Museum of Victoria 56: 611–616

Simberloff D and Stiling P (1996) Risks of species introduced for biological control. Biological Conservation 78: 185–192

Smith HS (1948) Biological control of insect pests. In: Reuther W, Calaran EC and Carman GE (eds) Biological Control of Citrus Insects. The Citrus Industry Vol IV, pp 276–320. University of California, Division of Agricultural Sciences Publications, Berkeley, California

Sweetman HL (1958) The Principles of Biological Control. Brown, Dubuque, Iowa, 560 pp

Tothill JD, Taylor THC and Paine RW (1930) The Coconut Moth in Fiji: a History of Its Control by Means of Parasites. Imperial Bureau of Entomology, London, 269 pp

Tscharntke T (2000) Parasitoid populations in the agricultural landscape. In: Hochberg ME and Ives AR (eds) Parasitoid Population Biology, pp 235–2253. Princeton University Press, Princeton, New Jersey

Wajnberg E, Scott JK and Quimby PC (eds) (2001) Evaluating Indirect Ecological Effects of Biological Control. CABI Publishing, Wallingford, UK, 261 pp