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Review Article

Mass rearing of entomophagous insects and predaceous mites: are the bottlenecks biological, engineering, economic, or cultural?

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Abstract

Commercial mass rearing of entomophagous insects on artificial diets has been a goal for five decades, and economical production of biological control agents is desperately sought because of mounting needs for environmentally safe pest management methods. Yet, there is still no commercial artificial diet-based rearing of entomophages. We consider here the potentials and pitfalls to commercial production of entomophagous arthropods. We discuss endoparasitoids, ectoparasitoids and predators, with emphasis on predators. We also consider the potentials and problems inherent in generalist versus specialist natural enemies both as targets of rearing efforts and in their potential market. Finally, we present a detailed analysis of what have been shown as liabilities and assets of rearing a predator that has been produced for well-over 150 generations and nearly 15 years on an artificial diet. We discuss the possible reasons why this research success has not become a commercial success, and suggest ways to speed the development/adoption of artificial diet-based mass rearing systems for biological control agents.

Introduction

More than fifty years ago, F. J. Simmonds (1944) proposed that the development of artificial diets for entomophages would greatly improve the potential for biological control of arthropod pests. Yet, after the ensuing five decades of research and dozens of published reports on such artificial diets, there are no commercial mass rearing programmes for entomophages based on using them. The purpose of this paper is to explore possible reasons for this apparent lack of progress. Our fundamental question is whether the failure is a result of biological, engineering, or cultural barriers.

Biological control technology has taken three basic forms in its century of existence: conservation, classical importation, and augmentation (see Nordlund, 1996 for a detailed discussion of approaches to biological control and its incorporation into integrated pest management). All three approaches have their share of potential value and certainly have a place in our efforts to reduce the use of expensive and environmentally harsh methods of pest management. We focus here on augmentation: actions taken to increase populations or beneficial effects of biological control agents (Rabb *et al.*, 1976) because of our belief that this approach is necessary for management of many of the key pests in most agricultural systems (Nordlund, 1996, in press). The primary means of increasing populations of biological control agents is periodic release of organisms that have been reared in the laboratory or insectary. Such releases can be inoculative or inundative.

If augmentation is to work, an adequate number of inexpensive organisms of suitable quality must be available (Nordlund, in press). It is very expensive to rear sufficient numbers of host/prey arthropods on live host plants to accommodate mass rearing of parasites or predators. The difficulty in terms of expense, room, and reliability of rearing two or three trophic levels of organisms to produce an entomophage justifies efforts to develop artificial diet-based rearing systems. Seasonality of host plants and host/prey arthropods further complicates efforts to produce biological control agents with ‘natural’ or factitious host/prey. Therefore, several laboratories have attempted to develop artificial diets for mass rearing of biological control agents. Also, the availability of an artificial diet facilitates automation of a rearing system, which should increase capacity, reduce costs and improve the quality (Nordlund & Greenberg, 1994; Nordlund, in press; Smith & Nordlund, in press).

Artificial Diets and Automation

Is there a market for natural enemies reared on artificial diet? Since there are no commercially available natural enemies reared on artificial diets, it is impossible to test this question. However, we must conclude that a potential market exists based on the proliferation of companies that supply entomophages reared on 'natural' or factitious hosts/prey (Cranshaw *et al.*, 1996; Hunter, 1997; van Lenteren *et al.*, 1997). It is reasonable to assume that if these producers could rear high quality natural enemies on artificial diets at prices competitive with those reared on 'natural' diets or factitious hosts, they would be able to market them equally well. We expect that this demand for natural enemies would increase if there were a significant reduction in price and increase in availability of high quality natural enemies. The use of artificial diets and automated rearing technology should decrease production costs and increase production capacity for mass-reared natural enemies. Artificial diets may also prove useful as food supplements during shipment, and such a practice would eliminate quarantine problems involved with use of natural or factitious hosts.

Barriers to overcome in successful mass rearing of natural enemies include: development of nutritionally adequate artificial diets, suitable packaging for the diets, nondestructive handling of insects and mites, adequate moisture, prevention of microbial contamination of diet or insects living in close association, prevention of loss of genetic fitness, adequate ventilation, appropriate thermal conditions, appropriate lighting, accommodation for moulting, oviposition sites, and accommodation for newly-eclosed first instars that are extremely vulnerable to desiccation and starvation (Cohen, 1992; Cohen & Staten, 1994; Grenier *et al.*, 1994; Nordlund & Greenberg, 1994). Of all these factors, probably the most complex are the development of an artificial diet that satisfies the nutritional *and* phagostimulatory needs and the efficient packaging of the diet. The problem of packaging is complicated by the need, in most cases, to maintain both moisture and a barrier to microbial attack while still keeping the diet accessible and phagostimulatory to the insects.

Another impediment to development of programmes in large-scale rearing of biological control agents is a long-standing prejudice against organisms produced on other than natural prey or hosts (National Academy of Sciences, 1969; King *et al*., 1985). The report by the National Academy of Sciences (1969) admonishes the biological control community to be cautious about predators and parasites not reared on their natural prey or hosts. Referring to the coccinellid, *Cryptolaemus montrouzieri* Mulsant, which was reared in large numbers on mealybugs on potato sprouts, the report read, "It is possible that a parasite or predator reared in this way may change its host preference and be less effective than if reared on the host it is expected to attack in the field." Although several cases have been documented to demonstrate that predators and parasites reared on factitious host/prey or artificial diets resume normal predation or parasitism (King *et al*., 1985; Cohen & Staten, 1994; Carpenter & Greany, 1998), scepticism expressed in the National Academy report remains. Also, Cohen & Patana (1984) demonstrated that phytophagous insects from colonies that had been maintained for 25 years on artificial diets lost none of their ability to revert to natural food sources. These reports indicate that suspicion may be unfounded about insects reared for prolonged time periods on artificial media.

Several laboratories have reported development of rearing techniques for maintaining small cultures of natural enemies on artificial diet, including some egg parasitoids (Morrison, 1985a, 1985b; Nettles, 1990; Nordlund *et al.*, 1997), ectoparasitoids (Grenier *et al.*, 1994; Carpenter & Greany, 1998) and predators (Morrison & King, 1976; Cohen & Staten, 1994; Grenier *et al.*, 1994; Cohen & Smith, 1998; De Clercq *et al.*, 1998). There are also a few reports of moderate to large-scale efforts at production of entomophages (Morrison, 1985a; Cohen & Staten, 1994; Morales-Ramos *et al.*, 1997). There has been considerable success with the use of artificial diets for rearing a broad range of insect pests, including the boll weevil, *Anthonomus grandis grandis* Boheman (Col., Curculionidae), various fruitflies, the screwworm fly, *Cochliomyia hominivorax* (Coquerel) (Dipt., Calliphoridae), and a number of Lepidoptera (Sikorowski *et al.*, 1984; Nakamori *et al.*, 1992; Leppla & King, 1996; Tillman *et al.*, 1997). However, none of the systems developed for using artificial diets for rearing entomophages has progressed to a commercial scale. For such ventures to be profitable, they must allow production of sufficient quantities of insects at a low enough cost to successfully compete with conventional pesticides. The appreciable costs of labour and materials, as well as the difficulty in rearing very large numbers of entomophages, even for glasshouse conditions, have evidently proved to be too great a barrier to development of artificial diet-based mass rearing techniques. Automation of certain processes in an insect rearing system would decrease the rearing costs and increase the number of insects that can be produced.

The life history of the insect impacts the potential difficulties in using diets for rearing entomophages. For example, endoparasitoids that have very exacting relationships with their hosts present such obstacles as timing of hormone systems and other cyclical cues that parasitoids may require for complete development (Grenier *et al.*, 1994). Ectoparasitoids and egg parasitoids may be less tied to hormonal cycles, but they may still require perpetually fresh materials that are inherent in living hosts that maintain homeostasis. Predators would require far less attention to these matters, but they have the unfortunate habit of cannibalism that could complicate rearing efforts. Furthermore, most predators use some form of extra-oral digestion that tends to accelerate the spoiling of food because of microbial and enzymatic contamination (Cohen, 1998). Thus, the problem of sanitation and removal of spent feeding containers may severely limit predator production.

Another life-style consideration that can have profound impact on the usefulness of an entomophage is whether it is a generalist or a specialist. There are widespread prejudices against generalist predators (Cohen & Staten, 1994), some with a sound basis and others unfounded. So the interest in generalist predators may be less than it would be for specialists. However, the probability of success in developing an artificial diet and automated mass rearing system for a generalist is probably much greater than the chances of meeting all of a specialist's needs.

One of the prejudices against generalist predators is that they can not regulate (maintain an organism's population density over an extended period of time between characteristic upper and lower limits (DeBach *et al.*, 1976)) a pest population because no density dependent relationship exists. However, in many agricultural systems, regulation is not the goal; instead, the goal is often an immediate one-time or series of pest population reductions. Such reductions can be accomplished by appropriate releases of generalist predators that can and do attack the target pest. In addition, because generalist predators can potentially be useful against a variety of pests, they should be more attractive to producers than many specialists (Nordlund & Legaspi, 1996).

Once the barrier of artificial diet development has been overcome, most of the remaining barriers to successful mass rearing of natural enemies can be confronted using engineering methods. Even the problems associated with making large amounts of an artificial diet become engineering problems. Automation, the replacement of mechanical and/or electrical components for human labour, is the most cost-effective method to obtain the large quantities of insects required by a mass rearing programme. Engineering expertise is required to design and integrate the machinery that is necessary to automate any or all of the mass rearing processes.

Suitable packaging for insect diet or for the actual insect can usually be accomplished using packaging or food processing machinery that is currently on the market (Edwards *et al.*, 1996; Tillman *et al.*, 1997). Sometimes slight modifications to the machinery may be required to accommodate the species-specific rearing processes. Form-fill-seal machines form a tray, fill the tray with a product (i.e. insect diet, insect life stages, etc.), and seal the tray. There are also machines that will perform a single process, such as filling bags, cups, trays, etc. or sealing packages. Large-scale food processing machinery is available for making the hundreds or thousands of kilograms of diet per day that may be required in a mass rearing facility (Rothrock, 1996). Prevention of diet contamination can usually be incorporated into the design of the machinery. The insectary worker is the major source of microbes in a rearing facility (Sikorowski, 1984; Sikorowski & Goodwin, 1985), and once the worker is removed from as much of the diet production and rearing process as possible, the contamination problem can be solved. A variety of diet sterilization options may be incorporated into the diet production system, including flash sterilization, pasteurization or irradiation to eliminate or reduce the microbial load of the diet (Sikorowski & Goodwin, 1985).

The availability of adequate ventilation, temperature, humidity, and lighting also becomes an engineering problem, once the optimum values of each are ascertained. Precise control of these values is often critical to the survival of an insect. Maintaining this critical environment often requires an engineer well experienced in environmental control systems.

Nondestructive handling of the insects is an extremely difficult problem to solve. We often think that humans are more adept at handling insects without harming them than machines. However, machines have been developed to perform many delicate tasks. When very large numbers of insects are being produced, it is not economically practical for humans to handle every single insect. Therefore, the handling of the insects must be automated for a mass rearing system to be cost-effective. It is the engineer's task to design machinery that will not harm the insects. After all, an engineer can design a machine that produces thousands or millions of insects per day, but the machine is useless if the insects are not viable.

Cages and their associated feeding and oviposition sites also require engineering. In a mass rearing programme, the cages need to be spaced efficiently, and they must be easy to work with. They must be clean to be cost-effective. They must also provide access to the proper environment and allow for as little handling of the insect as possible.

Solutions to all of the above mentioned problems not only require knowledge of engineering principles, but also knowledge of the biology and behaviour of the insect. Often a team of entomologists, insect physiologists/biochemists, pathologists, field ecologists, extensionists, and engineers is the best combination of expertise for designing optimized mass rearing systems. Advancement of augmentative biological control would also greatly profit from a team of specialists in post-rearing distributional technology, field release and field evaluation systems. Finally, once all of these technologies have been developed, agricultural economists will also be necessary for the demonstration of cost-effective pest management.

A Case Study

A case study with *Geocoris punctipes* Say (Het., Lygaeidae) will serve to illustrate the problems and potentials of developing a rearing programme based on artificial diets. An artificial diet and rearing system was developed for *G. punctipes* (Cohen, 1985a) on which this generalist predator has been in continuous culture for more than 150 generations, and the colony has been maintained for nearly 15 years. The colony was subcultured from 1991 to 1997 by the US Department of Agriculture (USDA), Animal and Plant Health Inspection Service (APHIS) whose personnel have made several improvements towards increasing the productivity of the colony while improving and simplifying the rearing process (Staten *et al.*, 1993). This is, to our knowledge, the longest-standing continuous culture of any entomophage reared on an artificial diet. It is also the most carefully tested colony in terms of quality assessment. In several laboratory and field tests, it has been shown to be indistinguishable from feral counterparts in terms of ability to return to natural prey, return to the field, and their metabolic efficiency and biochemical/physiological characteristics (Cohen, 1985a, 1985b, 1990; Cohen & Staten, 1994). It is, therefore, very informative to examine the work performed on this culture over the last 15 years.

The colony was originated from a test group of 30 *G. punctipes* nymphs that had been reared from a colony held on 'natural' diet for three years in the former USDA, ARS (Agricultural Research Service), Tucson Biological Control of Insects Laboratory. It is, therefore, not a genetically diverse colony. This is a laboratory-selected culture that has passed through a severe 'bottleneck' of selection for laboratory conditions. In its first seven years, this colony was provided with no plant materials whatsoever; only free water provided with a petri dish and sponge was used to supplement water. The diet was always presented in a paste form enclosed in Parafilm®[1] that was stretched to one-third its original thickness (i.e., from 120 to about 45 μm. Various supplements were added to the diet on a trial basis, including green plant materials, wheat germ, vitamins, chicken egg whites or yolks, etc., but the most productive mixture was found to be that which was originally reported (Cohen, 1985b; Cohen & Urias, 1986, 1988). After the culture was adopted by the APHIS laboratory, green beans were added as a supplementary source of moisture, cages were made of pressed plastic, cotton flannel was used as oviposition sites, food packets were redesigned in the form of flat, stretched pillows, and diet was changed every day. Occasional efforts were made to provide first instar nymphs with pink bollworm (*Pectinophora gossypiella* (Saunders); Lep., Gelechiidae) eggs to increase the rate of development and survival of the earlier nymphs. Such efforts were successful but were considered too expensive to be feasible on a long term basis.

The fact that this colony has survived for nearly 15 years and could be increased in size with an increase in number of cages and diet provisions establishes the 'minimal hypothesis' that an artificial rearing system exists that includes an artificial diet that is fully adequate nutritionally and physically. The long term survival is clear proof that the concerns (discussed by Cohen & Staten, 1994) are unfounded that entomophages could never be cultured on a long term basis on completely artificial diets (that which contains no insect-derived ingredients). The extensive quality assessments made of this colony over the past ten years demonstrate that an insect product, comparable in most ways to counterparts derived from the wild, can be reared on an artificial diet. This pertains to parity in prey kill capacity (Hagler & Cohen, 1991; Cohen, 1992), selection and preference for prey (Cohen, 1989; Hagler & Cohen, 1991, Cohen, 1992), adult weight (Cohen & Staten, 1994), and metabolic capabilities (Cohen, 1984, 1985a; Cohen & Urias, 1986, 1988; Cohen, 1992). In other respects (including weight, oviposition rate, and development time), artificial diet-reared predators were slightly inferior to those reared on 'natural' or factitious prey (Cohen & Debolt, 1983; Cohen & Staten, 1994; A. C. Cohen, unpublished data). Tables 1 and 2 are summaries of the development rates and adult weights of *G. punctipes* reared on artificial diets, natural diets and in the field.

[1]Mention of a commercial or proprietary product does not constitute an endorsement by the USDA.

Table 1. Development time of *Geocoris punctipes* fed six different diets.

Diet	Duration of nymphal instar (days)					
	1st	2nd	3rd	4th	5th	Total
H. zea eggs & beans[1]	5.1	3.3	4.3	4.1	5.8	22.7
L. hesperus eggs & beans[1]	4.8	3.9	4.5	4.3	6.1	23.6
L. hesperus eggs & H_2O[1]	5.1	4.1	4.3	4.3	6.4	24.2
H. zea eggs & H_2O[1]	5.4	4.8	4.1	4.9	7.6	26.8
Meat diet & water[2]	6.1	6.2	5.0	4.2	7.1	28.6
Meat diet & beans & water[2]	4.3	4.5	3.5	4.0	6.4	22.7

[1]Cohen & Debolt (1983); *Helicoverpa zea* (Boddie) (Lep., Noctuidae) and *Lygus hesperus* Knight (Het., Miridae).

[2]Cohen & Urias (1986).

Table 2. Weights of *Geocoris punctipes* from the laboratory compared with weights from field-collected samples (means ± S.E.).[1]

	Laboratory females	Field females	Laboratory males	Field males
Mean weight (mg)[2]	1.47 ± 0.042	1.84 ± 0.044	0.95 ± 0.023	1.05 ± 0.034

[1]Data from Cohen & Staten (1994).

[2]Field females were significantly larger than diet-fed females (T = 5.14; $P < 0.05$; $n = 22$); field males were significantly larger than diet-fed males (T = 2.28; $P < 0.05$; $n = 22$).

Although the ultimate measure of the efficacy of augmentation is control of the targeted pest, the penultimate tests are survival in the field and ability to suppress pest populations in the field. *G. punctipes* from our cultures were tested in both of these arenas and were found to survive for at least ten days in the field under extreme temperatures, rains and battering winds near Tucson, Arizona, in August (Cohen & Staten, 1994). Studies by Cohen & Byrne (1992) indicated that *G. punctipes* demonstrated a type II functional response when predating whitefly nymphs, and that both laboratory and field-originated individuals could kill about 50 whiteflies per day in a laboratory study. These predators, in one-week cage studies, suppressed populations of silverleaf whiteflies, *Bemisia argentifolii* Bellows & Perring (Hom., Aleyrodidae), surviving and reproducing in heavily infested cages of whiteflies on cotton during a summer in Phoenix, Arizona (Cohen & Staten, 1994). The predators in this study did not control the whiteflies, which eventually destroyed the plants, which terminated the study. Subsequently, Cohen & Brummett (1997) demonstrated that whiteflies were not good prey for *G. punctipes* because of size disparities and low concentrations of nutrients present in *Bemisia* spp. Studies by Champlain & Scholdt (1966), Dunbar & Bacon (1972), Tamaki & Weeks (1972), Crocker & Whitcomb (1980), and Cohen & Brummett (1997), however, indicate that *G. punctipes* is well-suited to other prey such as lepidopteran eggs, larger aphids, and other slow-moving, soft-bodied arthropods. These tests showed that the survival and killing capacity were not lost from predators that had been held in captivity for ten years prior to these tests.

Of course, the ultimate test of the ability of natural enemies to do their job would be the economical suppression of pests in a crop. However, such suppression would require several factors that have not yet been put in place: (1) The availability of an adequate number of entomophages to release at rates of tens of thousands per hectare over a large enough area that the vagaries of weather, patchy distributions of prey, inadvertent introduction of pesticides, etc. could not conspire to negate or compromise the integrity of the demonstration. (2) The entomophage is appropriately selected in relation to the pest that it is charged with controlling. (3) The timing is such that the entomophage release is timed with the population dynamics of the pest and the phenology of the crop, allowing a maximization of the search and kill capacity of the predator or parasite. Obviously, neither (2) nor (3) could be achieved since (1) has not been accomplished and is a necessary pre-requisite for the other two.

Hunter (1997) lists only one commercial producer of *G. punctipes*, BioFac Crop Care, Inc. We know (M. A. Maedgen, pers. comm.) that the artificial diet in question is used by BioFac, but that it is also supplemented with prey. Why, after almost 15 years of availability of an effective artificial diet and numerous demonstrations of the ability of diet reared *G. punctipes* to perform in the field, has *G. punctipes* not become a commercial augmentative biological control success? Basically, the answer to this question is two-fold. First, despite improvements in the rearing system for *G. punctipes* over the past ten years or so, there has been no concerted effort to develop an optimized and automated mass rearing system for this potentially valuable generalist predator. Techniques being used are labour intensive and thus, not cost effective. Second, the costly rearing system and limited rearing capacity have made it impossible to conclusively demonstrate reliable and cost competitive pest management based on use of *G. punctipes*. It is also important to note that the outcome of these tests would have indicated greater economic promise in a high cash crop such as those produced in greenhouses. Pest treatments for most open field crops need to be less costly than can be afforded in high cash crop settings.

Only after a major investment, as described above, will there be a definite answer to questions about the efficacy of natural enemies reared on artificial diet. Private industries and public funding agencies have been timid about investing in such huge and costly operations because of the high risks and strong doubts about the efficacy of such natural enemies. Thus, there has been a circular trap wherein the timidity of investors results from the lack of definitive results, and the lack of results stems from the lack of adequate commitment. We hope that the case study described here offers enough impetus or credibility to justify bolder and more dedicated efforts at making augmentative release of entomophages reared on artificial diet a realistic and commercially feasible enterprise. In fact, it is our contention, if augmentation of entomophages is to provide a viable alternative to conventional pesticides, automated mass rearing systems using artificial diets for most entomophages will be a practical necessity.

Future Prospects and Conclusions

There appears to be a worldwide market for entomophages. The retail prices for relatively small quantities of parasites and predators ranges from US$ 0.005 per *Chrysoperla carnea* (Stephens) (Neur., Chrysopidae) egg to $ 0.17 per *Orius* sp. adult (Cranshaw *et al.*, 1996). If prices could be reduced to one-hundredth of that amount, it may be feasible to expand the market to include field crops, rather than greenhouses and protected cropping systems or other very high value production systems. Cohen & Staten (1994) estimated that production of *G. punctipes* could be reduced from $ 0.065 to $ 0.028 per adult with a few simple changes in diet packaging. Automated diet packaging to further reduce labour would drive costs down even further. Recent advances in diet technology for *Chrysoperla rufilabris* (Burmeister) (Cohen & Smith, 1998) will permit production of eggs of this species for less than $ 0.00005 each.

With the development of artificial diets for entomophages such as those mentioned here, one of the main bottlenecks that has impeded mass rearing has been overcome. There remain some further impediments to the biological and engineering aspects of mass rearing. Even the most nutritious and phagostimulatory artificial diet is useless in a mass rearing system if it is not presented in a manner acceptable to the entomophage. However, a packaging system that is acceptable for small numbers may not meet the needs of a mass rearing facility. For example, our experience at the Biological Control and Mass Rearing Research Unit has taught us that packaging the Cohen & Smith (1998) diet for *C. rufilabris* in stretched Parafilm® is very labour intensive, greatly increasing the cost of using an otherwise inexpensive diet. Automation of the diet preparation and packaging process would result in an ability to produce very large amounts of ready-to-use diet. As a result, we are working on a small machine to prepare packages of artificial diet that will produce about five packages per minute, each containing about 0.16 kg of diet. This small machine, then, will produce 2100 packages and require about 340 kg of diet per seven-hour production run. This will necessitate the existence of a rearing system capable of efficiently preparing and using this amount of diet, as well as systems for shipping and distributing the large number of insects that will be produced. In other words, something seemingly as simple as cost-effective use of an inexpensive artificial diet essentially requires the existence of a complete system for rearing, packaging and distributing very large numbers of insects.

Rapid progress in the development of artificial diets for entomophagous insects is being made in many parts of the world (Grenier *et al.*, 1994). However, as the case study of the *G. punctipes* diet demonstrated, the diet is one of the first in a long series of steps that are necessary before a high quality and cost competitive entomophage can be brought to the market place, permitting the development of a market for that entomophage. Many of the bottlenecks in the process are biological. However, while biological issues have long been recognized, we believe that the importance of engineering bottlenecks is at least equally important, and that they have been continuously under-appreciated. This contributes to a 'can't do' culture, in which many believe that we cannot produce enough quality entomophages at a sufficiently low cost to allow augmentative biological control to become a significant component in 'mainstream' pest management in agricultural commodities. This 'can't do' culture limits investment and even our willingness to think in terms of rearing a million, billion, or trillion entomophages per day. We believe that augmentative biological control can and should play a major role in IPM in mainstream production agriculture. For this to happen, teams of entomologists, insect physiologists/biochemists, geneticists, engineers, pathologists, and even agricultural economists and marketing specialists will need to focus on development and demonstration of optimized, automated, and cost-effective systems for rearing, packaging, shipping, and using the biological control agents. Such teams are currently being assembled.

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