Review Article

PARASITOIDS AS INSECT PEST CONTROL AGENTS

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A R T I C L E I N F O	A B S T R A C T
	Scientific evidence points to the fact that the use of synthetic pesticides is fraught with problems. Therefore, entomologists continue searching for more friendly control measures to use. One of such methods handy is biological control using parasitoids, which are insects that control other insects. Though, a number of parasitoids have been scientifically chronicled to control insect pests, and a number of studies conducted about them, still there is more to know about parasitoids and how they function to control their host pests. Hence, this paper was intended to review works that have been done to bring to the fore matters relating to important issues to consider when contemplating using parasitoids as insect pest control agents. The paper reviewed how parasitoids are categorized and used in biological control, factors that influence parasitoid host range, host location and recognition, development of parasitoids, specialization of parasitoids, sources of information on host range for introducing parasitoids, how accurately can host range be predicted, factors influencing host–parasitoid interactions, as well as concerns about use of parasitoids as biological control agents and the ways out. The paper ends with some conclusions.

INTRODUCTION

Since the introduction of DDT in the 1940s to control insect pests, man's use of pesticides has increased. Many millions of tonnes of formulated pesticides are used each year to control a wide range of pests in agriculture and health (Thyagaran, 1988). However, the use of such pesticides does not go without problems (Deedat, 1994). Thus they are health hazards to humans and can destroy the natural control agents of the pests.

Since chemical pesticides have become health hazard than solution to agricultural problems alternative means of pest control are being developed everyday. These include the use of host plant resistance (Barrow, 1989; Bosque-Perez et al., 1989; Harris and Nwanze, 1992); use of cultural practices (Shanower et al., 1991; Setamou et al., 1995); and biological control (Bosque-Perez and Dabrowski, 1989; IITA, 1986; Kfir, 1988). Biological control involves the use of pathogens, predators or parasitoids. Biological control has been used more often against insect pests than against any other group of organisms. The most commonly used agents in these efforts are other insects or related arthropods. These beneficial species are classified as either predators or parasitoids (Strand and Obrycki, 1996).

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Parasitoids are basically insects whose larvae may feed internally (endoparasitoids) or externally (ectoparasitoids) (Metcalf and Luckmann, 1975) on other arthropods. Fraser *et al.* (2007) also observed that parasitoids are insects, mainly wasps (Hymenoptera) that develop to maturity by feeding on the body of another host arthropod, eventually killing it. Cox and Wilkin, 1996) consider parasitoids as obligate parasites in their juvenile stages with free-living adult stages. They are tiny wasps belonging to the order Hymenoptera, the adult typically reaching a length of 1-2 mm although those of *Venturia canescens* can grow to a length of 6 mm long. The female uses the ovipositor to lay eggs inside the body of the host insect which is eventually killed after the egg hatches and the larva feeds on the host's internal tissues (Cox and Wilkin, 1996).

Parasitoids may be about the same size as their hosts, kill their hosts, and require only one host (prey) for development into a free-living adult (Metcalf and Luckmann, 1975). In South Africa, several parasitoids have been introduced as biological control agents against stem borers (Skoroszewski and Van Hamburg, 1987; and Kfir et al., 1989). Since *Xanhtopimpla stemmator* established itself on stem borers in Mauritius, it was also introduced into South Africa (Moore and Kfir, 1996) to control lepidopterous stem borers. Several other examples of insect pest parasitism have been reported. For example, in South Africa, several parasitoids were found to be associated with *Busseola fusca*, a lepidopterous stemborer pest. Kfir (1995) recorded eighteen parasitoid species from *B. fusca* (Fuller) on maize and grain Sorghum in Delmas and Cedara.

The larval parasitoid, *Cotesia sesamiae* (Cameron) (Hymenoptera: Braconidae) was discovered emerging from about 90% of parasitized *B. fusca* larvae (Kfir, 1995).

The use of parasitoids in controlling insect pests has many advantages over traditional chemical controls. The parasitoids leave no harmful chemical residues. In case they are released in a storage facility, they continue to reproduce as long as hosts are available and environmental conditions are suitable. Unlike chemicals that need to be applied to a wide area, natural enemies can be released at a single location. They will actively spread, find, and attack pests. Parasitoids are typically very small and have short life cycle and high reproductive capacity. It is likely that resistance to parasitoid pest control will develop more slowly, or not at all, because the parasitoids are coevolving with their hosts and will tend to overcome host resistance. It is possible for insect pathogens to be spread by the activities of parasitoids thereby promoting pest control (Flinn and Schöller, 2012).

The story of parasitoids on various crops all over the world is an unending one. However, the story is a mixed bag comprising successes and failures. This is mainly due to the fact that the whole process of using parasitoids in controlling insect pests is highly scientific and needs comprehensive understanding from biological control scientists. A number of studies have been conducted but still there is more to know about parasitoids and how they function to control their host pests. Therefore this write up is an attempt to bring some pertinent issues about parasitoids and their mode of operation to the fore for the benefit of entomologists, especially those interested in biological control.

Categorization of parasitoids

In terms of species and absolute numbers, parasitoids are generally abundant in almost every ecosystem. However, they are taxonomically more restricted, in that they occur most often in the orders Hymenoptera (ants, bees, and wasps) and Diptera (flies) (Clausen, 1940). According to Hassell (2000) parasitoids comprise some 10% or more of all metazoan species, and largely belong to two families, the Diptera (two-winged flies) and the Hymenoptera (sawflies, bees, wasps and ants). Some authorities are of the opinion that there are parasitoid species belonging to five orders and over 80 families in all (Sweetman, 1958, cited by Coulson and Witter, 1984). However, it seems only Hymenoptera and Diptera contain families with numbers that play an important role as parasites of lepidopterous stem borer pests. For the Gramineae or Poaceae alone, approximately 100 genera of parasitoids (Hymenoptera and Diptera) have been recorded attacking cereal stem borers in Africa and surrounding Islands (Polaszek, 1992).

In the opinion of Crosskey (1980); LaSalle and Gauld (1991), estimates vary widely. However, the parasitic Hymenoptera is considered to have more than 1 million species, while the exclusively parasitic family Tachinidae is regarded as the most species-rich groups of Diptera. Despite the fact that parasitoids are restricted in terms of orders they have high levels of species diversity. As a result they are usually categorized by the hosts they parasitize and where their offspring develop (Godfray 1994). Conti and Colazza (2012) take the issue further by saying that parasitoids representing some 15 families of Hymenoptera develop in insect eggs; three of these families, Platygastridae (Scelionidae), Mymaridae, and

Encyrtidae, are associated with Heteroptera. Several species of heteropteran egg parasitoids are or may be important for biological pest control (Conti and Colazza, 2012).

Parasitoids have long been popular subjects for ecological study for several reasons (Hassell, 2000). This is because they are important for biological pest control and this has stimulated much empirical and theoretical work on the attributes that make parasitoids effective pest control agents. It is also because parasitoids are ideal subjects for developing relatively simple population models. This is mainly because it is only the adult females that search for hosts, and because the act of finding a host is normally followed by oviposition (Hassell, 2000).

Hassell (2000) went on to assert that the success in finding and attacking hosts therefore closely defines parasitoid reproduction, which means that (i) host-parasitoid models can have a much simpler structure than corresponding predator-prey models in which all predator stages may attack prey with different effectiveness, and (ii) reproduction is less closely defined by prey consumption. Also, many species of parasitoids and their hosts can readily be cultured in laboratory microcosms, and this has greatly increased the amount of empirical information on host-parasitoid interactions under controlled conditions The common phenomenon is that hosts are found by the adult female who lays eggs (oviposits) directly on or into the host (Strand and Obrycki, 1996). Some hymenoptera such as parasitic wasps have specialized ovipositors that they use to pierce the cuticle of their hosts or to drill through plant material to reach hosts that are hidden within leaves or sterns. Some parasitic flies also oviposit directly on or into hosts whereas others deposit their progeny near hosts. For those who deposit their progeny near hosts, the hosts become parasitized by consuming the fly's eggs or when the eggs hatch and mobile larvae enter the hosts (Strand and Obrycki, 1996).

In spite of the different mechanisms of how hosts are parasitized, most parasitoids attack just one life stage of their hosts. Some of the species oviposit and complete their development in the egg stage of the host, and they are called egg parasitoids. On the other hand some other parasitoids attack other life stages and they are referred to as larval, pupal, or adult parasitoids depending on the specific life stage being attacked. In some cases parasitoids oviposit in one host stage but their offspring complete development in another. Depending on the situation they are referred to as egg- larval or larval- pupal parasitoids (Strand and Obrycki, 1996)

Parasitoids can also be classified according to where their progeny feed. Species that develop within hosts are called endoparasitoids and those that feed externally are called ectoparasitoids. If only a single individual develops per host the parasitoid is referred to as solitary. On the other hand species in which more than one individual develops per host are referred to gregarious parasitoids. Superparasitism occurs when more individuals of the same parasitoid species are present in a single host than can complete development in a normal way. Yet there is another group known as hyperparasitoids. They are species that parasitize other species of parasitoids present in a host (Strand and Obrycki, 1996). Walter (1983) reported a more unusual group which are heteronomous hyperparasitoids. They are found in the hymenopteran family Aphelinidae, where the female wasps

develop as primary parasitoids of Homoptera and the male wasps develop as hyperparasitoids in females of their own species or another.

Askew and Shaw (1986) observed that recent scientific discovery has come out with two new parasitoid categories which have gained favour in the host range literature. One category is a group of parasitoids whose hosts continue to grow after parasitism and they are called koinobionts. These are contrary to idiobionts whose hosts do not develop further after parasitism. Generally, ectoparasitoids that permanently paralyze their hosts as well as endoparasitic egg and pupal parasitoids are usually idiobionts. Endoparasitoids of larvae and adults are usually koinobionts (Strand and Obrycki, 1996). Jervis and Kidd (1986) also reported that some parasitoids feed on hosts as adults by drilling a hole in the host with their ovipositor and consuming its body fluids. Some of such species feed and oviposit on the same host, whereas others use different hosts for feeding and oviposition.

How parasitoids are used in biological control

According to Strand and Obrycki (1996), there are three general approaches to using parasitoids as biological control agents. The first is importation, or classical biological control. Strand and Obrycki (1996) went on to say that many insect pests are introduced species. Therefore the rationale behind classical biological control is to seek natural enemies from the native range of the pest and release them into the pest's introduced range. If successful, the natural enemy becomes permanently established and maintains the pest population below levels that cause economic problems. Greathead (1986) buttressed this further by stating that approximately 16% of classical biological control programs worldwide using parasitoids or predators have resulted in complete control of the pest (Greathead 1986).

The second method is referred to as the conservation approach. It employs cultural methods such as intercropping or adjusting the timing of insecticide applications to enhance the abundance or efficacy of endemic natural enemies (Strand and Obrycki, 1996). The third approach is known as augmentative biological control. Here, natural enemies are reared in insectaries or collected from the field and then released at sites where it is anticipated that a pest population might exceed economic threshold. In the words of Hunter (1994) this approach to biological control has expanded considerably in recent years with more than 50 commercial insectaries across the United States selling parasitoids. For example, Quilici and Rousse (2012) indicated that augmentative releases of parasitoids may be a useful tool for the area-wide management of tephritid pests. The phenomenon of commercial insectaries is refreshing news because the expertise already exists and this can make biological insect pest control a viable one with less hustle.

Factors that influence parasitoid host range

It has been established that no parasitoid attacks all insects in a given area, and those that are successfully attacked often share certain characteristics (Strand and Obrycki, 1996). Hence, when talking about parasitoids the issue of host range becomes very important. The term host range refers to the set of species that can support development of a parasitoid (Strand and Obrycki, 1996). Therefore life history of parasitoids plays prominent role in their host range and development. The most important aspects of life history that are likely to influence

host range are foraging behaviour and factors that influence feeding habits, oviposition decisions, and development of offspring (Strand and Obrycki, 1996).

The process of locating and accepting prey or hosts is called host selection. Habitats and hosts vary in quality. Meanwhile, all arthropods, especially insects in a given habitat are potential hosts of parasitoids, but some habitats contain more hosts and some hosts will yield offspring of higher fitness. Therefore, the theoretical foundation for understanding how parasitoids select their prey or hosts adopts the approach of optimal foraging theory (Stephens and Krebs, 1986). The model is based on the assumption that natural selection acts to maximize fitness through a factor such as the number of surviving offspring produced from hosts by the parasitoids. Several of such models have been developed. They explore how travel times between parches, risks of mortality in the process of oviposition, and competition between individuals are likely to influence foraging decisions of parasitoids (Strand and Obrycki, 1996). Mangel and Clark (1986); and McNamara and Houston (1986) reported that other more recent dynamic optimization approaches have been developed that take into account the changes that occur in the internal state of parasitoids as they forage over a lifetime. The most important aspect of these theoretical studies is that host selection behaviour varies with ecological circumstances. Under this each species of parasitoid is able to attack a given range of hosts that can be ranked from high to poor in quality.

An example of a specialist is the egg-larval parasitoid *Copidosoma floridanum*. The female of this wasp parasitizes only the eggs of certain moths in the subfamily Plusiinae (Lepidoptera: Noctuidae). The host egg quality of this species varies with age where younger eggs produce offspring of higher fitness than older eggs (Ode and Strand, 1995).

The main factor that determines the acceptability of a host by a specialist or generalist parasitoid is the quality of other hosts in the environment. In the actual fact the range of hosts attacked is narrower in good habitats that contain high-quality hosts, but it is broader in poor habitats that contain fewer hosts of high quality (Strand and Obrycki, 1996). These assertions are supported by results of work done by Godfray (1994) in which parasitoids often attacked hosts in which their progeny could not survive when given no other choice for oviposition, but they ignored such hosts whenever they were presented in conjunction with a preferred host. The implication of this is that one needs to probe the factors contributing to making a parasitoid a specialist or a generalist. If a particular parasitoid species is found attacking several host species it might mean that it does not have a quality host in the ecosystem and for it to survive it must attack different host species.

Factors influencing host location and recognition

The host selection processes of parasitoids have been hierarchically divided into distinct components such as host habitat location, host location, host acceptance, and host suitability (Vinson, 1976). Vet et a1. (1990) emphasized that these components frequently blend together and that learning plays an important role in the foraging responses of parasitoids. Learning here is talking about the experience of particular parasitoid species. It is also an established fact that parasitoids use both physical (visual and tactile) and chemical cues during the host selection process (Waage and Greathead, 1986; New, 1991).

According to Tumlinson *et al*. (1993) the location of the habitat and host by female parasitoids is a theoretically sequential behaviour leading a parasitoid to a potential host. The host is then examined for its suitability (host acceptance phase) (Tumlinson *et al*., 1993). During the location process, the female parasitoids respond to various stimuli from the plant, the host population, the host itself or their interactions. Those stimuli are mainly volatile semiochemicals, though visual and/or mechanical cues are also used (Tumlinson *et al*., 1993; Quicke, 1997; Vinson, 1998).

Quilici and Rousse (2012) also take the argument further when they stated that parasitoids rely on chemical, visual, and mechanical stimuli, often strongly related to their ecology. Behavioral modulation factors include biotic and abiotic factors including learning, climatic conditions and physiological state of the insect (Quilici and Rousse, 2012). Generally, female parasitoids are under selection pressure to efficiently invest their limited time on the location and exploitation of host-derived stimuli. In general, the levels of reliability and detectability of a particular stimulus are inversely correlated. Female parasitic wasps adopt differing strategies to solve this dilemma (Conti and Colazza, 2012). It is also known that successful parasitism of insect herbivores by insect parasitoids arises through several phases of host searching, which lead female wasps to the vicinity of, or in contact with their hosts. During the host location process, females encounter and explore a variety of stimuli, among which chemical cues (semiochemicals or infochemicals) play a pivotal role (Conti and Colazza, 2012).

Chemical cues: Strand and Obrycki (1996) observed that parasitoids respond to odours associated with the microhabitat of their host(s). Giving an example, Turlings *et al*. (1990) stated that the parasitoid *Cotesia marginiventris* is strongly attracted to plants damaged by hosts but not to plants damaged mechanically. The chemical cue is saliva from the hosts which induces plants to produce specific compounds that attract the parasitoid. While in the microhabitat, the parasitoids locate the hosts using cues associated with the host itself. Again, chemicals in faeces, honeydew, and saliva are often present in the proxirnity of hosts and are used as orientation cues by parasitoids. Furthermore, factors such as movement and nonvolatile chemicals mediate the final stages of host location. The abundance of hosts often varies between generations and microhabitats. This is one of the reasons that parasitoids are capable of learning novel cues that improve searching efficiency (Strand and Obrycki, 1996). In many cases parasitoids exhibit preferences based on the types of host odours present on their pupal cocoons (Strand and Obrycki, 1996).

Vet and Dicke (1992) observed that generally, stimuli which are reliably associated with the presence of hosts are preferably used. Volatile semiochemicals have been by far the ones most studied. They have been classified into kairomones, allomones or synomones according to cost/benefit considerations (Nordlund and Lewis, 1976)

Visual, tactile and other cues: The site of emergence and experiences gained while foraging serve as sources of information about the location of hosts. For example, the larval endoparasitoid wasp, *Microplitis demoitor* responds to cowpea plants if reared on hosts fed on cowpea while wasps reared on hosts fed on artificial diet do not (Herard et a1. 1988). Many parasitoids also exhibit associative learning after emergence. This involves the ability to form associations between previously meaningless stimuli. In other examples, parasitoids exhibit the ability to learn visual and/or chemical cues associated with hosts, and in the process developing innate preferences for microhabitats (Vet and Dicke, 1992). Meanwhile, other ways that parasitoids respond to fluctuations in abundance of hosts include seasonal dormancy, use of alternative hosts and dispersal (Tauber *et al*. 1983).

The location of both the host habitat and host is a plastic and flexible behaviour. In addition to the genetic background and the physiological state of the parasitoid, the experience acquired by the female is an important factor inducing variability in foraging behaviour of many parasitoid wasps, after (Vet and Dicke, 1992); Vet and Groenewold,1990);. Turlings *et al*., 1993) or even prior (Corbet, 1985) to the emergence of the adult parasitoid. Thus, if the host is located in hard to reach microhabitat and the parasitoid is not properly placed to find it, parasitization will be difficult. This could also be mediated by genetics.

Factors affecting development of parasitoids

The physiological characteristics of hosts influence the host range of parasitoids, especially koinobiont parasitoids. Development of such endoparasitoids is strongly influenced by the host's endocrine and immune systems (Lawrence and Lanzrein, 1993, Strand and Pech 1995). Hosts that do not meet the developmental requirements of a parasitoid are referred to as refractory or resistant hosts whereas those that me*et al*l developmental requirements are known as being suitable hosts (Strand and Obrycki, 1996). Koinobionts fall into two broad categories, namely, those that depend directly or indirectly on host endocrine factors to synchronize their own growth, and those that alter host endocrine state in a manner that promotes their own growth. Bachrecke et a1. (1993) gave an example that embryos from the gregarious parasitoid wasp *Copidosoma floridanum* form larvae in response to a rise in the hormone (ecdysone) that regulates moulting of the host. However, many solitary endoparasitoid wasps prevent the host from moulting or completing metamorphosis. They rather maintain the host in a juvenile state which appears to be essential for the successful development and emergence of their progeny (Strand and Obrycki, 1996). The implication of this is that if the host matures beyond the juvenile states it may curtail further development of the parasitoid and thereby hampering progenies. It is possible that the advanced stage of the host may produce substances that would affect the physiology of the progeny and hence must be stopped before it develops.

Strand and Obrycki (1996) also intimated that the factors responsible for altering host development are produced by either the adult parasitoid or the developing larva. Factors produced by adults include venoms and symbiotic polydnaviruses. Most parasitic wasps produce venoms in a specialized venom gland associated with the female's reproductive system. However, polydnaviruses are found in only certain species of parasitic wasps in the families Braconidae and Tchneumonidae (Strand and Obrycki, 1996).

According to Strand and Obrycki (1996) polydnaviruses replicate in a region of the wasp's ovary called the calyx and they are injected into the host during oviposition. Viral transcripts then affect development of the host which has been made a juvenile in such a way as to promote the survival of the

wasp's offspring (Lawrence and Lanzrein, 1993). Some parasitoids can produce specialized cells called teratocytes, which are liberated from the eggs of some parasitoids at hatching. These teratocytes are also considered to alter the endocrine physiology of hosts (Dahlman 1991).

In considering whether a host is suitable for development of an internal parasitoid, the host's immune system is equally important. A host's system defense against parasitoids depends mainly on innate capacity to recognize and respond to the invading species, which is genetically determined. Incompatible hosts often eliminate parasitoids by encapsulation, a process in which circulating blood cells (hemocytes) form a multilayered cellular envelope around the parasitoid, eventually killing it (Strand and Obrycki, 1996). Strand and Obrycki (1996) further observed that to avoid encapsulation, parasitoids have adopted a variety of counter-strategies. For example, some species avoid host defenses passively by developing in locations inaccessible to host hemocytes or by possessing surface features that prevent the host from recognizing it as foreign. Also, other species actively disrupt the host immune system by using the same factors that alter the development of hosts. Polydnaviruses in particular have been shown to disrupt the ability of hemocytes to attach to foreign surfaces and to selectively kill cells involved in capsule formation (Strand and Pech 1995).

Specialization of parasitoids

It is difficult understanding the ecological and evolutionary conditions selecting for host specialization (Futuma and Moreno, 1988). Therefore, most discussions in connection with this subject matter is based on the differences between the efficiency gained in resource use by specialists and the benefits of using several resources as food by generalists (Strand and Obrycki, 1996). Generally, the host ranges of parasitoids are considered to be specialized (Price 1980). Therefore, environmental constancy and degree of niche specialization of the organisms attacked by a given parasitoid are also considered to be important in specialization. Extreme specialization on the part of hosts may, however result in resources that are too rare in space and time to support specialist parasitoids (Janzen, 1981). In any case, the small size of insects compared to that of vertebrates affords considerable opportunity for niche specialization and speciation by insect herbivores. This has probably contributed in part to the high species diversity in parasitic Hymenoptera, whose hosts are mainly herbivores, and other insect natural enemies, which feed on herbivorous insects (Strand and Obrycki, 1996).

Sources of information on host range for introducing parasitoids

Literature review is one of the means of establishing host range of parasitoids. Such information on the host ranges of many species can be found in large catalogues of taxonomic associations such as Krombein et a1. (1979).The primary literature provides important information on life histories and potential host ranges. However, caution should be taken when trying to get insight about the trends of host ranges of species in particular taxa on the basis of information in catalogues. Some major factors contribute to this need for caution (Strand and Obrycki, 1996). The first one is that most information on the field biology of natural enemies has been collected in agricultural ecosystems, which are not necessarily representative of natural habitats. A biased view of what the host range of a species might be in its native range or what it might parasitize outside of the agricultural crop being sampled may result.

The second factor is that the few community level studies that have been published in the primary literature indicate that natural enemy complexes vary spatially and temporally. Further to that, since many field studies are carried out at a single time and location, potentially erroneous conclusions about host ranges and species loads can arise. Thirdly, the lack of detailed systematic information on many taxa, combined with the anomalous host records reported in many catalogues, render these summaries almost useless for predicting host ranges of individual species (Askew and Shaw 1986, Wharton 1993).

In spite of the stated shortcomings, Hawkins and Sheehan (1994) are of the opinion that several community-level and phylogenetic studies provide important insight on the host ranges of natural enemies. Such studies suggest that biological control workers generally overestimate specificity. Relatively few parasitoids are strictly monophagous, and some are highly polyphagous. However, it cannot be said that insect parasitoids exhibit no specialization. Rather, most species restrict themselves to attacking relatively few species, a condition considered as oligophagous, where they either share similar life-history traits or exist in a common habitat (Strand and Obrycki, 1996). The argument here therefore puts the onus on the one trying to introduce a particular parasitoid species for insect pest control to search thoroughly through the literature in order to understand the biology of such parasitoid before introducing it.

In spite of all the arguments about the sources of information on host range for introducing parasitoids, three connections appear to be important when making inferences about the host range of individual species. These are phylogeny, shared ecology, and how the natural enemy develops (Strand and Obrycki, 1996).

Influence of phylogeny

For phylogeny, one is considering a tree of life which is a theory about how organisms are related to one another through evolutionary time. It is based on the assumption that more closely related species will be more similar to one another, and they are commonly built using genetic sequences or physical characters. When making inferences about host range, phylogenetic knowledge is often important. The degree of specialization for some groups is clearly conserved phylogenetically but not for others. Taking parasitoids of the family Braconidae for example, they attack insects in more than 120 families and yet most subfamilies are restricted to a single order of insects. In this case major lineages are often restricted to single families of hosts (Wharton 1993). Some species attack only a single species, whereas others parasitize specific genera and a few parasitize nearly all agromyzids in their environment. In other cases, subfamilies and genera of wasps in a paraphyletic group such as the Pteromalidae (Hymenoptera) consist of species whose hosts occur in several orders or families (Strand and Obrycki, 1996). Other parasitoid taxa are highly specialized in the host stage that they attack but exhibit extremely broad host ranges in a taxonomic sense. Examples are iehneumonids in the tribe Ephialtini which do parasitize only concealed larvae or pupae, but the host taxa

include Lepidoptera, Coleoptera, Diptera, and Hymenoptera (Gauld 1986). According to Strand and Obrycki (1996) this variation reflects in part the quality of existing phylogenies.

Gauld (1986) suggested that holophyletic groups will often exhibit similar biological characteristics, but paraphyletic groups usually will not. As such, predictions about the host range of a natural enemy belonging to a holophyletic group will be more accurate than for a species in a paraphyletic group. The nonsystematist should recognize the fact that the quality of available phylogenies greatly influences how much inferences can be made from catalogues or the primary literature. A group, the Ephialtini is well-studied. However, its classification and inferences about its biology is still difficult to deal with because of the lack of character states for subdividing the paraphyletic group into well defined holophyletic groups (Strand and Obrycki, 1996).

Influence of shared ecology

In the attempt to predict host range of parasitoids it is also important to consider the type of ecological relationship that exists between the parasitoid and its hosts. Resource partitioning or niche differentiation is common among groups of insect herbivores. Many examples of niche specialization by parasitoids also exist. There are examples where generalist parasitoids attack a diversity of insect pests occurring in a defined habitat. For example, the braconid *Bracon mellitor* parasitizes many species of insects found in cotton squares (Vinson *et al.*, 1977). Contrary to that, iehneumonids in the genus *Scambus* parasitize hosts from several orders present in grass sterns, seed pods, and flower heads (Fitton *et al.*, 1988).

It is also documented that there are parasitoids that restrict their foraging activities to particular habitats but can feed across different trophic levels (Polis and Holt 1992; Rosenheim et a1. 1995; Strong 1992). A common example is the braconid parasitoid *Aphidius rhopalosiphi*, which when in the laboratory can successfully parasitize several species of aphids. However, *A. rhopalosiphi* preferentially searches leaves of wheat plants. Therefore it heavily parasitizes aphids such as *Metopolophium* spp., which feed on leaves in the field than aphid species that feed in other regions of the plant (Gardner and Dixon1985).

In a study Fraser *et al.* (2007) discovered that parasitoids in the ichneumonid subfamilies Pimplinae, Poemeniinae and Diacritinae tended to be more abundant and species rich in woodlands with a high broadleaf content and tree species richness. However, the ichneumonid subfamily Diplazontinae was found to vary in abundance and richness within rather than between woodlands and showed no association with measured habitat variables. Reserve selection analysis indicated that coniferous woodlands, and woodlands with a low abundance and richness of parasitoids, nonetheless can contribute to maximizing parasitoid diversity at the landscape scale.

At the individual woodland scale, Fraser *et al.* (2007) found that broadleaved woodlands with high tree species richness appear best for conserving parasitoid abundance and diversity. At a landscape scale however, a variety of woodland habitat types can maximize diversity of all parasitoid taxa. They hypothesized that the degree of association between parasitoid abundance and diversity, and characteristics of the vegetation within habitats will decrease with an increase in the number of trophic links that separate them (Fraser *et al.*, 2007). This points to differences in trophic structure across the habitat and niches.

Influence of mode of development on host range of individual species

Scientifically, categorizing parasitoids as koinobionts and idiobionts is especially useful for predicting host range (Askew and Shaw, 1986). In general terms, larval endoparasitoids (koinobionts) often form intimate physiological associations with their hosts, while many egg and pupal parasitoids (idiobionts) kill their hosts at oviposition or shortly afterwards and their progenies developing mainly as saprophytes (Strand 1986). As a result, koinobionts are predicted to have narrower, more taxonomicaly defined host ranges than idiobionts. Askew and Shaw (1986); and Sato (1990) stated that studies of parasitoids attacking leaf miners found narrower host ranges among the koinobionts. Sheehan and Hawkins (1991) also pointed out that ichneumonids in the subfamily Pimplinae which are all idiobionts have wider host ranges than the *Metopiinae* which are koinohionts.

All parasitoids whose host ranges cut across ordinal line are also idiobionts. Examples are *B. mellitor* and *Scambus* sp. The implication is that generally, shared ecology may be the better predictor for host range of idiobionts. However, generalizations need to be made with caution. For example, a conserved complex of phytophagous insects coexist in stored grain habitats, whereas the idiobiont wasp *Bracon bebetor* parasitizes only larvae in the moth subfamily Phyeitinae (Lepidoptera: Noctuidae), such as *Plodia interpunctella*. Furthermore, although this wasp is reported to parasitize a wide variety of moths in the laboratory, the progenies generally develop poorly on larvae outside the Phycitinae (Antolin *et al.* 1995).

How accurately can host range be predicted?

This is practically a difficult task and the answer varies with various taxa. Sufficient information abounds in literature for predictions to be made for some genera and subfamilies. However, for other genera it is difficult because of poor powers of prediction. It is important to start the evaluation process with a search of the literature taking into consideration taxonomic affiliation, the quality of existing phylogenies, and all preexisting information on life history (Strand and Obrycki, 1996).

It is possible to access a large literature covering species that attack economically important pests in their native habitat or that have been used previously as a biological control agent. However, most often the literature is unable to give adequate biological information if the species under consideration attacks non-pest species in its native range or it is endemic to regions of the world that are economically underdeveloped. In such cases, life history studies and evaluation of phylogenetic information on related species can be of help in developing a profile on the natural enemy under consideration (Strand and Obrycki, 1996).

In order to achieve the desired results, experimental evaluation should include both field studies in the native range of the parasitoid and controlled laboratory studies on host specificity. Test species should include potential hosts that are phylogenetically related to the target pest as well as unrelated species (Haley and Forno, 1992). Specifically, the categories of potential hosts that should be considered in host specificity

testing would include: hosts closely related to the target, hosts attacked by species related to the parasitoid being evaluated and unrelated species from the region where the agent would be introduced. How extensive the list of test organisms should be and how host specificity trials should be conducted must be tailored to the characteristics of the species under evaluation. Similarly, how trials are conducted in evaluating the host specificity of a potential parasitoid must take into account its potential hosts and their habitat(Strand and Obrycki, 1996).

It must be noted that no matter the level of host specificity testing, risk cannot be ruled out to non-target organisms when introducing a parasitoid. Such types of studies also provide little insight into whether an introduced parasitoid is likely to disrupt native communities through indirect effects and competition or not. However, we can have some modicum of hope because most examples in which biological control agents have had documented negative impacts (Howarth 1991; Smith and Remington 1996) occurred in the nineteenth and early twentieth centuries, when little or no evaluation took place before introduction. It is further assuring because many biological control workers have touted the successes of using parasitoids in managing several major pests. What is necessary is to pay attention to experimental detail, to the biology of natural enemies, and to evaluation of the host ranges of natural enemies after establishment to enhance the credibility of biological control using parasitoids in the future (Strand and Obrycki, 1996).

Factors influencing host–parasitoid interactions

A study by Staab, *et al*. (2016) indicates that host–parasitoid interactions in species-rich forests are related to the phylogenetic diversity of the tree community, which influences parasitism rates through parasitoid abundance. In the same study it was shown that effects of tree community phylogenetic diversity (PD) are much stronger than effects of tree species richness and this can cascade to high trophic levels, and promote trophic interactions (Staab, *et al*., 2016). The authors continued to say that consumptive and antagonistic interactions between species are central processes in ecosystems (Staab, *et al*., 2016). All variables describing parasitoids decreased with elevation, and were, except parasitism rate, dependent on host abundance (Staab, *et al*., 2016). A range of studies mostly from anthropogenically influenced ecosystems showed that parasitism and trophic interactions are influenced by habitat age (Tscharntke *et al*., 1998), habitat fragmentation or land-use type (Tylianakis, *et al*, 2007) mostly via lower parasitoid diversity and abundance in more severely modified habitats. Thus, the activities of humans in the ecosystem can positively or negatively affect the host-parasitoid interactions.

In a study to examine the factors affecting the orientation, reproduction, and sex ratio of the egg parasitoid *Ooencyrtus kuvanae* Howard, Hofsteter and Raffa (1998) found out that adult females were attracted to airborne volatiles from the egg mass and accessory gland of the primary host, the gypsy moth *Lymantria dispar* L. Hofsteter and Raffa (1998) further found out that visual cues also affected host selection of *O. kuvanae*. Background colours against which egg masses were placed affected oviposition preference. In the absence of egg masses, colour variation did not affect wasp behaviour. Light is required for parasitism by *O. kuvanae*. The age and density of both the host and parasitoid affected wasp reproduction and

sex ratios. Older egg masses issued relatively fewer wasps and higher proportions of males than did young egg masses. Likewise, wasp reproduction and the proportion of females declined with wasp age. Larger egg masses produced more wasps and lower proportions of males than did smaller egg masses. The number of offspring per female, and the proportion of female offspring were inversely related to wasp density (Hofsteter and Raffa, 1998). Here, obviously, presence of fewer females implies lower rates of parasitism because it is the females that do the parsitization. Therefore, size of egg masses and age of egg masses are important factors for host-parasitoid interaction so far as *O. kuvanae* is concerned.

Cesar and Papaj (2001) observed that oviposition behaviour in phytophagous insects and entomophagous parasitoids is often modified by the presence of conspecific brood (eggs and larvae). Often, females avoid laying eggs on or in hosts bearing brood, a behaviour that acts to reduce the level of competition suffered by their offspring. Avoidance of occupied hosts is typically mediated by cues and/or signals associated with brood. Typically, females avoid depositing eggs on previously exploited host resources, a behaviour thought to reduce competition suffered by their offspring (Prokopy, 1981). Females of a variety of species, for example, assess the presence of conspecific brood on the basis of visual or tactile stimuli associated with eggs (Shapiro, 1981; Takasu and Hirose, 1988; Williams and Gilbert, 1981) or larvae (Mappes and Mäkelä, 1993), implying that host-parasitoid interaction in some parasitoid species depends on what happens between the host and other parasitoids previously.

Concerns about use of parasitoids as biological control agents and ways out

According to Strand and Obrycki, (1996), as a result of species diversity, it will not be easy having comprehensive knowledge of the biology of insect pest parasitoids. Assuming that host and habitat preferences for a given species are well characterized, there will still be shifts in host range, especially where a species is introduced into completely new habitat or exposed to intense levels of selection. Thus, in biological control there is always the risk that a natural enemy could adverse1y affect non-target organisms when introduced into a new habitat. The scientific community needs to come to a consensus about how large this risk is and how it is to be measured relative to the monetary and environmental costs of managing pests by alternative means. This is necessary to avoid introducing parasitoids which in the long run will become pests themselves.

The aforementioned brings the idea that the risk of a parasitoid shifting its host range must also be balanced against the changes pests undergo through evolutionary time. The development of resistance to pesticides and documented shifts in host plant preferences by insect pests (Strong et a1. 1984) have demonstrated that selection on pest populations can result in severe environmental and economic problems. Undoubtedly, some groups of parasitoids have broad host ranges and should not be introduced into new habitats. However, the groups that exhibit levels of specificity that merit their continued use in insect pest management can continue to be used.

Flinn and Schöller (2012) asserted that biological control which involves the use of parasitoids requires more information and careful timing compared to traditional

chemical insecticides. Many parasitoids are host-specific, implying that the right complex of parasitoids needs to be released to attack the insect pests in a particular field or bulk of grain. Timing of the release is also critical. For biological control using parasitoids to be practical, releases have to be made early enough in the pest growth cycle so that adult parasitoids outnumber the pests. If parasitoids are released too late, extremely high numbers of parasitoids will need to be released to control the pests. Unlike fumigants, parasitoids cannot be used successfully if the manager waits until pest numbers have reached damaging levels (Flinn and Schöller, 2012).

Designing a biological control program using parasitoids requires careful planning. Many natural enemies are host-specific, so it is necessary to determine which pest species are causing the problem before releasing the appropriate parasitoid species. A well-designed sampling programme should indicate which pest species typically exceed economic threshold (Flinn and Schöller, 2012).

In some cases parasitoids can be stored and refrigerated for a short time up to one week and it must be obtained directly from the producer as needed. In many countries, little expertise and infrastructure exists to supply control agents or support the use of parasitoids in controlling insect pest such as stored product pests. However, in a country such as United State of America (USA) seven species of parasitoids are commercially available for pest control, especially stored product protection (Wilson *et al*. 1994; White and Johnson 2010). It is possible for countries with less expertise to approach more endowed countries such as the US and the like to be of help in controlling insect pests using parasitoids.

CONCLUSIONS

Once chemical pesticides have become health hazards biological control using parasitoids has become one of the most acceptable means of insect pest control worldwide. This is so because the use of parasitoids in controlling insect pests has many advantages over traditional chemical controls. Parasitoids are variously categorized depending on a number of factors. The categorization could be based on the host stage that is being parasitized and the development of the parasitoid or the number of hosts in which the parasitoid develops before becoming an adult, or where their progenies feed.

There are three general approaches to using parasitoids as biological control agents. This can be importation, or classical biological control, conservation approach which employs cultural methods, and augmentative biological control, where natural enemies are reared in insectaries or collected from the field and then released at sites where it is anticipated that a pest population might exceed economic threshold. Each approach has its own intricacies and the one employing it needs to understand it before proceeding to use it.

It can also be said that the host range of parasitoids and host location and recognition are influenced by factors and theories which every biological control scientist needs to understand before making the attempt of employing it in insect pest control. Furthermore, documented evidence points to the fact that the host range and host location by parasitoids is largely influenced by stimuli in the form of chemical cues, visual, tactile, ecological, phylogenetic, mode of development or physiological in nature. These stimuli bring about differences

in specialization of parasitoids. Meanwhile, a catalogue of scientific information exists on mode of operation of parasitoids for any entomologist interested in it. In order to achieve successful biological control using parasitoids it is important to predict the host range and biology as well as study the factors that influence host-parasitoid interactions of the parasitoid to be introduced.

Insect pest parasitoids are much diversified. This makes it difficult to have comprehensive knowledge of their biology. Meanwhile, there are advantages and disadvantages of using parasitoids as control agents. However, extensive research has already been done about the subject matter and there is large literature and expertise existing. These expertise and existing knowledge can serve as the basis for any non-expert interested in biological insect pest control using parasitoids.

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