DO INTRODUCED PARASITOIDS DISPLACE NATIVE ONES?

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ABSTRACT

An attempt was made to determine from the literature and from experience whether native parasitoids of native pests are eliminated by introduced parasitoids. Several native or previously-introduced parasitoids of exotic pest species have become scarce or apparently have disappeared completely following the introduction of additional natural enemies. It is concluded that native parasitoids can be displaced over much of their range, but there usually are favorable habitats where they are able to co-exist with the introduced species.

RESUMEN

Se quiere determinar en base a lo reportado en la literatura y en base a experiencia propia si los parasitoides nativos de las plagas nativas son eliminados al introducir parasitoides foraneos. Algunos parasitoides nativos o introducidos previamente contra plagas exoticas se han reducido en numero o han desaparecido completamente despues de la introduccion de enemigos adicionales. Se concluye que los parasitoides nativos pueden ser desplazados fuera de su rango, pero usualmente encuentran habitats favorables donde ellos pueden co-existir con las especies introducidas.

During the discussion period in one of the biological control symposia of the XIX International Congress of Entomology held in Beijing, China, I inquired whether anyone could cite an example in which an introduced parasitoid had displaced a native parasitoid of a native pest to the point of extinction. Nobody could provide an example. If there are instances where this occurred, the chances that they would be recorded are very slim, mainly because of the frequent absence of intensive pre-introduction studies of the parasitic fauna. Hence, later, if only introduced parasitoids were reared from a native pest, we could not be certain whether they in fact had displaced native parasitoids or whether there had been any native parasitoids in the first place. Flanders (1966), in his excellent discussion of species replacement among the parasitic Hymenoptera, provided several examples where one introduced parasitoid of a pest displaced another, but he did not cite any examples of displacement of native parasitoids of pests.

Rosen & DeBach (1979), in their monograph on *Aphytis* (all species of which are primary parasitoids of armored scales), predicted that, on average, there should be one species of *Aphytis* for each species of armored scale. There are more than 130 species of armored scales recorded from Florida (Dekle 1976), and hence we should expect a large number of species of this aphelinid genus particularly from native diaspidids for which there were no prior records of parasitism by *Aphytis*. Over the past 7 years, aided by Dr. David Rosen during his sabbatical in 1991, I collected, and held for parasitoid emergence, diaspines from many native as well as adventive plants. Although we reared specimens of this genus from many of the scales, most proved to be introduced species of *Aphytis* or species previously recorded from other scales. Whether or not introduced species displaced native ones, or whether there were no specialized native ones attacking many species of the scales, is debatable. The natural enemies of scales on most plants other than citrus had not been studied before the introduction of *Aphytis holoxanthus* DeBach and *A. lingnanensis* Compere (Hymenoptera: Aphelinidae). Hence we have no basis to determine whether native species of *Aphytis* have actually been displaced. We are left with anecdotal accounts about the partial or complete displacement of native parasitoids by introduced parasitoids. There are examples where a native parasitoid, which turned its attention to an adventive pest, may have been displaced on that particular host by an introduced parasitoid. There are several examples wherein one, or more, introduced parasitoids has been displaced by a further introduction. By reviewing some of these examples perhaps we can deduce whether in fact native parasitoids are likely to have been completely displaced (eradicated) by introduced ones. I will refer to examples where an introduced parasitoid eliminated its host, to examples where at least partial displacement of a native parasitoid of a native host by an introduced parasitoid occurred and to several examples where introduced parasitoids were displaced by subsequent introductions.

EXTINCTION OF A HOST

During the final quarter of the last century and the first quarter of the current century, a small moth, *Levuana iridescens* Bethune-Baker (Lepidoptera: Zygaenidae), virtually destroyed the coconut industry in Fiji. Although at the time it was not known to occur elsewhere, and subsequently was not found during extensive surveys for natural enemies in the Pacific islands and southeast Asia, it was concluded that this moth was not native to Fiji (Tothill et al. 1930). These authors remark on the rarity of parasitoids of it in Fiji and use this as one of the criteria in concluding that the moth was not native. Only three specimens of hymenopterous parasitoids had been reared from *Levuana* pupae. Two of the specimens were not adequate for identification beyond the family level (Chalcididae). The third specimen (also Chalcididae) escaped! Before escape, it was identified tentatively as a species of *Brachymeria* known to be parasitic on the pupa of another moth and therefore likely to be polyphagous on lepidopterous pupae.

The tachinid *Bessa remota* (Aldrich) is a parasitoid of the coconut moth *Cathartona catoxena* (Hampson) in Malaysia. When introduced into Fiji in 1925, it attacked the Levuana moth so successfully that the Levuana moth became extinct (Robinson 1975, Howarth 1991). Hence, had there been specialized monophagous parasitoids of Levuana moth in Fiji, they would also have become extinct! Perhaps, if indeed the Levuana moth had originated elsewhere, it has been eliminated in its area of origin by the arrival of *B. remota* in the same dramatic manner that occurred following the deliberate introduction of this tachinid into Fiji. This could account for lack of success in locating the area of origin of the moth. *Heteropan dolens*Druce, an unrelated zygaenid moth, disappeared from Fiji about the same time apparently due to suppression by *B. remota* (Robinson 1975, Howarth 1991). Fortunately, *H. dolens* still occurs in Aneityum Island, New Hebrides (Robinson 1975).

Another example of the elimination of an immigrant host by an introduced polyphagous parasitoid is that of the nigra scale in California. Flanders (1959, 1966) described the discovery in California of the nigra scale, *Saissetia nigra* (Nietner), and its disappearance following the introduction of an encyrtid parasitoid, *Metaphycus helvolus* Compere, which also attacks several other soft scales.

Howarth (1991), while reviewing the negative impacts of classical biological control, cited known examples where extinctions of the nontarget as well as the target species have been reported. These, in addition to the zygaenid moths cited above, include the sharp decline of native pentatomids in the genera *Coleotichus* and *Oechalia* in Hawaii after the introduction of the tachinid *Trichopoda pilipes* (F.) and the scelionid *Trissolcus basalis* (Wollaston) in 1962 for the control of the immigrant southern green stink bug *Nezara viridula* (L.). Also, apparently as a result of these introductions, another immigrant pentatomid *Murgantia histrionica* (Hahn) as well as its deliberately introduced parasitoid *Trissolcus murgantiae* (Ashmead) became extinct in Hawaii. Additionally the disappearance of at least 15 species of the larger native moths of Hawaii was attributed aby Howarth (1991) to the direct or indirect impact of biological control introductions, though this is disputed by Funasaki et al. (1988).

DISAPPEARANCE OF A NATIVE PARASITOID

Although the following examples are not conclusive and have not resulted in extinction, they suggest that competitive suppression of native parasitoids does occur.

Sugarcane Borers

The Caribbean. In the Caribbean and much of Latin America, the most concerted effort in the field of biological control has been against the sugarcane borer *Diatraea saccharalis* (F.) and related species. In most of the Caribbean islands, both pest and natural enemies are adventive species. However, in Trinidad, four economically important species of *Diatraea* are considered native; several native parasitoids also occur there. Despite attempts to introduce additional control agents, the only species known to have become established permanently is the Asian braconid *Cotesia flavipes* Cameron, a parasitoid of species of *Chilo*, a genus closely allied to *Diatraea.* Levels of parasitism of *Diatraea* spp. in sugarcane by *C. flavipes* are generally low, and there appears to be little likelihood that, in Trinidad, it will have much effect on the dominant native parasitoid *Paratheresia claripalpis* Wulp. This is not so in maize, where *Diatraea lineolata* Wlk., the most abundant stalk borer, is not heavily parasitized by *P. claripalpis.* Until the introduction of *C. flavipes*, the dominant native parasitoid was *Apanteles diatraeae* Muesebeck, a braconid which seldom parasitized *Diatraea* spp. in sugarcane. Levels of parasitism of *D. lineolata* by *A. diatraeae* reported in the earlier literature (Kevan 1945) seldom exceeded 10%, although levels of 30% were found in later surveys (Bennett unpubl.). However, after the establishment and build-up of *C. flavipes* in Trinidad, parasitism by *A. diatraeae* diminished to the point where it was not represented in extensive collections of *D. lineolata* during 1984-85 (Bennett unpubl.).

Brazil. In Brazil occur species of *Diatraea* additional to *D. saccharalis.* An additional native tachinid, the Amazon fly, *Metagonistylum minense* Townsend, is widespread in Brazil. In 1974, *C. flavipes* was introduced into northeast Brazil where it established readily on *Diatraea flavipennella* Box and *D. saccharalis*; however, when it was released in Saõ Paulo State, it barely established, and required frequent supplementary releases to have any effect on borer populations. A cool-weather strain was acquired from Pakistan in 1978; it performed well and is now the dominant parasitoid (Botelho 1992). The native tachinid parasitoids *Metagonistylum minense* and *P. claripalpis* have become scarce. While they are no longer represented in survey collections in many fields they occur sporadically in collections from other fields.

Florida Red Scale

Florida. The success story of the biological control of the Florida red scale *Chrysomphalus aonidum* L. has been chronicled several times (Selhime et al. 1969, Browning 1990). Considered to be one of the most serious pests of citrus, Florida red scale was brought under excellent biological control by the introduction of *Aphytis holoxanthus* DeBach (Aphelinidae) in 1960. By 1964, scale populations had been reduced to a non-economic level. Selhime et al. (1969) report that it successfully replaced *Pseudhomalopoda prima* Girault (Encyrtidae) as the main control agent. Displacement was so complete that it is often difficult to find this encyrtid in Florida red scale on citrus. Despite its common epithet, the Florida red scale is not native to Florida, whereas *P. prima* is. *P. prima* is restricted to the neotropics and to the southern States from Florida west to Texas and the host range is given as *C. aonidum* and *Aonidiella aurantii* Maskell, both citrus pests of Asian origin. Therefore, even if *P. prima* disappeared completely from the citrus ecosystem (which is not a native ecosystem in Florida, and *P. prima* hasn't disappeared completely) it would merely be a retreat to its native host or hosts. I have reared it as the dominant parasitoid of *Acutaspis morrisonorum* Kosztarab on southern red cedar, *Juniperus silicicola* (Small) Bailey, as recently as 1990. Hence, although it has been displaced to a great extent by *A. holoxanthus* on Florida red scale, it still is the most important parasitoid on at least one of its native hosts.

Brazil. Following its success in the USA, *A. holoxanthus* was colonized, in 1962 by Paul DeBach, in the State of Saõ Paulo, where previously the native aphelinid *Aphytis costalimai* (Gomes) was the most common parasitoid (Rosen & DeBach 1979). In 1984, while in Brazil to collect *A. costalimai* for dispatch to India for trial on *Melanaspis glomerata* (Green), I examined several thousand Florida red scale; several hundred *Aphytis* pupae were obtained. The following excerpt of my unpublished tour report explains the findings:

"A few of the parasites emerging from *Chrysomphalus aonidum* were slide-mounted in Hoyer's. None proved to be *A. costalimai*, a species readily recognizable by its distinctively mottled fore-wing. Similarly, none of the pupae examined appeared to be as extensively pigmented as those of *A. costalimai* (Rosen & DeBach 1979). The specimens proved to be *Aphytis holoxanthus*. The ease with which *A. costalimai* was encountered in the past on this host (Rosen & DeBach 1979) suggests that, if present, it should have been represented in the sample size obtained. If the *Aphytis* material shipped to India proves to be *A. holoxanthus*, a species introduced into Brazil for the control of Florida red scale (Rosen & DeBach 1976), it is evident that this species has completely displaced *A. costalimai* as a parasite of *C. aonidum*. In view of the relative scarcity of *C. aonidum*, *A. holoxanthus* appears to have effected excellent control." (F. D. Bennett 1984 unpubl. report).

All specimens of *Aphytis* shipped to India were indeed *A. holoxanthus*. In 1987 I reared a few specimens of *A. costalimai* from *Lindingaspis* sp. (Diaspididae), collected on *Ligustrum* sp. at Curitiba, Parana, Brazil proving conclusively that this parasitoid had not been driven to extinction.

DISPLACEMENT OF INTRODUCED PARASITOIDS BY OTHERS

Rhodesgrass Mealybug

The Rhodesgrass mealybug, *Antonina graminis* (Maskell), a pest of Asian origin, threatened to ruin the cattle industry in Texas in 1945 because of its deleterious effect on pasture grasses. Excellent biological control was achieved following the introduction of parasitoids (Dean et al. 1979). The mealybug, following its discovery in 1945, also was considered a serious pest in Florida, where it attacked a wide range of grasses (Questel & Genung 1957). Biological control efforts in Florida commenced with the introduction of *Anagyrus antoninae* Timberlake (Hymenoptera: Encyrtidae) in 1954 (Questel & Genung 1957). In July, parasitoids obtained from Texas were released in the Clewiston area, and in November in the Homestead area (Questel & Genung 1957, Dean

& Schuster 1958). In 1956, parasitoids were recovered several miles from the nearest release sites. Some were distributed to new areas by collecting grass, infested with parasitized mealybugs, and placing it in areas where parasitoids did not occur. In areas where parasitoids were released first, the mealybug had become scarce by 1957. Questel & Genung (1957) noted that establishment had occurred at every release site, and considered that the continued dissemination of this parasitoid would aid in controlling Rhodegrass mealybug throughout southern Florida.

The introduction into Florida of *Neodusmetia sangwani* (Subbo Rao), the encyrtid parasidoid which provided successful control of Rhodesgrass mealybugs in Texas, were recommended. Large-scale releases of this parasitoid were made in 1959. Although establishment occurred, there are no published accounts of a thorough post-release survey. The late Professor Reece I. Sailer collected extensively and reared parasitoids of Rhodesgrass mealybug from 1975-1985. During 1985-1991 I continued to collect and rear parasitoids from localities throughout Florida. *N. sangwani* was widespread and abundant. In contrast, *A. antoninae* was never found during Sailer's or my surveys. These results suggest strongly that *A. antoninae*, which initially established readily and showed promise as an effective control agent, has been displaced completely by *N. sangwani*. Another encyrtid *Pseudectroma* sp. of unknown origin (not *P. europaea* (Mercet) which had been introduced as a control agent), was encountered frequently and, although never as abundant as *N. sangwani*, might also have been a contributory factor to the disappearance of *A. antoninae*. Schuster & Dean (1976) reported the competitive displacement of *A. antoninae* by *N. sangwani* in Texas and suggested that the "lack of competitiveness of *A. antoninae* was a result of its inability to develop at high vapor deficits" and at high seasonal temperatures prevailing during the summer months. They found that *A. antoninae* was displaced but not eliminated. In Florida despite a more equitable rainfall distribution *A. antoninae* appears to have been driven to extinction or at least to a non-detectable level.

Fruitflies in Hawaii.

The Oriental fruitfly (*Bactocera* (= *Dacus*) *dorsalis* (Hendel)) and the Mediterranean fruitfly (*Ceratitis capitata* (Wiedemann)) both became serious pests after their arrival in Hawaii. Three of several braconid parasitoids introduced in rapid succession in 1948 for the control of the Oriental fruit fly became established. Initially *Biosteres* (= *Opius) longicaudatus* (Ashmead) became widely established, but eventually *Biosteres vandenboschi* and finally *Biosteres arisanus* (Sonan) (= *Opius oophilus* Fullaway) became dominant to the extent that the other two species have been relegated to the status of rare species in some of the islands (Van den Bosch et al. 1982). *B. arisanus* now accounts for 74 to 92% of all parasitoids reared from *B. dorsalis* and *C. capitata* in both tropical and temperate zones in Hawaii (Ramadan et al. 1992). This provides us with an example of competitive displacement of introduced parasitoids of immigrant pests by another introduced parasitoid. However, after forty years, the other parasitoids are still well represented in samples and there is no apparent likelihood that any species will be driven to extinction.

Competition Among *Aphytis* Species

Perhaps the most conclusive evidence for competitive displacement and likelihood of extinction over large areas is to be found in the extensive studies on *Aphytis* spp. by DeBach & Sundby (1963). *Aphytis chrysomphali* (Mercet) was eliminated from nearly all of its range (4,000 sq. miles) in southern California within 10 years of the introduction of *A. lingnanensis* which in turn was displaced over much of its range within 4 years by *A. melinus* DeBach from India. However, *A. lingnanensis* precluded the establishment of *A. melinus* in the milder climatic areas of San Diego County. In some areas, host scarcity was not a limiting factor. In laboratory studies, whenever any two of three species (*A. fisheri* DeBach, *A. melinus*, and *A. lingnanensis*) were cultured together, one species was eventually eliminated: the species surviving was influenced by the temperature and humidity regimes of the particular experiment. Even when an abundance of hosts was present at all times, *A. lingnanensis* eliminated *A. fisheri* after 9 generations. While the laboratory studies largely confirmed field events, *A. chrysomphali* was able to compete successfully and to coexist with *A. lingnanensis* in a few coastal areas where conditions for its survival were optimal.

The elimination of one parasitoid by another under laboratory conditions has been demonstrated. Using her ovipositor, the female of *A. lingnanensis* mutilated the prepupae and pupae of *Encarsia lounsburyi* (Berlese & Paoli) (Flanders 1951). Similarly, in laboratory culture with black scale as host, *Coccophagus pulvinariae* Compere (Aphelinidae) displaced *Coccophagus cowperei* Girault. However, in the field both were able to co-exist because the host preference of the females was not the same (Compere 1940). DeBach (1965, 1966) discussed competitive displacement of ecological homologues; included among the factors accounting for displacement were temperature, humidity, natural enemies, disease, type or condition of the food source as well as other factors. He dealt with numerous examples including those where one parasitoid succeeded another and stated, in the case of the *Aphytis* spp. introduced for control of California red scale referred to earlier, that displacement could occur in the presence of "surplus, even abundant, food". Huffaker & Laing (1972) attempted to clarify this statement and concluded that "competitive displacement must involve competition for some requisite (a resource or relatively enemy-free space), however low its intensity".

INEFFECTIVE INTRODUCED PARASITOIDS, EFFECTIVE IMMIGRANTS, AND REFUGIA

Introduced parasitoids do not always dominate native species (DeBach 1966). In fact, in classical biological control, failure to obtain establishment at all is frequent (Hoy 1985). DeBach (1965) stated that perhaps only 25% of imported colonized entomophagous insects become established. In other instances establishment occurs but there is only minor effect on the host or on native parasitoids. The introduction of parasitoids and predators has reduced host densities adequately to replace chemical pesticides in approximately 16% of more than 600 projects (Myers et al. 1989). The reasons for non-establishment of introduced parasitoids, in most instances, remain unclear and have been debated repeatedly by biological control practitioners, ecologists and modelers (e.g., Hoy 1976, Ehler & Hall 1982, 1984, Keller 1984, Myers et al. 1989 and DeBach & Rose 1992). Competitive exclusion is a frequently debated issue, but in their analysis Elher & Hall (1982, 1984) and Keller (1984) were considering exotic insect introductions and not native natural enemies.

Tallamy (1983), when analyzing the results of the numerous parasitoid introductions into the USA for the control of the gypsy moth, *Lymantria dispar* (L), in the context of equilibrium biogeography notes that "parasite extinction events are regular occurrences".

Assessment prior to the intensive programs for the importation of parasitoids from Europe indicated that the level of parasitism of gypsy moth by native species was negligible (Howard & Fiske 1911, Burgess 1926). If these native species were not detected in post-introduction surveys for gypsy moth parasitoids they should not necessarily be judged as having been driven to extinction. In all probability they retreated to the hosts which they attacked before the arrival of the gypsy moth. It is possible that certain of the introduced parasitoids could have had a negative impact on native parasitoids on their native hosts. For example *Brachymeria intermedia* (Nees) (Hymenoptera: Chalcididae) is polyphagous in its native range, where it parasitizes at least 15 species of Lepidoptera. Following its introduction into the USA it has been reared from several leaf rollers as well as from gypsy moth (Leonard 1981). Similarly the introduced tachinid fly *Compsilura concinnata* (Meigen) has been reared from several hosts including non-forest dwelling species such as the imported cabbage worm *Pieris rapae* (L.) and the cabbage looper *Trichoplusia ni* (Hübner) in eastern USA (Headland & Schroeder 1981). The three species of native Tachinidae reared from gypsy moth (Howard & Fiske 1911) all have a very broad host spectrum (see Arnaud (1978) for current nomenclature and recorded hosts). Hence introduced parasitoids are unlikely to displace them over their entire host range.

There are several other examples in the literature where successive introductions of additional parasitoids have led to improved biological control. In some instances, the parasitoid introduced earlier became scarce and the more recently introduced species provided effective control. In others, the second introduction complemented the first and both species co-existed, as occurred during the olive scale biological control program in California (Huffaker & Kennett 1966). In several biological control programs, the successive introduction of different biotypes has led to improved control (Caltagirone 1985, LaSalle & Gauld 1992) and to the apparent disappearance of the first biotype. This may have occurred more frequently than reported, but was not recognized because of the lack of criteria to differentiate between successive introductions of the same species carrying a different genome.

Introduced parasitoids do not necessarily compete well with native species. In experimental releases of parasitoids in feed lots in northern Nebraska for fly control, the native pteromalid *Muscidifurax raptor* Kogan & Legner outperformed the introduced *Pachycrepoideus vindemiae* (Rondani) (Hymenoptera: Pteromalidae) (Petersen et al. 1992).

Examples heretofore given of adventive parasitoids have dealt with introduced species. There is necessarily much less documentation of immigrant species, i.e., those which arrived as stowaways or hitchhikers or even by flight (Simberloff 1986). This is because there is no record of immigrant parasitoids which fail to establish.

Parasitoids sometimes do immigrate. In Hawaii, studies by Sembel (1980) suggested that the immigrant *Trichogramma papilionis* Nagarkatti, first recorded on Oahu in 1979, multiplied rapidly. It became dominant over *Trichogramma chilonis* Ishii as an egg parasitoid of several but not all lepidopterous hosts. Hirose et al. (1988), when discussing their studies on the coexistence and interspecific competition of three species of *Trichogramma* as parasitoids of the swallowtail *Papilio xuthus* L. in Japan, concluded that habitat differences of the parasitoids over the entire range of the hosts precluded any one of the three species being driven to extinction.

In short, in addressing the question of whether introduced parasitoids replace native parasitoids, there is, as is true for most other biological phenomena, no unequivocal simple answer. The examples cited above suggest that sometimes native parasitoids can be displaced over much of their range, but usually there are restricted habitats or refugia where they are able to co-exist with introduced parasitoids. Where host extinctions do occur they are more likely the result of the introduction of a generalist parasitoid like *Bessa remota* that can survive on alternate hosts than from the introduction of host-specific parasitoids.

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ANT BEHAVIOR AND MICROBIAL PATHOGENS (HYMENOPTERA: FORMICIDAE)

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ABSTRACT

The effectiveness of microbial controls for pest ants can be reduced by ant behaviors. Introductions of pathogens, including nematodes, into ant nests result in behavioral responses by ants that affect infection rates to ants exposed to inocula, affect the dissemination of inocula among nestmates, and affect the dispersal of inocula outside the nest. These behaviors include grooming, secretion of antibiotics, nest hygiene, avoidance, and dispersal. Ant behaviors must be considered in developing microbial control agents. Approaches to overcoming the behavioral responses of the red imported fire ant to the entomopathogen *Beauveria bassiana* (Balsamo) Vuillemin are discussed.